HABITAT CORRELATES OF SPECIES PRESENCE AND CONSERVATION STRATEGIES: IDENTIFYING REINTRODUCTION SITES FOR THE BROOK FLOATER AND ASSESSING *CORBICULA FLUMINEA* PRESENCE IN THE UPPER SAVANNAH RIVER DRAINAGE

by

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(Under the Direction of Peter D. Hazelton)

ABSTRACT

Habitat degradation and invasive species are major threats to North American freshwater ecosystems. Many freshwater mussel (Order: Unionida) species exist in isolated populations, leaving them vulnerable to disturbances and invasive species. Using a standardized habitat survey protocol, I: 1) determined habitat similarity between sites in South Carolina and Georgia to sites containing Brook Floater (*Alasmidonta varicosa*) in other watersheds across their range, using principal component analysis to inform potential reintroduction sites; and 2) determined habitat and landscape variables linked to presence of invasive *Corbicula fluminea*. Results identified possible reintroduction sites of Brook Floater and found that landscape variables, particularly upstream reservoirs and developed land density, were associated more with *C. fluminea* site presence than site-specific habitat variables. By identifying habitat capable of supporting the reintroduction of mussel populations and identifying habitat variables that aquatic invasive species may exploit in their expansion, this work can improve decisions for freshwater mussel conservation.

INDEX WORDS: aquatic management, southeast, impoundment, dam, freshwater mussel management, upper Savannah River watershed, aquatic invasive species

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DEDICATION

I would like to dedicate this document to Taylor Miller, thank you for all your help at home, and without you I would not even be here at all. Your words of encouragement during all of the late nights have helped me reach this enormous milestone in my life. Thank you for your continued support through everything.

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CHAPTER 1

CURRENT STATUS OF FRESHWATER MUSSEL'S HABITAT AND LANDSCAPE VARIABLE PREFERENCES

Introduction to North American freshwater mussels

In North American, freshwater mussels represent species in the order Unionida. This order is distributed worldwide with the exception of Antarctica (Bogan & Roe, 2008). The family Unionidae is the most diverse and found commonly in North America, South and Central America, Europe, Asia, and Africa (Bogan, 2008). Margaritiferidae is the only other family of Unionida found in North America (Graf & Cummings, 2007). Within North America, freshwater mussels can be found in every state except Hawaii, but their diversity is greatest in the eastern half of the continental United States. The epicenter of freshwater mussel diversity is located in the southeast (Elkins *et al*. 2019); this area contains 91% of freshwater mussel species found in the country. The southeast is also a global hotspot for other freshwater species, including crayfish, fish, salamanders, turtles, and aquatic insects (Collen et al., 2014; Richman et al., 2015).

Over the past 100 years, North America has lost 30 species of mussel to extinction, and nearly 65% of the remaining taxa are vulnerable, threatened, or endangered (Haag, 2012; Williams et al., 1993). Unfortunately, the imperilment rate of freshwater species in the southeast is increasing at an alarming rate, where the number of imperiled or at-risk species of fish is increasing faster than the species can recover (Jelks et al., 2008). Freshwater mussel species in the southeast have imperilment rates higher than fish and many other taxa (Elkins et al., 2019). Into the 1900's, many of North America's streams and rivers still held healthy and dense populations of mussels. Then, in the 20th century, habitat degradation caused by humans impounding and polluting North America's aquatic ecosystems dramatically affected freshwater mussel populations, leading many to become extinct or endangered (Williams et al., 1993).

Many of the factors that negatively affect freshwater mussel populations can be attributed to a degradation of habitat (Downing et al., 2010). In the southeast, the impoundment and alteration of rivers was fueled by the need for navigation corridors. For example, the Tennessee-Tombigbee waterway was constructed to provide a water navigation corridor to remote regions of Mississippi and Alabama, which resulted in the destruction of crucial freshwater mussel habitat (Abell et al., 2000; Haag, 2012). Impoundments are cited as the primary reason why many freshwater mussel populations are fragmented (Downing et al., 2010) and accepted as the leading cause of extinction for 12 species of mussels (Haag, 2009). The widespread construction of dams has altered habitat for freshwater mussels in major ways, changes to habitats, flow and temperature fluctuations, and ecological function (Poff et al. 2007; Poole & Downing, 2004). Urban growth, deforestation, and agriculture are known to negatively affect freshwater mussel populations (Brown et al., 2010; Poole and Downing, 2004). Alterations to flow patterns often seen in urban settings caused by channelization can affect the complex life-cycle of both adults and juveniles (Gates et al., 2015).

Even after the influx of impoundments ceased and land use practices improved, delayed effects from the alteration of stream habitat still threatened many mussel populations (Haag, 2012). Isolated assemblages of mussels persist in unaltered reaches of stream habitat, but these populations and assemblages are rarely consistent with the number and diversity of their historical population (Haag, 2012). Natural population recovery of freshwater mussels is slow, mostly due to their comparatively lower dispersal rates among other aquatic fauna, and their reliance on host fish and passive dispersal makes their long-distance dispersal slow (Haag, 2012). Such isolation and slow recovery create scenarios that allow localized events such as pollution or extreme flooding to wipe out remaining individuals of a population.

Impacts from invasive species

Among the greatest threats to freshwater ecosystems is the introduction of invasive species (Sala et al., 2000). Around the world, aquatic invasive species (AIS) have been introduced either accidentally or deliberately through human activity (Strayer, 2010). AIS can completely alter ecosystems and the food webs in which they become established (Vander Zanden et al., 1999; Strayer, 2012). For instance, Zebra Mussels (*Dreissena polymorpha*) were introduced in North America in 1988 and have caused significant alterations to ecosystems. Zebra Mussels have disrupted food webs by reducing the amount of phytoplankton and zooplankton populations in water columns, altering nutrient dynamics and water clarity, resulting in increased growth of submerged plants and algae (Caraco et al., 1997). High filtration rates of Zebra Mussels have led to an increase in benthic macrophytes and periphytic algae, which caused significant decreases in dissolved oxygen levels and declines in native filter feeders (Caraco et al., 2000). Native freshwater unionids have been significantly affected by Zebra Mussels, leading to population declines as the result of competition for food and habitat (Ricciardi et al., 1998; Strayer & Malcom, 2007). Zebra Mussels also attach directly to shells of native freshwater mussels, limiting their ability to move, burrow, feed, and reproduce (Ricciardi et al., 1996; Schloesser et al., 1996; Strayer & Smith, 1996). Despite the widespread ecological impacts of Zebra Mussels, management is difficult and solutions to dealing with the invasion has not been identified (Strayer et al., 2006).

Most often, AIS are introduced by overland dispersal using a human vector, and traits like dormant eggs, or resistance to drying out are favorable traits when traveling long distances during inhospitable conditions (Hairston & Cáceres, 1996; Havel et al., 2014). Some AIS are also capable of using a more natural means of transportation by sticking to the feet or feathers of wading birds, or passing through the digestive tract of predators (Bilton et al., 2001), thus allowing further dispersal in a new ecosystem. Certain traits are going to improve an AIS' success at establishing and proliferating in a new system (Kolar & Lodge, 2001). One effective trait is the ability to reproduce asexually, allowing a single individual to successfully establish and reproduce in a novel environment. Other traits like rapid growth and reproduction rates (McMahon, 2002), greater thermal tolerances, larger native geographical ranges (Bates et al., 2013), a greater tolerance of water pollution, and generalized habitat use (Karatayev et al., 2009) all increase a species likelihood of being a successful AIS. Once an invasive species is established, it is almost impossible to eradicate from an area and best management recommendations are always to avoid colonization in the first place (Pimentel et al., 2005).

"Invasibilty" of communities and landscapes

I consider the "invasibility" of an aquatic community to be its vulnerability to, or lack of resilience to, an invasive species becoming established when an exposure occurs. The invasibility of a community changes depending on their biotic and abiotic conditions that are naturally exhibited. The competition exhibited between species is correlated with preventing invasibility, creating an inverse relationship between the species richness of a community and the invasibility. This phenomenon was first described by Elton (1958) and is known as the biotic resistance hypothesis. This hypothesis was further elaborated by MacArthur (1965) who described species packing as the self-organization between species to maximize non-overlapping niche space. Species themselves are limiting the occupiable space of other species, and by having more narrow niches more species are able to exist in a community and prevent other species from invading. These interactions are influenced by the amount of resources available in the community; an abundance of resources increases competition and increases the diversity of species that can exist in an ecosystem (Macarthur, 1965).

