ECOLOGICAL INDICATORS IN NORTHEASTERN GEORGIA FLOODPLAINS

by

BRYANA M. BUSH

(Under the Direction of Darold Batzer and Michael Ulyshen)

ABSTRACT

Wetlands, including floodplains, are valuable but threatened ecosystems. Wetlands face threats including: loss, fragmentation, degradation, invasion of exotic species, and the effects of climate change. The objective of my dissertation was to establish environmental indicators which may aid in monitoring possible future changes in wetland structure and function. To do this I evaluated ecological indicators in two riparian Northeastern GA wetland systems, both in the Oconee River watershed. I assessed invertebrate community structure and beta diversity in beaver (*Castor canadensis*)-created wetlands across several successional stages in stream-wetland complexes. I evaluated the effect of litter bag mesh size (used to control invertebrate access) on microclimate and leaf litter breakdown. I also estimated the effects of the invasive shrub Chinese privet (*Ligustrum sinense*), on decomposition dynamics and litter-dwelling invertebrates on privet-invaded floodplains.

My results suggest that beaver activity could be an important conservation tool by substantially contributing to alpha diversity, and stabilizing beta and regional diversity in regions where they are present. Mesh did not significantly impact litter bag microclimate, but I found evidence that mesh size may instead cause unintended impacts on litter breakdown by changing decomposer trophic dynamics. Chinese privet leaves disappeared from litter bags more quickly than native sweet gum (*Liquidambar styraciflua*) or a privet-sweet gum mixture, but invertebrate abundance and community structure did not differ among litter types. However, the effect of Chinese privet invasion on decomposition dynamics on active floodplains varied depending on hydrologic conditions. Organic material decomposed more quickly in privet invaded plots when the floodplain was dry but not when significant flooding occurred.

INDEX WORDS: Floodplain, beaver, *Castor fiber*, *Castor canadensis*, invertebrate, wetland, stream, dam, pond, beta diversity, turnover, species replacement, Chinese privet, litter breakdown, mesh, invertebrate, microclimate, sweet gum, *Liquidambar styraciflua*

ECOLOGICAL INDICATORS IN NORTHEASTERN GEORGIA FLOODPLAINS

by

BRYANA M. BUSH

BS, Coastal Carolina University, 2010

MS, Coastal Carolina University, 2013

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

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2018

ECOLOGICAL INDICATORS IN NORTHEASTERN GEORGIA FLOODPLAINS

by

BRYANA M. BUSH

Major Professors:	Darold Batzer Michael Ulyshen
Committee:	Joseph McHugh Stephen Golladay

Electronic Version Approved:

Suzanne Barbour
Dean of the Graduate School
The University of Georgia
December 2018

DEDICATION

I would like to dedicate this dissertation to my family who are the most incredible, large, loud group of cheerleaders anyone could ask for. For my grandfather, Rev. Robert Jewell, who believed deeply in education and demonstrated that earning an advanced degree was both possible and worth while no matter age or life circumstances. For my mother, Robin Libby, who demonstrated how much a tireless work ethic could accomplish and that the value of the work you do, not the recognition for it, was the point of working hard. For my sister, Jennifer Alexander, who’s incredible resilience and bravery inspired me to keep going even when I was scared, tired, or faced adversity. For my husband, William Bush, who encourages me to take on new challenges (no matter how big or scary) and has an unwavering belief in my ability to succeed. He helped me accomplish this goal in every conceivable way (including but not limited to: experimental construction, field work, spot checking data entry, technology problems, and support of all dissertation related crying). If anyone ever deserved an honorary doctorate, it is my husband and words cannot express my appreciation for all his support.

ACKNOWLEDGEMENTS

First, I would like to thank my advisors, Darold Batzer and Mike Ulyshen. Darold has been an extraordinary mentor. He treated me with the respect of a colleague, which gave me the confidence to explore my ideas, while also taking every opportunity to teach. I could not have done this without Darold and I am a better scientist and teacher because of him. I hope I can someday guide my students with even a fraction of the skill and compassion he has shown me. Mike took me on as a student part-way through my dissertation and has provided an important alternate perspective (and patience) along the way. Mike has especially challenged me to think critically about my approach to experimental design and analysis which has been enormously useful. Working with both of my (very different) advisors has been an incredible advantage and demonstrates the value of collaborative work.

I also want to thank my committee, Joe McHugh and Steve Golladay. Joe and Steve have been available whenever I needed them and have provided me with help and suggestions which have strengthened my work. Joe was incredibly patient in teaching me about terrestrial invertebrates (even when I really didn’t want to) which proved to be invaluable as I learned that there are an incredible number of terrestrial invertebrates in wetlands. Steve has made incredibly stressful experiences, like comps, positive learning experiences which I am grateful for.

Scott Horn, of the US Forest Service, has helped me in more ways than I can count. He is always willing to lend a hand with field work, get supplies, teach a technique, or help with identification. Beyond that, Scott makes work fun and is a good friend. Likewise, my fellow UGA Entomology graduate students are an amazing network of people who help one another with all things bug ID, R, and anything else someone might need, and I am proud to have been part of that team. I am especially grateful to my long-time lab mates and friends: Courtney Holt McDaniel, Conor Fair, Brittany Clark, Kelly Murray, Tom Sheehan, and Emilee Poole. I would also like to acknowledge the work of two wonderful undergraduates, Yared Aklilu and Nyree Riley, who I was fortunate to work with. I'd also like to thank my co-authors and collaborators outside of UGA: Scott Wissinger, Cristina Stenert, Leo Maltchik, and Vlad Gulis. They significantly contributed to this work and helped be become a better writer.

Lastly, I would like to thank those organizations which have provided me with financial support. The US Forest Service supported the privet study and my associated assistantship, the Society for Wetland Scientists provided research funds, and the UGA Graduate School supported my travel to academic meetings.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Wetlands are the most economically valuable terrestrial ecosystem globally in terms of ecosystem services (Costanza et al. 2014). Unfortunately, wetlands are also among the most threatened ecosystems; losing 142 million hectares worldwide between 1997 and 2011 (Costanza et al. 2014). Wetlands are not only in peril due to loss but fragmentation and degradation as well, resulting from a variety of threats which include urbanization, agriculture, invasive species, and climate change among others. For example, in a 2011 US EPA survey only 48% of existing wetlands in the United States were considered in “good” condition (US EPA 2016) which may impair the availability and quality of ecosystem services.

Given numerous threats to wetlands it may be useful to establish environmental indicators, which may help us better understand the current structure and function of specific types of wetlands. Use of ecological indicators such as community structure and ecosystem processes may aid in monitoring changes to wetlands over time. I aimed to evaluate ecological indicators in two riparian Northeastern GA wetland systems both in the Oconee River watershed. First, I assessed invertebrate community structure and beta diversity in beaver-created wetlands across several successional stages. Secondly, I evaluated leaf decomposition and associated invertebrates on privet-invaded floodplains and investigating litter bag methodological approaches.

Literature Cited:

Costanza R, de Groot R, Sutton P, van der Ploeg S, Anderson SJ, Kubiszewski I, Farber S, Turner RK (2014) Changes in the global value of ecosystem services. Global Environmental Change 26:152-158.

US EPA (2016) National wetland condition assessment 2011 report: A collaborative survey of the nation’s wetlands. U.S. Environmental Protection Agency; Office of Wetlands, Oceans, and Watersheds Office of Research and Development. Washington. D.C. 119 pp.

CHAPTER 2

INVERTEBRATES IN BEAVER-CREATED WETLANDS AND PONDS[1]

---

[1] Bush BM, Wissinger SA (2016) In: Batzer D, Boix D (eds) Invertebrates in Freshwater Wetlands: An International Perspective on their Ecology. Springer International Publishing, Cham, pp 411-449.

Reprinted here with permission from the publisher.

ABSTRACT

Eurasian (*Castor fiber*) and North American (*Castor canadensis*) beavers are semi-aquatic mammals that modify the hydrology of streams and other water bodies by constructing dams throughout the temperate and boreal zones of North America and Europe. Our review suggests that beaver wetlands support high invertebrate taxon richness primarily due to high habitat heterogeneity. Beaver created wetlands have a variety of sub-habitats and beaver activities (damming of streams, building of channels, etc.) create a mosaic of lentic and lotic hydrology that provides habitat for stream, pond, and semi-aquatic invertebrates. Beaver also create and maintain new wetlands as well as enhancing existing ones which may help maintain wetland habitat for invertebrates in the face of climate change and habitat destruction.

INTRODUCTION

Eurasian (*Castor fiber*) and North American (*Castor canadensis*) beavers are semi-aquatic mammals that modify the hydrology of streams and other water bodies by constructing dams. The modified aquatic habitats associated with beaver activities were once a ubiquitous feature of the post-Pleistocene landscape throughout the temperate and boreal zones of North America and Europe. By the end of the 19th century, trapping and hunting by humans had extirpated beavers across much of their former range (e.g. Johnson and Chance 1974; Danilov et al. 2011). Since then, the recovery and/or reintroduction of populations in North America and Europe (Naiman 1988; Hartman 1994, 1995; Nolet and Rossell 1998; Bluzma 2003; Halley and Rossell 2012; Law et al. 2014) have led to 1) caused dramatic changes in the structure and function of headwater and middle orders streams and adjacent riparian zones (Naiman et al. 1988; Rosell 2005), and 2) the creation and maintenance of wetland habitats both within and beyond the boundaries of stream valleys (McCall et al. 1996; Syphard and Garcia 2001).

Research on invertebrate communities in aquatic habitats associated with beaver activities can be divided into general groups of studies: 1) those with a distinctly "running water perspective" that focus on how beaver dams change stream invertebrate communities at multiple scales (reach, stream segment, stream system; Allan 2004); and 2) those with a distinctly wetlands/pond perspective on the plant and animal life that inhabit the many types of shallow lentic habitats outside of stream channels. We first briefly summarize the major themes from the large literature focused on how beavers affect stream invertebrate communities, and then turn to focus on the distinctly lentic invertebrate communities that occur in non-channel wetlands created by beavers.

STREAM ECOLOGY PERSPECTIVE ON BEAVER DAM INVERTEBRATES

BEAVER RE-ESTABLISHMENT IN NATIVE RANGE & CHANGING STREAMSCAPES

Robert Naiman established the general paradigm for the effects of beaver activity on stream invertebrates by describing how the presence of beaver dams in stream channels modifies nearly every aspect of the physicochemical (water chemistry, carbon budgets, nutrient spiraling, flow regimes, physical substrates, retention/turnover of organic matter, etc.) and biological (hetero- and auto-trophic microbial assemblages, community metabolism, plants, invertebrates, fish, waterfowl) environment in stream channels and adjacent riparian habitats (Naiman and Melillo 1984; Naiman et al 1986, 1988a,b; also see Rosell et al. 2005). From the perspective of stream ecologists, hydrologists, and fluvial geomorphologists, the recovery of beaver populations in North America and Eurasia during the past 100 years has prompted a re-evaluation of the structure and function of headwater and middle-order streams as compared to when and where beavers had (have) been extirpated (Naiman et al. 1986, 1988; Cirmo and Driscoll 1993; Devito and Dillon 1993; Hammerson 1994; Pollock et al. 1995; Klotz 1998; Snodgrass and Meffe 1998; Collen and Gibson 2001; Butler and Malanson 2005; Pollock et al. 2007; Burchsted and Daniels 2014; Curran and Cannetelli 2014). The hydrology of beaver ponds in this context is dominated by stream flow inputs and outputs and the dams, and can reduce peak channel discharge by temporarily storing water and shunting it to the adjacent riparian zone /floodplain (Fig 1.1a). This one of three potential losses of water between channel inflow and outflow in beaver dams. A second is through evapotranspiration because of the increased surface area and residence times, especially in arid environments (Andersen et al. 2011), and a third is through downwelling into the shallow ground water that moves down valley through unconsolidated sediments. In arid land streams, groundwater recharge from beaver ponds and wetlands can enhance shallow groundwater storage, which later supplements channel flow during low-flow conditions, potentially converting intermittent to perennial streams (Fig. 2.1b, Gibson and Olden 2014).

In steep gradient headwater and middle-order streams, beaver activity in North America and Eurasia leads to the replacement of erosional (riffle) assemblages of invertebrates typical of high-oxygen, turbulent-flow, hard-substrate habitats (e.g. stoneflies, mayflies, riffle beetles, net-spinning caddisflies, etc.) with communities that are more typical of depositional environments (pools, runs) that have relatively slow, laminar flow, relatively low oxygen, and a predominance of soft substrates (e.g. chironomids and other dipterans, odonates, dytiscid beetles, hemipterans, annelids, epibenthic crustaceans, etc.). At the reach scale, invertebrate biomass is much higher (1.3–11.1 g m^{-2}) in pools behind beaver dams than in adjacent riffles (0.01–0.6 g m^{-2}), but taxonomic diversity between the habitats is similar (McDowall and Naiman 1986; Naiman et al. 1986). However, at the stream-segment or beta diversity scale (Allan 2004), the longitudinal sequences of these alternating habitat types results in an increase in the overall taxonomic and trophic (functional-feeding-group) diversity as compared to streams lacking beaver dams (e.g. Sprules 1935 [Ontario]; McDowall and Naiman 1986 [Quebec]; Harthun 1999 [Hesse, Germany]; Smith et al. 1999 [New York]; Margolis et al. 2001 [Pennsylvania]; Pliūraitė and Kesminas 2011 [Lithuania]).

The patches of large woody debris associated with dams (Fig. 2.2) and huts can harbor unique assemblages of invertebrate species dominated by grazers and filter feeders (e.g. simuliid larvae; Clifford et al. 1993; Adler and Mason 1997). Rolauffs et al. (2001) found higher invertebrate diversity and higher secondary productivity on coarse woody substrates of dams than in either riffles or the pools created by the dams, perhaps as a result of some combination of the 1) extensive surface area of these complex structures, 2) availability of organic materials (wood substrate with biofilm and flow-through suspended particulates), 3) high organic turnover rate, and 4) aerobic conditions at the water-air interface.

Several studies have compared stream invertebrate communities between comparable habitats above and below beaver dams. In a small, low gradient stream in northeastern North America (New York state), Smith et al. (1999) found that stream invertebrate assemblages below dams are less diverse and had lower densities of Plecoptera, Trichoptera, and filter feeders (taxa not specified). In contrast, Fuller and Peckarsky (2011a) found no systematic differences among functional feeding groups (FFGs) above and below ponds and no differences driven by dam morphology among FFG with the exception of suspension feeders. The abundance of suspension feeders, and especially simuliids, increases below beaver ponds with high hydraulic head dams which is also typical downstream of man-made reservoirs due to high seston pulses (Mackay and Waters 1986; Richardson and Mackay 1991). However, suspension feeders decrease below ponds with a low hydraulic head dam, and the difference between high- and low-head dams is not driven by algae spillover from dams. Fuller and Peckarsky (2011a) hypothesize that higher abundance of suspension feeders below high head dams could be related to a higher availability of bacterial seston or increased scour downstream of high head dams, but not below low head dams, both of which are favorable for simuliids. Invertebrates were not influenced by any differences in nutrients, algal biomass, and benthic organic matter among stream reaches above and below ponds related to dam morphology.

In a related study, Fuller and Peckarsky (2011b) studied the impact beaver pond morphology had on mayfly life history (Fig. 2.2). They evaluated downstream effects of beaver pond morphology on *Baetis bicaudatus* size and timing of emergence. Reaches downstream of high head, low surface area ponds produced larger females than low head ponds with larger surface area, and females found below the pond were larger than those found above. Male size differences followed similar patterns but were not significantly different. Because large female *B. bicaudatus* are more fecund than small females, Fuller and Peckarsky hypothesize that the next generation could vary in size by +11 to -12% depending on pond morphology. Larger female size downstream of high head ponds corresponds with colder water temperatures in these areas. Outflow water is colder than pond, probably as a result of groundwater upwelling below the high hydraulic head dams. Despite temperature differences, pond morphology did not predict timing of emergence of mayflies downstream of dams. In general, where groundwater lost through the hyporheic in beaver ponds resurfaces as channel flow (see Fig. 2.1a,b) should have important consequences for how beaver dams affect downstream stream invertebrate communities.

Impounded reaches of channels in low gradient streams are likely to have an enhanced wetted area of overhanging vegetation and snag habitats along flooded shoreline margins (Johnston and Naiman 1987). The importance of channel-margin overhanging vegetation as substrate for aquatic invertebrates is well described in other stream contexts (e.g. coastal plain rivers - Benke et al. 1984). The secondary production of aquatic invertebrates on these substrates can dwarf that on channel substrates and can be the most important source of production for fisheries in slow-moving, soft-sediment channels (as in Benke et al. 1985). Indeed, literature reviews and meta-analyses of the positive effects of beavers on stream fish cite the high invertebrate productivity in stream habitats associated with beaver activity (pools, wetted margins, dams, huts) as an important positive effect on stream fish abundance, growth, and productivity (reviews by Collen and Gibson 2001; Kemp et al. 2012). Other positive effects of beavers on fish are related to the habitat heterogeneity in the streamscape on overwintering success, juvenile refugia, recruitment, and connectivity between juvenile and adult habitats; whereas barriers to fish movement and increased temperatures (and decreased oxygen) towards upper tolerance thresholds are cited as negative effects in those same reviews. The degree to which beavers have a positive or negative effect on native brook trout, the top predator in high gradient, headwater streams in northeastern North America, appears to vary across locations and geomorphological context (White and Rahel 2008; Niles et al. 2013). From the perspective of our focus here on invertebrates, we did not find any studies that consider how the changes in fish communities associated with beaver activity feedback on invertebrate communities.

There is also a large literature on the positive effects of beaver activity on the growth, survival, and diversity of waterbirds that is attributed to the creation of structurally favorable habitats for breeding and survival (e.g. Brown et al. 1996; McKinstry et al. 2001), and to the high primary and secondary productivity in beaver-created wetlands, including invertebrate production (e.g. Nummi and Hahtola 2008; Nummi and Holopainen 2014). However, it is not clear how increased density, diversity, and production of waterbirds in turn affects beaver pond invertebrate communities.

In relatively flat landscape settings, it appears that the invertebrate communities in the pools that develop upstream of dams are comparable to those typical in standing water habitats. For example, in low gradient streams in Hesse, Germany, the macroinvertebrate communities in beaver ponds are distinctly different from those in un-impounded reaches with high diversity of taxonomic groups (e.g. 11-18 odonates, 11-22 caddisflies including many limnephilids that are typically lentic; Harthum 1999). In contrast, in the Bigoray River in Alberta, Canada, Clifford et al. (1993) found that, although the percent composition varied between habitats, there were 7 taxa that were common to both unimpounded and impounded reaches. For example, Simuliidae represented more than 80% of the most abundant taxa in dams but less than 3% in unimpounded sites. Chironomidae made up less than 12% of the most abundant taxa in dams however it comprised more than 48% in streams. In addition, unimpounded sites contained taxa frequently associated with slower reaches (*Pisidium* spp., *Leptophlebia cupida*, *Caenis* spp.) and both cluster and principal component analysis separated dam sites and stream sites. Thus, it appears that in some hydrologic and geomorphic contexts, beaver dams can be important refugia for lotic taxa in slow moving streams, and in others, are more likely to reduce the available habitat for those taxa. It is possible that in relatively small streams with confined valleys, beaver activities may overwhelm the capacity and competence of low stream discharge to create truly lentic-like habitats, whereas in the context of higher flows and unconfined channels, the redistribution and artificially cascaded nature of channel flows across multiple distributaries may actually enhance the lateral presence of erosional (riffle) and depositional (pool) habitats.

In unconfined geomorphological settings (e.g. broad valleys), the in-channel invertebrate diversity at the stream-segment scale should be complemented by the creation of lateral habitats that support other types of invertebrate assemblages on adjacent shoreline margins (see Johnston and Naiman 1987), and out-of-channel riparian habitats including paleochannels with active and abandoned beaver dams. For example, in relatively flat stream segments in the U-shaped valleys created by mountain glaciers in western North America (Fig. 2.3a.), single, meandering channels can be transformed into valley wide systems of distributaries, each with a complex longitudinal and lateral sequence of habitat types associated with beaver activities including open ponds, systems of channels connecting those ponds, and extensive willow (*Salix* sp.) and sedge (*Carex* sp.) meadow wetland habitats (Fig. 2.3b). The hydrology of floodplain beaver ponds outside of the main channel will vary depending on proximity to the main channel. The hydrology of ponds close to the main channel will be more affected by changes in stream flow conditions than those isolated laterally from the channel. The hydrology of the latter will be dominated by inputs and outputs dominated by the down valley movements of shallow groundwater and lateral hyporheic losses from the main channel (Fig. 2.1c, 2.3b). In this geomorphologic setting, there is likely to be a continuum of invertebrate communities ranging from those dominated by taxa typical of pools in stream channels to those dominated by lentic taxa typical of non-riparian wetlands and ponds (see discussion below of Western Beaver Wetlands; Appendix).

Beaver Impacts Outside of Native Range

Finally, given the transformative effects that beavers can have on nearly every aspect of running water systems, it is not surprising that they are having profound impacts as invasive species on stream ecosystems outside of their native range. In streams of south-temperate South America, Anderson and colleagues studied the impacts of invasive beavers on stream ecosystem structure and function, including the effects on stream invertebrate diversity, community composition, and productivity (Anderson et al. 2007, 2009, 2010). In a comprehensive review of the impacts of beavers on the physical and biological environments of stream systems in south temperate South America, they concluded that the impacts of beavers as exotic invasive species was of similar magnitude and direction as that observed in studies in the native range of beavers (Anderson et al. 2009). In South America, they compared un-impacted reaches to reaches with beaver ponds to reaches below beaver ponds and found lower taxonomic and FFG diversity in the pools associated with dams than in either upstream or downstream reaches, which did not differ from unimpacted reaches (Anderson et al. 2007). They attributed this difference to the relatively homogenous microhabitat in the soft sediments of the pools, although they did not appear to include other types of habitats (wetted margins, dams, hut). Examining other beaver-associated habitats could be important in obtaining a full picture of invertebrate diversity as these other connected habitats increase habitat heterogeneity, which has increased diversity in beaver-influenced habitats elsewhere. They also found invertebrate abundance, biomass, and secondary production were higher in the pools associated with dams as compared to above or below undammed reaches (Anderson et al. 2007), which was consistent with the literature from North America and Eurasia (Anderson et al. 2009). They tested the hypothesis that this higher productivity was associated with increased production and input of allochthonous detritus using stable isotopes and found a slight increase in reaches with vs. without beaver dams (Anderson and Rosemond 2010). Anderson and colleagues argued that because the in-stream productivity and metabolism in these forested catchments is naturally driven primarily by allochthonous subsidies, beaver impacts are small. They predict that in streams where autochthonous production contributes a larger fraction of the overall energy budget, beavers will have a bigger impact on shifting the metabolism of a stream reach towards autochthonous production (as in Naiman et al. 1986, 1988).

LENTIC INVERTEBRATE COMMUNITIES IN BEAVER WETLANDS

BEAVER-MEADOW WETLAND COMPLEXES IN NORTHEASTERN NORTH AMERICA

In relatively flat-lying landscapes, beaver activities beyond the main channels of streams can create extensive and persistent wetland complexes that are distinctly lentic in character (Fig. 2.4a). These habitats are variably described as “beaver-pond wetlands,” “beaver meadow wetlands” or “valley beaver impoundments (Burchsted et al. 2010; Polvi and Wohl 2012). As a result of the recolonization of beavers over the past 100 years, these wetland complexes have become a ubiquitous feature of the landscape in northeastern North America (from west to east - Minnesota, Wisconsin, Michigan, Ontario, Ohio, Pennsylvania, New York, New England, Quebec, New Brunswick and non-urbanized areas of the coastal Atlantic states). Along the northern tier of this region (i.e. southern Canada and border states of the U.S.), beaver dams that occur beyond the margins of stream courses can transform vast tracts of saturated-soil peatlands into complexes of open ponds, marshes, and shrub swamps that are interconnected by beaver-constructed standing-water canals (Naiman et al. 1986, 1988; Rebertus 1986; Johnston and Naiman 1990; Woo and Waddington 1990; McCall et al. 1996; Donkor and Fryxell 2000; Ray et al. 2004). Beaver wetland complexes that are not part of peatlands are also common further to the south in glaciated and unglaciated landscapes of Ohio, Pennsylvania, Ontario, and New York, often at the boundary between upland and lowland terrain (Johnston and Naiman 1987; Grover and Baldassare 1995; Wissinger and Gallagher 1999). The hydrologic budget of beaver wetland complexes is often tied to upwelling areas of groundwater discharge with the outflows below the complexes forming perennial headwater streams (Fig. 2.1d). These wetland complexes are distinctly different from the pools created by beaver dams in large stream channels (Hodkinson 1975; Ray et al. 2001; Burchsted et al. 2010).

Compared to the many detailed studies of how beaver dams change stream invertebrate communities at the streamscape level (see above), there are relatively few studies that describe the invertebrate communities in beaver-meadow wetland complexes. These complexes are ubiquitous in the hummocky glaciated terrain of northwestern Pennsylvania (Fig. 2.4), and the complexes are long-lived, especially where beaver colonies are protected (e.g. PA State Game Lands, Erie National Wildlife Refuge). Wissinger and Gallagher (1999) studied the invertebrate communities in two such complexes (Robinson-South Marsh Complex; and Church-Kiser Marsh Complex in Allegheny College's Research Reserve). The beaver dams at these sites are located on terraces along the edges of the valley and impound groundwater discharge as it resurfaces at the base of the slopes of uplands. The complex of habitats created in the relatively flat-lying terrain include:

1) relatively deep (> 1 m) ponds immediately behind the dam structure that have complex plant zonation ranging from an open-water zone of floating pads of spatterdock (*Nuphar variegata*) and submergent vegetation (e.g. *Potamogeton* spp., *Ceratophylum* spp.) towards shoreline vegetation with deep (e.g. *Typha angustifolia and T. latifolia)* and shallow water emergents (e.g. *Scirpus cyperinus*, and *Sparganium eurycarpum*) (Fig. 2.4a);

2) shallow marshes of emergent vegetation that grade into moist-soil herbaceous communities that develop on flooded fields adjacent to active dams, and then invade pond basins when dams are abandoned. In addition to the emergent vegetation surrounding the ponds *per se* (see above), seasonally inundated wet meadow plant assemblages are dominated by rushes and sedges (e.g. *Juncus effusus, Carex hystericina, and C. lurida)* and herbaceous plants (e.g, *Eupatorium maculatum* and *Verbena hastata*);

3) shrub-swamps along margins of active or abandoned ponds that are dominated by alder (*Alnus rugosa*), wetland dogwoods (*Cornus ammomum* and *C. stolonifera*), and willows (*Salix* spp.) and buttonbush (*Cephalanthus occidentalis*), and wet meadow shrubby species including meadowsweet (*Spirea alba*) and sweet gale (*Myrica gale*) (Fig. 2.4b);

4) back-flooded forests with dead snags of trees that are intolerant of anaerobic soil conditions soils (e.g. *Prunus serotina, Fagus grandifolia, and Quercus* spp.); and

5) living red-maple/hemlock moist-soil swamps with vernal woodland pools that develop in the depressional micro-topography from the raised water table in back-flooded forests (Figure 15.1 in Wissinger and Gallagher 1999; Fig. 2.4c). Despite the apparent remoteness of these woodland pools to beaver activity, the hydrologic dependence becomes apparent when beaver dams are abandoned, and the adjacent water table falls.