Land alteration is the second greatest threat to freshwater communities behind invasive species (Sala et al., 2000), but land use change and invasive species often cooccur. Alterations in watershed land use can physically affect freshwater ecosystems by increasing sedimentation, altering hydrologic patterns, and polluting waterways (Allan, 2004). These changes often disrupt critical habitats, such as riparian zones, and negatively affect both the physical environment and biological communities, leading to reduced biodiversity among fish and macroinvertebrates (King et al., 2011; Kovalenko et al., 2014). Degraded habitats often become more susceptible to invasion by non-native species, which can further alter community structure and ecosystem function (Hobbs & Huenneke, 1992; Didham et al., 2005). For example, urban land use has also been found to be correlated with invasive species abundance, most likely because of significant alterations to the stream communities (Riley et al., 2005). And the degradation of both physical and chemical habitat parameters has been correlated with invasive macroinvertebrate presence (Früh et al., 2012). It is not always evident whether degraded habitat is more invadable because of reduced biodiversity, or because the invasive species has greater tolerance to those conditions

(Hobbs & Huenneke, 1992; Didham et al., 2005). But invasive species and reduced native diversity are often both associated with altered habitat.

Reservoirs and impoundments are estimated to affect over 60% of the world's freshwater rivers (Rosenberg et al., 2000). Reservoirs and impoundments provide favorable habitat for invasive species that can tolerate degraded conditions (Früh et al., 2012), and act as steppingstones for invasive species to spread (Havel, 2005a; Havel, 2005b) By degrading the dynamic habitat that native species rely on (Agostinho et al., 2004), newly formed reservoirs creates early successional and species poor systems, making them more susceptible to invasions than natural systems (Johnson et al., 2008). Results from a study evaluating reservoirs in the Mediterranean region supported claims that richness of invasive fish was inversely correlated with the richness of native fish. And that invasive fish species richness was correlated with the size of a reservoir and the human pressures the reservoir receives (Clavero et al., 2013).

Corbicula fluminea background

The basket clam, *Corbicula fluminea* (Müller, 1774) is a freshwater bivalve native to Southeast Asia, but because of its invasive success, has an almost worldwide distribution (Crespo et al., 2015). First accounts of this species, outside of its native range, come from Vancouver Island in Canada in the 1920's. Today, the species is found in almost every major watershed in North America (USGS, 2024). *C. fluminea* represents a typical r-strategist species; its lifespan is relatively short at around 5 years maximum but is capable of producing 75,000 offspring during its lifetime. Outside of *C. fluminea's* native range, the species grows larger at a maximum of 50mm (Sousa et al., 2006) and is capable of both sexual and asexual reproduction (Hedtke et al., 2008), with three or more reproductive events annually (Mouthon, 2001)

The larval veliger stage of *C. fluminea* is released from the siphons of adults at around 250µm and can disperse long distances in the water column (Graf & Cummings, 2007). Once the veliger reaches 500µm, it will anchor to a substrate via a single mucous byssal thread. The ideal habitat for *C. fluminea* is sandy substrates in rivers with moderate flows (Graf & Cummings, 2007; Schmidlin & Baur, 2007), but the species can occupy many habitats. They have been found in substrate compositions ranging from bedrock to silt (Hakenkamp et al., 2001; Sousa et al., 2006; Vaughn & Spooner, 2006), in varying flow conditions in rivers, streams, and lakes (Graf & Cummings, 2007), and a full range of suspended solids conditions (Aldridge et al., 1987). The distribution of *C. fluminea* in invaded regions is often positively correlated to human activity. In one study *C. fluminea* were positively correlated to the percentage of agriculture land use within a watershed (Ferreira-Rodríguez et al., 2022). In another study, it was hypothesized that the amount of recreational pressure on reservoirs in Texas was the reason for the disproportional presence of *C. fluminea* in large reservoirs rather than small ones (Karatayev et al., 2005). Around the world, this small invasive clam has become a widespread problem due to the ecological damage it causes (Sousa et al., 2014).

C. fluminea have the potential to seriously alter the biotic and abiotic conditions of ecosystems due to high densities and abundances, the deposition of shell, bioturbation and filtering activity markedly (Sousa et al., 2009). In high densities, massive die-offs can cause elevated ammonia concentrations in the water from soft tissue deterioration of dead *C. fluminea*, creating toxic conditions for other aquatic species (Ilarri et al., 2011). These conditions affect adult freshwater mussels and may affect juvenile and glochidia mussels to higher degree because of increased sensitive to ammonia toxicity produced during mass die-offs of *C. fluminea* (Cherry et al., 2005). During changes in water chemistry or disease outbreak, elevated ammonia levels from *C. fluminea* die-offs are more prevalent and cause a greater impact to freshwater mussels during low-flow and high temperature events (Vaughn & Hakenkamp, 2001).

C. fluminea and freshwater mussels have overlapping diets, they filter feed a mix of phytoplankton, zooplankton, bacteria, fine particles, and organic detritus (Vaughn & Hakenkamp, 2001; Vaughn et al., 2008). During times of low food availability, species of freshwater mussel with thinner trophic niches may be at risk of competition with *C. fluminea* for food (Modesto et al., 2021). This is because *C. fluminea* can consume a wide spectrum of food in the water column, often greater than freshwater mussels who may specialize on a very specific food type in an ecosystem (Atkinson et al., 2010; Chiarello et al., 2022; Modesto et al., 2021). In addition to filter feeding, *C. fluminea* can pedal feed from the substrate (Modesto et al., 2021). The competition for food resources favors *C. fluminea*, who in high enough densities and when in degraded habitat conditions have the potential to cause considerable growth reduction in native freshwater mussels (Haag et al., 2021). *C. fluminea* also compete with native mussels for space, and may displace the native mussels from more favorable habitat (Hakenkamp et al., 2001).

Challenges to native mussel conservation

Native freshwater mussels are negatively affected by alterations to the landscape including the change in land use and the creation of reservoirs. In many ecosystems, invasive species now compete with native freshwater mussels for resources, further endangering existing populations already under threat. Such conditions may create isolated populations of mussels persisting in remaining unaltered reaches of stream habitat rarely consistent with the abundance and richness of their historical assemblages. Fragmentation and isolation leaves mussels vulnerable to stochastic events such as floods, droughts, or disease (Haag, 2012). Because native freshwater mussel colonization is slow, isolated populations remain at risk for longer periods, even after the surrounding habitat has improved. Adult freshwater mussels exhibit very minimal movement and are almost entirely reliant on host fish for dispersal (Haag, 2012). Techniques such as reintroductions are valuable and useful tools to prevent extinctions, extirpations, and future listings when the natural colonization of a species is unlikely to occur in a timely manner (Mcmurray & Roe, 2019).

Some species of freshwater mussels have a broad range of suitable habitat conditions, while some species are more specialized in habitat use. In North Carolina, different species of freshwater mussels were associated with varying physical habitat (Pandolfo et al., 2016). The federally listed *Alasmidonta heterodon* was found in a very narrow range of physical habitat conditions, while the highly distributed common *Elliptio complanata* occupied a broader niche breadth. Evidence also suggested a non-random habitat use for an additional eight species in the study (Pandolfo et al., 2016). When working with a rare mussel species low numbers of occurrences are often problematic for identifying species-habitat relationships (Box et al., 2002). With more habitat observations for a given species, researchers and managers would have been able to improve inferences related to habitat needs. Such information can be useful in cases of site determination for reintroductions of an imperiled species (Fisk et al., 2014), and has been used previously to relocate freshwater mussels whose sites were being threatened by channel alterations (Johnson & Brown, 2000). An understanding of what high-quality habitat is for a species is crucial to conserve freshwater mussels through reintroductions (IUCN, 2013).

Brook Floater

The Brook Floater (Alasmidonta varicosa) is a medium sized (<100 mm) species of freshwater mussel with a patchy distribution along the Atlantic slope from New Brunswick, Canada to Georgia, U.S.A. Of the 16 states in which this species historically occurred, they have been presumably extirpated from two (Rhode Island and Delaware), and are listed as vulnerable throughout their range (NatureServe, 2024). In 2010, the species was petitioned for listing as endangered or threatened, with a final decision not to list under the Endangered Species Act (USFWS, 2018). Brook Floater have been weakly associated with macrohabitats consisting of small, upland streams with medium (0.25-1 mm) sandy substrates (Strayer & Ralley, 1993), though typically not in headwater or higher gradient streams that may be prone to scouring (Nedeau, 2008). In a report from Nova Scotia, a study attempted to classify the habitat of Brook Floater, they found that the species prefers substrate composed of cobble or small boulder with sand filling the gaps between (Marshall & Pulsifer, 2010). In the same study, researchers also concluded that the land use adjacent to Brook Floater occupied sites were a mix of protected forests to heavy agriculture. In Massachusetts (USA), Brook Floater were often found alongside other species (Skorupa et al., 2024). Of the five co-occurring species found alongside Brook Floater, evidence suggested that Brook Floater abundances were greater at the center of rivers when compared to the edges, in areas where substrate is mixed with sand between cobble, and in mesohabitats of dammed pools, runs, and scour pools (Skorupa et al., 2024).

The Brook Floater Working Group was formed to increase cooperative conservation efforts and reduce further population losses of Brook Floater across its range. The group consists of thirty-nine representatives from three federal and fourteen state agencies and four academic institutions in the United States, as well as Canadian federal and provincial partners. Member specialties range from mussel ecology, conservation planning and management, population genetics, survey methods, propagation, and decision making. The group and their partners developed the Brook Floater Rapid Assessment Protocol to assess the status of Brook Floater throughout its range (Sterrett et al., 2018). For years, the group has been assessing the status of Brook Floater and other native freshwater mussels with this protocol, which collects habitat data related to substrate composition, mesohabitat characteristics, flow characteristics, and other site level characteristics as well as freshwater mussel occurrence data. Collectively the group has data sites from Brook Floater occupied watersheds across five states.

At the southern extent of its range, Brook Floater inhabit the Chattooga River between the border of South Carolina and northeast Georgia (Krause et al., 2020). This river is valued as an important ecosystem for conservation and supports a well-documented population of Brook Floater. The current status of the freshwater mussel populations is unknown in the watersheds surrounding the Chattooga River. This portion of the upper Savannah River drainage is home to five of the largest reservoirs in South Carolina, including Lake Hartwell (227 km^2) and Lake Keowee (75 km^2) (Wachob et al., 2009). Historic observations from South Carolina Department of Natural Resources (SCDNR) show two records of Brook Floater captured in tributaries surrounding the Keowee Reservoir during the 1950s. These collections were recorded before the formation of the Keowee Reservoir and the other large reservoirs in the area.

Research needs and objectives

Identification of habitat correlates associated with species presence and abundance are critical for the management of both invasive and imperiled species. Further, the identification of suitable habitat for both imperiled and invasive species may be complicated when the species is not locally abundant or is found within a patchy distribution; a condition that may exist during the initial spread of an invasive species or after local declines of a native species. Determining efficient detection techniques for AIS like *C. fluminea*, will yield a more cost-effective solution to their prevention than removal or sustained management (Coughlan et al., 2020). However, monitoring aquatic environments to prevent the spread of invasive species often lags behind establishment of new populations (Beric & MacIsaac, 2015). Understanding the habitat and landscape variables that promote *C. fluminea* dispersal may allow more effective preventative measures through prioritization of habitat type for monitoring and rapid response.

As native species decline it can become increasingly difficult to identify habitat needs for potential reintroduction and population restoration. In 2016, the Freshwater Mollusk Conservation Society revised a national strategy toward the conservation and restoration of freshwater mussel biodiversity in the United States (FMCS, 2016). Emphasis was placed on restoring mussel communities to self-sustaining levels and included reintroduction of species at the watershed level as an important component to the plan. Within the historic range of a species, if the goal is to establish new populations, then the best course of action is to reintroduce the species at the best available sites (Mcmurray & Roe, 2019). Reintroduction of freshwater mussels can be an important tool in restoration of mussel diversity under the assumption of some risk. To be most effective, this strategy requires a full evaluation of a species before implementation, such as the extent of the current wild populations, historical distribution, and that the newly proposed habitat is suitable for long-term success (Haag & Williams, 2014). Wild populations of Brook Floater and their preferred habitat have been studied across the species range by researchers and the Brook Floater Working Group (Strayer & Ralley, 1993; Pandolfo et al., 2016; Skorupa et al., 2024).

The first objective of my research (Chapter 2) is to identify potential Brook Floater reintroduction sites in the upper Savannah River basin in South Carolina based on multivariate habitat analysis informed by sites with known Brook Floater presence. The second objective of my research (Chapter 3) is to quantify how habitat and landscape variables of forested, agricultural, and developed watersheds relate to the presence of *C. fluminea* in the upper Savannah River drainage in South Carolina and Georgia, USA. This may expand our knowledge of how AIS move across a landscape and the locations most likely to be invaded. Data and analysis from this research could aid in the recovery of Brook Floater, as well as relate habitat and landscape characteristics to *C. fluminea*.

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CHAPTER 2

USING MULTIVARIATE HABITAT ASSOCIATIONS TO IDENTIFY REINTRODUCTION SITES FOR AN IMPERILED FRESHWATER MUSSEL, THE BROOK FLOATER (*ALASMIDONTA VARICOSA)*

Introduction

Freshwater mussels are integral to freshwater ecosystem function, their burrowing, shell deposition, and feeding provide structural habitat, aid in nutrient mixing and coupling, and stabilize the benthos (Vaughn et al., 2008). In some cases, freshwater mussels compose more than half of the benthic biomass in a river (Strayer et al., 1994), and play a critical role in the aquatic food web by linking the pelagic and benthic communities through filtration and excretion (Vaughn & Hakenkamp, 2001). North America is home to the highest diversity of freshwater mussels, boasting nearly 300 species. Unfortunately, over the past 100 years North America has lost 30 species of mussels as the result of extinctions, and nearly 65% of the remaining taxa are vulnerable, threatened, or endangered (Haag, 2012). Many factors negatively affect freshwater mussel populations, but most can be attributed to habitat degradation (Downing et al., 2010). Siltation in southern Sweden, caused by excessive agriculture and poor land use practices has been shown to affect the recruitment of *Margaritifera margaritifera* by reducing the survival of early life stages (Österling et al., 2010). Mussel populations in southeastern Oklahoma, already affected by urban development and reservoirs, are even more at-risk during droughts that occur more frequently (Vaughn et al., 2015). In the Clinch River watershed in Virginia and Tennessee, mussel species abundance and richness are declining, in part due to legacy mining contaminants from a tributary river in the system (Cope et al., 2021), and elsewhere because of newly discovered pathogens (Richard et al. 2020). And sometimes, even in relatively pristine systems, mussel population declines are occurring without any clear cause (Hornbach et al., 2018; and Haag 2019).

In 1998, a document was published that outlined the most important issues surrounding the conservation and restoration of freshwater mussels (NNMCC, 1998). The document has been revised and updated by the Freshwater Mollusk Conservation Society to reflect the same issues but in a more recent context (FMCS, 2016). In the latest version, emphasis is placed on restoring mussel communities to self-sustaining levels. For instance, the reintroduction of species at the watershed level is a potential strategy. Reintroductions can aid in the conservation of freshwater mussel species, but success is correlated with suitability of habitat within the historic range of a species (Mcmurray & Roe, 2019). The reintroduction of freshwater mussels can be an important tool in the conservation of freshwater mussels with relatively low risk. This strategy should only be implemented after information on the species has been fully evaluated, such as the extent of the current wild populations, historically where the species was found, and that the habitat is suitable for long-term success (Haag & Williams, 2014). Finding suitable habitat for a single mussel species can be difficult; however, some species are associated with specific ranges of depth, velocity, substrate, vegetation, canopy, and mesohabitat type (Skorupa et al., 2024; Strayer, 1993).

The Brook Floater (*Alasmidonta variacosa*) is a freshwater mussel native to much of the Atlantic slope (Williams *et al.* 1993). The species has been presumably extirpated from many watersheds throughout their range from New Brunswick, Canada to Georgia, USA (NatureServe, 2024). Across its range, the species is listed as vulnerable and, in 2010 was petitioned for listing as endangered under the United States Endangered Species Act, resulting in a decision not to list (USFWS, 2018). Brook Floater are considered habitat specialists among freshwater mussels and occur in streams and rivers of varying sizes with stable substrate usually occurring in forested watersheds with intact riparian zones (Nedeau, 2008). They are often associated with habitats containing larger substrate (i.e., cobble or boulders), interstitial sand, and avoid shallow riffles, deep pools, and areas of higher velocity or scouring (Strayer & Ralley, 1993; Skorupa et al., 2024). The Brook Floater Working Group, consisting of partners who specialize in mussel ecology, conservation, survey methods, propagation, and decision making, has designed and implemented a standard survey protocol, the Brook Floater Rapid Assessment Protocol, in many watersheds across the Atlantic Slope (Sterrett et al., 2018). This protocol was designed to assess the status of Brook Floater in current or previously occupied watersheds, while also collecting data on mussel communities and physical habitat characteristics at the site level.