Across all of these subhabitats in these beaver-pond wetland complexes, there is a remarkable diversity of wetland plants (Wissinger et al. 2001) and animals (amphibians, reptiles, fishes, invertebrates) (Wissinger and Gallagher 1999). Wissinger and Gallagher studied the resiliency of the invertebrate communities to short-term drought in the main pond communities by monitoring the multiple pathways by which species recolonized after drought, and experimentally by rehydrating soil cores that were extracted from dried basin sediments. They found that 1) the invertebrate assemblages in semi-permanent basins (abandoned beaver ponds and marginal wetland habitats) were more resilient after drought than those in the permanent basins, 2) the overall rapid recovery of the invertebrate diversity prior to drought (>90% after 18 months in semi-permanent basins) was attributable to a variety of recolonization modes (e.g. use of micro-refuges in dried basins (see Strachan et al. 2014), desiccation tolerance of eggs, larvae, adults, flexible life history traits, and seasonally-timed emergence), and 3) high dispersal rates among habitats with different hydroperiods lead to metapopulation and metacommunity dynamics that stabilize beta diversity across the complex of habitats (Wissinger and Gallagher 1999).

Combining the species identified in the original surveys (see taxonomic list in Wissinger and Gallagher 1999) with subsequent annual surveys (2000-2009; S. Wissinger unpublished data) reveals the presence of >250 invertebrate taxa including 40+ species of odonates, 16 species of caddisflies, 30+ species of beetles, 18 species of water bugs, 50+ dipteran taxa, 11+ molluscs, and 20+ crustaceans (see Appendix for list of families). The taxonomic resolution attainable for odonates and caddisflies (species-level identification in the field) provides insight into two levels of habitat heterogeneity that underlie this diversity. First, there is considerable habitat heterogeneity *within* types of subhabitats in the complexes. For example, different species of anisopteran and zygopteran dragonfly larvae are encountered at different depths and in different vegetation zones within main beaver ponds (Table 2.1). This type of spatial niche segregation within ponds (also see Crowley and Johnson 1982; Wissinger 1988; Van de Meutter et al. 2008) is not limited to dragonflies—in general, plant zonation is a well-described axis of niche segregation for invertebrates in many types of wetlands (Batzer and Wissinger 1996; Wissinger 1999; De Szalay and Resh 2000; Batzer 2013). Thus, the high diversity of habitat types and distinct plant communities associated with beaver-meadow wetland complexes (Grover and Baldassarre 1995; Wright et al. 2002, 2003) should in turn translate into a diverse invertebrate fauna (Hood and Larson 2014). Other microhabitats that create hotspots of diversity within beaver ponds include those associated with the structural complexity of beaver huts and dams (France 1997).

A second scale of heterogeneity in beaver-meadow wetland complexes is related to variation *between* different types of wetland habitats. Although specific patterns are difficult to predict across wetland types (Batzer 2013), for wetlands and ponds of similar size, species richness decreases along a gradient from permanent to temporary habitats, with species in temporary habitats often being a nested subset of those in the permanent habitats. In addition to nestedness patterns in ponds (see review by Batzer and Ruhí 2013), invertebrate community composition can also shift from permanent, relatively deep-water (1–2 m depth) ponds that typically have large-gaped predatory fish that prey on invertebrates (bass, sunfish, pickerel), to semi-permanent marshes and shrub-swamps habitats with small-gaped fish (stickleback, mudminnows) and/or salamander predators, to temporary habitats in which salamander larvae and invertebrates are the top predators (Batzer and Wissinger 1996; Welborn et al. 1996). In the beaver-wetland complex studied by Wissinger and Gallagher (1999), all of these types of habitats are present and odonates and caddisflies provide evidence for shifts in species composition along predator-permanence gradients. Although there are generalists that occur across habitat types, some species tend to occur mainly at one end (permanent) or the other (temporary) of this gradient (Tables 2.1 and 2.2). Similar differences are observed for beetle assemblages in temporary habitats vs. permanent ponds including beaver ponds beyond stream channels (Fairchild et al. 2000, 2003). Such shifts in species composition are expected for nearly every invertebrate taxon (beetles, bugs, odonates, caddisflies, true flies, crustaceans, molluscs, etc.) associated with wetland habitats; i.e. different combinations of species within genera and different genera within families will be present in different types of basins as a result of differential dispersal and colonization rates combined with the different biological and physicochemical filters that affect establishment and survival (Batzer and Wissinger 1996; Welborn et al. 1996; McCauley 2008). The mechanisms that underlie species replacements across permanence gradients (as in Tables 2.1, 2.2) are well described for odonates and caddisflies, and typically involve tradeoffs between physiological, behavioral, and morphological traits that facilitate coexistence with different types of predators, or tradeoffs between traits that facilitate coexistence with predators and those that expedite the completion of life cycles in temporary habitats. (e.g. Stoks and McPeek 2006; Wissinger et al. 2006; McCauley 2008; McCauley et al. 2010). Patterns of species replacements across habitat types in beaver wetland complexes may be confounded by cycles of dam building and abandonment that lead to legacy effects associated with shifts in permanence and in the presence/absence of large-gaped predatory fish. This temporal variability may be even more likely for beaver ponds and wetlands in the floodplains of major streams because of the stochastic arrival of fishes and unpredictable filling and drying events associated with floods (e.g. Kohler et al. 1999).

In summary, the habitat heterogeneity observed within and between the different types of basins in beaver-meadow wetland complexes combined with the potential for diversity-enhancing metacommunity dynamics associated with dispersal and high connectivity among basins should lead to an overall higher diversity of plants and animals as compared to in structurally simple and isolated wetland basins (Wissinger and Gallagher 1999; Wright et al. 2002, 2003; Caudill 2005; McCauley et al. 2010). Moreover, because the combinations of habitats in beaver-meadow complexes that are part of the cyclic and multi-successional pathways associated with beaver activity (see Fig. 7 in Naiman et al. 1988; also McMaster and McMaster 2001) are constantly changing, understanding the degree to which assemblage structure and composition at a given point in time at a given location is a result of extant vs. legacy conditions will require long-term and wetlandscape-level study.

BEAVER DAM WETLANDS IN WESTERN NORTH AMERICA

Wetland habitats associated with beaver activity in western North America occur in a variety of geomorphological contexts including 1) northern peatlands (e.g., Hood and Bayley 2008a,b, 2009); 2) on rivers of the “High Plains” to the east of the Rocky Mountains and in arid intermountain basins among the major North American Cordilleran ranges where created ponds and wetlands expand the riparian ecotone of stream systems and create perennial wetland habitats in arid landscapes (e.g. Andersen and Shafroth 2010; Gibson and Olden 2014); 3) on relatively small tributaries in the foothills of mountain ranges (e.g. Hodkinson 1975; Clifford et al. 1993; Morrison et al. 2015); 4) in the riparian zone of montane and subalpine rivers that flow through the U-shaped valleys carved by mountain glaciers in the Rockies and Sierras (Malanson and Butler 1990; Butler and Malanson 1995; Fuller and Peckarsky 2011a,b; Polvi and Wohl

2012; Levine and Meyer 2014) (Fig. 2.3,2.5), and 5) on streams flowing on terraces and other valley-side and headwater habitats in montane and alpine valleys (Caudill 2002; Fig. 2.5b).

Beaver Activity Enhances Habitat Heterogeneity in Northern Peatlands

As described for northeastern North America above, beaver activity in the peatlands of western Canada and Alaska, enhances existing habitat heterogeneity in these wetland landscapes. In Miquelon Lake Provincial Park, Alberta, Canada, beavers alter existing shallow isolated wetlands via channel digging (Hood and Larson 2014, 2015). Beavers dig long, deep channels perpendicularly from the wetland edge outward that connect to other wetlands or upland areas, thereby increasing habitat heterogeneity (Hood and Larson 2014) and wetland connectivity (Hood and Larson 2015). Hood and Larson (2014) found that beaver activity increased the amount of vegetated-edge habitat, which had higher species richness, diversity, and evenness than open water and beaver channels. Invertebrate richness, diversity, abundance, and density varied by year and yearly differences were driven by precipitation. Drought resulted in higher densities while higher water levels resulted in more diversity. *Daphnia* spp. were the most abundant taxon regardless of hydrologic conditions. Invertebrates were compared between active and inactive beaver wetlands and between different types of habitats (open water, beaver channels, and vegetated edges) within each category (active, inactive). Predators were the most species-rich group in both active and inactive wetlands, and Chaoboridae larvae were numerically dominant, especially in active beaver channels. Gerridae and Gyrinidae were unique to active channels despite low numbers of individuals. Tabanidae were unique to inactive channels and Culicidae were associated with all three sub-habitats in inactive wetlands. Amphipoda were associated with active vegetative edges and Hood and Lawson posit that amphipods are influenced by an increase of organic material brought in by beaver and that beaver maintain deeper water, which may reduce habitat for mosquito larvae. The strongest differences were seen at the within-wetland level with beaver channels and vegetated edges having more functional feeding groups than open water.

Abandoned Beaver Pond Invertebrate Communities

Beaver ponds are notorious sinks for mineral and organic sediments and patterns of accumulation of these various types of sediments should have multiple consequences for the development of benthic invertebrate communities. In general, the sediments at old dam sites contain higher amounts of organic material than those at relatively young sites (Butler and Malanson 1995). Hodkinson (1975a,b) studied the aquatic invertebrates in abandoned beaver ponds in forested landscapes in the foothills of the Rocky Mountains in Alberta, Canada, with a particular focus on understanding patterns of distribution and abundance of dipteran larvae, which were the dominant taxa in the organic-rich sediments in these habitats. Although the invertebrate communities in these abandoned beaver ponds included surface-dwelling Ephemeroptera, Plecoptera, Megaloptera, and Trichoptera, the great majority of taxa listed (67/ 83 species listed) were dipterans living in the soft organic-laden sediments in these basins. Tipulid larvae were particularly diverse (26 species), and Hodkinson determined that their distribution and abundance varied among substrate types. Coarse-grained, lotic-like gravel substrates in stream courses were dominated by non-tipulid lotic taxa. The abundance and species composition of the dipteran assemblages in the organic-laden, soft-sediments of the abandoned ponds varied along a gradient that varied in 1) particle size; 2) degree of compaction (flocculent to firm); and 3) amount (mostly organic to mostly mineral) and type (herbaceous, woody deciduous leaves, conifer needles) of detrital plant material. Invertebrate biomass was higher in loose, flocculent, detrital substrates than in relatively compacted, mainly mineral substrates. Dietary analyses by Hodkinson combined with those in previous studies Pritchard and Hall (1972) and Pritchard and Leischner (1973) revealed that 1) allochthonous vascular plant detritus dominated the diets of most species in these wetlands; and 2) that habitat partitioning led to dietary partitioning in terms of the type of vascular plant detritus ingested.

Succession in Riverine Floodplains

Beaver dams are frequently breached, rebuilt, relocated, or abandoned in relatively large streamscapes. Malison et al. (2014) studied invertebrates in different successional stages on a large river floodplain in Alaska, USA. Invertebrate communities in beaver ponds differed from flood-channel spring brooks but were similar among early-, mid-, and late-successional ponds despite the fact that early-successional ponds had a greater degree of connectivity to the main channel. The return of beavers to large river systems in arid landscapes is an area of intensive study because of the potential effects on conservation efforts—both on the positive side of the re-establishment of natural flora and fauna, and on the negative side as a interactor with invasive species (Gibson and Olden 2014). While there is evidence for how beaver re-establishment and subsequent cyclical changes associated with damming and abandonment can influence successional changes in vegetation, there are few data on changes to invertebrate communities (Gibson and Olden 2014).

Metapopulation dynamics in Montane Beaver Wetland complexes

Beaver activity on small streams in montane settings often creates step-like complexes of multiple ponds and wetlands that cascade along the relatively flat terrain of mountainside terraces and along the sides of montane valleys (Fig. 2.5b). The lateral development of these complexes creates multi-basin clusters of active and abandoned ponds with hydrologic budgets akin to those described above for the wetland complexes in northeastern North America; i.e., inputs are often dominated by first order streams, springs, and/or groundwater upwellings at valley margins (Fig 2.1d). The proximity of multiple habitats makes it likely that aquatic insects with even moderate dispersal abilities can move between ponds. In a series of related studies Caudill (2003b, 2003a, 2005) evaluated the dynamics of a mayfly (*Callibaetis ferrugineus hageni*) metapopulation in beaver ponds of the upper East River Valley of Colorado, USA with and without trout (Fig. 2.5b,c). Caudill found that late instar larval mayflies densities are significantly higher and adult emergence nearly an order of magnitude greater in troutless ponds than in those with trout. Surprisingly, trout ponds with few or no emerging adults subsequently have similar larval recruitment to ponds with high emergence rates (Caudill 2003a). Isotope labeled adult females move between trout and troutless ponds and there is no relationship between oviposition and trout (Caudill 2003b). A comparison of adult emergence compared to larval recruitment rates point to a source-sink population dynamic among beaver ponds, and models based on these empirical data predict that this mayfly cannot persist in ponds with trout in the absence of adult dispersal from neighboring troutless habitats (Caudill 2005).

Beaver-Pond vs. Non-Beaver Pond Montane Invertebrate Assemblages

Caudill's beaver-pond study sites are located in the Elk Mountains of Colorado, USA where Wissinger and colleagues have surveyed the invertebrate community composition of both beaver and non-beaver ponds for the past 25 years (Wissinger et al. 2003; Wissinger, unpublished data). The spatial configurations of the different types of montane wetland and pond habitats in the Elk Mountains are characteristic of many glaciated mountain valleys throughout the central Rocky Mountains - i.e. beavers dam the main stem of the East River as it meanders through a U-shape glacial valley creating wetland complexes with some ponds highly connected to main channel flow (as in Fuller 2011a,b; Malison et al. 2014), and others that are less directly connected hydrologically (see Fig. 2.3 and 2.5). Beavers also dam headwater side tributaries where they traverse glacier-formed terraces on valley walls (as in Caudill; Fig. 2.5c). Kettle ponds and other non-beaver dam wetland habitats associated with the glacial landscape also occur in these valleys. A comparison of the invertebrate communities in these various wetland habitats within the same valley reveals several patterns (Table 2.3). First, assemblages in main-stem and valley-floor complexes have a higher number of running-water invertebrates including stream-dwelling mayflies, stoneflies, and caddisflies, than those on valley terraces. Inlet and outlet areas of ponds at the upper and lower extent of beaver-pond complexes include some of these stream-dwelling EPTs that, in addition to a distinctly lentic group of organisms (see taxa lists in Appendix; Table 2.3), create a much higher total diversity than in communities in valley-floor complexes with an amalgam of relatively lotic and lentic taxa. There is considerable overlap in the dominant taxa in upland beaver pond complexes and those in non-beaver kettle ponds, with the former often as a nested subset of the species of the caddisflies, odonates, water bugs, and beetles that dominate (in terms of biomass) the large-bodied invertebrate fauna in non-beaver wetlands (Table 2.3; Fig. 2.6). There are several large-bodied taxa that characteristically dominate the biomass in upland beaver ponds but are rare or absent in non-beaver ponds including 1) *Callibaetis* mayflies (Fig. 1.6b); 2) tipulid flies (6- 8 species (Fig. 2.6e); 3) dixid flies; and 4) amphipod crustaceans. There are also subtle, species-level differences that are consistently observed between beaver- and non- beaver upland wetlands. For example, the water boatman *Callicorixa audeni* and *Cenocorixa bifida* are common in montane kettle ponds, whereas several species of *Hesperocorixa* (a relatively lotic genus) dominate in nearby beaver wetlands Caudill (2002). Many of the dominant taxa in temporary non-beaver ponds are rare or absent in beaver ponds. (Wissinger unpublished data). Whether the presence of trout in valley bottom beaver pond complexes explains the rarity of many of the larger bodied lentic taxa (odonates, beetles, water bugs, cased caddisflies; Table 2.3) found in upland habitats (beaver and non-beaver) bears further study.

Finally, beaver dam wetlands have the potential to play a stabilizing role in maintaining beta and regional diversity in wetland habitats in the face of climate change. Wetlands, ponds, and other shallow, temporary basins are considered to be the most vulnerable aquatic habitats to changes in temperature and precipitation regimes, especially at relatively high latitudes and elevations (Barnett et al. 2005; Corcoran et al. 2009; Tutyens et al. 2014). Ponds and other wetland habitats associated with beaver activity are typically permanent because of their hydrological connection to stream courses or their proximity to points of groundwater discharge (Fig. 2.1d). This permanence has the potential for creating refuges for species in habitats that are becoming increasingly temporary (see Smol and Douglass 2007). For example, in the East River Valley, the cased caddisfly, *Limnephilus externus* (Fig. 2.6a), is ubiquitous in beaver and non-beaver ponds and wetlands (also see Hodkinson 1975). The local habitat range of this species is limited by pond drying because of the extended time spent in the final instar during late summer (Wissinger et al. 2003). Censuses of the presence and abundance of this species throughout the valley for 25 years and have observed that during the past decade (2005-2015), early pond drying has resulted in complete cohort failures not observed in the previous 15 years (Wissinger, unpublished data). For example, in 2009 and 2012, a combination of a light snow pack, early snow melt, and a dry early summer, led to the disappearance of over 30 populations of this species in temporary wetland habitats in the East River Valley. The only populations of this species that survived to pupate and emerge in the valley in both years were associated with beaver dam wetlands (both main-valley and terrace complexes; see Fig. 2.3 and 2.5), which remained permanent as a result of their landscape position in stream courses. Spatial patterns of recolonization in non-beaver pond basins after these drought events suggest that beaver-pond populations provide a regional haven for this species in drought years and source of colonists for the re-establishment of populations in non-beaver habitats (Wissinger unpublished data).

BEAVER WETLANDS OF THE SOUTHEASTERN US

Southeastern US beaver wetlands are typically unstable transitory systems due to regional weather and a history of extreme sedimentation. The Southeastern US receives more annual precipitation (1300+ mm per year) than most other areas with beaver-created wetlands and is subject to intense tropical and winter storms that create large stream pulses. These pulses can breach many beaver dams, and at least temporarily drain beaver wetlands. In addition, river and stream beds in the Southeast, particularly the Piedmont region, are particularly unstable (Mukundan et al. 2011) due to poor cotton-era farming practices in the late 1800s and early 1900s that eroded 10 to 30 cm of topsoil into streams and floodplains (Trimble 1974). At current export rates, Jackson et al. (2005) estimate that six to ten millennia will be required to export sediment mobilized during the cotton-era from a Georgia Piedmont watershed. The precipitation patterns in the Southeast combined with unstable, sand and silt substrates limit vegetation growth in and around beaver wetlands to relatively simple communities (e.g. *Panicum* grasses) adapted to shifting hydrologic conditions. Exceptions include ponds built to incorporate old roadbeds or those isolated from main channel flows. Overall, however, most beaver wetlands in the Southeast are small, unstable habitats.

Succession in Invertebrate Communities in Southeastern Beaver Wetlands

Beaver wetlands in the Southeastern US are typically formed from damming small streams that then flood adjacent riparian forest (Fig. 2.1a). In early-stage beaver wetlands, many terrestrial trees persist. The wetlands overall are rather shallow other than the area immediately adjacent to the dam, and in the original stream channel. As beaver wetlands persist, terrestrial vegetation dies under stress from flooding, creating open pond-like wetlands with emergent and submergent vegetation. However, because dams often breach due to frequent and intense storms, these wetlands are frequently abandoned by beaver, and subsequently drain. Abandoned ponds can develop complex braided drainage networks, as the original channel becomes sediment filled and numerous secondary channels develop. Abandoned beaver wetlands usually fill with some seasonal standing water, and upland tree species are slow to reinvade. Typically, abandoned ponds are large open meadow-like wetlands with aquatic, semiaquatic, and terrestrial sub-habitats. A few studies have examined invertebrate communities in abandoned wetlands in other regions (Hodkinson 1975a,b; Wissinger and Gallagher 1999; Hood and Larson 2014), but not in southeastern North America.

To compare invertebrate communities of beaver wetlands among three basic stages of habitat succession, invertebrates were sampled in newly formed (created within 2 years; n = 4), mature (established for >15 years; n = 4), and abandoned wetlands (breached dams; n = 3) in October 2013 and May 2014 in Oconee National Forest in Georgia, USA (Bush and Batzer, unpublished data). There were a relatively high number of taxa (> 60 families; Appendix) in each wetland type, with strong seasonal variation in invertebrate communities (Fig. 2.7). In October, invertebrate communities differed among all successional stages, while in May only the mature beaver wetland communities differed from newly-formed or abandoned ponds (Fig. 2.7). Ostracoda, Copepoda, Branchiopoda (mainly daphniids), Chironomidae, and Ceratopogonidae collectively accounted for 89-95% of total invertebrates, regardless of condition, with ostracods alone accounting for 49-76% of all individuals (Fig. 2.8). Ostracods can be particularly abundant in systems with copious benthic organic detritus combined with relatively shallow, warm water, which is typical in Southeastern beaver wetlands (Smith and Delorme 2010). This preponderance of small, benthic taxa suggests that fish predation is important in these wetlands (Welborn et al. 1996), and most beaver wetlands of the Southeastern US support large populations of *Gambusia* mosquitofish (Poecilidae). Given that all three successional types were dominated by the same five small-bodied taxa, the differences among successional states (Fig. 2.7) are likely driven by rarer, larger-bodied invertebrate taxa.

The greatest differences among successional states were observed in October when terrestrial and semi-aquatic taxa such as springtails (Entomobryidae), scale bugs (Coccoidea), and spiders (Araneae) were among the most abundant macroinvertebrates in abandoned wetlands (Table 2.4). Macroinvertebrates in newly formed and mature beaver wetlands were dominated by common lentic taxa (e.g. Coenagrionidae, Libellulidae, Baetidae, Caenidae), and differences between communities were more likely driven by variation in relative abundance than community composition, *per se*.

In May, invertebrate communities were more similar among successional states, with only the more-stable mature wetlands exhibiting a unique community structure (Fig. 2.7). This seasonal difference suggests that both seasonal change as well as longer-term succession strongly control invertebrate community structures in these beaver wetlands.

While one might expect a linear successional pattern as a stream changes into a pond and then into a wet meadow (see Fig. 7 Naiman et al. 1988), the succession we observed appears more stochastic. In the Southeastern US, beaver wetlands are frequently changing from one stage to another, and back again. Dams in new beaver wetlands are frequently breached and abandoned before the wetland ever becomes mature. In fact, in our study ponds, two of the newly-formed wetlands were abandoned due to dam breaches soon after we sampled, and two newly-formed wetlands had been recreated from formerly abandoned sites. Thus, invertebrates in these wetlands have to be able to adapt to constantly changing conditions or be highly mobile colonizers. Where mature beaver wetlands persist, pond-like communities of lentic invertebrates develop that are able to take advantage of both permanent water and high habitat heterogeneity, and can tolerate high fish predation rates (e.g. Benke et al. 1999). Invertebrate communities in abandoned ponds may be 1) former residents of more mature wetlands that are able to take advantage of residual channels and seasonal filling, 2) migrants from near-by newly created or mature wetlands in the complex (Hodkinson 1975a; Wissinger and Gallagher 1999), or 3) semi-aquatic or terrestrial residents taking advantage of damp soil conditions or lush vegetation (as in abandoned pond in Hodkinson 1975a, tussock zone of Benke et al. 1999, marsh habitat in Wissinger and Gallagher 1999, and vegetative edges in Hood and Larson 2014 table S2).

Zonation and Habitat Heterogeneity Within Beaver Wetlands

Mature beaver wetlands in southeastern North America can be complex heterogeneous habitats with a variety of semi-aquatic, emergent, and submergent vegetation, as well an abundance of woody debris (Benke et al. 1999). Benke and colleagues examined the distribution of invertebrate communities in different habitat zones in a mature beaver wetland in Talledega National Forest, Alabama, USA. This wetland is the largest in a series of beaver-created wetlands on a low gradient small stream in the coastal plain of Alabama, and is sub-divided into three distinct vegetative zones each containing several sub-habitats. These zones consist of: 1) a small, deep unvegetated area of open water adjacent to the beaver dam, with a thin benthic layer; 2) a moderately shallow area in the middle of the pond dominated by floating white water lily (*Nymphaea odorata*), with a thicker benthic layer and extensive woody debris; and 3) a shallow semi-aquatic region at the edge of the pond dominated by emergent rush (*Juncus effuses*), which had two distinct subhabitats: rivulets and *Juncus* tussocks.

The taxon richness of the invertebrate community in the Talledaga beaver pond is tightly coupled with increasing habitat heterogeneity from the open water zone to the *Nymphaea* zone to the *Juncus* zone. The open water has the simplest invertebrate community (Hood and Larson 2014). Copepods are common to both open water and the benthic substrate, while cladocerans dominate the open water. The benthic layer here is dominated by Chironomidae larvae (as was the case for the *Nymphaea* and *Juncus* zones; McDowell and Naiman 1986; Clifford et al. 1993; Margolis et al. 2001; Hood and Larson 2014), oligochaetes, and microcrustaceans. Ceratopogonidae larvae are also common (similar to Georgia wetlands above) in all three zones, and are the most important predator by relative abundance in the benthos of the open water zone.

Taxon richness is higher in the structurally complex *Nymphaea* habitat. There is a higher species richness of microcrustaceans in the *Nymphaea* zone, compared to open water. Chironomids are the dominant insect in all three sub-habitats (vegetation, woody debris, and benthos) of this zone. *Hyalella azteca* is the most common non-insect invertebrate. Overall community structure is similar between the benthos and woody debris, and consisted of many typical lentic taxa. Caenids and baetids were the most abundant mayfly taxa, and dytiscid beetles were the dominant coleopterans. Hydroptilidae and Phryganeidae caddisfly larvae are observed, but in low numbers. The most important predators are Odonata larvae (Coenagrionidae and Libellulidae). The invertebrates on vegetation of the *Nymphaea* zone are similar to woody debris and benthos (although less abundant) with two exceptions: Chrysomelidae beetle larvae (*Donacia* spp.) and Pyralidae moth larvae which are both specifically associated with *Nymphaea* leaves.

The *Juncus* zone has the highest overall taxon richness of all three zones (>100 taxa), which reflects the presence of both aquatic and semi-aquatic sub-habitats. The second most abundant taxa (behind Chironomidae) are semiaquatic/terrestrial collembolans in both tussocks and rivulets (similar to the abandoned Georgia wetlands). Semiaquatic/terrestrial Carabidae and Staphylinidae beetles, and Lycosidae spiders, along with aquatic Dyticidae beetles, are the most common predators. Mites are another common predator in the *Juncus* zone, especially in the tussocks. Sciaridae larvae are only found in the *Juncus* zone and are only abundant in the tussocks. While insects are more taxonomically diverse in the *Juncus* zone, there are fewer microcrustacea taxa than in the *Nymphaea* zone, and those present are dominated by copepods and ostracods rather than copepods and cladocerans (as in the *Nymphaea* and open water zones). Curiously, the preponderance of Ostracoda seen in the Georgia beaver wetlands described above (Bush and Batzer, unpublished data) does not develop in the Talladega beaver pond.

Benke et al. (1999) and Stagliano et al. (1998) also studied insect emergence in all three zones of the Talledaga beaver pond. Insects emerge in every month of the year, and chironomids are the most frequently collected insects in emergence traps, and the only group collected in the open water zone. Chironomid emergence is highest in the *Nymphaea* zone, which was several times higher than the open water zone even at its lowest point and is annually twice that of the *Juncus* zone. Insect emergence year-round coupled with continuously high chironomid larval abundance likely means that growth continues year round in this warm water wetland. While chironomid emergence is lower in the *Juncus* zone than the *Nymphaea* zone, ceratopogonid emergence is highest in the *Juncus* zone. Sciaridae, Cecidomyiidae and Lepidoptera also emerge in high numbers from the *Juncus* zone. The majority of emerging insects from the *Juncus* zone are semi aquatic or terrestrial.

CONCLUSIONS

Beaver wetlands have high invertebrate taxon richness. A recent analysis of macroinvertebrate family richness and composition from 447 individual wetlands by Batzer and Ruhí (2013) included five beaver wetlands (four from Wissinger and Gallagher 1999 and one from Benke et al. 1999). These beaver wetlands ranked 1st, 3rd, 4th, 6th, and 9th overall as supporting the most families out of the 447 sites, not including the semi-terrestrial invertebrate families that are discussed above as being prevalent in abandoned beaver ponds (e.g. beaver complexes in the Southeastern US; see Table 2.4 and Appendix). Our review suggests that beaver wetlands support high taxon richness primarily due to high habitat heterogeneity (e.g. Benke et al. 1999; Wissinger and Gallagher 1999; Hood and Larson 2014), which has several components:

- Beaver wetlands have a variety of sub-habitats including: open water, emergent and submergent vegetation, varying water depths, wetted semi-aquatic edges, mud substrates, highly organic benthic layers of varying complexity, and woody debris, which can each support unique organisms (e.g. Benke et al. 1999; Wissinger and Gallagher 1999).

- Beavers increase habitat heterogeneity of existing wetlands by digging long, deep channels that increase connectivity to other wetlands (e.g. Hood and Larson 2014).
- Beaver dams themselves create unique habitats with water flowing through complex woody debris structure (e.g. Clifford et al 1993; Rolauffs et al. 2001).
- Beaver activities (damming of streams, building of channels, etc.) creates a mosaic of lentic and lotic hydrology that provides habitat for both stream and pond invertebrates (e.g., Table 2.3; Appendix A).
- Beaver wetland environments are constantly changing through time, which creates dynamic, frequently non-linear, multidimensional succession in habitat conditions and invertebrate community structure (Naiman et al. 1988).
- Beaver dam complexes often include multiple basins that are hydrologically connected and within dispersal distances that foster metapopulation dynamics that enhance alpha and beta diversity (e.g. Caudill 2005).
- Wetted edges, shallow regions, and abandoned beaver wetlands create refuge for many terrestrial taxa (see discussions in Western and Southeastern North America vignettes).
- A variety of predators of invertebrates (other macroinvertebrates, amphibians, fishes, and birds) exploit beaver wetlands, and because predation pressure changes spatially across and temporally within beaver wetlands, heterogeneity should be enhanced. Few studies have considered these potential feedbacks on invertebrate communities in beaver wetlands.
- At the continental scale, conservation efforts to recover and reintroduce beaver populations in their native range (North America and Europe) have been successful and

beaver now have healthy populations that create wetlands across a wide variety of geomorphological, hydrological and climactic conditions (e.g., Gibson and Olden 2014).

Our review further identifies important ecological values and services to our society that emanate from beaver activities and associated invertebrate communities including:

- Creation and maintenance of new wetlands (e,g., Fustec et al. 2001; Syphard and Garcia 2001; Cunningham et al. 2006; Nummi et al. 2014; Morrison et al. 2015), in the face of on-going wetland loss in Europe and North America (Zedler and Kercher 2005; Dahl 2011).
- Enhancement of existing wetlands, which aids in increasing wetland density important to conserving wetland dependent organisms as human populations increase (Gibbs 2000).
- Restoration of water quality and quantity in arid lands that has important consequences for regional water management issues and for conservation of plants and animals in those regions (Maret et al. 1987; Gibson and Olden 2014).
- Maintenance of natural flows (Wild 2011) during drought and flood buffering against extreme precipitation events, both of which are likely to become more frequent and severe in the face of climate change (IPCC 2014).
- Creation of refuges for invertebrates during drought which are then able recolonize other wetlands post-drought, stabilizing regional diversity (e.g. Wissinger and Gallagher 1999).
- Maintenance of abundant and rich aquatic invertebrate communities that provide important ecosystem services such as the processing of organic matter (e.g., Klemmer et al. 2012; Prather et al. 2013) and linking primary energy sources to wetland fish and waterfowl (Kemp et al. 2012; Nummi and Halopainen 2014).

Beavers and beaver wetlands will likely become especially crucial management partners and resources as climate change and population growth continue to threaten wetlands overall (Wild 2011).

Literature Cited:

Adler PH, Mason PG (1997) Black flies (Diptera:Simuliidae) of East-Central Saskatchewan, with description of a new species and implications for pest management. The Canadian Entomologist 129 (01):81-91.

Allan JD (2004) Landscapes and riverscapes: The influence of land use on stream ecosystems. Annual Review of Ecology, Evolution, and Systematics 35:257-284.

Anderson CB, Pastur GM, Lencinas MV, Wallem PK, Moorman MC, Rosemond AD (2009) Do introduced North American beavers Castor canadensis engineer differently in southern South America? An overview with implications for restoration. Mammal Review 39 (1):33-52.

Anderson CB, Rosemond AD (2007) Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. Oecologia 154 (1):141-153.

Anderson CB, Rosemond AD (2010) Beaver invasion alters terrestrial subsidies to subantarctic stream food webs. Hydrobiologia 652 (1):349-361.

Barnett TP, Adam JC, Lettenmaier DP (2005) Potential impacts of a warming climate on water availability in snow-dominated regions. Nature 438 (7066):303-309.

Batzer DP (2013) The seemingly intractable ecological responses of invertebrates in North American wetlands: A review. Wetlands 33 (1):1-15.

Batzer DP, Ruhí A (2013) Is there a core set of organisms that structure macroinvertebrate assemblages in freshwater wetlands? Freshwater Biology 58 (8):1647-1659.

Batzer DP, Wissinger SA (1996) Ecology of insect communities in nontidal wetlands. Annual Review of Entomology 41 (1):75-100.

Benke A, Henry III R, Gillespie D, Hunter R (1985) Importance of snag habitat for animal production in southeastern streams. Fisheries 10 (5):8-13.

Benke A, Ward G, Richardson T (1999) Beaver impounded wetlands of the southeastern coastal plain. In: Batzer D, Rader R, Wissinger S (eds) Invertebrates in freshwather wetlands of North America: Ecology and management.Wiley, Toronto, Ontario, pp 217-245.

Benke AC, Arsdall TCV, Jr., Gillespie DM, Parrish FK (1984) Invertebrate productivity in a subtropical blackwater river: The importance of habitat and life history. Ecological Monographs 54 (1):25-63.

Bluzma P (2003) Beaver abundance and beaver site use in a hilly landscape (Eastern Lithuania). Acta Zoologica Lituanica 13 (1):8-14.

Brown DJ, Hubert WA, Anderson SH (1996) Beaver ponds create wetland habitat for birds in mountains of southeastern Wyoming. Wetlands 16 (2):127-133.

Burchsted D, Daniels M, Thorson R, Vokoun J (2010) The river discontinuum: Applying beaver modifications to baseline conditions for restoration of forested headwaters. Bioscience 60 (11):908-922.

Burchsted D, Daniels MD (2014) Classification of the alterations of beaver dams to headwater streams in northeastern Connecticut, U.S.A. Geomorphology 205 (0):36-50.

Butler DR, Malanson GP (1995) Sedimentation rates and patterns in beaver ponds in a mountain environment. Geomorphology 13 (1–4):255-269.

Butler DR, Malanson GP (2005) The geomorphic influences of beaver dams and failures of beaver dams. Geomorphology 71 (1–2):48-60.

Caudill CC (2002) Metapopulation biology of the mayfly Callibaetis ferrugineus hageni in high-elevation beaver ponds. Dissertation, Cornell University, Ithaca, New York.

Caudill CC (2003a) Empirical evidence for nonselective recruitment and a source-sink dynamic in a mayfly metapopulation. Ecology 84 (8):2119-2132.

Caudill CC (2003b) Measuring dispersal in a metapopulation using stable isotope enrichment: high rates of sex-biased dispersal between patches in a mayfly metapopulation. Oikos 101 (3):624-630.

Caudill CC (2005) Trout predators and demographic sources and sinks in a mayfly metapopulation. Ecology 86 (4):935-946.

Cirmo CP, Driscoll CT (1993) Beaver pond biogeochemistry: Acid neutralizing capacity generation in a headwater wetland. Wetlands 13 (4):277-292.

Clifford HF, Wiley GM, Casey RJ (1993) Macroinvertebrates of a beaver altered boreal stream of Alberta, Canada, with special reference to the fauna on the dams. Canadian Journal of Zoology 71 (7):1439-1447.

Collen P, Gibson RJ (2001) The general ecology of beavers (Castor spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish – a review. Reviews in Fish Biology and Fisheries 10 (4):439-461.

Corcoran RM, Lovvorn JR, Heglund PJ (2009) Long-term change in limnology and invertebrates in Alaskan boreal wetlands. Hydrobiologia 620 (1):77-89.

Crowley PH, Johnson DM (1982) Habitat and seasonality as niche axes in an odonate community. Ecology 63 (4):1064-1077.

Cunningham JM, Calhoun AJK, Glanz WE (2006) Patterns of beaver colonization and wetland change in Acadia National Park. Northeastern Naturalist 13 (4):583-596.

Curran JC, Cannatelli KM (2014) The impact of beaver dams on the morphology of a river in the eastern United States with implications for river restoration. Earth Surface Processes and Landforms 39 (9):1236-1244.

Dahl TE (2011) Status and trends of wetlands in the conterminous United States 2004 to 2009. US Department of the Interior, Fish and Wildlife Service, Washington, DC.

Danilov P, Kanshiev V, Fyodorov F (2011) Characteristics of North American and Eurasian beaver ecology in Karelia. In: G S, P BJ (eds) Restoring the European Beaver: 50 Years of Experience. Pensoft Publishers, Sofia, pp 55-72.

De Szalay FA, Resh VH (2000) Factors influencing macroinvertebrate colonization of seasonal wetlands: responses to emergent plant cover. Freshwater Biology 45 (3):295-308.

Devito KJ, Dillon PJ (1993) Importance of runoff and winter anoxia to the P and N dynamics of a beaver pond. Canadian Journal of Fisheries and Aquatic Sciences 50 (10):2222-2234.

Donkor NT, Fryxell JM (2000) Lowland boreal forests characterization in Algonquin Provincial Park relative to beaver (*Castor canadensis*) foraging and edaphic factors. Plant Ecology 148 (1):1-12.

Fairchild GW, Faulds AM, Matta JF (2000) Beetle assemblages in ponds: effects of habitat and site age. Freshwater Biology 44 (3):523-534.

Fairchild GW, Jason C, Faulds AM, Short AEZ, Matta JF (2003) Microhabitat and landscape influences on aquatic beetle assemblages in a cluster of temporary and permanent ponds. Journal of the North American Benthological Society 22 (2):224-240.

France RL (1997) The importance of beaver lodges in structuring littoral communities in boreal headwater lakes. Canadian Journal of Zoology 75 (7):1009-1013.

Fuller MR, Peckarsky BL (2011a) Does the morphology of beaver ponds alter downstream ecosystems? Hydrobiologia 668 (1):35-48.

Fuller MR, Peckarsky BL (2011b) Ecosystem engineering by beavers affects mayfly life histories. Freshwater Biology 56 (5):969-979.

Fustec J, Lode T, Le Jacques D, Cormier JP (2001) Colonization, riparian habitat selection and home range size in a reintroduced population of European beavers in the Loire. Freshwater Biology 46 (10):1361-1371.

Gibbs JP (2000) Wetland loss and biodiversity conservation. Conservation Biology 14:314–317.

Gibson PP, Olden JD (2014) Ecology, management, and conservation implications of North American beaver (*Castor canadensis*) in dryland streams. Aquatic Conservation: Marine and Freshwater Ecosystems 24 (3):391-409.

Grover AM, Baldassarre GA (1995) Bird species richness within beaver ponds in south-central New York. Wetlands 15 (2):108-118.

Halley D, Rosell F, Saveljev A (2012) Population and distribution of Eurasian beaver (Castor fiber). Baltic Forestry 18 (1):168-175.

Hammerson GA (1994) Beaver (*Castor canadensis*) ecosystem alterations, management, and monitoring. Natural Areas Journal 14 (1):44-57.

Harthun M (1999) The influence of the European beaver (*Castor fiber albicus*) on the biodiversity (Odonata, Mollusca, Trichoptera, Ephemeroptera, Diptera) of brooks in Hesse (Germany). Limnologica 29 (4):449-464.

Hartman G (1994) Long-term population development of a reintroduced beaver (*Castor fiber*) population in Sweden. Conservation Biology 8 (3):713-717.

Hartman G (1995) Patterns of spread of a reintroduced beaver *Castor fiber* population in Sweden. Wildlife Biology 1 (2):97-103.

Hodkinson ID (1975a) A community analysis of the benthic insect fauna of an abandoned beaver pond. Journal of Animal Ecology 44 (2):533-551.

Hodkinson ID (1975b) Energy flow and organic matter decomposition in an abandoned beaver pond ecosystem. Oecologia 21 (2):131-139.

Hood GA, Bayley SE (2008a) Beaver (Castor canadensis) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. Biological Conservarion 141 (2):556-567.

Hood GA, Bayley SE (2008b) The effects of high ungulate densities on foraging choices by beaver (*Castor canadensis*) in the mixed-wood boreal forest. Canadian Journal of Zoology 86 (6):484-496.

Hood GA, Bayley SE (2009) A comparison of riparian plant community response to herbivory by beavers (Castor canadensis) and ungulates in Canada's boreal mixed-wood forest. Forest Ecology and Management 258 (9):1979-1989.

Hood GA, Larson DG (2014) Beaver-created habitat heterogeneity influences aquatic invertebrate assemblages in boreal Canada. Wetlands 34 (1):19-29.

Hood GA, Larson DG (2015) Ecological engineering and aquatic connectivity: a new perspective from beaver-modified wetlands. Freshwater Biology 60 (1):198-208.

Jackson CR, Martin JK, Leigh DS, West LT (2005) A southeastern piedmont watershed sediment budget: Evidence for a multi-millennial agricultural legacy. Journal of Soil and Water Conservation 60 (6):298-310.

Johnson DR, Chance DH (1974) Presettlement overharvest of Upper Columbia River beaver populations. Canadian Journal of Zoology 52 (12):1519-1521.

Johnston CA, Naiman RJ (1987) Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. Landscape Ecology 1 (1):47-57.

Johnston CA, Naiman RJ (1990) Aquatic patch creation in relation to beaver population trends. Ecology 71 (4):1617-1621.

Kemp PS, Worthington TA, Langford TEL, Tree ARJ, Gaywood MJ (2012) Qualitative and quantitative effects of reintroduced beavers on stream fish. Fish and Fisheries 13 (2):158-181.

Klemmer AJ, Wissinger SA, Greig HS, Ostrofsky ML (2012) Nonlinear effects of consumer density on multiple ecosystem processes. Journal of Animal Ecology 81:770–780.

Klotz RL (1998) Influence of beaver ponds on the phosphorus concentration of stream water. Canadian Journal of Fisheries and Aquatic Sciences 55 (5):1228-1235.

Kohler SL, Corti D, Slamecka MC, Schneider DW (1999) Prairie floodplain ponds - Mechanisms affecting invertebrate community structure. In: Batzer DP, Rader

RD, Wissinger SA (eds) Invertebrates in Freshwater Wetlands of North America. pp 711-730.

Law A, Jones KC, Willby NJ (2014) Medium vs. short-term effects of herbivory by Eurasian beaver on aquatic vegetation. Aquatic Botany 116 (0):27-34.

Levine R, Meyer GA (2014) Beaver dams and channel sediment dynamics on Odell Creek, Centennial Valley, Montana, USA. Geomorphology 205:51-64.

Mackay RJ, Waters TF (1986) Effects of small impoundments on hydropsychid caddisfly production in Valley Creek, Minnesota. Ecology 67 (6):1680-1686.

Malanson GP, Butler DR (1990) Woody debris, sediment, and riparian vegetation of a subalpine river, Montana, U.S.A. Arctic and Alpine Research 22 (2):183-194.

Malison RL, Lorang MS, Whited DC, Stanford JA (2014) Beavers (Castor canadensis) influence habitat for juvenile salmon in a large Alaskan river floodplain. Freshwater Biology 59 (6):1229-1246.

Margolis BE, Raesly RL, Shumway DL (2001) The effects of beaver-created wetlands on the benthic macroinvertebrate assemblages of two Appalachian streams. Wetlands 21 (4):554-563.

Maret TJ, Parker M, Fannin TE (1987) The effect of beaver ponds on the nonpoint source water quality of a stream in Southwestern Wyoming. Water Resources 21:263–268.

McCall TC, Hodgman TP, Diefenbach DR, Owen RB (1996) Beaver populations and their relation to wetland habitat and breeding waterfowl in Maine. Wetlands 16 (2):163-172.

McCauley JS (2007) The role of local and regional processes in structuring larval dragonfly distributions across habitat gradients. Oikos 116 (1):121-133.

McCauley SJ (2008) Slow, fast and in between: habitat distribution and behaviour of larvae in nine species of libellulid dragonfly. Freshwater Biology 53 (2):253-263.

McCauley SJ, Brodin T, Hammond J (2010) Foraging rates of larval dragonfly colonists are positively related to habitat isolation: Results from a landscape-level experiment. The American Naturalist 175 (3):E66-E73.

McDowell DM, Naiman RJ (1986) Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). Oecologia 68:481–489.

McKinstry MC, Caffrey P, Anderson SH (2001) The importance of beaver to wetland habitats and waterfowl in Wyoming. Journal of the American Water Resources Association 37:1571–1577.

McMaster RT, McMaster ND (2001) Composition, structure, and dynamics of vegetation in fifteen beaver-impacted wetlands in western Massachusetts. Rhodora 103(915):293–320.

Morrison A, Westbrook CJ, Bedard-Haughn A (2015) Distribution of Canadian Rocky Mountain wetlands impacted by beaver. Wetlands 35 (1):95-104.

Mukundan R, Radcliffe DE, Ritchie JC (2011) Channel stability and sediment source assessment in streams draining a piedmont watershed in Georgia, USA. Hydrological Processes 25 (8):1243-1253.

Naiman RJ, Décamps H, Pastor J, Johnston CA (1988a) The potential importance of boundaries of fluvial ecosystems. Journal of the North American Benthological Society 7 (4):289-306.

Naiman RJ, Johnston CA, Kelley JC (1988b) Alteration of North American streams by beaver. Bioscience 38 (11):753-762.

Naiman RJ, Melillo JM (1984) Nitrogen budget of a subarctic stream altered by beaver (Castor canadensis). Oecologia 62 (2):150-155.

Naiman RJ, Melillo JM, Hobbie JE (1986) Ecosystem alteation of boreal forest streams by beaver (Castor canadensis). Ecology 67 (5):1254-1269.

Naiman RJ, Melillo JM, Lock MA, Ford TE, Reice SR (1987) Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. Ecology:1139-1156.

Niles JM, Hartman KJ, Keyser P (2013) Short-term effects of beaver dam removal on brook trout in an Appalachian headwater stream. Northeastern Naturalist 20 (3):540-551.

Nolet BA, Rosell F (1998) Comeback of the beaver Castor fiber: An overview of old and new conservation problems. Biological Conservation 83 (2):165-173.

Nummi P, Hahtola A (2008) The beaver as an ecosystem engineer facilitates teal breeding. Ecography 31 (4):519-524.

Nummi P, Holopainen S (2014) Whole-community facilitation by beaver: ecosystem engineer increases waterbird diversity. Aquatic Conservation: Marine and Freshwater Ecosystems 24 (5):623-633.

Pliuraite V, Kesminas V (2012) Ecological impact of Eurasian beaver (Castor fiber) activity on macroinvertebrate communities in Lithuanian trout streams. Central European Journal of Biology 7 (1):101-114.

Pollock MM, Beechie TJ, Jordan CE (2007) Geomorphic changes upstream of beaver dams in Bridge Creek, an incised stream channel in the interior Columbia River basin, eastern Oregon. Earth Surface Processes and Landforms 32 (8):1174-1185.

Pollock MM, Naiman RJ, Erickson HE, Johnston CA, Pastor J, Pinay G (1995) Beaver as engineers: Influences on biotic and abiotic characteristics of drainage basins. In: Jones CG, Lawton JH (eds) Linking Species & Ecosystems. Springer US, pp 117-126.

Polvi LE, Wohl E (2012) The beaver meadow complex revisited – the role of beavers in post-glacial floodplain development. Earth Surface Processes and Landforms 37 (3):332-346.

Polvi LE, Wohl E (2013) Biotic drivers of stream planform: Implications for understanding the past and restoring the future. Bioscience 63 (6):439-452.

Polvi LE, Wohl EE, Merritt DM (2011) Geomorphic and process domain controls on riparian zones in the Colorado front range. Geomorphology 125 (4):504-516.

Pritchard G, Hall HA (1971) An introduction to the biology of craneflies in a series of abandoned beaver ponds, with an account of the life cycle of Tipula sacra Alexander (Diptera; Tipulidae). Canadian Journal of Zoology 49 (4):467-482.

Pritchard G, Leischner TG (1973) The life history and feeding habits of Sialis cornuta Ross in a series of abandoned beaver ponds (Insecta; Megaloptera). Canadian Journal of Zoology 51 (2):121-131.

Ray AM, Rebertus AJ, Ray HL (2001) Macrophyte succession in Minnesota beaver ponds. Canadian Journal of Botany 79 (4):487-499.

Ray HL, Ray AM, Rebertus AJ (2004) Rapid establishment of fish in isolated peatland beaver ponds. Wetlands 24 (2):399-405.

Rebertus AJ (1986) Bogs as beaver habitat in north-central Minnesota. American Midland Naturalist 116 (2):240-245.

Richardson JS, Mackay RJ (1991) Lake outlets and the distribution of filter feeders: An assessment of hypotheses. Oikos 62 (3):370-380.

Rolauffs P, Hering D, Lohse S (2001) Composition, invertebrate community and productivity of a beaver dam in comparison to other stream habitat types. Hydrobiologia 459:201-212.

Rosell F, Bozser O, Collen P, Parker H (2005) Ecological impact of beavers Castor fiber and Castor canadensis and their ability to modify ecosystems. Mammal Review 35 (3-4):248-276.

Smith AJ, Delorme LD (2010) Ostracoda. In: Covich JH, Thorp AP (eds) Ecology and Classification of North American Freshwater Invertebrates Third edn. Academic Press, San Diego, pp 725-771.

Smith ME, Driscoll CT, Wyskowski BJ, Brooks CM, Cosentini CC (1991) Modificatiom of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack mountains, New York. Canadian Journal of Zoology 69 (1):55-61.

Smol JP, Douglas MSV (2007) Crossing the final ecological threshold in high Arctic ponds. Proceedings of the National Academy of Sciences 104 (30):12395-12397.

Snodgrass JW, Meffe GK (1998) Influence of beavers on stream fish assemblages: Effects of pond age and watershed position. Ecology 79 (3):928-942.

Sprules WM (1940) The effect of a beaver dam on the insect fauna of a trout stream. Trans Amer Fish Soc 70:236-248.

Stagliano DM, Benke AC, Anderson DH (1998) Emergence of aquatic insects from two habitats in a small wetland of the southeastern USA: temporal patterns of numbers and biomass. Journal of the North American Benthological Society 17 (1):37-53.

Stoks R, McPeek MA (2003) Predators and life histories shape Lestes damselfly assemblages along a freshwater habitat gradient. Ecology 84 (6):1576-1587.

Stoks R, McPeek MA (2006) A tale of two diversifications: Reciprocal habitat shifts to fill ecological space along the pond permanence gradient. The American Naturalist 168 (S6):S50-S72.

Strachan SR, Chester ET, Robson BJ (2014) Microrefuges from drying for invertebrates in a seasonal wetland. Freshwwater Biology 59:2528–2538.

Syphard AD, Garcia MW (2001) Human- and beaver-induced wetland changes in the Chickahominy River watershed from 1953 to 1994. Wetlands 21 (3):342-353.

Trimble SW (1974) Man-induced soil erosion on the southern piedmont. Soil Conservation Society of America:1700-1970.

Tuytens K, Vanschoenwinkel B, Waterkeyn A, Brendonck L (2014) Predictions of climate change infer increased environmental harshness and altered connectivity in a cluster of temporary pools. Freshwater Biology 59 (5):955-968.

Van de Meutter F, Cottenie K, De Meester L (2008) Exploring differences in macroinvertebrate communities from emergent, floating-leaved and submersed vegetation in shallow ponds. Fundamental and Applied Limnology 173 (1):47-57.

Welborn GA, Skelly DK, Werner EE (1996) Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27:337-363.

White SM, Rahel FJ (2008) Complementation of habitats for Bonneville cutthroat trout in watersheds influenced by beavers, livestock, and drought. Transactions of the American Fisheries Society 137 (3):881-894.

Wild C (2011) Beaver as a climate change adaptation tool: concepts and priority sites in New Mexico. Seventh Generation Institute, Santa Fe.

Wissinger SA (1988) Life history and size structure of larval dragonfly populations. Journal of the North American Benthological Society 7 (1):13-28.

Wissinger SA, Brown WS, Jannot JE (2003) Caddisfly life histories along permanence gradients in high-altitude wetlands in Colorado (U.S.A.). Freshwater Biology 48 (2):255-270.

Wissinger SA, Gallagher LJ (1999) Beaver pond wetlands in northwestern Pennsylvania. Modes of colonization and succession after drought. In: Batzer D, Rader R, Wissinger S (eds) Invertebrates in freshwater wetlands of North America: Ecology and management. Wiley, Hoboken, New Jersey, pp 333-362.

Wissinger SA, Whissel JC, Eldermire C, Brown WS (2006) Predator defense along a permanence gradient: roles of case structure, behavior, and developmental phenology in caddisflies. Oecologia 147 (4):667-678.

Wissinger SA, Whiteman HH, Sparks GB, Rouse GL, Brown WS (1999) Foraging trade-offs along a predator-permanence gradient in subalpine wetlands. Ecology 80 (6):2102-2116.

Woo M-k, Waddington JM (1990) Effects of beaver dams on subarctic wetland hydrology. Arctic 43 (3):223-230.

Wright JP, Flecker AS, Jones CG (2003) Local vs landscape controls on plant species richness in beaver meadows. Ecology 84 (12):3162-3173.

Wright JP, Jones CG, Flecker AS (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132 (1):96-101.

Zedler JB, Kercher S (2005) Wetland resources: Status, trends, ecosystem services, and restorability. Annual Review of Environment and Resources 30 (1):39-74.

Table 2.1. Distribution of odonates in different subhabitats within a beaver-meadow wetland complex in northwestern Pennsylvania. Top vertebrate predators in parentheses (salamanders = *Ambystoma maculatum* and *Notopthalmus viridescens*). Larval occurrences based on Wissinger and Gallagher (1999) and subsequent D-net and aerial surveys taken during May–October between 2000 and 2009. Data are cumulative; i.e., not all species were collected in a given year. Larvae of all species are encountered along shorelines during their emergence periods.