The Chattooga River, in the upper reaches of the Savannah River watershed, along the border of South Carolina and Georgia holds a robust population of Brook Floater near the southern extent of the species' range (Krause et al., 2020). The Chattooga River drains approximately 730km^2, with 493km^2 being under federal management in national forests. This population of Brook Floater represents an outlier among the watersheds occupied by the species because the river is large and prone to high flows, not typical of the species' preferred habitat (Nedeau, 2008). This area of South Carolina is home to five of the largest reservoirs in the state, dating back to the 1950's (Wachob et al., 2009). Since the construction of the reservoirs, little effort has been given to survey this area of the upper Savannah River drainage outside of the Chattooga River, leaving gaps of data in the mussel communities, including Brook Floater, in the watershed. Currently there are no other known populations of Brook Floater in the upper Savanah River watershed outside of the Chattooga River. But because of the large amount of forested land protection in some basins, the watersheds adjacent to the Chattooga River may provide an option for strategic reintroduction.

In this study, I evaluated habitat suitability for reintroduction of Brook Floater across five HUC 10 watersheds in the upper Savannah River basin in South Carolina and Georgia. I used a multivariate approach (principal component analysis, PCA) to compare habitat condition in novel sites with those sites occupied by Brook Floater in four other watersheds throughout the species range. Watersheds within South Carolina and Georgia (hereinafter referred to as "target watersheds") were then prioritized for inclusion as potential reintroduction sites based on mean similarity to occupied Brook Floater sites. Target watersheds were ranked in priority for potential reintroduction based on (1) mean Euclidean distance of sites to the multivariate centroid of Brook Floater occupied sites, (2) the number of surveyed sites with distances lower than the median distance of all target watershed sites to the centroid of Brook Floater sites in multivariate space, and (3) the percent forested landscape for each target watershed as a proxy for habitat condition and protection. We propose this analysis as a case study of how multivariate datasets can be used to identify potential sites or watersheds for reintroduction of imperiled species.

Methods

Study Area

Target watersheds included five HUC10 watersheds in the upper Savannah River watershed: the Chattooga River, Chauga River, Little River, Lower Tugaloo River, and Coneross Creek. The Chattooga River HUC10 supports a strong population of Brook Floater in certain stretches (Krause et al., 2020). Historical observations of Brook Floater pre-date the impoundments of Lake Jocassee and Lake Keowee reservoirs (SCDNR unpublished data), of which the Little River, Lower Tugaloo, and Coneross Creek watersheds are tributaries. Information on the habitat characteristics of sites with Brook Floater comes from four occupied HUC10 watersheds from three states: the Farmington River and Ware River in Massachusetts, the Neversink River in New York, and the John's River in North Carolina (Figure 2.1). Information and locations of watersheds can be found in Table 2.1 and Figure 2.2 below.

Site Selection

Site selection processes vary depending on watershed, but in general the approach involves random selection of stream-road crossing or other locations of surveyor access to streams within the watershed of interest. In the five HUC10 target watersheds, sites were randomly chosen based on the methods of the Brook Floater Rapid Assessment Protocol (Sterrett et al., 2018). In each HUC10 watershed, 40 bridge crossings were randomly chosen in the entire watershed. Those 40 bridge crossings were randomly separated into 20 priority sites and 20 replacement sites. Sites were chosen using ArcGIS Pro version 3.0.3 (ESRI, Redlands, California). To find bridge crossings, ESRI's "Transportation" layer and the United States Geological Survey's (USGS) National Hydrography Dataset were intersected to create points at all possible bridge crossings within a HUC10 watershed. Sites were first checked for suitability, sites were considered suitable if they met the following criteria: < 1m in depth and ≥ 3m in width, legally and safely accessible from the bridge, and safe to traverse. If there were more than 10 suitable sites in the priority list, 10 would be randomly chosen for sampling. If there was less than 10 suitable sites in the priority list, then the remaining sites would be randomly chosen from the replacement list. To avoid habitat bias associated with bridge crossings, surveys were initiated at a random distance between 100-200 meters upstream of the bridge crossing.

Habitat Survey

The site level habitat survey performed in each watershed (John's: Sep-Oct 2017, Farmington: June-Aug 2017-18, Ware: July-Sep 2017-18, Neversink: June-Aug 2019, Aug 2020, Chattooga: May-Sep 2023, Chauga: May-Sep 2023, Lower Tugaloo: May- Sep 2023, Little: May-Sep 2023, Coneross: May-Sep 2023) followed the methodology of Sterrett et al. (2018), which is designed to apply a rapid approach to collecting site habitat variables. The survey required at least 3 observers who each maintained a longitudinal transect (lane) in which they searched for native mussels. Surveys were standardized for a total of 2-person hours and observers were trained to search at a rate of 10 m^2 per minute. The width of each observer's lane was determined by dividing stream width by the number of observers. An observer's lane width was a minimum of 1 meter and no more than 3 meters. If the width of the steam was too wide and the calculated observer's lane width was greater than 3 meters, more observers could have been used for the survey, or the surveyors could implement a bank survey. In this survey method, observers kept lane widths of 3 meters but lane one stayed anchored to a randomly chosen bank (left or right). Observers were confined to the search area in their lanes with a similar search rate of 10 m^2 per minute.

Data gathered for selected variables in the habitat survey also followed the protocol outlined in Sterrett et al. (2018). Site depth (cm) was measured using a meter stick at five locations within each lane: at the top (upstream) of the reach, at the bottom (downstream) of the reach, and three more at 25%, 50%, and 75% of the survey reach distance. The maximum and minimum depth were the deepest and shallowest measurements in any lane throughout a lane's reach. Substrate was measured by assessing the bed texture at five equidistant locations within each observer's lane. Observers classified substrate into size classes designated by the National Rivers and Streams Assessment (USEPA, 2013) (Table 2.2). The vegetation at a site was classified into either emergent, submergent, or algae categories. For each lane, a categorical percentage of the lane occupied by each vegetation type was provided (1 = 0%, 2 = 1-5%, 3 = 5-15%, 4 = 15-25%, 5 = >25%). Stream width (m) was the wetted width distance (meters) at the top, bottom and 50% of the reach. A modified spherical densiometer was used to count the amount of canopy cover of a site. Canopy cover was taken at the middle of the reach along both banks. This measurement was taken in four directions at each bank: upstream, downstream, towards river-right, and towards river-left. Mesohabitat description was the visually estimated proportion of riffle, run, and pool habitat the entire reach occupies. Large wood was the total number of large wood pieces in a lane's reach. Each observer counted the number of large wood pieces (>10 cm in diameter and 1.5 m long) in their lane. If it was in the form of snags, jams, or root wads, that singular clump could be counted as one large wood. Velocity code is a categorical measurement given by the surveyor of each lane representing a visual assessment of the general velocity for their respective lane, using descriptors from the EPA National Rivers and Streams Assessment Field Manual for Benthic Macroinvertebrate sampling (USEPA, 2013) (Table 2.3).

Data Analysis

Habitat variables were removed from the analysis if the respective variable occurred at less than 10% of all sites. The following substrate characteristics had occurrences too low to be included: smooth bedrock, rough bedrock, concrete, organic material, and hardpan. Substrate measurements were modified to represent the proportion of the site represented by each substrate size class. This was done by taking the number of occurrences per site for a single substrate size class divided by the total number of substrate measurements (i.e., # of lanes * 5 measurements). To represent depth for the entire site, mean depth was calculated across the five measurements of depth from each lane. Width was represented in a similar style, averaging the three width measurements at a site.

Vegetation classes (i.e., % submerged, emergent or algae) were modified to accommodate the variability of measurements between surveyors in different watersheds who may have been using different versions of the protocol's datasheet. Because there were multiple surveyors measuring data in different watersheds, some categorical bounds did not follow the default bounds set by current version of the protocol (i.e., 25-50%, 50-75%, etc.). To remedy this, each lane's measurement for each categorical vegetation type was represented by a singular percentage as the calculated median (e.g., 25-50% = 37.5%) of that class range across sites. This lane's vegetation measurement was then averaged across all lanes for each of the three vegetation classes for each site. The variable for canopy cover was reduced by averaging the measurements of canopy from eight measurements at a site. Large wood was reduced by combining the number of large wood from all lanes for each site. And velocity code was reduced by averaging the measurement of velocity for all lanes at a site. These methods reduced the number of measured predictor variables to 20 for each site.

To prepare data for my analysis and reduce the skewness of my predictors, proportional data (% of sand at a site) was either logit- or arcsine- transformed when the distribution of observations did not resemble a normal distribution. All other data was either log or square root transformed. After the data was transformed, the prepared data was standardized using the scale() function in R studio (Team, 2024). Data was scaled using this function by subtracting the mean of each variable and dividing by the standard deviation.

I used a principal component analysis (PCA) based on correlation matrices to examine patterns of habitat between watersheds containing Brook Floater. To do this, I compiled data from four watersheds containing Brook Floater (John’s River, Ware River, Farmington River, Neversink River), performed a PCA, and chose principal components based on the amount of variance they explained. To determine the habitat similarities between watersheds containing Brook Floater, I measured the Euclidean distance along three principal components of each site containing Brook Floater to its own watershed’s centroid, and the centroid of Brook Floater sites. I considered a site to be more similar to the habitat found in its’ own watershed if the distance to its own watershed’s centroid was lower than that of the distance to the Brook Floater centroid.

To determine which target watershed sites were most similar to sites occupied by Brook Floater, I compiled a data set of sites including South Carolina and Georgia and only those sites with Brook Floater presence in other watersheds. I performed a PCA and chose to investigate the top three principal components based on the amount of variance they explained. To determine similarity, I measured the Euclidean distance between each target watershed site and the centroid of sites with Brook Floater presence. For each watershed, I calculated the mean Euclidean distance to the Brook Floater centroid, the number of sites with a distance shorter than the median Euclidean distance, and the % forested land use. I then ranked the five watersheds from 1-5 for each of these categories where 1 was the best. Ranks were summed and a composite rank was created on the rank sums to infer watersheds that were most suitable for potential reintroduction.

Results

Watershed characteristics

Sites were sampled across five different months in multiple years (John's: Sep-Oct 2017, Farmington: June-Aug 2017-18, Ware: July-Sep 2017-18, Neversink: June-Aug 2019, Aug 2020, Chattooga: May-Sep 2023, Chauga: May-Sep 2023, Lower Tugaloo: May- Sep 2023, Little: May-Sep 2023, Coneross: May-Sep 2023). Brook Floater were found at 18 of 191 sites surveyed across ninewatersheds and five states. In South Carolina and Georgia, Brook Floater were not present at any of the randomly sampled 50 sites (Table 2.1).). Watersheds where Brook Floater were present had a minimum forested land cover percentage of 83% in the Ware River HUC 10. Only two watersheds in South Carolina had a forested land cover percentage above 68%, the Chattooga (90%) and the Chauga (86%). The Little, Lower Tugaloo, and Coneross Creek HUC 10's in South Carolina had the highest percentage of agriculture and urban land cover. The greatest proportion of sites surveyed where Brook Floater were present occurred in the John's River watershed with 30% (6/20) of sites containing Brook Floater observations.

PCA1: Differences in Brook Floater Habitat among Watersheds

PCA1 was performed on sites from watersheds containing Brook Floater (John's, Ware, Farmington, Neversink), using 20 site habitat variables. Six principal components (PCs) with eigenvalues > 1 accounted for 66 % of the total variance. The first three PCs were selected for further analysis because they captured the most variance in the data (44.57%%). A scree plot depicting the amount of variance explained by each PC, shows diminishing returns of variance explained after the third PC (Figure 2.3).

PC1 explained 19.82% of the variation in the data and represented a gradient from streams with larger size class substrate with high flows (negative) to streams that are slower moving with finer substrates (positive). PC2 (14.92 % variance explained) represented a gradient of streams that have narrow and shallow sections (negative) to streams with more riffle habitat and deep pools, large wood, and the presence of large boulders (positive). PC3 (9.83% variance explained) captured a gradient of streams with larger amounts of algae over finer substrate habitat in runs (positive) to the sites with silty depositional pools (negative) (Figure 2.4 and Table 2.4).

Minimal separation was observed between Brook Floater site habitat and their respective watersheds (Figure 2.5 & 2.6). Euclidian distances in multivariate habitat space along all three PCs were calculated between each Brook Floater occupied site and the centroid of the corresponding watershed, and between the site and the centroid for all Brook Floater sites. The median distance of Brook Floater sites to the centroid of their own respective watershed was 2.34 (0.9-5.4), while the median distance of Brook Floater sites to the centroid of all Brook Floater sites was 2.65 (0.63-4.85) (Figure 2.7). In three of the four watersheds, the median distance of Brook Floater sites to the Brook Floater centroid was lower than the median distance of Brook Floater sites to the centroid of their own respective watershed (1.32 to 2.03 in the Ware, 2.32 to 4.14 in the Farmington, 3.07 to 3.32 in the Neversink); however in Brook Floater occupied sites in the John's River watershed (n=6), the median distance value to the Brook Floater centroid was higher than the median distance of Brook Floater sites to the centroid of their own respective watershed (1.76 to 1.62) (Figure 2.8). Out of the seven Brook Floater sites in the Neversink watershed, five sites were closer in Euclidean distance to the Neversink watershed centroid and only two were closer in Euclidean distance to the Brook Floater centroid. Out of the six Brook

Floater sites in the John's River watershed, four sites were closer in Euclidean distance to the John's watershed centroid and only two were closer in Euclidean distance to the Brook Floater centroid. In the Farmington (n=4) and Ware (n=1), all sites were closer in Euclidean distance to the Brook Floater centroid than to their respective watershed's centroid (Table 2.5).

PCA2: Similarity of South Carolina sites to Brook Floater sites

PCA2 was performed on 50 sites from South Carolina and Georgia, and 18 sites where Brook Floater were present in four other watershed (Farmington, Ware, Neversink, John's). Using the same 20 habitat variables from PCA1, six principal components were extracted with eigenvalues > 1, accounting for 69% of the variance. The first 3 PCs were selected because they captured the most variance in the data at 50.28% (Figure 2.9). This selection was supported by eigenvalues > 1 for all 3 PCs and a scree plot showing diminishing returns past the third PC (Figure 8) (Table 2.6).

PC1 (24.18%) showed a gradient between habitats containing emergent and submergent vegetation with larger substrate and higher velocities versus habitats with slower moving and deep water covered in finer sandy substrates. PC2 (15.01%) covered the variation between deep-wide depositional pools with heavy riparian covers and swift moving run dominated sites. PC3 (11.09%) contrasted riffle-dominant sites with shallow run sites (Figure 2.10A & 2.10B).

Greater separation was observed between target sites and Brook Floater occupied sites in PCA2 than was seen between watersheds in PCA1 (Figure 2.11A & 2.11B), but multiple sites from target watersheds were within the 90% confidence ellipses of Brook Floater sites. Mean Euclidean distance along PC1, PC2, and PC3 between target sites and the centroid for Brook

Floater habitat was 4.36 (std. dev. = 1.09, and median distance was 4.62. The 18 sites that Brook Floater occupied had an average distance of 2.58 (± 1.39 std. dev.) to the centroid of Brook Floater habitat. Sites from the Chattooga watershed were most similar to those of Brook Floater (mean distance = 3.44 ± 1.35 std. dev.), and seven of the ten sites in this watershed had Euclidean distances below the median distance from the Brook Floater centroid (Table 2.7). The Chattooga watershed also ranked as the best site in the % forested landscape, resulting in the best composite rank priority for reintroduction consideration (Table 2.8). The Chauga watershed ranked second in the composite ranking system and second across all three ranking criteria. The Chauga watershed had a mean Euclidean distance of 4.31 (std. dev. = 1.04), five sites in the lowest 50^{th} percentile of distances, and 86% forested land use. The remaining three watersheds varied in ranks across the three criteria (Table 2.8).

Discussion

I used a non-parametric ordination technique (PCA) to compare multivariate habitat parameters of sites occupied and unoccupied by Brook Floater (*Alasmidonta varicosa*). My ojectives were to: (1) evaluate similarity in habitat use across watersheds, and (2) to inform decisions on potential reintroduction through habitat similarity. In my first analysis I compared habitat similarity across four basins containing Brook Floater occurrences (Neversink, Ware, Farmington and John's). Sites containing Brook Floater (n = 18) were equally similar to occupied sites from other watersheds as they were to unoccupied sites from within the same basin (Figure 2.7. Given considerable overlap among watersheds along PC1, PC2, and PC3 (Figure 2.5A & 2.6A), there were not marked differences in habitats surveyed in each of the four watersheds, nor were habitat parameters markedly different between occupied and unoccupied sites (Figure 2.5B & 2.6B).