Active Beaver Ponds 1-3 m depth & **permanent** (pumpkinseed, bluegill, grass pickerel, bass)			**Abandoned pond, marsh, shrub swamp** < 1 m depth, **semi-permanent** (mudminnow, stickleback, salamander larvae)		**Temporary** < 0.5 m depth (salamanders)
Benthic open basin	**Submergent vegetation**	**Shoreline with emergent veg.**	**Marshes – emergent & submergent veg.**	**Shrub Swamps**	**Woodland pools/margins**
Libellula lydia	*Libellula luctuosa*	*Libellula luctuosa*	*Libellula pulchella*	*Libellula pulchella*	*Aeshna umbrosa*
Libellula julia	*Libellula incesta*	*Libellula incesta*	*Libellula luctuosa*	*Libellula luctuosa*	
Gomphus exilis	*Erythemis simplicicollis*	*Erythemis simplicicollis*	*Libellula quadrimaculata*	*Aeshna constricta*	
Gomphus spicatus	*Sympetrum vicinum*	*Sympetrum vicinum*	*Anax junius*	*Aeshna canadensis*	
Argiogomphus forcifer	*Leucorrhinia intacta*	*Leucorrhinia intacta*	*Sympetrum vicinum*	*Sympetrum ambiguum*	
Perithemis tenera	*Pachydiplax longipennis*	*Pachydiplax longipennis*	*Sympetrum semicinctum*		
Epitheca cynosura	*Celithemis elisa*	*Celithemis elisa*	*Sympetrum obtrusum*		
Epitheca canis	*Celithemis eponina*	*Celithemis eponina*	*Aeshna tuberculifera*		
	Argia fumipennis	*Ischnura verticalis*	*Tramea lacerata*		
	Ischnura verticalis	*Ischnura posita*	*Tramea carolina*		
	Ischnura posita	*Enallagma civile*	*Pantala flavescens*		
	Enallagma signatum	*Enallagma signatum*	*Ischnura verticalis*		
		Enallagma vespersum	*Ischnura posita*		
		Nehalennia irene	*Enallagma civile*		
		Lestes vigilax	*Enallagma boreale*		
			Enallagma aspersum		
			Nehalennia irene		
			Lestes disjunctus		
			Lestes eurinus		
			Lestes congener		

Table 2.2. Distribution of cased caddisflies (Limnephilidae and Phryganeidae) across subhabitats in two beaver-meadow wetland complexes in northwestern Pennsylvania. Larval occurrences based on Wissinger and Gallagher (1999) and subsequent D-net samples taken October-November, and April-May from 2000-2009. Top predators in a) permanent ponds (active beaver ponds) are large-gaped fishes (sunfish, bass, grass pickerel); b) in semi-permanent marshes (herbaceous emergent) and shrubswamps are mudminnows, brook stickleback, and newts; and c) backflooded temporary habitats and woodland pools are *Ambystoma* salamander predators. Seeps and rivulets are small flowing water habitats between various standing water habitats in the beaver meadow complexes (see Fig 15.1 Wissinger & Gallagher 1999).

Permanent Ponds	**Semi-perm marshes & shrub swamps**	**Temporary woodland pools**	**Seeps & Rivulets**
Banksiola crotchii	*Nemotaulius hostilis*	*Ptilostomus ocellifera*	*Ironoquia punctatissima*
Platycentropus radiatus	*Limnephilus indivisus*	*Ptilostomus postica*	
Pycnopsyche subfasciata	*Limnephilus submonilifer*	*Ironoquia parvula*	
Agrypnia vestita	*Limnephilus moestus*		
Anabolia consocia	*Banksiola doussaria*		
Fabria Inornata	*Bansiola crotchii*		
	Anabolia bimaculata		
	Ptilostomus occellifera		
	Phryganea spp. (*sayi?*)		

Table 2.3. Number of species in relatively lentic vs. lotic aquatic insect groups in ponds and wetlands in the upper East River Valley in the Elk Mountains of Colorado near the Rocky Mountain Biological Laboratory. 1) Valley beaver = ponds with hydrologic connections to the East River (Fig. 2.5b); 2) upland beaver = beaver ponds on small tributaries along the valley sides (Fig 2.5c); and 3) non-beaver = kettle ponds in mid-valley moraines. Data combined from Caudill (2001), B. Peckarsky (unpub. data), and S. Wissinger (unpub. data).

Order	Family	Valley Beaver	Upland Beaver	Non-Beaver
Ephemeroptera	Total taxa	7	3	2
	Baetidae	1	2	1
	Caenidae		1	1
	Ephemerellidae	1		
	Heptageniidae	3		
	Leptophlebiidae	1		
	Siphlonuridae	1		
Plecoptera	Total taxa	7	2	0
	Chloroperlidae	2	1	
	Nemouridae	2	1	
	Perlidae	2		
Odonata	Total taxa	1	11	18
	Aeshnidae	1	3	3
	Coenagrionidae		3	4
	Corduliidae		1	2
	Lestidae		2	3
	Libellulidae		2	6
Coleoptera	Total taxa	7	16	22
	Chrysomelidae		1	1
	Dytiscidae	4	10	15
	Gyrinidae	1	1	1
	Haliplidae	1	1	2
	Helophoridae	1	1	1
	Hydrophilidae		2	2
Hemiptera	Total Taxa	3	8	11
	Corixidae	1	2	3
	Gerridae	1	2	3
	Mesoveliidae		1	1
	Notonectidae		1	1
	Saldidae	1	1	2
	Veliidae		1	1
Trichoptera	Total Taxa	8	8	10
	Hydropsychidae	1		
	Leptoceridae		1	1
	Limnephilidae	5	6	8
	Phryganeidae		1	1
	Polycentropodidae	2		
	Rhyacophilidae	1		

Table 2.4. Ten most abundant large-bodied taxa (excluding Ostracoda, Branchiopoda, Copepoda, Chironomidae, and Ceratopogonidae) in new, mature, and abandoned beaver wetlands of Georgia, in October 2013. Shaded taxa represent exclusively terrestrial taxa.

Newly-created	**Mature**	**Abandoned**
Oligochaeta	Caenidae	Entomobryidae
Dogielinotidae	Dogielinotidae	Coccoidea
Coenagrionidae	Coenagrionidae	Oligochaeta
Non-oribatid Acarina	Non-oribatid Acarina	Non-oribatid Acarina
Libellulidae	Libellulidae	Araneae
Sphaeriidae	Sphaeriidae	Coenagrionidae
Caenidae	Baetidae	Sphaeriidae
Baetidae	Veliidae	Oribatidae
Dytiscidae	Oribatidae	Corethrellidae
Araneae	Scirtidae	Delphacidae

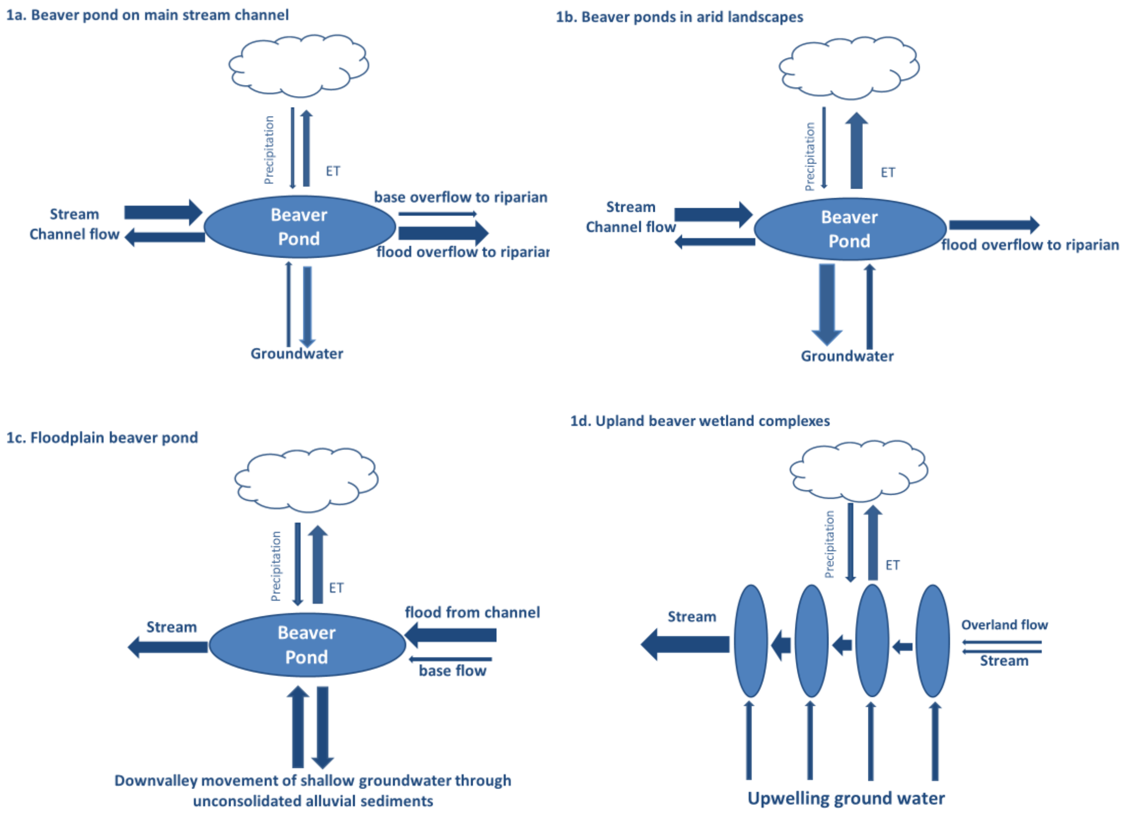

Figure 2.1 The hydrology of ponds and wetlands associated with beaver activity. **A**. The hydrology of beaver ponds in main channels will be dominated by stream flow inputs and outputs, and hence be temporally dynamic. Channel flow can be greater than outflow because of 1) bank overflow to the adjacent riparian zone, 2) enhanced evapotranspiration, and/or 3) hyporheic loss with the downstream return flow path dependent on the geomorphologic context (Rosell et al. 2005). **B**. In arid landscapes, the three losses between stream input and output will be exaggerated because of enhanced evaporation and lateral and vertical losses to shallow groundwater. The temporary storage in that shallow groundwater can being especially important for ameliorating downstream low-flow conditions (Gibson and Olden 2014). **C**. In beaver ponds and wetlands situated in floodplains away from the main stream channel, the hydrologic

budget will be strongly influenced by shallow ground water and lateral hyporheic flow moving down valley through unconsolidated sediments. Proximity to the main channel will determine the frequency and duration of inputs from floods (see Fig. 2.3b). **D**. Beaver dam wetland complexes in relatively upland landscapes (perched water tables, along valley margins) receive much of their hydrologic input from springs and upwelling groundwater discharge that then leaves the wetland complex as the channel flow of headwater streams. This hydrology model fits beaver meadow complexes in Northeastern North America and those on valley-margins in Western North America (see text).

Figure 2.2 Beaver dams on a high gradient stream (West Brush Creek) in the Elk Mountains of Colorado (see Fuller and Peckarsky 2011a,b; photo by Matt Fuller).

Figure 2.3 Beaver pond wetlands in the lower East River Valley in the Elk Mountains of central Colorado below the Rocky Mountain Biological Laboratory. A. Overview of meandering river in a glacially widened montane valley in spring (photo by Scott Wissinger). B. Arrow indicates location of zoom to floodplain complex of beaver ponds (note beaver hut in pond on lower left) and difference in water color between channel (spring runoff) and beaver-created riparian wetlands which include open ponds, channels connecting ponds, and extensive willow-thicket and sedge-meadow wetlands that cover most of the valley bottom (photo by Susan Washko).

Figure 2.4 Habitats associated with beaver meadow wetland complex in northwestern Pennsylvania, USA. A. Active beaver pond embedded in a series of ponds and other beaver-affected wetland habitats on Allegheny College's Biology Reserved. Habitats include open water zone in the foreground, lily pad zone, and shrub swamp (plant species given in text) at the forest edge in the background (photo by Ben Plohr). B. mixed species shrub swamp on the upslope edge of pond, and C. vernal pool in adjacent woodland enhanced by locally raised water table (photo by Scott Wissinger).

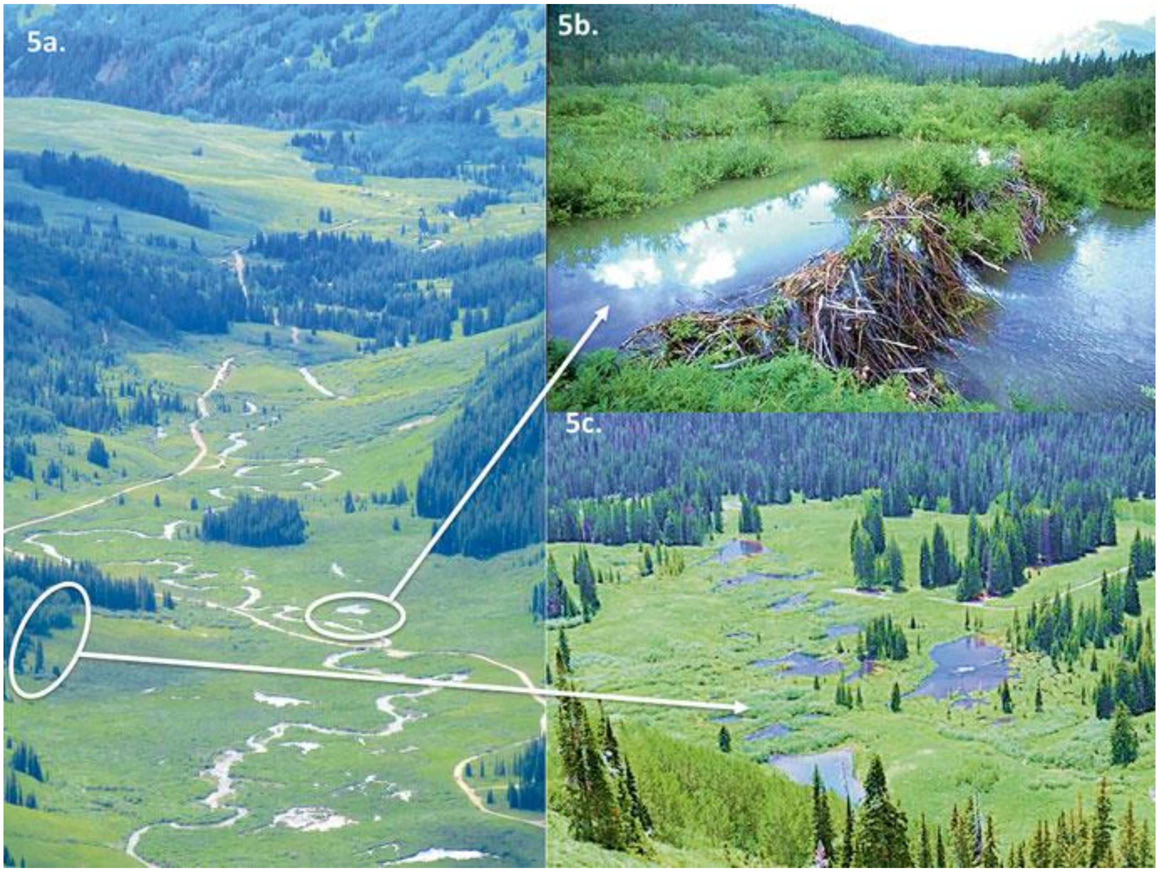

Figure 2.5 A. Overview of geomorphological settings of beaver dam wetlands in the upper East River Valley of in the Elk Mountains of central Colorado (photo by Scott Wissinger). B) valley bottom riparian beaver pond (photo by Chris Caudill), and C) upland beaver wetland complex along valley margin (photo by Susan Washko).

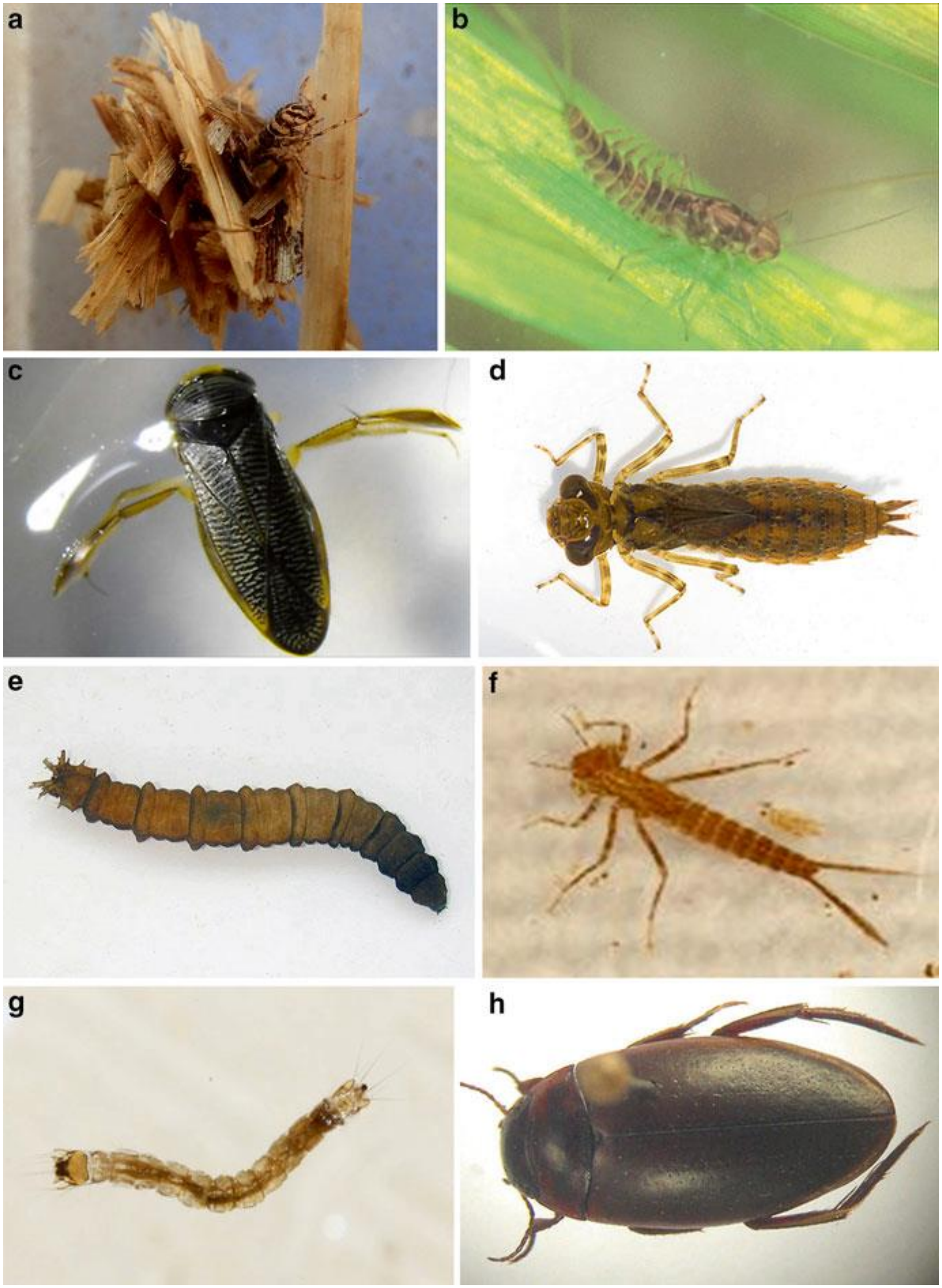

Figure 2.6 Frequently encountered abundant invertebrates in upland beaver wetlands in the East River Valley in the Elk Mountains of central Colorado studied by Caudill (2002)

and Wissinger (unpublished data). A) the limnephilid caddisfly, *Limnephilus externus* (photo by Nixie Boddy), B) *Callibaetis ferrugineus hageni* (photo by Chris Caudill), C) *Hesperocorixa* (photo by Timothy Loh), D) *Aeshna palmata* (photo by Susan Washko), E) tipulid fly larva (photo by John Meyer). F) larva of the damselfly, *Coenagrion resolutum* (photo by Susan Washko) G) larva of the meniscus midge *Dixella* (photo by Stephen Luk). H) the dytiscid diving beetle, *Agabus tristus* (photo by Susan Wasnko).

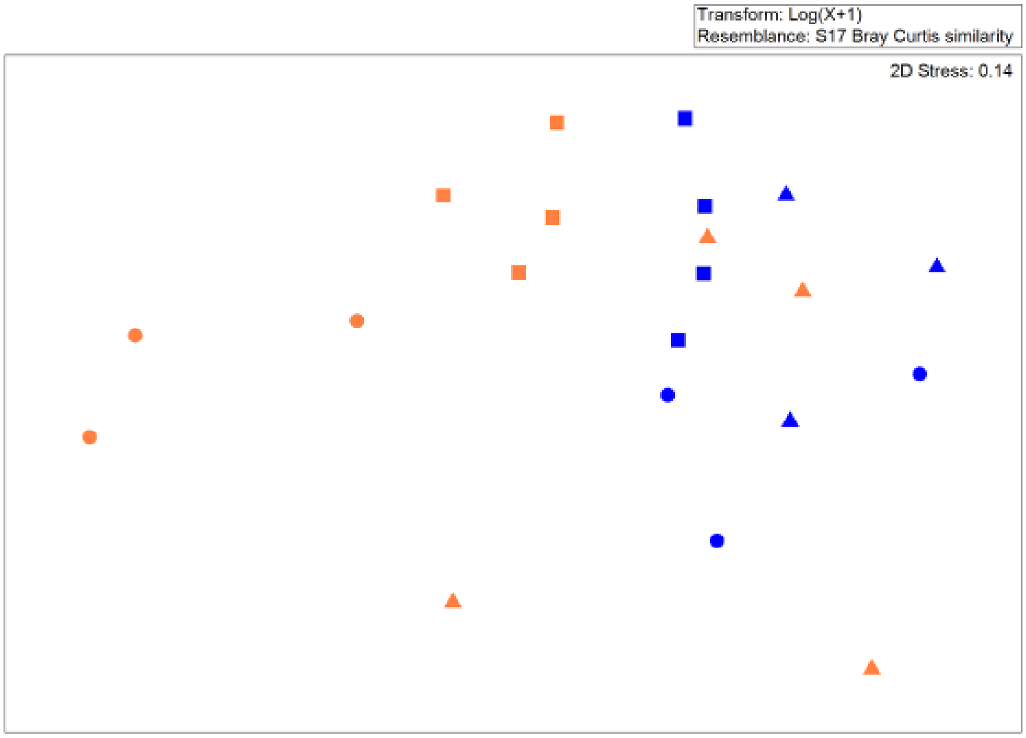

Figure 2.7 Nonmetric multidimensional scaling plot showing patterns among newly-created (▲), mature (■), and abandoned (●) beaver wetland invertebrate communities (Bray-Curtis similarity, Kruskal fit scheme 1,25 restarts) in October 2013 (orange fill; new vs mature R=0.344, P=0.029; new vs abandoned R=0.704, P=0.029; mature vs abandoned R=0.741, P=0.029) and May 2014 (blue fill; new vs mature R=0.685, P=0.029; new vs abandoned R=0.630, P=0.1; mature vs abandoned R=0.556, P=0.029).

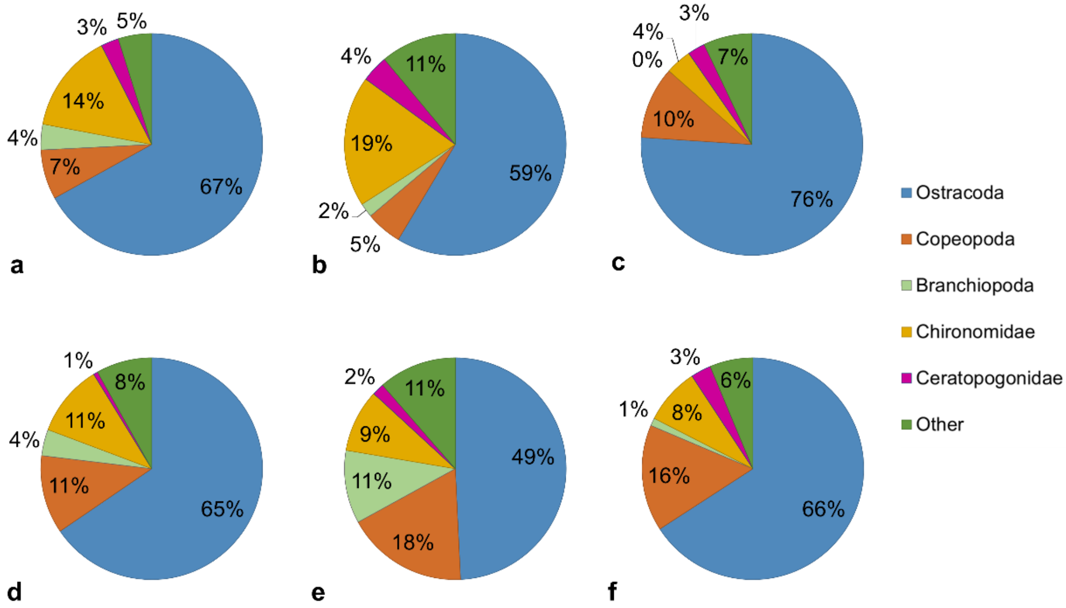

Figure 2.8 Relative abundance of most dominant taxonomic groups in a) October newly-created, b) October mature, c) October abandoned, d) May newly-created, e) May mature, and f) May abandoned beaver wetlands of Georgia.

CHAPTER 3

BEAVER-CREATED SUCCESSIONAL GRADIENTS INCREASE BETA DIVERSITY OF INVERTEBRATES BY TURNOVER IN STREAM-WETLAND COMPLEXES[2]

---

[2] Bush, B.M., C. Stenert, L. Maltchik, and D.P. Batzer. Submitted to *Freshwater Biology*, May 2018.

Abstract:

North American beaver (*Castor canadensis*) are well known ecosystem engineers which modify existing waterbodies primarily via dam building. Beaver dams in the southeastern US are regularly created, breached, rebuilt, relocated, or abandoned which creates complexes of newly-created, mature, and abandoned beaver wetlands within a stream network. A well accepted successional framework exists for beaver wetlands, but it has not been adequately evaluated in terms of invertebrate community dynamics and there are no studies in the southeastern US that have compared invertebrate communities across all successional stages. Our study assesses invertebrate community patterns along the natural successional gradient created by beaver and further assesses how this succession affects beta (β) diversity.

To compare invertebrate communities among successional stages, invertebrates were sampled in each of four stages of habitat succession, 1) natural stream channels (n=3), 2) forested wetlands created by newly formed beaver dams (n = 4), 3) mature open wetland marshes (n = 4), and 4) abandoned wetland meadows (n = 3), during autumn 2013 and spring 2014 in the Piedmont region of Georgia, USA. We then calculated β-diversity values for each stage and the overall study-area, partitioning nestedness and turnover dissimilarity, and evaluated invertebrate assemblage differences among successional stages.

In autumn, invertebrate communities were different among all successional stages, with the exception of new vs. abandoned wetlands, which were only marginally different, and streams vs. abandoned wetlands. In spring, only the mature beaver wetland communities were unique, differing from both streams and from newly-formed or

abandoned wetlands. Beta diversity was nearly twice as high for the overall study-system than any individual successional stage, which all had similar diversity. Additionally, turnover was significantly higher than nestedness in all stages.