In my second analysis PCA2, I conducted principal component analysis on a dataset that combined habitat variables from occupied Brook Floater sites from the four original watersheds and sites from our targeted watersheds. This resulted in better separation than PCA1 between occupied and unoccupied sites (Figure 2.11A and 2.11B). Specifically, along PC1 Brook Floater sites were associated with greater stream width, larger substrate sizes, and higher mean velocities, whereas sites from target watersheds were associated with finer substrates, large wood, and pool habitats (Figure 2.10A and 2.10B). Nevertheless, multiple target sites fell within the 90% confidence ellipses around the centroid of Brook Floater habitat, and two target sites had Euclidean distances less than the mean distance of occupied Brook Floater sites to the centroid of all Brook Floater occupied sites, suggesting some sites from the target watersheds were more similar in habitat than the average Brook Floater occupied site.

When ranking target watersheds by mean distance and frequency of top sites, the Chattooga River watershed was the best performing watershed across all three ranking criteria. This is of particular significance as the Chattooga River mainstem has an extant and robust population of Brook Floater (Krause et al., 2020), whereas the other four watersheds have no currently known occurrences. Even though we did not record any Brook Floater occurrences during our surveys, the closer proximity in habitat space of Chattooga River sites to occupied sites from outside of the Savannah supports the utility of this multivariate approach.

Measuring site habitat to inform management decisions related to reintroduction or stocking has previously been successful for freshwater mussels. In the River Irt in the UK, researchers found success when they measured physical stream habitat like substrate class sizes, flow velocity, and vegetation, to make decisions on the best sites to release juvenile Freshwater Pearl Mussel (*Margaritifera margaritifera*) (Lavictoire & West, 2024). The analysis used in the present study only incorporated physical habitat metrics to prioritize watersheds for potential reintroduction. This is because the Brook Floater Rapid Assessment Protocol (Sterrett et al., 2018) was designed to assess the status of Brook Floater; however, it may be a useful screening tool in identifying habitat similarities among sites with and without Brook Floater. Other studies using habitat parameters to predict mussel habitat include land use (Pandolfo et al., 2016; Shea et al., 2013), host fish presence (Schwalb et al., 2013) and other mussels' presence (Ruellan et al., 2023).

In addition to habitat suitability of individual sites, managers might also consider the number of suitable sites in a watershed and the distance between those sites. Connectivity of suitable habitat is often overlooked in freshwater mussel conservation (Newton et al., 2008), but could minimize the risk of stochastic events to small populations. In this study, the Chauga watershed in South Carolina was ranked 2nd in terms of total habitat distance from Brook Floater habitat, had the 2nd greatest number of sites lower than the median distance value (Table 2.8), and the 2nd highest % forest among the watersheds evaluated. The Chauga watershed is similar to the Chattooga watershed as both are located in the foothills of the Blueridge Region, contain a large amount of forested land cover, and contain sites most similar to that of Brook Floater elsewhere in their range.

Managers must take many considerations into account prior to embarking on population restoration of freshwater mussels. First, understanding why a freshwater mussel population experienced a decline is a crucial step before reintroductions begin (Mcmurray & Roe, 2019; Strayer et al., 2019). When the cause of mussel extirpation is unknown, managers and researchers should gain as much information about the species as possible, like important life history characteristics, population genetics, and host fish use. Successful reintroduction requires combining additional information of a species with their in-stream physical habitat requirements. Others have further expanded on considerations and needs for successful reintroductions of freshwater mussel populations beyond the scope of this study, including: brood stock collection and genetic management (Neves 2004; Jones et al., 2006; George et al., 2009; Patterson et al., 2018; McMurray & Roe, 2019; Roy et al. 2022); water use and property ownership at introduction sites (Skorupa et al. 2023); the presence of stable mussel communities (McMurray & Roe, 2019); and monitoring of introduced populations (FMCS 2016; McMurray & Roe, 2019; Strayer et al. 2019). The data and analysis presented in this study is one approach for evaluating similarity in multivariate habitat space of occupied and unoccupied mussel sites, and may be useful as part of a well-crafted conservation and reintroduction plan.

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Tables and Figures

Table 2.1. Information on watersheds used in analysis. Using USGS's National Land Cover Database, land cover for forest (deciduous forest/evergreen forest/mixed forest/shrub/scrub/grassland/herbaceous/woody wetlands/emergent herbaceous wetlands), urban (developed open space/developed low intensity/developed medium intensity/developed high intensity/barren land), and agriculture (pasture/hay/cultivated crops) could be calculated.

HUC 10	State	%forest/ urban/ agriculture/ open water	Area(km^2)	Number of sites	Number of sites w/ Brook Floater
Chattooga River	SC/GA	90/7/2/1	722	10	0
Chauga River	SC	86/6/6/1	286	10	0
Little River	SC	68/14/9/9	424	10	0
Lower Tugaloo	SC	47/13/31/9	727	10	0
Coneross Creek	SC	53/20/24/3	722	10	0
Farmington River	MA	88/6/1/5	387	31	4
Ware River	MA	83/9/6/2	564	21	1
Neversink River	NY	87/8/3/2	716	69	7
John's River	NC	93/3/3/1	542	20	6

Table 2.2. Abbreviation and size class of US EPA National Wadeable Stream Assessment (2013-2014) habitat survey form (USEPA, 2013)

Abbreviation	Size class
RS	Bedrock (smooth) – larger than a car
RR	Bedrock (rough) – larger than a car
RC	Concrete/Asphalt
XB	Large boulder (1000-4000mm) – meterstick to car
SB	Small boulder (250-1000mm) -basketball to meter stick
CB	Cobble (64-250mm) -tennis ball to basketball
GC	Coarse grave (16-64mm) -marble to tennis ball
GF	Fine gravel (2-16mm) -ladybug to marble
SA	Sand (0.06-2mm) -gritty -up to ladybug size
FN	Silt / clay / muck -not gritty
HP	Hardpan -firm, consolidated fine substrate
OT	Other
OR	Organic

Table 2.3. EPA National rivers and Stream Assessment stream velocity descriptions (USEPA, 2013).

1: Still water; low velocity; smooth, glassy surface; usually deep compared to other parts of the channel

2: Water moving slowly, with smooth, unbroken surface; low turbulence

3: Water moving, with small ripples, waves, and eddies; waves not breaking, and surface tension is not broken; “babbling” or “gurgling” sound.

Table 2.4. Principal component loadings from PCA1. Loadings indicate the direction and strength an original variable has on each principal component. Analysis was performed on sites from watersheds containing Brook Floater (John's, Ware, Farmington, Neversink), using 20 site habitat variables and 141 sites. Correlations greater than 0.40 and less than -0.40 are bolded.

	PC1(19.82%)	PC2(14.92%)	PC3(9.83%)
Riffle	**-0.6336183**	**0.4381380**	0.1803324
Run	0.3401405	**-0.6042504**	**0.4762799**
Pool	0.2331027	0.3483043	**-0.6578581**
Small Boulder	**-0.7320557**	0.1489701	-0.0931811
Cobble	-0.3257330	-0.3979218	-0.3655408
Course Gravel	**0.5412197**	-0.3480491	0.3335994
Fine Gravel	**0.5132921**	0.1474436	**0.4879116**
Sand	**0.5635412**	0.1737966	0.1742144
Submergent Vegetation	-0.1259349	0.3497655	0.1890500
Algae	-0.0763870	0.2152161	**0.4003601**
Large Boulder	**-0.4381413**	**0.4013089**	0.0140635
Emergent Vegetation	0.1089880	0.3529429	-0.0286388
Silt	**0.4027344**	0.2152912	**-0.5295890**
Large wood	0.2579206	**0.6339547**	-0.0984709
Average Depth	**0.6017387**	0.2644492	-0.0630477
Minimum Depth	**0.5181220**	-0.2883685	-0.2816433
Cover	0.1438881	-0.2874449	-0.0866140
Width	-0.0933222	**-0.7131725**	-0.3026812
Max Depth	**0.4701097**	**0.5485819**	0.1125682
Velocity	**-0.7356630**	-0.0692783	0.2627942

Table 2.5. Expanded table showing the sites where Brook Floater were present and the Euclidean distance to their respective watershed's centroid and the Euclidean distance to Brook Floater centroid. Distance was calculated using PC1, PC2, and PC3.