Community differences combined with high turnover among successional stages indicates that beaver wetland communities are not merely a subset of more stable mature wetlands or streams; instead each stage has a different taxonomic make-up. Our results strengthen the idea that beaver activity can be an important conservation tool by contributing substantially to diversity in areas where they are present. Beaver wetlands have the potential to help stabilize beta and regional diversity in the face of wetland loss from climate change and other human impacts.

Introduction:

The North American beaver (*Castor canadensis*) is among the most well-known ecosystem engineers – an organism that physically creates or significantly modifies an ecosystem (Jones, Lawton & Shachak, 1994; 1997). Beaver modify existing waterbodies via dam building and channel alteration. Beaver most frequently create new wetlands by impounding streams but may also alter existing wetlands by creating dams, huts, and tunnels, increasing wetted area margins, and altering water depths (Bush and Wissinger 2016). Alteration of waterbodies by beaver acts as an environmental filter influencing successional patterns – change to an ecosystem over time resulting from a disturbance (e.g., beaver activity) (Horn, 1974; Connell & Slatyer, 1977). Successional patterns of beaver wetlands have been well described by Naiman *et al.* (1988) based on patterns in the boreal forests of North America. Typically, a stream is impounded creating a cycle of wetland creation, maturation, and abandonment by beaver, and an eventual return to a forested stream over a period of time ranging from decades to centuries.

In the southeastern US, the successional pathway appears to be similar. Beaver wetlands usually result from damming of small forested streams which then flood riparian area. Newly-created wetlands are relatively shallow, and many trees persist. Over time, flooding stress kills upland vegetation creating mature pond-like marshy wetlands. However, in the southeastern US and the Piedmont region in particular, streambeds are relatively unstable resulting from a combination of frequent, strong storms and extensive deposits of sand and silt from historical erosion from poor cotton-era farming practices (Trimble, 1974; Mukundan, Radcliffe & Ritchie, 2011). As a result, dams are frequently breached and abandoned by beaver, and the ponds drain. Abandoned wetlands usually become wet meadows - that seasonally flood and contain braided channel networks; this creates a mosaic of aquatic, semi-aquatic, and terrestrial habitat. While the overall successional framework for beaver wetlands outlined by Naiman *et al.* (1988) remains well accepted, it has not been adequately evaluated in terms of invertebrate community dynamics (but see Malison *et al.* 2014, Bush and Wissinger 2016). Furthermore, there are no studies in the southeastern US, a non-boreal biome, that have compared invertebrate communities across all successional stages. The mechanisms underlying beta diversity (nestedness and turnover) across all successional stages will help indicate how beaver influence invertebrate community structure.

Beta (β) diversity, as defined by Whittaker (1960; 1972), assesses the relative uniqueness of local communities when compared among similar habitats across a larger spatial scale. Beta diversity as a measure of the dissimilarity among communities, can result from two different components; turnover and nestedness (Legendre, 2014). The turnover component indicates that species tend to replace each other along spatial or environmental gradients, while the nestedness component represents a type of richness difference pattern characterized by the composition of species-poor sites being subsets of species-rich ones (Baselga, 2012; Legendre & De Cáceres, 2013; Legendre, 2014). High turnover rates imply that community dissimilarities may be the result of environmental filtering, competition, and historical events (Qian, Ricklefs & White, 2005; Leprieur *et al.*, 2011). In comparison, the predominance of the nestedness mechanism reflects a non-random process of species loss (Gaston & Blackburn, 2000).

Partitioning the relative importance of turnover and nestedness diversity patterns can directly assist conservation planning by addressing diversity at broader spatial and temporal scales than species richness or local (alpha) diversity alone (Socolar *et al.*, 2016). A high proportion of turnover implies that conservation should target multiple sites, while a high proportion of nestedness suggests that conservation may only need to target the richest sites (Gianuca *et al.*, 2017; Socolar *et al.*, 2016). Invertebrates have successfully been used as model organisms for evaluating diversity and conservation targets in this way (Ruhí, Datry & Sabo, 2017; Sor, Legendre & Lek, 2018). Furthermore, the use of beaver populations as a management tool for restoration of freshwater systems has become an increasingly popular idea (Pollock *et al.*, 2014; Pollock *et al.*, 2015; Law *et al.*, 2017). Given the high rates of wetland loss and a changing climate, and that beaver are able to successfully create and maintain new wetlands, investigating invertebrate diversity across beaver wetlands is an important conservation priority.

Evidence suggests that habitat heterogeneity resulting from beaver activity in streams and wetlands increases plant species richness (Wright, Jones & Flecker, 2002; Wright, Flecker & Jones, 2003; Law *et al.*, 2017) as well as having a positive effect on fishes (Collen & Gibson, 2001; Kemp *et al.*, 2012), amphibians (Hossack *et al.*, 2015; Vehkaoja & Nummi, 2015), and water birds (McKinstry, Caffrey & Anderson, 2001; Nummi & Holopainen, 2014). While a few studies have found high invertebrate richness in individual beaver wetlands (Benke, Ward & Richardson, 1999; Wissinger & Gallagher, 1999; Hood & Larson, 2014), there is a dearth of research on invertebrates, including diversity research, across beaver-created wetland complexes. The majority of research relating to invertebrates and beaver activity has focused on the impact on associated stream reaches (i.e. the replacement of lotic with lentic taxa when a stream reach is converted to a wetland; McDowell and Naiman 1986, Bush and Wissinger 2016) rather than on the dynamics of the wetlands themselves. Beaver wetlands are typically found in large complexes, creating a spatio-temporal mosaic of habitats within a region. We hypothesize that the interspersion of lentic habitats and taxa along lengths of stream habitat containing lotic taxa will increase regional (β) diversity, and that chains of hydrologically connected wetlands of varying successional characteristics will further increase invertebrate β diversity. Additionally, we hypothesize that any differences in invertebrate beta diversity among successional stages will mainly be from turnover-resultant dissimilarity. Our study assessed invertebrate community patterns along the natural successional gradient created by beaver (i.e., stream channels, newly-created ponds, mature ponds, abandoned ponds), and determined how this succession affected β diversity.

Methods:

Study Design:

Invertebrate communities were sampled in each of four stages of habitat succession, 1) natural stream channels that were not altered by beaver activity and fed downstream beaver wetlands (n=2), 2) forested wetlands created by newly formed beaver dams (created within 2 years of sampling; n = 4), 3) mature open wetland marshes (established for >15 years; n = 4), and 4) abandoned wetland meadows (with breached dams; n = 3) in October 2013 and May 2014 in Oconee National Forest in Greene County, Georgia, USA. Wetlands were part of large complexes associated with two stream catchments (33.44^{o}N, 83.15^{o}W and 33.38^{o}N, 83.15W) within the Upper Oconee River watershed; the overall complexes encompassed stream reaches of 1-2 km lengths, with the wetlands scattered across floodplains that ranged in widths from 50-300 m. Sample sites were interspersed with other beaver modified wetlands in various stages of succession. Stream reaches associated with the two beaver wetland complexes, but not affected by beaver activity, were sampled upstream of the beaver influenced areas. To generate a third natural stream channel replicate, we selected and sampled another stream, Harris Creek (33.41^{o}N, 83.16W), which had no evidence of beaver activity, and was spatially located midway between the other two catchments. Sample wetlands ranged from approximately 0.5 to 2.0 ha, and all were < 1 meter deep. Successional history of each of the sample locations was known from annual observations by DPB since 1998.

Eight, 0.5-m D-frame net sweeps (Wildlife Supply Company, mouth dimensions 305-mm wide x 254-mm high, 500-micron mesh) were taken in each wetland or stream habitat, partitioned to comprise all representative subhabitats present, in October 2012 (autumn) and May 2013 (spring). Samples were preserved in 95% alcohol, rinsed over a 300-µm sieve, and subsampled (all subsamples had ≥ 200 individuals) using a modified grid system. Invertebrates, both aquatic and non-aquatic, retained were identified to the lowest possible taxonomic level (usually family; Stehr 1987, Stehr 1991, Goulet and Hubert 1994, Triplehorn and Johnson 2005, Merritt *et al*. 2008, Thorp and Covich 2009, Bellinger *et al.* 2014, Evans 2014).

Statistical Analyses:

Community Succession Analyses

Non-metric multidimensional scaling (NMS, Bray-Curtis similarity, Kruskal fit scheme 1,25 restarts) was used to visualize patterns among habitat successional stages and seasons. Significant differences in invertebrate communities among successional stages (based on relative abundances of taxa present) were assessed using analysis of similarity (ANOSIM; Bray-Curtis similarity, Kruskal fit scheme 1,25 restarts), for fall (October) and spring (May), separately. All abundance data were log(x+1) to limit influence of highly abundant taxa, and rare taxa were included in the analyses. NMS ordination and ANOSIM analyses were performed using PRIMER v6 software (Clarke & Gorley, 2006). Additionally, the *multipatt* function (IndVal.g, 999 permutations) of the R package *indicspecies* (De Cáceres & Legendre, 2009) was used to assess the presence of invertebrate indicator species among successional stages for fall (October) and spring (May), separately.

Beta diversity Analyses

Beta diversity was calculated as Sorensen pairwise dissimilarity in the macroinvertebrate composition between wetlands (βsor). Baselga (2012) proposed a method for partitioning total dissimilarity in species composition (βsor) into two separated components: (i) turnover (βsim, Simpson pairwise dissimilarity) that indicates species replacement between sites, and (ii) nestedness (βnes, nestedness-resultant dissimilarity) that indicates the loss of species from site to site if the species from poorer areas are a subset of richer areas. Analyses were conducted in the statistical program R, version 3.4.0 (R Core Development Team, 2017) using the command *beta.pair* of the *betapart* package (Baselga *et al.*, 2013).

The values of βsor, βsim and βnes generated by the analysis of the 14 wetlands studied were separated into ten sets: (i) pairwise comparisons between newly created beaver wetlands (6 pairs), (ii) between long established mature wetlands (6 pairs), (iii) between abandoned wetlands (3 pairs), (iv) between forested stream reaches (3 pairs), (v) between newly created and mature wetlands (16 pairs), (vi) between newly created and abandoned wetlands (12 pairs), (vii) between newly created wetlands and streams (12 pairs), (viii) between mature and abandoned wetlands (12 pairs), (ix) between mature wetlands and streams (12 pairs, although this is not a natural transition), and (x) between abandoned wetlands and streams (9 pairs).

The values of βsor were compared among the different successional stages using a Kruskal-Wallis test, by comparing the values of βsor for the group of pairs of each habitat type. The values of βsim and βnes were compared through Wilcoxon signed-rank test (non-normal distributions) or paired *t*-tests (normal distributions) within each group previously determined. Prior to that, the homogeneity of variances and normality of the data set were checked using the Bartlett and Shapiro-Wilk tests, respectively.

Results:

Community Patterns Among Successional Stages

Invertebrate community analysis revealed strong seasonal differences between spring and autumn (Fig. 3.1). In spring, only mature wetland invertebrate communities displayed a unique community structure (new vs. stream R=0.815, P=0.1; new vs. mature R = 0.704, P = 0.029; new vs. abandoned R = 0.852, P = 0.1; mature vs. stream R=0.852, P=0.029; mature vs. abandoned R = 0.593, P = 0.029, abandoned vs. stream R=0.519, P=0.1). In autumn, invertebrate communities were less similar among successional stages. Invertebrate communities were different among stages (new vs. stream R=0.778, P= 0.029; new vs. mature R=0.313, P=0.029; mature vs. stream R=0.815, P=0.029; mature vs. abandoned R=0.741, P=0.029), with the exception of the comparisons of new vs. abandoned wetlands which was only marginally significant (R=0.722, P=0.057) and of streams vs. abandoned wetlands (R=0.889, P=0.1). Indicator analysis revealed 11 taxa which were significantly associated with a successional stage in autumn (Table 3.1), with six terrestrial or semi-aquatic taxa being associated with abandoned wetlands and three lotic aquatic taxa being associated with natural stream channels. No indicator taxa were significantly associated with individual successional stages in spring. Some lentic aquatic taxa were general indicators of wetland conditions, regardless of successional stage. In both autumn and spring, Coenagrionidae damselfly nymphs and Ostracoda microcrustaceans were strong ($P \leq 0.01$) indicators for new wetlands, mature wetlands, and abandoned wetlands collectively, and Libellulidae dragonfly nymphs were indicators of new and mature wetlands collectively.

Beta Diversity

The overall βsor value for the study area was 0.770. βsor values did not change among the different successional pond stages (H = 7.271, P = 0.064; median, $\beta_{\text{newly created wetlands}}$ = 0.381, $\beta_{\text{mature wetlands}}$ = 0.278, $\beta_{\text{abandoned wetlands}}$ = 0.287, and β_{streams} = 0.341) (Fig. 3.2).

Contributions of Succession to Beta Diversity

Along the temporal successional gradient, the turnover component consistently had a higher contribution to βsor than the nestedness component, between streams and newly-created wetlands (U = 78, P < 0.001), between newly-created and mature wetlands (t_{15}= -9.232, P < 0.001), between mature and abandoned wetlands (t_{11} = 8.685, P < 0.001), and between abandoned wetlands and streams (t_8 = 22.075, P < 0.001) (Fig. 3.3). Similarly, the turnover component exceeded the nestedness component between newly-created and abandoned wetlands (U = 78, P = 0.002), a transition that could happen naturally with early abandonment. Finally, while not part of any natural successional pathway, the turnover component contributed most to the contrast between mature wetlands and streams (U = 78, P < 0.001).

Contributions of Geographic Variation to Beta Diversity

The beta diversity resulting from species turnover between paired watersheds for newly-created beaver wetlands, mature wetlands, and streams was also greater than that resulting from nestedness (new-new: U = 21, P = 0.035; mature-mature: U = 21, P = 0.031; stream-stream: t_2 = 12.765, P = 0.006). However, the value of beta diversity resulting from species turnover between paired abandoned wetlands did not differ significantly from the value resulting from the nestedness ($U = 6$, $P = 0.250$) (Fig. 3.4).

Discussion:

Investigations into invertebrate dynamics associated with beaver activity have typically focused on the replacement of lotic with lentic taxa (e.g. see Appendix in Bush and Wissinger 2016), and our analyses also found a dramatic shift as stream habitat was converted to wetland habitat. However, we also found that invertebrate communities were markedly different among successional wetland types, especially in autumn. McDowell and Naiman (1986) and Naiman *et al*. (1988) hypothesized that due to similar numbers of taxa among beaver wetlands and streams as well as the existing hydrologic connection within stream-wetland networks, invertebrates in beaver wetlands were likely comprised of stream depositional-pool taxa. Richness and diversity values were similar among successional stages in our system, yet, our analysis found high turnover among successional stages indicating that beaver wetland communities are not merely a subset of stream species pools. Higher turnover rather than nestedness may also explain a nearly two-fold increase in β diversity for the whole study-area over individual successional stages, which were similar. Newly-created and abandoned wetlands are not merely a subset of more stable mature wetlands or streams; instead each stage has a different taxonomic make-up. These results support our hypotheses that chains of hydrologically connected wetlands of varying successional characteristics could further increase invertebrate β diversity mainly by turnover-resultant dissimilarity.

The taxonomic makeup of each successional state may relate to metacommunity dynamics within beaver wetland complexes. In wetlands, studies of metacommunities - sets of communities linked within a region by the dispersal of several interacting species (Wilson, 1992; Leibold *et al.*, 2004) – most frequently focus on the effect of relative connectivity among depressional wetlands (Snodgrass *et al.*, 1996; Semlitsch, 2000; Cottenie & Meester, 2003; Roe & Georges, 2007; Heino *et al.*, 2015). Like depressional wetlands, beaver wetlands exist as a spatial mosaic within the landscape and dispersal distance among wetlands is likely important (Wissinger & Gallagher, 1999; Caudill, 2003; Caudill, 2005). However, because wetland complexes are made up of varying successional stages (with varying biotic and abiotic conditions) there is an additional temporal component that adds to the spatial heterogeneity of beaver wetland complexes. For example, Wissinger and Gallagher (1999) found that invertebrates in abandoned beaver wetlands recovered differently (more rapidly) from drought than did those of mature wetlands. Invertebrates in abandoned wetlands were more drought tolerant and had more micro-habitat available for refuge from drought, whereas, mature wetland taxa relied more on aerial recolonization from neighboring wetlands.

Abandoned wetlands do not appear to be transitioning back to streams, as might be expected, but instead are a unique habitat unto themselves. While channel habitat exists, most of the surface area of abandoned ponds is wet meadow, which is dominated by herbaceous vegetation and partially fills seasonally depending on hydrologic conditions – favoring the semi-aquatic and terrestrial taxa found to be associated with abandoned wetlands in our analysis. Semi-aquatic and terrestrial invertebrates are found in herbaceous sub-habitats in other beaver wetlands (Hodkinson, 1975; Benke, Ward &

Richardson, 1999; Wissinger & Gallagher, 1999; Hood & Larson, 2014) but the great extent of vegetation and damp soil may explain the preponderance of these taxa in abandoned wetlands. The grassy channels likely also support some unique invertebrate taxa, as they do for fishes (Snodgrass & Meffe, 1998). Longer term successional processes likely result in an eventual transition back to a stream condition (Naiman, Johnston & Kelley, 1988), although the temporal scale of our study (decadal) failed to capture this.

Successional patterns, while generally cyclical, can be either short-circuited or more prolonged than described elsewhere. Personal observations revealed that all of our newly-created wetland study sites were abandoned soon after our study ended, and prior to becoming mature. Unpredictability may further contribute to diversity and differences among successional stages (Chase & Myers, 2011; Heino *et al.*, 2015). The relative influence of stochastic versus deterministic community assembly in beaver wetlands requires more careful study. Successional patterns also varied seasonally. Seasonal differences are likely the result of a combination of factors including hydrology, vegetation and canopy cover, predation, and invertebrate life histories (Batzer & Wissinger, 1996; Wissinger, 1999; De Szalay & Resh, 2000; Batzer, Palik & Buech, 2004) but interactions among these factors in wetlands are complex and would require intensive study to elucidate (Batzer, 2013). Finally, high turnover within specific successional stages (Fig. 3.4) suggests that some differences among invertebrate communities resulted from geographic variation, which is to be expected. Invertebrate community dynamics in beaver influenced systems are likely the result of a longer term successional pattern in combination with seasonal and geographic variation.

Recently, it has been suggested that using ecosystem engineers, like beaver, to restore ecosystems may lessen the need for direct human intervention (Byers *et al.*, 2006; Law *et al.*, 2017). Our results strengthen the idea that beaver activity can be an important conservation tool by contributing to diversity in areas where they are present. Beavers may be especially important in geologically ancient landscapes like the Southeastern US Piedmont, where lentic aquatic habitats other than beaver wetlands are rare (Jackson, Thompson & Kolka, 2014). Beaver wetlands are typically considered permanent due to a connection to existing surface water bodies. As such, these wetlands have the potential to help stabilize beta and regional diversity in the face of climate change. This will be especially important for pond and wetland biota because these small, shallow habitats are considered among the world's most vulnerable ecosystems to changes in temperature and precipitation (Winter, 2000; Barnett, Adam & Lettenmaier, 2005; Johnson & Poiani, 2016; Zhu *et al.*, 2017). Conservation of all successional stages within watersheds is essential, as no single stage contains the full range of diversity present in the larger wetland-stream complex. High stochasticity of beaver impacted habitats as well as temporal and geographic variation may have further impacts on diversity, and long-term research on these systems would be useful in understanding the full range of impacts of beaver on invertebrate diversity and succession.

Literature Cited:

Barnett TP, Adam JC, Lettenmaier DP (2005) Potential impacts of a warming climate on water availability in snow-dominated regions. Nature 438:303-309.

Baselga A (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Global Ecology and Biogeography 21:1223-1232.

Baselga A, Orme D, Villegér S, De Bortoli J, Leprieur F (2013) Betapart: Partitioning beta diversity into turnover and nestedness components. R package version 1.3. https://CRAN.R-project.org/package=betapart.

Batzer DP (2013) The seemingly intractable ecological responses of invertebrates in north american wetlands: A review. Wetlands 33:1-15.

Batzer DP, Palik BJ, Buech R (2004) Relationships between environmental characteristics and macroinvertebrate communities in seasonal woodland ponds of Minnesota. Journal of the North American Benthological Society 23:50-68.

Batzer DP, Wissinger SA (1996) Ecology of insect communities in nontidal wetlands. Annual Review of Entomology 41:75-100.

Bellinger P, Christiansen K, Janssens F (2014) Checklist of the collembola of the world. http://www.collembola.org.

Benke A, Ward G, Richardson T (1999) Beaver impounded wetlands of the southeastern coastal plain. In: Batzer D, Rader R, Wissinger S (eds) Invertebrates in freshwater wetlands of North America: Ecology and management. Wiley, Toronto, Ontario, pp 217-245

Bush BM, Wissinger SA (2016) Invertebrates in beaver-created wetlands and ponds. In: Batzer D, Boix D (eds) Invertebrates in freshwater wetlands: An international perspective on their ecology. Springer International Publishing, Switzerland, pp 411-449.

Byers JE et al. (2006) Using ecosystem engineers to restore ecological systems. Trends in Ecology & Evolution 21:493-500.

Caudill CC (2003) Empirical evidence for nonselective recruitment and a source-sink dynamic in a mayfly metapopulation. Ecology 84:2119-2132.

Caudill CC (2005) Trout predators and demographic sources and sinks in a mayfly metapopulation. Ecology 86:935-946.

Chase JM, Myers JA (2011) Disentangling the importance of ecological niches from stochastic processes across scales. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2351-2363.

Clarke K, Gorley R (2006) Primer v6: User manual/tutorial. PRIMER-E, Plymouth.

Collen P, Gibson RJ (2001) The general ecology of beavers (castor spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish – a review. Reviews in Fish Biology and Fisheries 10:439-461.

Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist 111:1119-1144

Cottenie K, Meester LD (2003) Connectivity and cladoceran species richness in a metacommunity of shallow lakes. Freshwater Biology 48:823-832.

De Cáceres M, Legendre P (2009) Associations between species and groups of sites: Indices and statistical inference. Ecology 90:3566-3574.

De Szalay FA, Resh VH (2000) Factors influencing macroinvertebrate colonization of seasonal wetlands: Responses to emergent plant cover. Freshwater Biology 45:295-308.

Evans AV (2014) Beetles of eastern north america. Princeton University Press, Princeton, New Jersey.

Gaston K, Blackburn T (2000) Pattern and process in macroecology. Blackwell Science, Oxford.

Gianuca AT, Declerck SAJ, Lemmens P, Meester LD (2017) Effects of dispersal and environmental heterogeneity on the replacement and nestedness components of β-diversity. Ecology 98:525-533.

Goulet H, Hubert JF (1993) Hymenoptera of the world: An identification guide to families. Agriculture Canada Publication, Ottawa, Canada.

Heino J, Melo AS, Siqueira T, Soininen J, Valanko S, Bini LM (2015) Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. Freshwater Biology 60:845-869.

Hodkinson ID (1975) A community analysis of the benthic insect fauna of an abandoned beaver pond. Journal of Animal Ecology 44:533-551.

Hood GA, Larson DG (2014) Beaver-created habitat heterogeneity influences aquatic invertebrate assemblages in boreal canada. Wetlands 34:19-29.

Horn HS (1974) The ecology of secondary succession. Annual Review of Ecology and Systematics 5:25-37.

Hossack BR, Gould WR, Patla DA, Muths E, Daley R, Legg K, Corn PS (2015) Trends in Rocky Mountain amphibians and the role of beaver as a keystone species. Biological Conservation 187:260-269.

Jackson CR, Thompson JA, Kolka RK (2014) Wetland soils, hydrology, and geomorphology. In: Ecology of freshwater and estuarine wetlands. 2 edn. University of California Press, Oakland, California, pp 23-60

Johnson WC, Poiani KA (2016) Climate change effects on prairie pothole wetlands: Findings from a twenty-five year numerical modeling project. Wetlands 36:273-285.

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem enigneers. Oikos 69:373-386.

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946-1957.

Kemp PS, Worthington TA, Langford TEL, Tree ARJ, Gaywood MJ (2012) Qualitative and quantitative effects of reintroduced beavers on stream fish. Fish and Fisheries 13:158-181.

Law A, Gaywood MJ, Jones KC, Ramsay P, Willby NJ (2017) Using ecosystem engineers as tools in habitat restoration and rewilding: Beaver and wetlands. Science of the Total Environment 605-606:1021-1030.

Legendre P (2014) Interpreting the replacement and richness difference components of beta diversity. Global Ecology and Biogeography 23:1324-1334.

Legendre P, De Cáceres M (2013) Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. Ecology Letters 16:951-963.

Leibold MA et al. (2004) The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters 7:601-613.

Leprieur F, Tedesco PA, Hugueny B, Beauchard O, Dürr HH, Brosse S, Oberdorff T (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. Ecology Letters 14:325-334.

Malison RL, Lorang MS, Whited DC, Stanford JA (2014) Beavers (castor canadensis) influence habitat for juvenile salmon in a large alaskan river floodplain. Freshwater Biology 59:1229-1246.

McDowell DM, Naiman RJ (1986) Structure and function of a benthic invertebrate stream community as influenced by beaver (castor canadensis). Oecologia 68:481-489.

McKinstry MC, Caffrey P, Anderson SH (2001) The importance of beaver to wetland habitats and waterfowl in wyoming. Journal of the American Water Resources Association 37:1571.

Merritt RW, Cummins KW, Berg MB (eds) (2008) An introduction to the aquatic insects of north america. 4 edn. Kendall Hunt Publishing Company, Dubuque, Iowa

Mukundan R, Radcliffe DE, Ritchie JC (2011) Channel stability and sediment source assessment in streams draining a piedmont watershed in Georgia, USA. Hydrological Processes

Naiman RJ, Johnston CA, Kelley JC (1988) Alteration of north american streams by beaver. BioScience 38:753-762.

Nummi P, Holopainen S (2014) Whole-community facilitation by beaver: Ecosystem engineer increases waterbird diversity. Aquatic Conservation: Marine and Freshwater Ecosystems 24:623-633.

Pollock MM, Beechie TJ, Wheaton JM, Jordan CE, Bouwes N, Weber N, Volk C (2014) Using beaver dams to restore incised stream ecosystems. BioScience 64:279-290.

Pollock MM, Lewallen G, Woodruff K, Jordan CE, Castro JM (2015) The beaver restoration guidebook: Working with beaver to restore streams, wetands, and floodplains. vol 1. United States Fish and Wildife Service, Portland, Oregon

Qian H, Ricklefs RE, White PS (2005) Beta diversity of angiosperms in temperate floras of eastern asia and eastern North America. Ecology Letters 8:15-22.

R Core Development Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/.

Roe JH, Georges A (2007) Heterogeneous wetland complexes, buffer zones, and travel corridors: Landscape management for freshwater reptiles. Biological Conservation 135:67-76.

Ruhí A, Datry T, Sabo JL (2017) Interpreting beta-diversity components over time to conserve metacommunities in highly dynamic ecosystems. Conservation Biology 31:1459-1468.

Semlitsch RD (2000) Principles for management of aquatic-breeding amphibians. The Journal of Wildlife Management 64:615-631.

Snodgrass JW, Bryan JAL, Lide RF, Smith GM (1996) Factors affecting the occurrence and structure of fish assemblages in isolated wetlands of the upper coastal plain, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 53:443-454.

Snodgrass JW, Meffe GK (1998) Influence of beavers on stream fish assemblages: Effects of pond age and watershed position. Ecology 79:928-942.

Socolar JB, Gilroy JJ, Kunin WE, Edwards DP (2016) How should beta-diversity inform biodiversity conservation? Trends in Ecology & Evolution 31:67-80.

Sor R, Legendre P, Lek S (2018) Uniqueness of sampling site contributions to the total variance of macroinvertebrate communities in the lower Mekong basin. Ecological Indicators 84:425-432.

Stehr FW (1987) Immature insects. vol 595.7039 I-33i. Kendall/Hunt Publishing, Dubuque, Iowa.

Stehr FW (1991) Immature insects, vol 2. Kendall/Hunt Publishing, Dubuque, Iowa.

Thorp JH, Covich AP (2009) Ecology and classification of North American freshwater invertebrates. Academic press, London, UK.

Trimble SW (1974) Man-induced soil erosion on the southern piedmont. Soil Conservation Society of America:1700-1970.

Triplehorn CA, Johnson NF (2005) Borror and Delong's introduction to the study of insects. 7th edn. Thomson Brooks/Cole, Belmont, California.

Vehkaoja M, Nummi P (2015) Beaver facilitation in the conservation of boreal anuran communities. Herpetozoa 28:75-87.

Whittaker RH (1960) Vegetation of the Siskiyou mountains, Oregon and California. Ecological Monographs 30:279-338.

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:213-251.

Wilson DS (1992) Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology 73:1984-2000.

Winter TC (2000) The vulnerability of wetlands to climate change: A hydrologic landscape perspective. Journal of the American Water Resources Association 36:305-311.

Wissinger SA (1999) Ecology of wetland invertebrates: Sythesis and applications of conservation and management. In: Batzer DP, Rader RB, Wissinger SA (eds) Invertebrates in freshwater wetlands of north america: Ecology and management. John Wiley & Sons, Inc, pp 1043-1086.

Wissinger SA, Gallagher LJ (1999) Beaver pond wetlands in northwestern pennsylvania. Modes of colonization and succession after drought. In: Batzer D, Rader R, Wissinger S (eds) Invertebrates in freshwater wetlands of North America: Ecology and management. Wiley, Hoboken, New Jersey, pp 333-362.

Wright J, Jones C, Flecker A (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132:96-101.

Wright JP, Flecker AS, Jones CG (2003) Local vs landscape controls on plant species richness in beaver meadows. Ecology 84:3162-3173.

Zhu J et al. (2017) Modeling the potential impacts of climate change on the water table level of selected forested wetlands in the Southeastern United States. Hydrology & Earth System Sciences 21:6289-6305.

Table 3.1 Indicator taxa by successional stage for autumn 2013, with their typical habitat associations from Merritt *et al*. (2008) and Johnson and Triplehorn (2005).

Successional Stage		Family	Indicator Value	P	Habitat association
Newly-created	Trichoptera	Leptoceridae	0.905	0.013	Aquatic, Lentic †
Mature	Coleoptera	Anthicidae	0.866	0.024	Terrestrial
Abandoned	Collembola	Entomobryidae	0.988	0.008	Semi-terrestrial
		Sminthuridae	0.920	0.014	Semi-terrestrial
	Hemiptera	Pseudococcidae	0.961	0.014	Terrestrial
		Hebridae	0.864	0.029	Semi-aquatic
		Mesoveliidae	0.863	0.041	Semiaquatic
	Coleoptera	Curculionidae	0.886	0.022	Terrestrial
Stream	Ephemeroptera	Ephemeridae	1.000	0.005	Aquatic, Lotic
		Perlodidae	1.000	0.005	Aquatic, Lotic
	Odonata	Gomphidae	0.929	0.006	Aquatic, Lotic

†The leptocerid genus occurring *Oecetis*, is a common inhabitant of Southeastern US wetlands (DPB personal observations).

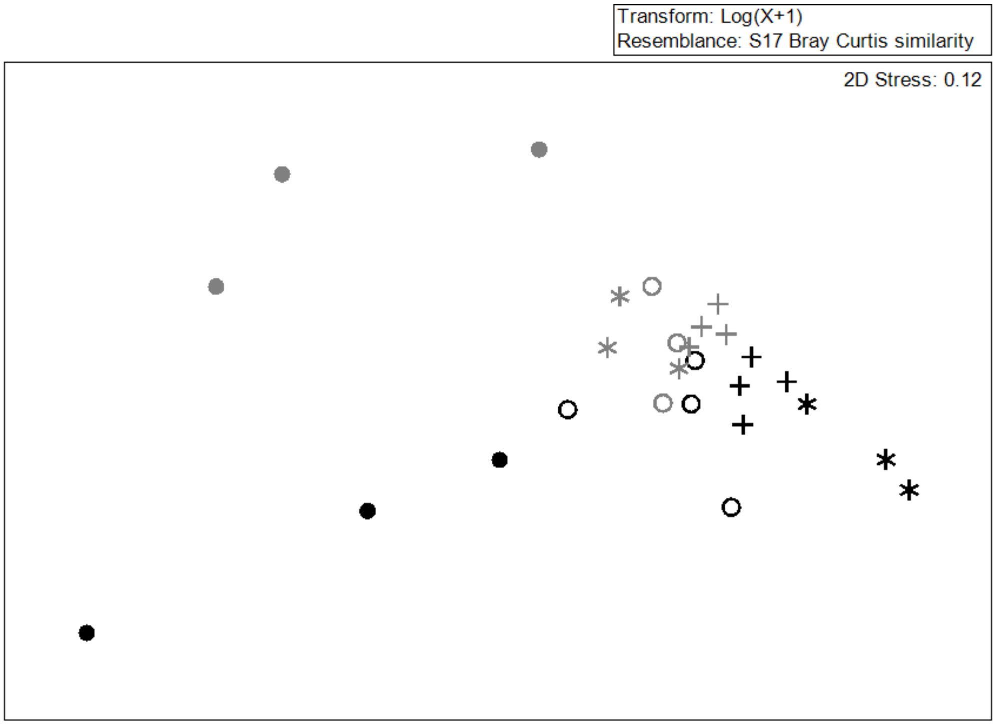

Figure 3.1 Nonmetric multidimensional scaling plot showing patterns among streams (filled circles), and newly-created (open circles), mature (+), and abandoned (*) beaver wetland in autumn 2013 (black) and spring 2014 (gray).

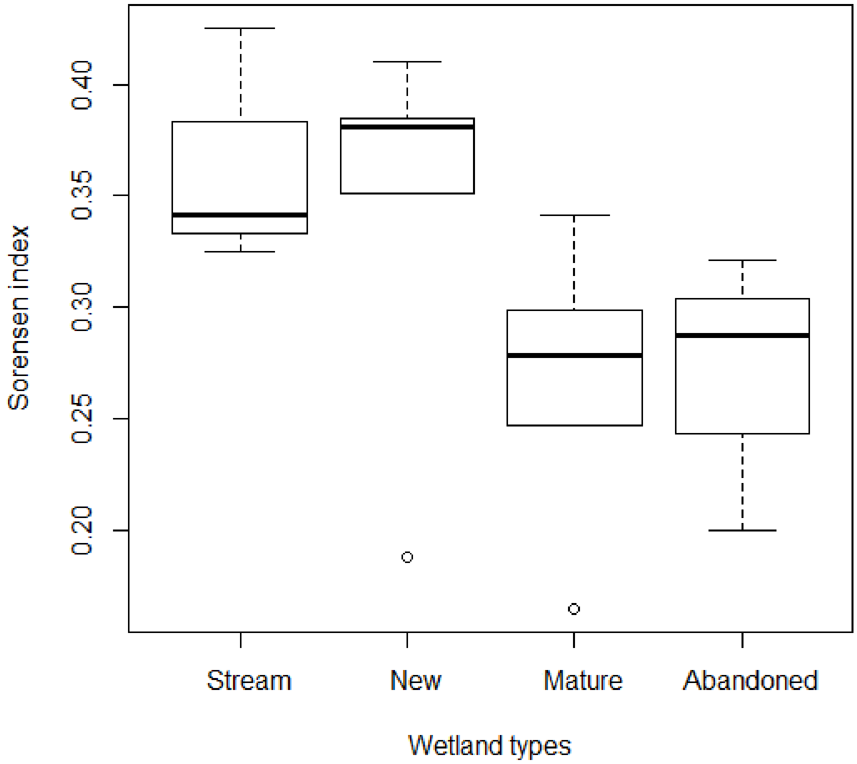

Figure 3.2 Sorensen pairwise dissimilarity index in the invertebrate composition among the different successional wetland stages.

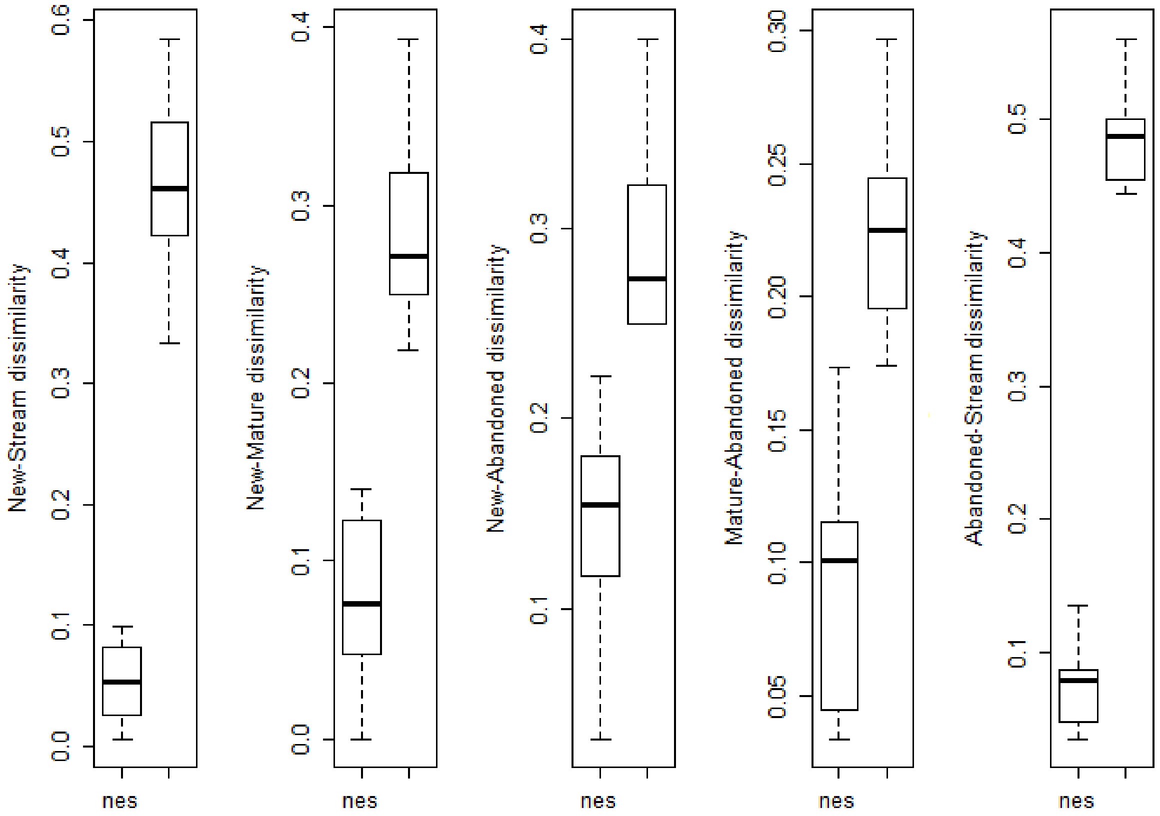

Figure 3.3 Contribution of the turnover and nestedness components to overall Beta Sorensen between pairs of the different successional wetland stages along the temporal successional gradient.

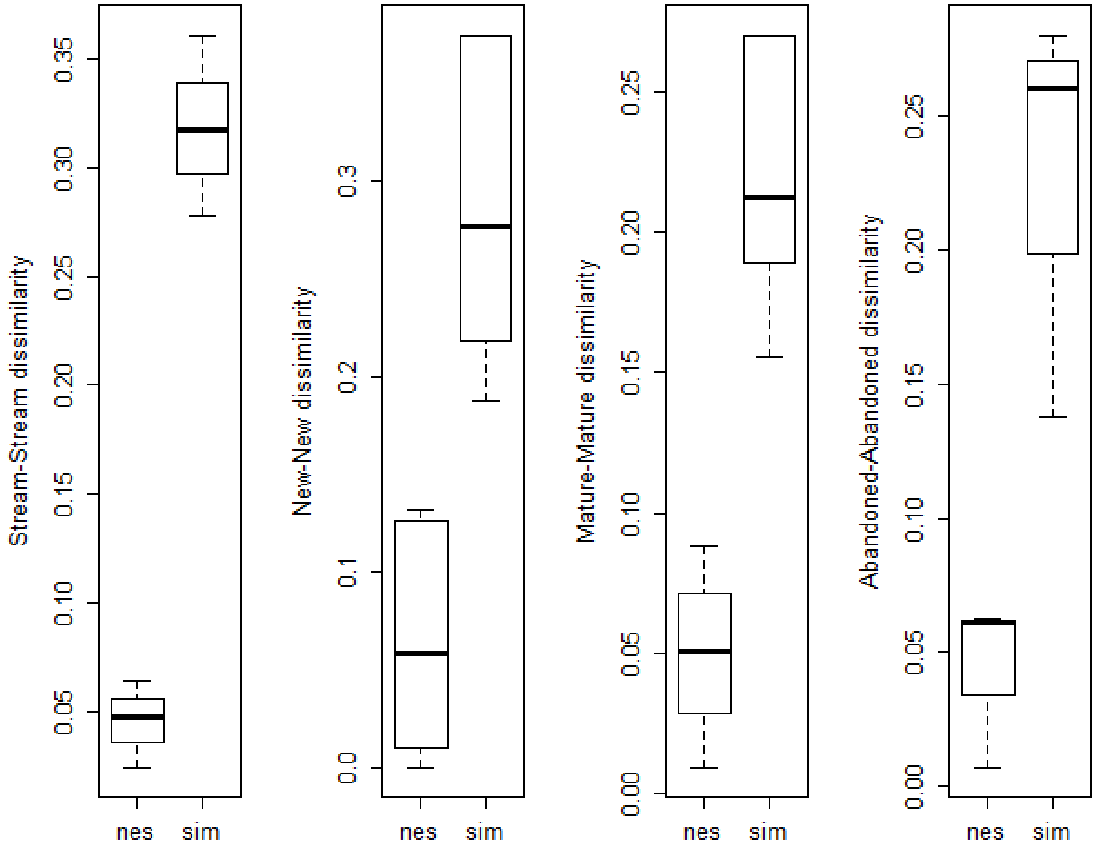

Figure 3.4 Beta diversity resulting from species turnover and nestedness between paired habitats of the same successional wetland stage.

CHAPTER 4

ASSESSING THE EFFECTS OF MESH ENCLOSURES ON INVERTEBRATES AND LITTER BREAKDOWN IN A FLOODPLAIN FOREST OF THE SOUTHEASTERN USA[3]

---

[3] Bush, B.M., M.D. Ulyshen, C.G. Fair, and D.P. Batzer. 2018. Accepted by *Wetland Ecology and Management*.

Reprinted here with permission of the publisher.

Abstract:

The litter bag method has been used to study litter breakdown for over 50 years but remains a criticized technique. One major criticism is the effect of mesh enclosures, specifically the use of two or more mesh sizes to evaluate the role of arthropods, on litter breakdown. We aimed to evaluate the effectiveness of a new basket-style mesh enclosure in mitigating microclimatic mesh effects while still excluding invertebrates. We evaluated 5 basket treatments constructed from 300-µm mesh: no basket, closed basket, closed basket with bottom slits, open basket, and open basket with bottom slits which held invasive Chinese privet (*Ligustrum sinense*) litter on the Oconee-River floodplain, GA, USA. After 134 days, we found that temperature and humidity did not vary among treatments but that litter breakdown rates (*k*) and invertebrate composition were different among treatments. Litter breakdown was faster in the no basket treatment (the most open treatment) than in closed baskets without slits (the most closed treatment). Microinvertebrates were not effectively excluded from baskets but most macroinvertebrates were excluded from baskets (open and closed) without slits, except for some small predators. Unexpectedly, we found some evidence that using litter bags of two different mesh sizes may have a secondary trophic effect on litter breakdown, further complicating how best to evaluate the impact of arthropods on litter breakdown.

Introduction:

The litter bag method has been the primary technique for studying leaf litter breakdown for over 50 years (Bocock and Gilbert 1957; Kampichler and Bruckner 2009). The litter bag method entails using mesh bags to hold a known mass of leaf litter, which is monitored over time to measure leaf litter breakdown rates. Often, litter bags are used to evaluate the role of arthropods in litter decomposition, typically by excluding arthropods from one set of litter bags and comparing breakdown rates of treatments with and without arthropods. Arthropods are most commonly excluded from litter bags in two ways: using differing mesh sizes, including one mesh which is sufficiently small to exclude invertebrates, or applying an insecticide to leaves to create an arthropod exclusion treatment. More recently, litter decomposition studies and the litter bag method have faced criticism (Prescott 2005; Kampichler and Bruckner 2009), especially when used to evaluate the role of arthropods on litter breakdown rates. However, some studies ignore the role of arthropods in litter breakdown altogether, asserting that soil arthropods are not important in their systems (Prescott 2005).

The most popular approach to assess arthropod impacts is the use of varying mesh size. This type of litter bag study employs at least two different sizes of mesh in bag construction to either exclude or allow access to arthropods of a certain body size. The use of varying mesh sizes has been employed nearly as long as the litter bag technique itself (Crossley and Hoglund 1962) and is still widely used today. However, this approach has been criticized because there may be confounding factors that are artifacts of mesh size creating a “mesh effect”. Mesh effects may arise from a higher proportion of litter fragments exiting bags with larger mesh in the field, or differential handling effects, leaching rates, and/or microclimate conditions for litter enclosed in mesh of differing size (Bradford et al. 2002; Kampichler and Bruckner 2009; Bokhorst and Wardle 2013). In a large meta-analysis of litter bag studies Kampichler and Bruckner (2009) found that only one study attempted to correct for mesh effects. Furthermore, the Kampichler and

Bruckner (2009) meta-analysis found that if a mesh effect influenced results by ≥ 7%, the arthropod effect was nullified. We were able to find only two other studies that directly tested for mesh effects in leaf litter breakdown (but see Stoklosa et al. 2016 & Ulyshen 2014, which evaluate mesh effects on woody substrates), only one of which evaluated arthropods, and both studies yielded conflicting results (Bradford et al. 2002; Bokhorst and Wardle 2013). Potential causes of mesh effects require further examination. We posit that microclimate is likely an important variable relating to mesh effects in litter breakdown studies. However, microclimate is difficult to control under field conditions, and the influences of temperature and moisture on microbes, which are integral in leaf decomposition, are likely crucial (Coûteaux et al. 1995).

We tested the application of the open-pan design described by Ulyshen et al. (2016), in a study addressing wood decomposition, to litter bags in an attempt to minimize mesh effects on microclimate when evaluating the role of arthropods. The purpose of this design is to exclude macroinvertebrates without completely enclosing the substrate within mesh bags. In this study, we created baskets out of fine mesh within which we placed litter bags. We sought to test whether basket walls could prevent colonization of macroinvertebrates while avoiding the unwanted effects that traditional mesh bags likely have on microclimate. Further, the study was conducted under floodplain forest conditions, a macrohabitat that has received scant attention in terms of assessing litter breakdown. Rather than using two mesh sizes, we created baskets of the same fine mesh size and used slit openings in the bottom of baskets to mediate arthropod access. We hypothesized that baskets with the same mesh size, despite having slits or not, would have similar temperature and humidity conditions. Additionally, we assessed whether having a lid, or having the top open to the environment, could still be used to control soil invertebrate access, while maintaining a largely natural microclimate. We hypothesized that litter placed in baskets with bottom slits, providing access to soil arthropods, would breakdown faster than those without slits.

Methods:

Study Sites:

Four study sites were selected on the Chinese privet (*Ligustrum sinense*)-invaded Oconee River floodplain in the Georgia Piedmont region (Athens-Clarke and Greene Counties). The four sites were the privet-invaded reference plots in a long-term privet eradication study, see Hanula et al. (2009) for descriptions of the sites.

Experimental Design:

Basket treatments consisted of two parts: an inner litter bag and an outer exclusion basket. A) Litter bags served as the base (an inner bag) for all 300-μm exclusion basket treatments to prevent loss of privet leaves through bottom slits or out of open-topped bags, and to inhibit entry of ambient privet leaf-fall. Thus, 5-mm mesh litter bags (this mesh size was the largest that would still contain the majority of privet leaves while also allowing free access to large invertebrates) containing 10-g air-dried privet leaves were placed inside each 300-μm basket before sealing and secured with fishing line, or secured alone on the soil surface for the no basket control treatment. As privet leaves can be quite small (some < 5mm) leaves were first sifted through 5-mm mesh before weighing so as not to unnecessarily lose leaves through the mesh which could cause an over estimate of mass-loss. B) Exclusion baskets constructed with 300-μm nylon-mesh in a box-shaped design 25-cm (L) X 25-cm (W) X 24.4-cm (H). All baskets also had a 0.6-cm folded over "lip" that protruded outward from each top edge intended to further impede invertebrates from crawling into the bags over the sides. In preliminary testing, 24.4 cm was estimated to be an adequate height to exclude most soil dwelling invertebrates from entry despite some treatments having an open top. 300-µm nylon-mesh was selected because it was the smallest mesh size that we estimated would still allow regular movement of microbes and air flow while excluding macroinvertebrates.

To evaluate different basket designs, one basket each of five basket treatments were placed at two subplots at each site (10 bags per site, n=40; Fig. 4.1). 1) The *no basket treatment* served as a control and consisted only of a 5-mm mesh leaf bag. For the other 4 treatments, 2) *Closed-top baskets* were fully intact on all sides with all seams sealed, intended to exclude invertebrates. 3) *Closed-top baskets with slits* were identical to closed-top bags except for three parallel slits (approximately 18.4 cm long, 8.9 cm apart, and 5 cm from the bag edge on all sides) on the bottom surface, intended to allow entry of soil-dwelling invertebrates. 4) *Open-top baskets* were also fully intact on all sides with seams sealed other than an absence of the top panel, intended to allow a more natural microclimate than closed-top bags. 5) *Open-top baskets with slits* were identical to the open-top treatment except for the addition of three slits in the bottom surface (identical in size and placement to the close-topped bags with slits) to allow access to soil dwelling invertebrates. All five treatments were placed underneath 1-m^2, 1-mm mesh canopies each standing 1-m high, to further inhibit ambient privet litter from entering open-top baskets.

Each bag contained one Hygrochron ibutton (Maxim Integrated, San Jose CA, USA) data logger that recorded temperature and humidity every two hours. Each logger was hung slightly above the ground inside an over-turned plastic cup and secured to the inside of the litter basket, for rain protection (loggers were not waterproof). For no basket bags, data logger cups were hung immediately next to the bag from a tent stake.

Exclusion baskets and associated litter bags were deployed in the field on 13 May 2015 to approximate the spring leaf fall of privet and capture maximal seasonal arthropod activity. Five additional baskets (one of each type) were also deployed in the field but were immediately retrieved to account for handling loss. All baskets were collected from the field on 24 September 2015 after 134 days.

Inner litter bags were carefully removed from outer baskets (if applicable), placed in paper bags and sealed for transport back to the laboratory, and immediately placed in Berlese funnels (BioQuip Products, Rancho Dominguez, CA) to extract invertebrates for ca. 48 hours. Following Berlese extraction, leaves were dried at 55 ^{o}C for 24 hours and then weighed, ashed, and reweighed to determine ash free dry mass (AFDM) remaining. Extracted invertebrates were counted and identified to the lowest practical taxonomic level and then categorized into trophic groups.

Statistical Analysis:

Temperature, humidity, and arthropod abundance differences among treatments were evaluated using a linear mixed-effects model (LME) using the nlme package (Pinheiro et al. 2017) in R (R Core Team 2017) with treatment (basket type) as a fixed effect and site as a random effect. Temperature and humidity values were averaged across the entire incubation period prior to analysis.

Litter breakdown (g AFDM litter remaining) was compared among treatments via an analysis of co-variance (ANCOVA) using a linear mixed-effects model (LME) using the nlme package for each site with days of exposure as the co-variate. In addition, the litter breakdown coefficient (*k*) was calculated for each treatment using a linear regression of ln-transformed AFDM values vs. days of exposure. All statistical analyses were conducted in R version 3.3.3 (R Core Team 2017). Data were Log (x + 1) transformed where necessary to meet statistical assumptions.

Results:

Mean temperature in litter baskets ranged from 20.4 to 25.4 ^{o}C, seasonally, and mean relative humidity in litter baskets ranged from 83.9 to 114.4 %, seasonally (Fig. 4.2). Neither temperature ($F_{4,29} = 0.17$, $P = 0.95$) nor humidity ($F_{4,29} = 1.03$, $P = 0.41$) were significantly different among basket types.

Leaf litter breakdown rates ranged from 0.0064 to 0.0240 (k, d^{-1}; Table 4.1) and ash-free dry mass (AFDM) lost over the course of the study ranged from approximately 54 – 96%. Leaf litter breakdown rates were significantly different among treatments ($F_{4,44}$=3.065, P=0.026). A post-hoc Tukey HSD test showed that the no basket treatment had a significantly faster breakdown rate than closed-top baskets without slits (Table 4.1).

As expected, we were unable to completely exclude invertebrates from any of the exclusion basket treatments as many small invertebrates (e.g., collembolans and oribatid mites) were able to pass through the holes in the mesh (Fig. 4.2d). Baskets with slits allowed access, as expected, to medium and large sized invertebrates. Closed baskets without slits were able to exclude most macroinvertebrates except for several very small predators (< 2mm) in some baskets. Open baskets without slits were successful in excluding large detritivores like millipedes, however large detritivores were rare in all treatments. Open baskets without slits were not very effective at excluding spiders (Fig. 4.3c), though most spiders found in these baskets were very small (< 2 mm) and were presumably capable of passing through the mesh openings. Detritivores, dominated by collembolans and oribatid mites, were the most abundant trophic group in all bag types comprising 40 - 98% of invertebrate abundance per bag. Predators, dominated by Araneae (spiders), ranged from 1 - 70% of invertebrate abundance per bag.

Total invertebrate abundance per sample was not significantly different among treatments (Fig. 4.2d; Table 4.3). Invertebrate abundance of trophic groups important to litter breakdown (detritivores and predators) were significantly different among treatments, however (Table 4.3). Tukey tests showed that detritivores were significantly more abundant in closed baskets without slits than in closed baskets with slits (Fig. 4.3a). Predatory invertebrates were significantly less abundant in closed baskets without slits than in all other bag types (Fig. 3a). Based upon overall abundance Collembola, Oribatida, and Araneae had the greatest potential to play important roles in the trophic dynamics associated with litter breakdown, so these individual taxa were also analyzed. Collembola abundance was significantly different among treatments (Table 4.3), with Tukey tests indicating that abundance was higher in open and closed baskets without slits than in all other treatments (Fig. 4.3b). Oribatida abundance was not significantly different among basket types (Table 4.3). Araneae abundance was significantly different among treatments (Table 4.3) and a Tukey test revealed that spiders were significantly less abundant in closed baskets without slits than in all other basket types (Fig. 4.3c).