Watershed	Site ID	Distance to watershed's centroid	Distance to BF centroid	Closer to
Neversink, NY	NY_Neversink_9-2019-06-27	2.4372369	3.3192859	Watershed
Neversink, NY	NY_Neversink_6-2019-06-26	2.0436641	3.0702209	Watershed
Neversink, NY	NY_Neversink_4-2019-08-14	3.3201038	4.0379951	Watershed
Neversink, NY	NY_Neversink_22-2020-07-22	3.9192458	3.0233567	BF
Neversink, NY	NY_Neversink_19-2020-07-21	3.5408726	2.9392943	BF
Neversink, NY	NY_Neversink_13-2019-08-15	4.306706	4.8512475	Watershed
Neversink, NY	Ny_Neversink_10-2019-06-27	2.2458422	2.6265133	Watershed
Ware, MA	MA_WareRiver_45-2017-08-14	2.0338475	1.3234458	BF
Farmington, MA	MA_Farmington_69-2018-08-08	3.2553788	0.7616821	BF
Farmington, MA	MA_Farmington_4-2017-07-12	3.1276935	1.4271069	BF
Farmington, MA	MA_Farmington_20-2017-07-12	5.0373256	3.223025	BF
Farmington, MA	MA_Farmington_10-2017-08-09	5.398964	4.0454131	BF
John's, NC	171017.2wtr-2017-10-17	1.3419115	1.6699231	Watershed
John's, NC	171005.4wtr-2017-10-05	0.9019374	0.6288277	BF
John's, NC	170927.2wtr-2017-09-27	1.7146164	1.0894818	BF
John's, NC	170927.1wtr-2017-09-27	1.6832068	1.965052	Watershed
John's, NC	170926.3wtr-2017-09-26	1.9944247	2.6782433	Watershed
John's, NC	170926.1wtr-2017-09-26	1.5767912	1.856478	Watershed

Table 2.6. Principal component loadings from PCA2. Analysis was performed on 50 sites from South Carolina, and 18 sites from four watersheds where Brook Floater were present (John's, Ware, Farmington, Neversink). Correlations greater than 0.40 and less than -0.40 are bolded.

	PC1(24.18%)	PC2(15.01%)	PC3(11.09%)
Riffle	0.1967394	-0.1941062	**0.7858605**
Run	0.1249783	**-0.4578847**	**-0.7597373**
Pool	**-0.4281923**	**0.6308566**	0.2302276
Small Boulder	**0.7063896**	0.1285161	0.0778372
Cobble	0.3485215	0.0276611	0.2268412
Course Gravel	**-0.7162475**	-0.2524335	-0.3480257
Fine Gravel	**-0.6198304**	0.3754844	-0.0153433
Sand	-0.3706789	-0.0716856	0.2240720
Submergent Vegetation	**0.4605938**	0.2061247	-0.0912716
Algae	0.2128154	0.0217066	-0.2336958
Large Boulder	**0.6096543**	-0.0569775	0.3853826
Emergent Vegetation	**0.6390185**	0.1859401	0.1272690
Silt	0.1960446	**0.4551303**	0.3023610
Large wood	**0.4162541**	-0.0160396	0.0839868
Average Depth	**-0.6933253**	0.1544912	0.1265320
Minimum Depth	**0.7022981**	0.3286693	**-0.4464092**
Cover	0.1745104	**0.8374972**	-0.2677701
Width	**0.4672137**	**0.5397497**	-0.3516367
Max Depth	-0.3283941	**0.7314216**	0.0407242
Velocity	**0.6030770**	**-0.4270760**	0.0597731

Table 2.7. Euclidean distance from 50 sites in Carolina to the centroid of Brook Floater habitat. Principal components were calculated using 68 sites, 50 sites from South Carolina, and 18 sites containing Brook Floater from 4 HUC10 watersheds (Neversink, Ware, Farmington, John's). Distance was calculated using PC1, PC2, and PC3.

Site	Distance
ChattoogaR15-2023-09-15	1.0935
ChaugaG14-2023-07-11	2.5495
ChattoogaG12-2023-07-12	2.6587
ChattoogaR16-2023-07-27	2.6925
ChattoogaR13-2023-07-13	2.8031
ChaugaG7-2023-06-27	2.9892
TugalooR4-2023-06-06	3.0604
ChattoogaG19-2023-08-18	3.1644
ChattoogaG8-2023-07-13	3.2044
ChattoogaG7-2023-07-13	3.2408
ConerossG18-2023-06-29	3.2418
ChaugaR2-2023-06-28	3.5463
TugalooR11-2023-07-07	3.4762
TugalooG13-2023-05-24	3.5388
ConerossG6-2023-05-30	3.5431
TugalooG16-2023-06-06	3.5463
ChaugaG13-2023-07-11	3.9775
LittleR7-2023-07-05	4.0302
ConerossG7-2023-05-31	4.2128
LittleG7-2023-06-07	4.2988
LittleG13-2023-06-26	4.3806
LittleG19-2023-06-07	4.3838
ChaugaR7-2023-06-28	4.4696
ConerossG20-2023-06-29	4.5347
LittleG20-2023-08-18	4.5989
ChaugaG6-2023-06-27	4.6452
ConerossG5-2023-09-15	4.6734
ConerossG10-2023-06-29	4.7253
ConerossG8-2023-05-31	4.8147
ConerossG14-2023-05-30	4.8177
ChattoogaG10-2023-07-12	4.9153
TugalooG4-2023-05-23	4.943
ChaugaG9-2023-05-25	5.1184
ChaugaG18-2023-07-07	5.1216
LittleG4-2023-07-11	5.1253

Table 2.7. Euclidean distance from 50 sites in Carolina to the centroid of Brook Floater habitat. Principal components were calculated using 68 sites, 50 sites from South Carolina, and 18 sites containing Brook Floater from 4 HUC10 watersheds (Neversink, Ware, Farmington, John's). Distance was calculated using PC1, PC2, and PC3.

Site	Distance
ChattoogaG16-2023-08-18	5.1284
ConerossG9-2023-05-25	5.2855
TugalooG20-2023-05-23	5.3408
TugalooG2-2023-05-24	5.3566
ChaugaG10-2023-06-28	5.357
TugalooG18-2023-05-23	5.3775
LittleG9-2023-07-05	5.4422
LittleG16-2023-06-26	5.4644
ChattoogaG17-2023-07-27	5.4828
ChaugaG3-2023-06-27	5.491
ConerossG19-2023-05-30	5.5273
LittleG11-2023-06-20	5.5848
LittleG12-2023-06-07	5.7434
TugalooG12-2023-05-24	5.8099
TugalooG15-2023-06-06	5.9152

Table 2.8. Rank analysis of South Carolina and Georgia HUC10 watersheds for reintroduction priority. Composite rank is ranked best-worst (1-5) based on unweighted summed rank of mean Euclidean distance to Brook Floater habitat centroid, rank of number of sites in watershed in the top 50th percentile distance to Brook Floater centroid, and % forested landscape in watershed.

	Euclidean Distance to Brook Floater Centroid		Number of sites in top 50th percentile		% Forested Landscape			
Watershed	Mean (st. dev.)	Rank	No. Sites	Rank	% Forested	Rank	Summed Rank	Composite Rank
Chattooga	3.44 (1.35)	1	7	1	90%	1	3	1
Chauga	4.31 (1.04)	2	5	2	86%	2	6	2
Coneross	4.54 (0.71)	3	4	4	53%	4	11	4
Little	4.91 (0.63)	5	5	2	68%	3	10	3
Tugaloo	4.64 (1.10)	4	4	4	47%	5	13	5

Figure 2.1. HUC 10 watersheds containing sites with known Brook Floater occurrence (Ware, Farmington, Neversink, John's) and target watersheds in the upper Savannah River watershed (Chattooga, Chauga, Little, Tugaloo, Coneross). These watersheds were surveyed using the Brook Floater Rapid Assessment Protocol.