Discussion:

We found no differences in temperature or humidity among basket types. While we predicted baskets with the same mesh size would have similar microclimates, it was unexpected that open and closed-top baskets and the control treatment lacking baskets also had similar microclimates. These results suggest that in our study, basket design has little influence on temperature or humidity. These results are similar to Bokhorst and Wardle (2013) who found that fine mesh bags were slightly warmer (0.7 ^{o}C) in the morning but otherwise there were no temperature differences among mesh sizes and no differences in water entry or evaporation rates among mesh sizes.

However, we did find that litter broke down faster in the no basket treatment (the most open treatment) than in closed baskets with no slits (the most enclosed treatment). It is difficult to compare our breakdown rates to other studies examining mesh effects because we were unable to restrict access of very small arthropods and we employed unique bag designs. However, in a laboratory microcosm study of defaunated litter bags, Bokhorst and Wardle (2013) did not find a difference in decomposition rate among bags with different mesh sizes which is contrary to our findings. Yet, in a field mesocosm experiment where arthropods were present, Bradford et al. (2002) found that increasing mesh size increased litter breakdown rates. While we did not find significantly different breakdown rates in intermediary basket types, we did find a difference between the treatment most restrictive to arthropods and most isolated from the environment (closed baskets with no slits) and those that were most open to arthropods and the environment (no basket), similarly to Bradford et al. (2002). While we cannot know for certain, we hypothesize that the differences in breakdown rates that we saw are likely related to differences in access of arthropods to litter and/or differences in fragmentation between treatments. We found breakdown rates within the range of those found by Lobe et al. (2012) who also used 100% privet leaves, but somewhat faster rates than those found by Mitchell et al. (2011), using 50% privet litter in mixed bags.

We found that bag design affected invertebrate composition. Total detritivore abundance of which 30% and 69% consisted of Collembola and oribatid mites, respectively, was higher in closed baskets without slits than in closed baskets with slits (Fig. 4.3a). By contrast, spider abundance was lower in closed baskets without slits than in closed baskets with slits (Fig. 4.3c), suggesting predation may explain the detritivore pattern. This interpretation is complicated, however, because Collembola abundance was similar in open baskets without slits than in closed baskets without slits (Fig. 4.3b) even though spider abundance in the former treatment did not differ from the no basket treatment (Fig. 4.3c). Another possibility is that the mesh bottom of baskets without slits reduced the egression rates of collembolans that had colonized litter in these treatments, resulting in elevated numbers of these invertebrates. (Fig. 4.3). While litter breakdown studies employing different mesh sizes usually aim to exclude larger detritivores, we found that a completely enclosed small mesh treatment (closed-top baskets without slits) also significantly reduced predator abundance. It is possible that differences found in breakdown rates among mesh sizes in other studies, may have also been mediated by predator effects as well as those of large detritivores. We hypothesize that in our system, large detritivores were so rare (3 total across all treatments) that if invertebrates influenced differences in breakdown rates, predator effects likely played a much larger role than those of large detritivores. We have designed supplemental studies to directly assess the possible importance of trophic interactions on leaf breakdown.

Importantly we were unable to exclude all invertebrates from any of our treatments, despite using a very fine mesh. Other studies assessing mesh effects on arthropods suggest exclusion requires ≤ 100-µm mesh (Bradford et al. 2002; Bokhorst and Wardle 2013). Such a fine mesh is very likely to create unrealistic breakdown conditions. Existing mesh-effect studies have not examined microclimate and arthropods concurrently, nor evaluated the impact of extremely fine mesh on the microbial community. Studies examining the interacting effects of extremely fine mesh, arthropods, microbes, and microclimate should be conducted. We were able to exclude most, but not all, macroinvertebrates from open and closed baskets without slits. However, those that were able to access these treatments were nearly exclusively very small predators, which may impact trophic interactions, albeit to a possibly small degree, but should not affect breakdown directly. Additionally, we found evidence which suggests that using two different mesh sizes may cause an unintended trophic effect on litter breakdown. Large mesh bags seem to create natural microclimate conditions and permit a natural arthropod community to develop, and thus may best reflect natural breakdown rates. The large mesh litter bag approach is already widely used in terrestrial forests (Coleman et al. 2004), and aquatic systems (Benfield 2007), and our work suggests the technique is similarly useful under floodplain conditions. Large mesh bags do not, however, allow for direct investigation of arthropod impacts on litter breakdown.

Overall, basket design did not influence microclimate in our study, but it did influence litter breakdown rates and the relative abundances of certain arthropod groups like spiders and springtails. This does not, however, indicate that microclimate should not be a concern when considering litter bag design, although the issue was minimally important in our floodplain system. The strong effect of complete mesh enclosure on spider abundance was also unexpected and may provide an opportunity to test how predators may indirectly affect breakdown rates by altering detritivore abundance. Future studies of the microclimate within different bag designs across different regions and ecosystems remain necessary.

Literature Cited:

Benfield EF (2007) Decomposition of leaf material. In: Hauer FR, Lamberti GA (eds) Methods in stream ecology, 2nd edn. Academic Press, San Diego, pp 711-720

Bocock KL, Gilbert OJW (1957) The disappearance of leaf litter under different woodland conditions. Plant and Soil 9:179-185.

Bokhorst S, Wardle DA (2013) Microclimate within litter bags of different mesh size: Implications for the ‘arthropod effect’ on litter decomposition. Soil Biology and Biochemistry 58:147-152.

Bradford MA, Tordoff GM, Eggers T, Jones TH, Newington JE (2002) Microbiota, fauna, and mesh size interactions in litter decomposition. Oikos 99:317-323.

Coleman DC, Crossley Jr DA, Hendrix PF (2004) Chapter 9 : Laboratory and field exercises in soil ecology. In: Coleman DC, Crossley DA, Hendrix PF (eds). Fundamentals of soil ecology, 2nd edn. Academic Press, Burlington, pp 299-325

Coûteaux M, Bottner P, Berg B (1995) Litter decomposition, climate and litter quality. Trends in Ecology and Evolution 10:63-66.

Crossley DA, Hoglund MP (1962) A litter-bag method for the study of microarthropods inhabiting leaf litter. Ecology 43:571-573.

Hanula JL, Horn S, Taylor JW (2009) Chinese privet (*Ligustrum sinense*) removal and its effect on native plant communities of riparian forests. Invasive Plant Science and Management 2:292-300.

Kampichler C, Bruckner A (2009) The role of microarthropods in terrestrial decomposition: A meta-analysis of 40 years of litterbag studies. Biological Reviews 84:375-389.

Lobe JW (2012) Effects of the removal of the invasive shrub, Chinese privet (*Ligustrum sinense*), on soil properties and earthworm communities. Thesis, University of Georgia.

Mitchell JD, Lockaby BG, Brantley EF (2011) Influence of Chinese privet (*Ligustrum sinense*) on decomposition and nutrient availability in riparian forests. Invasive Plant Science and Management 4:437-447.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2017) nlme: Linear and nonlinear mixed effects models. R package version 3.1-131. Available from: https://CRAN.R-project.org/package=nlme.

Prescott CE (2005) Do rates of litter decomposition tell us anything we really need to know? Forest Ecology and Management 220:66-74.

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: https://www.R-project.org/.

Stoklosa AM, Ulyshen MD, Fan Z, Varner M, Seibold S, Müller J (2016) Effects of mesh bag enclosure and termites on fine woody debris decomposition in a subtropical forest. Basic and Applied Ecology 17:463-470.

Ulyshen MD (2014) Interacting effects of insects and flooding on wood decomposition. PLOS One 9:e101867.

Ulyshen MD, Müller J, Seibold S (2016) Bark coverage and insects influence wood decomposition: Direct and indirect effects. Applied Soil Ecology 105:25-30.

Table 4.1 Leaf breakdown rates (*k*) expressed per day for each treatment (basket-type)

Treatment	k (day^{-1})	R^2
Loose bag	0.0159	0.6509
Open-top + slits	0.0143	0.5500
Open-top	0.0093	0.8731
Closed-top + slits	0.0113	0.7428
Closed-top	0.0074	0.8546

Table 4.2 Summary of mixed-effects models (LME) testing for the effects of treatment (basket-type) on invertebrate abundances (per sample) for detritivores, predators, and total invertebrate abundance. Significant results ($P \leq 0.05$) are indicated in bold type

Trophic Group	Numerator Df	Denominator Df	F	P
Detritivores	**4**	**25**	**3.393**	**0.024**
Predators	**4**	**25**	**9.148**	**< 0.001**
Total Abundance	4	25	1.703	0.181

Table 4.3 Summary of mixed-effects models (LME) testing for the effects of treatment (basket-type) for Collembola, Oribatida, and Araneae. Significant results ($P \leq 0.05$) are indicated in bold type

Taxa	Numerator Df	Denominator Df	F	P
Collembola	**4**	**25**	**4.818**	**0.005**
Oribatida	4	25	1.904	0.141
Araneae	**4**	**25**	**13.941**	**<0.001**

Figure 4.1 Example of litter basket treatments.

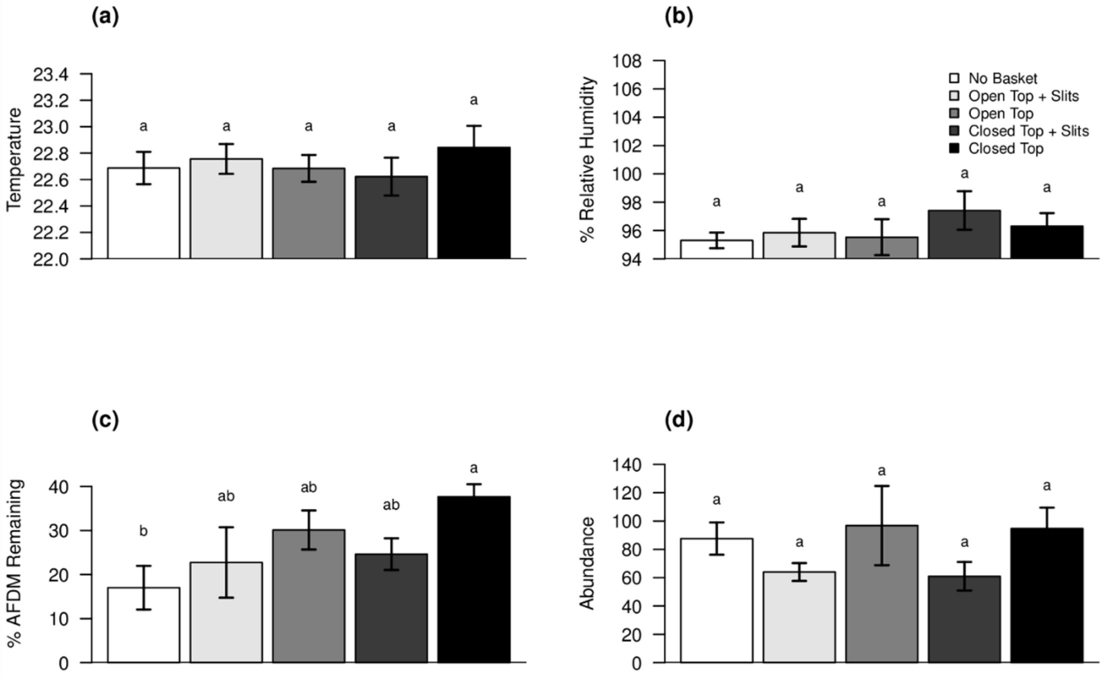

Figure 4.2 Mean (± SE) a) temperature (^{o}C), b) percent relative humidity, c) percent AFDM remaining and, d) total invertebrate abundance per sample for all basket types. Bars indicated by the same letter, within each graph, are not significantly different.

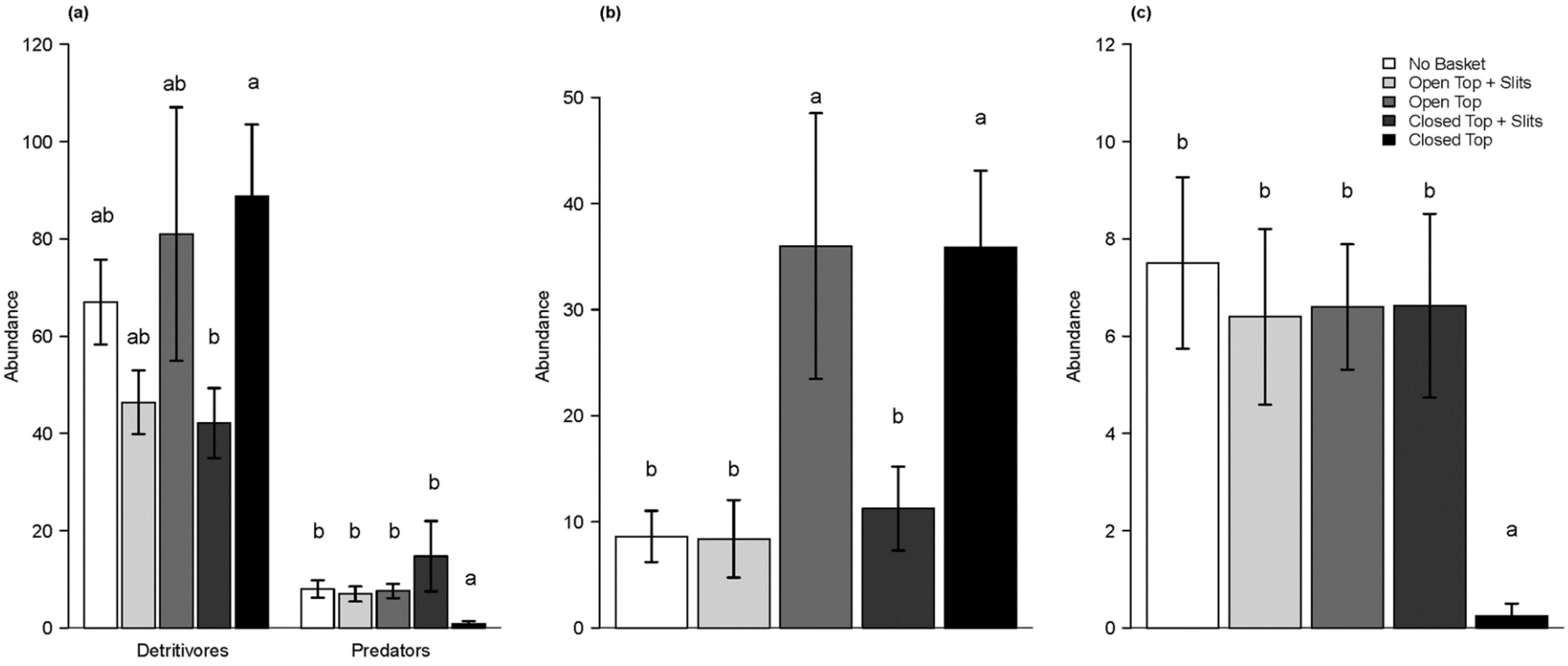

Figure 4.3 Invertebrate abundances (mean ± SE) for all basket types: a) by trophic group, b) for Collembola, and c) Araneae. Bars indicated by the same letter, within each trophic group, are not significantly different.

CHAPTER 5

EFFECTS OF CHINESE PRIVET (*LIGUSTRUM SINENSE)* INVASION ON DECOMPOSITION AND LITTER-DWELLING INVERTEBRATES IN SOUTHEASTERN U.S. FLOODPLAIN FORESTS[4]

---

[4] Bush, B.M., M.D. Ulyshen, and D.P. Batzer. To be submitted to *Biological Invasions*.

Abstract: Chinese privet (*Ligustrum sinense*) is one of the most problematic invasive plants in many parts of the world where it often dominates the shrub layer in riparian forests. In this study, we aimed to evaluate the role of privet invasion on litter inputs, rates of litter decomposition and litter-dwelling arthropods in the Southeastern United States. To do this we: 1) evaluated the relative contribution of privet to total litter-fall, 2) compared breakdown of artificial leaves (filter paper) in plots which had or had not been subjected to experimental privet removal, and 3) compared litter breakdown and arthropod communities among the following litter types: a) native sweet gum, b) invasive Chinese privet, and c) a mixed sweet gum-privet litter treatment (to examine the effect of privet litter on sweet gum breakdown). Privet accounted for 10% of annual litter-fall. After 134 days, while the floodplain was dry, the percent ash-free dry mass (AFDM) remaining of filter paper two-fold lower in reference plots than in privet removal plots. Over 166 days, which encompassed flooded and dry periods, the percent ADFM remaining in privet litter bags was significantly lower than that of sweet gum or mixed bags, which were not different from one another, regardless of plot type. Additionally, the proportion of litter remaining was not different between reference and privet removal plots. There were no differences among treatments (litter or plot types) in invertebrate community composition or in abundances of detritivore and predator invertebrates. We hypothesize that effects of flooding and privet invasion on decomposition dynamics interact, and that the effect of privet may vary depending on the hydrologic condition of the floodplain.

Introduction:

Floodplain wetlands are among the most valuable ecosystems on earth in terms of ecosystem services (Costanza et al. 2014) but are also one of the most threatened. Floodplain area has declined by 106 million hectares globally between 1997 and 2011 (Costanza et al. 2014) and is additionally being impacted by a myriad of other threats including invasion by exotic species. Wetlands are especially vulnerable to invasive plant species which frequently form monotypic stands able to impact biodiversity, food webs, and nutrient cycling (Zedler and Kercher 2004). Additionally, projected changes in hydropattern resulting from climate change, are predicted to reduce competitiveness of native Southeastern U.S. plants and (along with other anthropogenic disturbances) increase the competitiveness of invasive plant species (Flanagan et al. 2015). Given the susceptibility of floodplain wetlands to invasive plant species it is important to understand their impacts on wetland ecosystem function.

Chinese Privet (*Ligustrum sinense*) is a highly invasive plant in the Southeastern U.S., estimated to cover > 1.09 million forested ha. as of 2008 (Miller et al. 2008). Chinese Privet (hereafter referred to as “privet”) is an ornamental shrub introduced into the U.S in the 1850s that experiences rapid growth and can reach 9m heights (Greene and Blossey 2014). In Georgia, our study location, privet is listed as a category one (most serious threat) invasive plant by the Georgia Exotic Pest Plant Council (GA-EPPC 2010) and is reported in 95% of counties in Georgia (EDDMapS 2018). It is especially prevalent in riparian areas. For example, as of 1999 privet covered 59% of the upper Oconee River Floodplain in north Georgia (Ward 2002). Because its dominance in floodplain areas there is potential for privet to contribute a significant amount of leaf litter. Privet invaded floodplain sites in western Georgia reported privet to account for 3.6 - 15% of annual litter fall in moderately invaded plots and 7.8 - 29.9% in those that were severely invaded (Mitchell et al. 2011). While several studies have examined the impact of privet on native plant communities in the Southeastern U.S. (Hanula et al. 2009; Greene and Blossey 2012; Greene and Blossey 2014; Hudson et al. 2014), few have examined the impact of this highly invasive shrub on wetland ecosystem processes such as leaf litter breakdown, which may impact nutrient cycling and carbon storage, both important ecosystem services of floodplains.

Invasive plants are known to alter the timing of leaf senescence and litter chemistry in forested systems (Ehrenfeld 2003), which is likely to alter the dynamics of litter breakdown because plant traits significantly influence rates of decomposition (Cornwell et al. 2008). The few studies that have examined the effect of exotic plant species on decomposition have found that exotic invasive plants are frequently more labile and decompose more quickly than native plant litter (Cameron and Spencer 1989; Ehrenfeld 2003; Allison and Vitousek 2004; Ashton et al. 2005; Mitchell et al. 2011). However, in an *in-situ* study of 78 deciduous forest plant species, Jo et al. (2016) found no overall differences in decomposition rates between native and non-natives with only a few non-native plants decaying more quickly than natives. To our knowledge, only Mitchell et al. (2011) and Lobe (2012) have examined the impacts of privet on breakdown. Privet had a higher litter quality than any native species (lower C:N ratio, lower lignin content, and higher N content) and as the ratio of privet to native litter increased the rate of decomposition increased (Mitchell et al. 2011). When privet accounted for 30% of leaf litter the carbon turnover rate was 2.6 times that of uninvaded plots (Mitchell et al. 2011). While these results are compelling, minimal data exist on litter-associated arthropods that are known drivers of decomposition; these organisms may also be affected by changes in litter quality due to invasive privet.

In 2005, an experiment investigating the ecological impacts of Chinese privet removal was initiated in floodplain forests in northeastern Georgia. So far, the study has consistently shown that privet removal strongly benefits native plant and flying insect communities (Hanula et al. 2009; Ulyshen et al. 2010; Hanula and Horn 2011a; Hanula and Horn 2011b; Hudson et al. 2013). Some non-native invertebrates, by contrast, may benefit from privet. For example, Ulyshen et al. (2010) found an association between privet and the non-native ambrosia beetle, *Xylosandrus crassiusculus*. Similarly, Lobe (2012) found European earthworms to be more common at sites invaded by privet whereas native earthworms were more abundant at sites never invaded by the species. Additionally, Lobe (2012) found that freshly harvested privet leaves decomposed at similar rates at sites that had or had not been cleared of privet. However, leaves from native tree species were not included in that study and no published efforts have explored the effects of privet on arthropods confined to the litter or soil layers.

The goal of our study was to evaluate the effect of privet invasion on decomposition rates and litter-associated arthropods in the context of a long-term privet removal experiment. To do this we: 1) evaluated the relative contribution of privet to total litterfall among our invaded study sites 2) compared breakdown of cellulose (using filter paper) in plots which had or had not been subjected to experimental privet removal, and 3) compared litter breakdown and arthropod communities among litter types: a) native sweet gum (found at all study sites), b) invasive Chinese privet, and c) a mixed sweet gum-privet litter treatment (to examine the effect of privet litter on sweet gum breakdown) in plots which had or had not undergone privet removal.

Methods:

Study Sites:

Four study sites were selected on floodplains of the severely privet-invaded Oconee-River Watershed in the Northeast Georgia Piedmont region (Athens-Clarke and Greene Counties). All selected sites were used in a long-term experimental privet removal study started in 2005 by Hanula et al. (2009) using one of three treatments: 1) Reference, no privet was removed, 2) Mulch, mechanical removal of all privet which was then mulched and layered on the soil surface, and 3) Chainsaw, hand removal of all privet using saws and leaving piles of cut privet on the soil surface. The mulch plots remain relatively privet-free approximately 10 years later, so we used reference and mulch plots to compare conditions with and without privet, respectively (see Hanula et al. 2009 for site descriptions).

Litter-fall:

To estimate the proportion of privet litter to both sweet gum and overall litter-fall at our study sites, we collected litter in leaf traps for approximately one year using protocol adapted from Harrison (2013) and the Center for Tropical Forest Science (CTFS) - Forest Global Earth Observatory (ForestGEO) (Anderson-Teixeira et al. 2015). Leaf traps consisted of a polyvinyl chloride (PVC) frame, with a 1-m^2, 1-mm nylon mesh surface which captured leaves, and was 1-m above ground. Four traps were placed within reference plots at each of the four sites (16 traps total) in subplots established by Hanula et al. (2009). Traps were placed on 20 October 2014 and litter was collected approximately once a month, except during peak leaf fall when it was collected every 2 weeks, until 21 October 2015. Leaves were transported from the field in cloth bags, dried at 55°C until a constant mass was reached (usually 72 hours), sorted, and weighed.

Filter Paper experiment:

In the summer of 2015, prior to evaluating different litter types, we placed 10 fine-mesh (300 µm) bags filled with 10 filter paper discs each (Fisherbrand, medium porosity, 9-cm diameter, Fisher Scientific, Waltham, MA) in the center of each plot as a cellulose control. Bags were placed along a transect at 1-m intervals. Fine-mesh bags were used to exclude most macroinvertebrates while still allowing moisture and gas exchange. These fine-mesh filter paper bags allowed us to examine the effect of plot type (reference or mulch, hereafter privet removal plot) without potential impacts of litter chemistry and macroinvertebrate community differences. Filter paper bags were placed *in situ* on 13 May 2015 and left in place until 24 September 2015, a total 134 days. Immediately after retrieval, filter paper was dried at 55˚C for ca. 24 hours and subsequently weighed, ashed in a muffle furnace at 550°C for 4 hours and reweighed to determine ash free dry mass (AFDM) remaining.

Leaf Litter experiment:

Leaf litter breakdown was evaluated using the litter-bag method. Leaves were collected at abscission and air dried. Leaf litter was placed within 5-mm mesh bags (the smallest size mesh that would both contain privet litter and allow access to large invertebrates) and consisted of 10g of leaf litter from: A) privet, B) sweet gum, or C) a 50% mixture of privet and sweet gum. A 50% mixture was chosen because it was approximately the average proportion, by dry weight, of privet to sweet gum that fell across the four sites over the course of the previous year (informed by litter-fall results, see above). Due to the small size of privet leaves (some < 5mm), litter was first sifted through 5-mm mesh before weighing so as not to cause an over estimate of mass-change via loss through mesh-bag windows.

Samples were placed at one randomly selected subplot within each reference and privet removal plot at all four sites (8 plots total). At each of the 8 subplots (four privet removal, four reference, one each at each of four sites), six bags each of the three litter treatments (privet, sweet gum, and mixture) were randomly placed at 1-m intervals along transects in two randomly chosen cardinal directions (n=144).

Litter bags were deployed in the field in January of 2016 and collected initially at approximately 2 weeks, and then approximately once a month depending on hydrologic conditions with a total time of 166 days in-situ. An additional set of 24 litter bags (1 bag for each litter type, brought to each of the 8 subplots) were also transported into the field in January 2016, placed on the substrates as per other bags, but then immediately retrieved to estimate handling loss. Upon retrieval (either at the start or end of the trial), litter bags were sealed in paper bags, returned to the laboratory, and placed immediately in Berlese funnels (BioQuip Products, Rancho Dominguez, CA) for ca. 48 hours to extract invertebrates. After Berlese extraction, leaves were handled similarly to filter paper. Extracted invertebrates were retained in 70% ethanol and then counted, identified (typically to family, but sometimes order or class), and categorized into trophic groups.

Statistical Analysis:

Litter-fall data were used primarily to inform the contents of the mixed litter treatment, so no statistical analyses were performed. Mass of three litter categories (privet, sweet gum, and all other litter) were totaled and proportions of each were determined.

Shortly after litter samples were placed in the field, significant natural flooding occurred which infiltrated litter bags with an abundance of fine, highly organic sediment. This intrusion resulted in some litter samples having higher ash-free dry masses relative to the baseline (i.e. handling loss bags), rather than a decreasing mass. Given that it was not possible to calculate the relative proportions of organic material from sediment versus experimental litter, we were prevented from calculating conventional litter breakdown coefficients (*k*) to compare breakdown rates among treatments. Instead, we compared percent AFDM remaining among treatments using a linear mixed-effects model (LME) with the nlme package (Pinheiro et al. 2017) in R (R Core Development Team 2017) with treatments (plot type and litter type) as fixed effects, days exposure as a categorical factor, and site as a random effect. To minimize the effects of extreme values found in some bags (resulting from complete burial by sediment), values for percent AFDM remaining were capped at 150%. (We did, however, test differences among treatments at both 200% AFDM remaining and without any caps on values, and the significance of our tests remained similar.)

Filter paper bags were not inundated because flooding levels were low in 2015, compared to 2016. However, for ease of comparison to litter type treatments (2016 data), we compared percent AFDM remaining between plot types for filter paper bags as well, using a one-way analysis of variance (ANOVA) in R. For all analyses, bags that were damaged or lost were omitted. Data for both litter and filter paper bags were square root transformed prior to analyses to meet statistical assumptions.

Invertebrate abundance data (individuals per sample) were pooled across sampling dates prior to all analyses and additionally, were log (x + 1) transformed to satisfy statistical assumptions and minimize the influence of highly abundant taxa. Immature invertebrates too small to be reliably identified were left out of analyses (< 1% of the total). Invertebrate community structure (based on relative abundances of taxa present) within litter bags was compared among plot and litter treatments via a two-way analysis of similarity (ANOSIM; Bray-Curtis similarity, Kruskal fit scheme 1,25 restarts), and non-metric multidimensional scaling (NMS, Bray-Curtis similarity, Kruskal fit scheme 1,25 restarts) was used to visualize patterns among treatments (but not presented here because no patterns were apparent). All identifiable taxa were included in the analysis at the family level, except for several taxa which were only identified to order or class (in this case all individuals within that group were combined at the higher level of organization). Invertebrate trophic group abundances (detritivores, predators) were compared among treatments using a two-way analysis of variance (ANOVA) in R. NMS ordination and ANOSIM analyses were performed using PRIMER v6 software (Clarke and Gorley 2006). All analysis in R were performed using version 3.4.0 (R Core Development Team 2017).

Results:

Litter-fall:

In total, after pooling results from the 16 traps, privet and sweet gum accounted for 10 and 13 % total annual litter-fall, respectively, with all other leaf types comprising the remaining 77%. Privet leaf-fall peaked twice; first in December 2014 – January 2015 when 34% of privet litter fell, and again in March – May 2015 accounting for another 44

% of annual privet litter. However, 95 % of sweet gum and 93% of other litter fell between the months of October and December.

Filter Paper experiment:

The percent AFDM remaining of filter paper ranged from 0.4 – 95.7% after 134 days. Additionally, the percent AFDM remaining in privet removal plots was approximately twice as high as those in reference plots, a significant difference ($F_{1,73}$=6.2, P=0.015; Fig. 5.1).

Litter Bags experiment:

The percent ash-free dry mass (AFDM) remaining in litter bags after 166 days ranged from 4.9 – 363.6%. Across all dates, percent AFDM ranged from 4.9 – 551%. Dominant detritivores in litter bags, across dates and treatments, were spring tails (Collembola) and oribatid mites. Spiders (Araneae) and ants (Formicidae) were the dominant invertebrate predators. Approximately 30,000 total individuals were collected from litter bags, across 98 taxa.

The percent AFDM remaining varied significantly among litter types (privet, sweet gum, mixed privet and sweet gum; $F_{2,130}$=10.3, P< 0.001) and there was no significant interaction between litter type and plot type ($F_{2,130}$=0.5, P=0.623). A post-hoc Tukey HSD test showed that privet bags had significantly less (~ 20 %) AFDM remaining than sweet gum bags, or mixed bags. However, sweet gum and mixed bags were not significantly different from one another (Fig. 5.2). Invertebrate community analysis revealed no difference among litter types (R= - 0.027, P=0.994). Detritivore invertebrate abundance per sample did not vary among litter types ($F_{2,138}$=0.035, P=0.966), nor did predator abundance ($F_{2,138}$=2.156, P=0.120).

Proportion AFDM remaining in litter bags did not significantly vary by plot type (reference or privet removal; $F_{1,130}$=0.3, P=0.599). Invertebrate community composition was not different between plot types (R=0.003, P=0.369). Detritivores were somewhat more abundant in reference plots than in privet removal plots, but this difference was not significant ($F_{1,138}$=3.5, P=0.060). There were no differences in predator invertebrate abundance between plot types ($F_{1,138}$=0.4, P=0.552).

Discussion:

We found that there was significantly less Chinese privet leaf litter remaining in litter bags over time, than in bags containing native sweet gum or a privet-sweet gum mixture, in both reference and privet removal plots. We had expected privet litter to disappear faster than sweet gum because previous work has shown that privet has a higher litter quality (Mitchell et al. 2011) and exotic invasive plants are typically more labile, decaying more quickly (Cameron and Spencer 1989; Ehrenfeld 2003; Allison and Vitousek 2004; Mitchell et al. 2011). It was unexpected, however, that leaf litter remaining in mixed bags would be similar in proportion to sweet gum. Mitchell et al. (2011) found that as the proportion of privet litter increased in mixed litter bags that the rate of decomposition also increased. We found a difference in percent AFDM remaining between mixed bags (50% privet) and sweet gum-only bags of only around 1 %, which is striking considering an approximately 20% difference between privet-only litter and each of the other two litter treatments (sweet gum only and a privet-sweet gum mixture).

It seems that the presence of sweet gum dramatically mitigated the effect of high privet litter quality on breakdown, rather than privet accelerating sweet gum breakdown as we had expected. In an analysis of 30 mixed-litter studies, Gartner and Cardon (2004) found it was more common for mixed-litter bags to accelerate decomposition, especially if one or more species in the mixture has a higher litter quality. However, that pattern was not ubiquitous and factors other than litter quality, such as secondary inhibitory compounds and physical structure, influenced the effects of litter mixtures on decay (Gartner and Cardon 2004). We hypothesize that, in our study, some influencing factors of litter mixture decomposition may have been affected by the extensive flooding seen during the study period. For example, McArthur et al. (1994) found that in stream and floodplain pools in South Carolina, water oak (*Quercus nigra*) had an inhibitory effect on decomposition of the more labile sweet gum in mixed litter bags. This was not the case on dry floodplains and addition of oak leachate (containing phenols and tannins) inhibited bacterial density in mixed-species packs. Flooding, which happened soon after litter placement in our study, had the potential to increase sweet gum leaching, subsequently decreasing the effect of privet litter chemistry decomposition.

Additionally, physical qualities of litter mixtures, like structural heterogeneity, can impact colonization of leaf litter by decomposers (Gartner and Cardon 2004; Korboulewsky et al. 2016). Mixed-litter initially increased both habitat heterogeneity and microarthropod abundance in a Japanese mixed-oak forest, but over time compaction and fragmentation of leaf litter minimized the effect of mixed-litter heterogeneity on decay and soil arthropods (Kaneko and Salamanca 1999). Flooding likely greatly increased the rate of litter compaction (and in some cases burial), reducing the influence of structural benefits of mixed-litter bags on decomposers. This idea is supported by the lack of differences found in invertebrate abundance and community composition among our litter treatments. However, the body of literature involving the effect of mixed-litter on soil invertebrates remains scant and results vary (Gartner and Cardon 2004; Korboulewsky et al. 2016).

We did not find a significant difference in the percent AFDM remaining in leaf litter bags, regardless of litter type, between reference and privet removal plots. Similarly, Lobe (2012) did not find a difference in privet litter decomposition in plots with or without privet. However, our results were unexpected given that the previous year (2015), the percent AFDM remaining in filter paper bags was two-fold higher in privet removal plots than in reference plots. Results from our filter paper analyses are consistent with Mitchell et al. (2011) who found higher carbon turnover in privet invaded plots. Differences between filter paper and litter bag studies may also relate to flooding. Flooding did not occur during the filter paper study, whereas multiple, large flood pulses took place during the litter bag study, depositing a great amount of highly organic soil onto the floodplain. It is widely accepted that flood pulses affect floodplain nutrient and organic matter cycling (Junk et al. 1989; Tockner et al. 2000) and temporary, intense floods have been shown to increase nitrogen mineralization and subsequent nitrification-denitrification processes during drying (Shrestha et al. 2014). Possibly, effects from large flood pulses experienced during our study, outweighed any impact of privet on floodplain soil nutrients and subsequent effects on litter decay that we may have otherwise detected. Conversely, it is also possible that there is a difference in soil chemistry among plots, which impacts decay of cellulose (filter paper), but that soil chemistry may be less important than other factors influencing decomposition of more structurally and chemically complex leaf litter. For example, Pavao-Zuckerman and Coleman (2005) found that litter breakdown was not influenced by soil chemistry but was affected by soil moisture and organic matter content, both of which would have been similar between reference and privet removal plots.

Furthermore, we did not see significant differences between reference and privet removal plots in either invertebrate community composition or abundances of detritivore and predator invertebrates. Patterns of abundance and diversity of soil invertebrates is multifactorial, including soil (especially pH and moisture) and litter quality, microhabitat types, and fungal communities, so the collective influence of one plant species, like privet, is likely influenced by the relative effects of that plant on a myriad of interacting factors (Korboulewsky et al. 2016). Because we were not able to detect any differences among these features, it is difficult to say specifically why we did not see significant differences in invertebrate patterns between plot types. Again, it is possible the impact of flooding minimized the relative influence that privet may have otherwise had on invertebrate abundances and community composition.

In general, we found relatively little impact of Chinese privet invasion on litter breakdown or litter associated arthropods. However, flooding greatly impacted our study, and it is difficult to know if flooding masked the impacts of privet invasion; especially considering that during a dry phase, filter paper decayed significantly faster in plots that contained privet. Yet, because privet is widespread in riparian areas the interplay of privet invasion and flooding is relevant to informing management decisions. It may also be important to explore the role differences in leaf-fall phenology among privet and native species may play, which to our knowledge has not yet been documented. We suggest on-going, long-term research among seasons and across wet and dry years to fully understand the relationship between privet invasion and floodplain carbon and nutrient cycling. Previous privet-related decomposition studies have taken place during dry phases of the flood pulse, and our results serve as a baseline for future examination of the role of privet invasion in active floodplain zones.

Literature Cited:

Allison SD, Vitousek PM (2004) Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. Oecologia 141:612-619.

Anderson-Teixeira KJ et al. (2015) CTFS-ForestGeo: A worldwide network monitoring forests in an era of global change. Global Change Biology 21:528-549.

Ashton IW, Hyatt LA, Howe KM, Gurevitch J, Lerdau MT (2005) Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. Ecological Applications 15:1263-1272.

Cameron GN, Spencer SR (1989) Rapid leaf decay and nutrient release in a Chinese tallow forest. Oecologia 80:222-228.

Clarke K, Gorley R (2006) Primer v6: User manual/tutorial. PRIMER-E, Plymouth.

Cornwell WK et al. (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11:1065-1071.

Costanza R et al. (2014) Changes in the global value of ecosystem services. Global Environmental Change 26:152-158.

EDDMapS. 2018. Early Detection & Distribution Mapping System. The University of Georgia - Center for Invasive Species and Ecosystem Health. Available online at http://www.eddmaps.org/; last accessed 25 September 201.

Ehrenfeld GJ (2003) Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503-523.

Flanagan NE, Richardson CJ, Ho M (2015) Connecting differential responses of native and invasive riparian plants to climate change and environmental alteration. Ecological Applications 25:753-767.

GA-EPPC (2010) Georgia exotic pest plan council list of non-native invasive plants in Georgia. The University of Georgia - Center for Invasive Species and Ecosystem Health. http://www.gaeppc.org/list/. Last accessed 26 September 2018.

Gartner TB, Cardon ZG (2004) Decomposition dynamics in mixed-species leaf litter. Oikos 104:230-246.

Greene B, Blossey B (2014) Patterns of privet: Urbanizing watersheds, invasive *Ligustrum sinense*, and performance of native plant species in piedmont floodplain forests. Ecosystems 17:990-1001.

Greene BT, Blossey B (2012) Lost in the weeds: *Ligustrum sinense* reduces native plant growth and survival. Biological Invasions 14:139-150.

Hanula JL, Horn S (2011a) Removing an exotic shrub from riparian forests increases butterfly abundance and diversity. Forest Ecology and Management 262:674-680.

Hanula JL, Horn S (2011b) Removing an invasive shrub (Chinese privet) increases native bee diversity and abundance in riparian forests of the Southeastern United States. Insect Conservation and Diversity 4:275-283.

Hanula JL, Horn S, Taylor JW (2009) Chinese privet (*Ligustrum sinense*) removal and its effect on native plant communities of riparian forests. Invasive Plant Science and Management 2:292-300.

Harrison M (2013) Standard operating procedure: Forest litter-fall. Orangutan Tropical Peatland Project, Palangka Raya, Indonesia.

Hudson JR, Hanula JL, Horn S (2013) Removing Chinese privet from riparian forests still benefits pollinators five years later. Biological Conservation 167:355-362.

Hudson JR, Hanula JL, Horn S (2014) Impacts of removing Chinese privet from riparian forests on plant communities and tree growth five years later. Forest Ecology and Management 324:101-108.

Jo I, Fridley JD, Frank DA (2016) More of the same? In situ leaf and root decomposition rates do not vary between 80 native and nonnative deciduous forest species. New Phytologist 209:115-122.

Junk WJ, Bayley PB, Sparks RE The flood pulse concept in river-floodplain systems. In: Dodge DP (ed) International Large River Symposium, 1989. Canadian Special Publications Fisheries Aquatic Sciences, pp 110-127.

Kaneko N, Salamanca E (1999) Mixed leaf litter effects on decomposition rates and soil microarthropod communities in an oak–pine stand in Japan. Ecological Research 14:131-138.

Korboulewsky N, Perez G, Chauvat M (2016) How tree diversity affects soil fauna diversity: A review. Soil Biology and Biochemistry 94:94-106.

Lobe JW (2012) Effects of the removal of the invasive shrub, Chinese privet (*Ligustrum sinense*), on soil properties and earthworm communities. The University of Georgia.

McArthur JV, Aho JM, Rader RB, Mills GL (1994) Interspecific leaf interactions during decomposition in aquatic and floodplain ecosystems. Journal of the North American Benthological Society 13:57-67.

Miller JH, Chambliss EB, Oswalt CM (2008) Maps of occupation and estimates of acres covered by nonnative invasive plants in southern forests using SRS FIA data. http://www.invasive.org/fiamaps. Last Accessed: 26 September 2018.

Mitchell JD, Lockaby BG, Brantley EF (2011) Influence of Chinese privet (*Ligustrum sinense*) on decomposition and nutrient availability in riparian forests. Invasive Plant Science & Management 4:437-447.

Pavao-Zuckerman MA, Coleman DC (2005) Decomposition of chestnut oak (*Quercus prinus*) leaves and nitrogen mineralization in an urban environment. Biology and Fertility of Soils 41:343-349.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2017) Nlme: Linear and nonlinear mixed effects models. R package version 3.1-131. https://CRAN.R-project.org/package=nlme.

R Core Development Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/.

Shrestha J et al. (2014) Flood pulses control soil nitrogen cycling in a dynamic river floodplain. Geoderma 228-229:14-24.

Tockner K, Malard F, Ward JV (2000) An extension of the flood pulse concept. Hydrological Processes 14:2861-2883.

Ulyshen MD, Horn S, Hanula JL (2010) Response of beetles (coleoptera) at three heights to the experimental removal of an invasive shrub, Chinese privet (*Ligustrum sinense*), from floodplain forests. Biological Invasions 12:1573-1579.

Ward RW (2002) Extent and dispersal rates of Chinese privet (*Ligustrum sinense*) invasion on the Upper Oconee River floodplain, north Georgia. Southeastern Geographer 42:29-48.

Zedler JB, Kercher S (2004) Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. Critical Reviews in Plant Sciences 23:431-452.

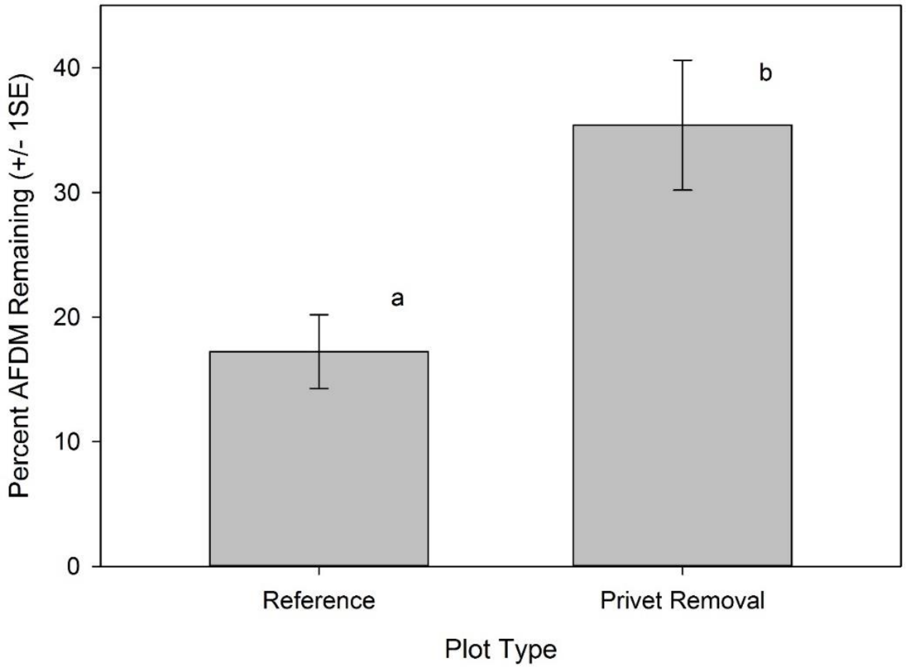

Figure 5.1. Average percent ash-free dry mass (AFDM) remaining (± 1 SE) of filter paper bags after 134 days. Bars indicated by the same letter are not significantly different.

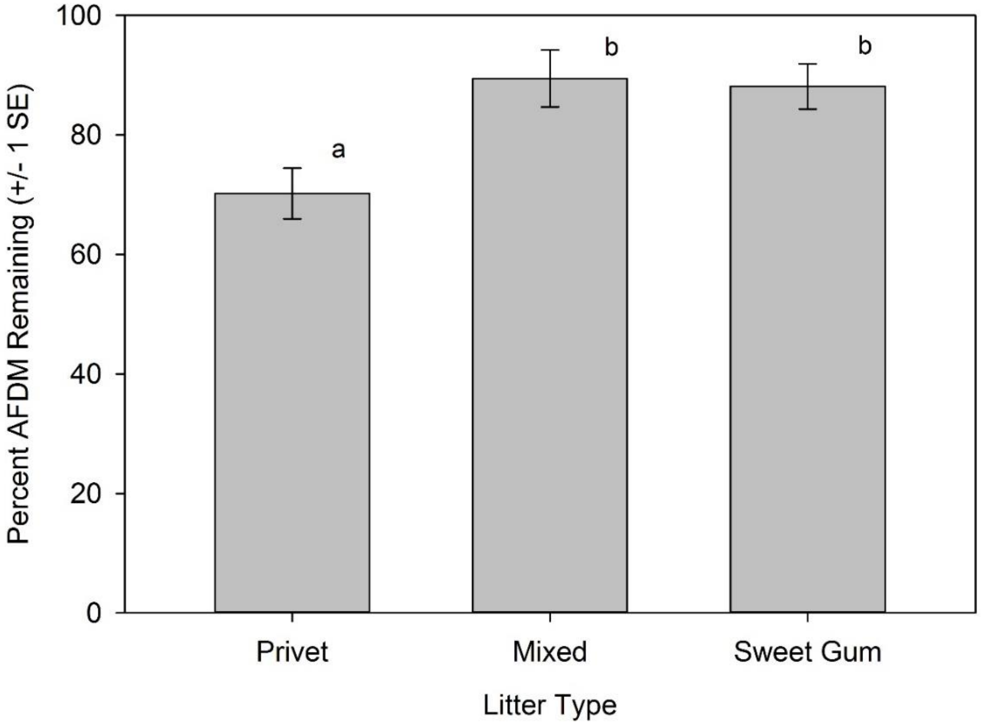

Figure 5.2. Percent ash-free dry mass (AFDM) remaining (± 1 SE) of privet, mixed, and sweet-gum litter bags averaged across all sampling dates and plot types. Bars indicated by the same letter are not significantly different.

CHAPTER 6

CONCLUSION

Wetlands are valuable ecosystems which remain under threat from loss, fragmentation, degradation, invasive species, and climate change (Zedler and Kercher 2004; Zedler and Kercher 2005; Dahl 2011; Costanza et al. 2014). Because of these threats, it is important to establish baseline information for ecological indicators of structure and function in certain wetland types so that changes in community structure and ecosystem processes can be monitored.

My research suggests that beaver activity increases invertebrate abundance and diversity by increasing habitat heterogeneity within and along a wetland-stream complexes. Community differences along with high turnover among wetland successional stages indicates that invertebrate communities of each type have a different taxonomic make-up. Beaver activity could be an important conservation tool by substantially contributing to alpha diversity, and stabilizing beta and regional diversity in regions where they are present.

Additionally, while investigating litter bag methodology, I found that microclimate within different litter bag types did not appear to influence litter breakdown, but that bag design did. Microinvertebrates, known to influence decomposition, were difficult to exclude from fine-mesh bags and we found evidence that the use of difference mesh sizes may have detected a trophic effect rather than an overall effect of invertebrates on breakdown. These results are important to consider when trying to evaluate the role of invertebrates on litter decomposition, an important ecosystem process.

Finally, the effect of the invasive shrub, Chinese privet (*Ligustrum sinense*) on decomposition and litter-associated invertebrates appeared to vary depending on hydrology. When the floodplain was dry, filter paper broke down twice as fast in plots which has substantial privet invasion. However, when subjected to flood pulses, there was no effect of privet invasion on decomposition of privet, sweet gum, or mixed privet-sweet gum litter or their invertebrate inhabitants. Privet litter did, however, disappear significantly faster than sweet gum or mixed sweet gum-privet litter, yet it is uncertain how these results may have been influenced by flooding. The interplay between privet invasion and flooding on decomposition processes is important to better understand because privet is prevalent in riparian areas like floodplains where carbon cycling is an important ecosystem process.

Literature Cited:

Costanza R et al. (2014) Changes in the global value of ecosystem services. Global Environmental Change 26:152-158.

Dahl TE (2011) Status and trends of wetlands in the conterminous united states 2004 to 2009. Washington, D.C.

Zedler JB, Kercher S (2004) Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. Critical Reviews in Plant Sciences 23:431-452.

Zedler JB, Kercher S (2005) Wetland resources: Status, trends, ecosystem services, and restorability. Annual Review of Environment and Resources 30:39-74.

APPENDICES

Appendix A – Chapter 2 Appendix. Invertebrates in beaver associated ponds and wetlands in Georgia (Bush and Batzer unpublished), Pennsylvania (Wissinger and Gallagher 1999; Wissinger unpublished), and Colorado, USA (Caudill 2002; B. Peckarsky, unpublished data; S. Wissinger unpublishded data). * indicates presence of at least one species.

	SE NA Beaver Dam Wetlands			**NE NA Beaver Pond Complexes**	**Central Colorado Montane Beaver Dam Ponds and Wetlands**	
Family	**New**	**Mature**	**Abandoned**	**All Basins**	**Valley Terrace Pond Complexes**	**Stream Channel / Riparian Distributary**
Turbellaria		*		*	*	*

Gastropoda	Lymnaeidae	*	*	*	*	*	*
	Physidae	*	*	*	*	*	*
	Planorbidae	*	*	*	*	*	*
Bivalvia	Sphaeriidae	*	*	*	*	*	*
Oligochaeta		*	*	*	*	*	*
Hirudinea		*	*	*	*	*	*
Aranaea		*	*	*	*	*	*
Acari		*	*	*	*	*	*
Pseudoscorpiones		*					
Ostracoda		*	*	*	*	*	
Cladocera	Bosminidae				*	*	*
	Chydoridae				*	*	
	Daphniidae	*	*	*	*	*	
Copepoda	Calanoida					*	
	Cyclopoida	*	*	*	*	*	*
Decapoda	Cambaridae	*	*		*		
Isopoda	Asellidae	*	*		*	*	
Amphipoda	Crangonyctidae	*	*	*	*	*	*

	Dogielinotidae	*	*	*	*	*	*
Collembola	Entomobryidae	*	*	*	*		
	Hypogastruridae	*		*	*		
	Isotomidae	*	*	*			
	Poduridae			*	*	*	*
	Sminthuridae		*	*			
Ephemeroptera	Baetidae	*	*	*	*	*	
	Caenidae	*	*	*	*	*	*
	Ephemeridae		*				
	Ephemerellidae						*
	Heptageniidae						*
	Leptophlebiidae						*
	Siphlonuridae						*
Odonata	Aeshnidae	*		*	*	*	*
	Coenagrionidae	*	*	*	*	*	*
	Gomphidae	*			*	*	*
	Lestidae		*		*	*	*
	Libellulidae	*	*	*	*	*	*

Plecoptera	Chloroperlidae					*	*
	Nemouridae					*	*
	Perlidae						*
Orthoptera	Gryllidae			*			
	Tettigonidae			*			
Psocoptera				*			
Thysanoptera	Terebrantia			*			
Hemiptera	Aphidae	*	*	*			
	Belostomatidae	*	*	*	*		
	Cercopidae			*			
	Cicadellidae	*	*	*			
	Coccoidea	*	*	*			
	Corixidae	*	*	*	*	*	*
	Delphacidae	*	*	*			
	Gelastocoridae				*		
	Gerridae	*	*		*	*	*
	Hebridae		*	*	*	*	
	Hydrometridae			*	*		

	Mesoveliidae	*	*	*	*	*	
	Miridae	*		*			
	Nepidae	*	*		*		
	Reduviidae		*	*			
	Veliidae	*	*	*	*	*	
Neuroptera	Corydalidae	*	*	*	*		
	Sialidae	*			*		
Coleoptera	Anthicidae		*				
	Carabidae		*	*	*	*	
	Chrysomelidae			*	*	*	
	Coccinellidae	*		*			
	Curculionidae		*	*	*		
	Dytiscidae	*	*	*	*	*	*
	Elateridae			*			
	Elmidae	*		*			*
	Gyrinidae			*	*	*	
	Haliplidae		*	*	*	*	
	Hydraenidae			*	*		

	Hydrophilidae	*	*	*	*	*	
	Lampyridae		*	*			
	Latridiidae			*			
	Noteridae		*	*	*		
	Phalacridae			*			
	Ptilodactylidae		*	*			
	Scirtidae		*	*	*		
	Silvanidae			*			
	Staphylinidae			*	*	*	
Trichoptera	Hydroptilidae	*	*	*			
	Hydropsychidae			*			
	Leptoceridae	*			*	*	
	Limnephilidae				*	*	*
	Phryganeidae				*	*	
	Polycentropodidae	*					*
	Rhyacophilidae	*					*
Lepidoptera	Crambidae	*					
	Noctuidae	*	*	*			

	Tineidae		*				
Diptera	Ceratopogonidae	*	*	*	*	*	*
	Chaoboridae				*	*	
	Chironomidae	*	*	*	*	*	*
	Corethrellidae	*	*	*			
	Culicidae	*	*	*	*	*	*
	Dixiidae				*	*	*
	Dolicopodidae				*		
	Empididae		*		*		
	Ephydridae	*	*		*		
	Psychodidae			*	*		
	Ptychopteridae	*	*	*	*		
	Simuliidae			*			*
	Stratiomyidae	*	*	*	*	*	
	Tabanidae	*	*	*	*	*	
	Tipulidae	*	*	*	*	*	*
Hymenoptera	Formicidae		*	*			
	Chalcidoidea			*			

Mymaridae	*					
Platygastroidea	*	*	*			