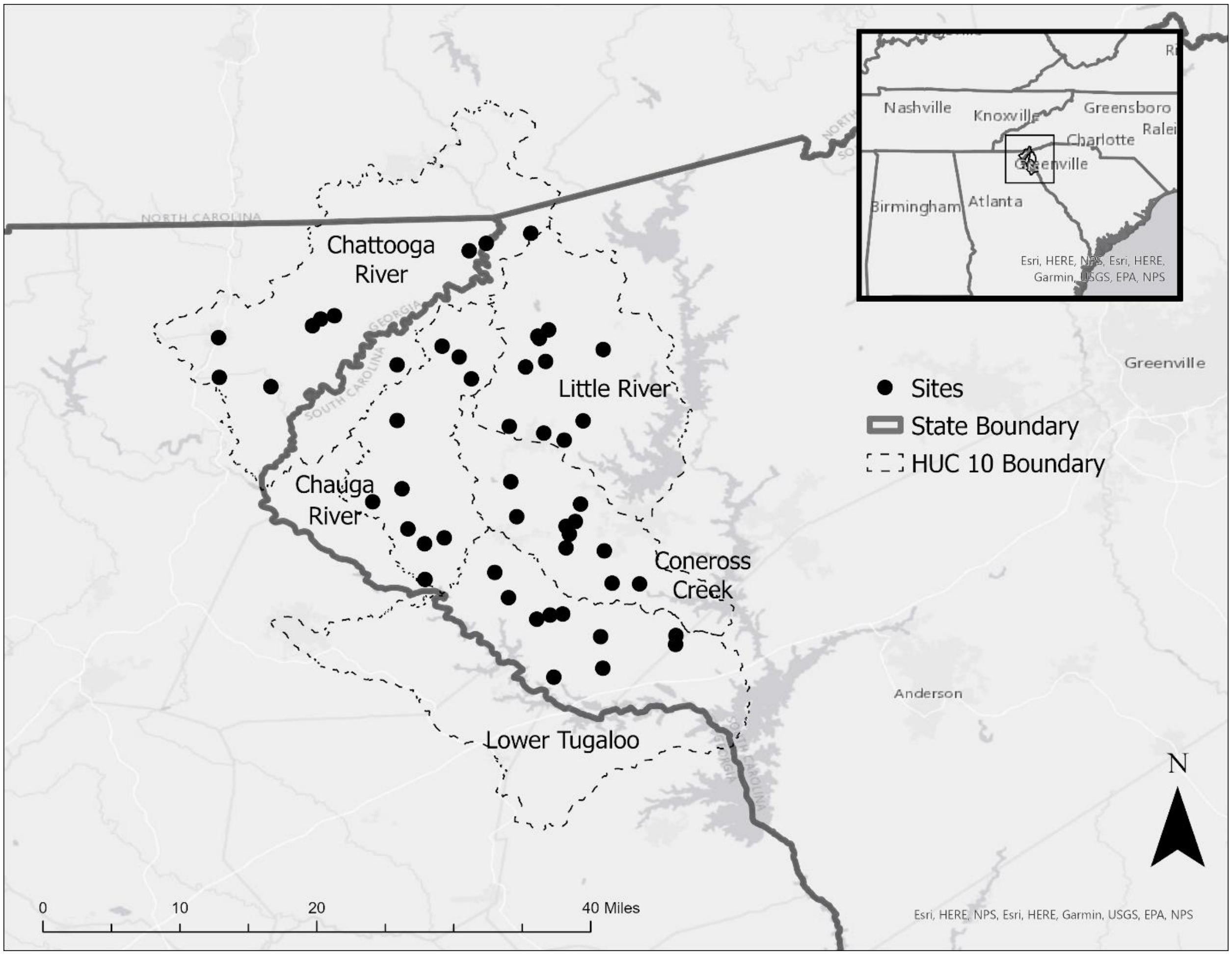

Figure 2.2. Five HUC 10 watersheds in the upper Savannah River Drainage surveyed May – September of 2023 using the Brook Floater Rapid Assessment Protocol. Brook Floater were not present at any of the 50 sites surveyed.

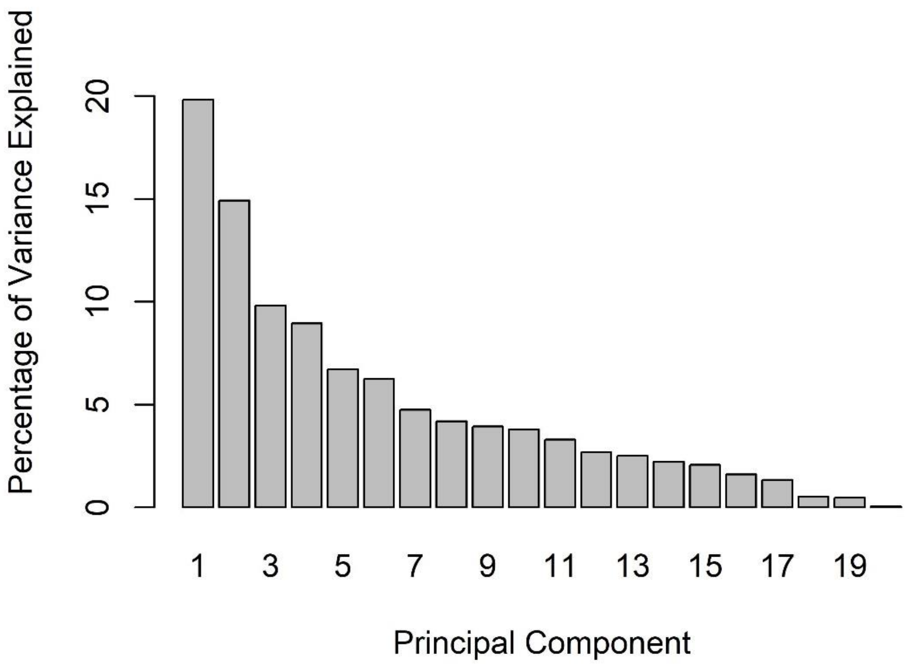

Figure 2.3. Scree plot of 20 principal components describing the variance explained of 141 sites between 4 HUC10 watersheds (Neversink, Ware, Farmington, John's) in PCA1.

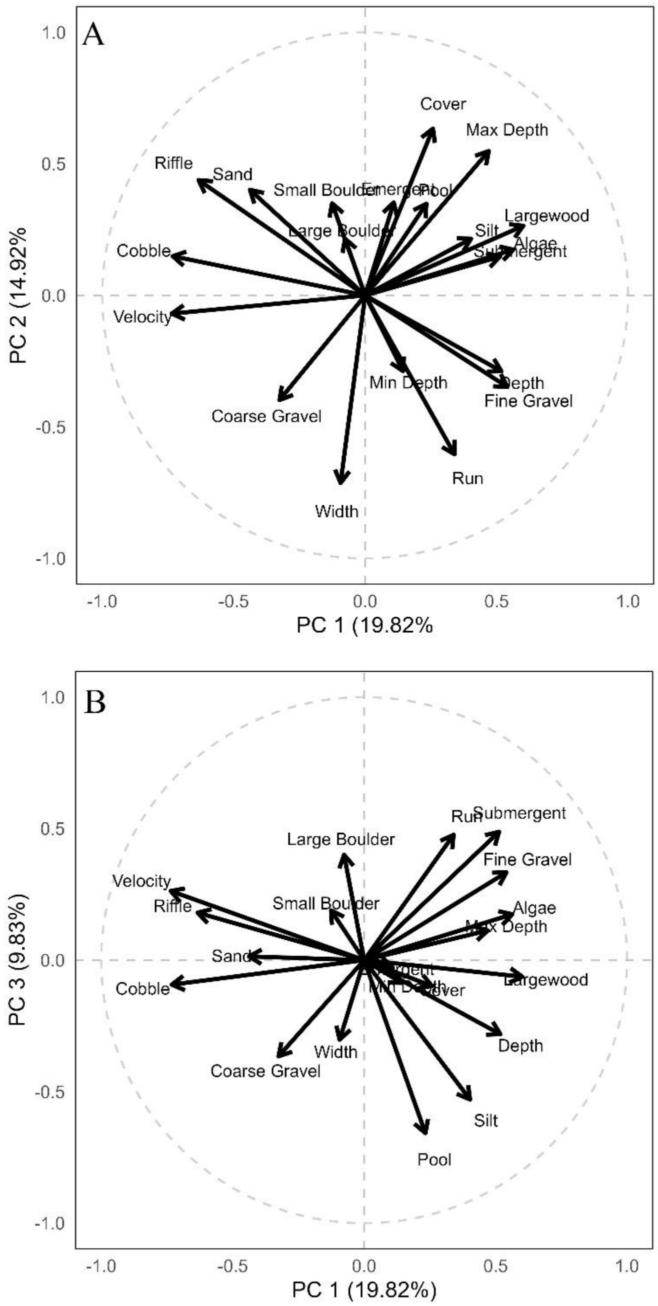

Figure 2.4. PCA1 was performed on 141 sites from four HUC10 watersheds (John's, Ware, Farmington, Neversink). PC1 versus PC2 (A) and PC1 versus PC3 (B) show the strength (arrow distance) and effect (positive or negative) an original habitat variable has on a principal component.

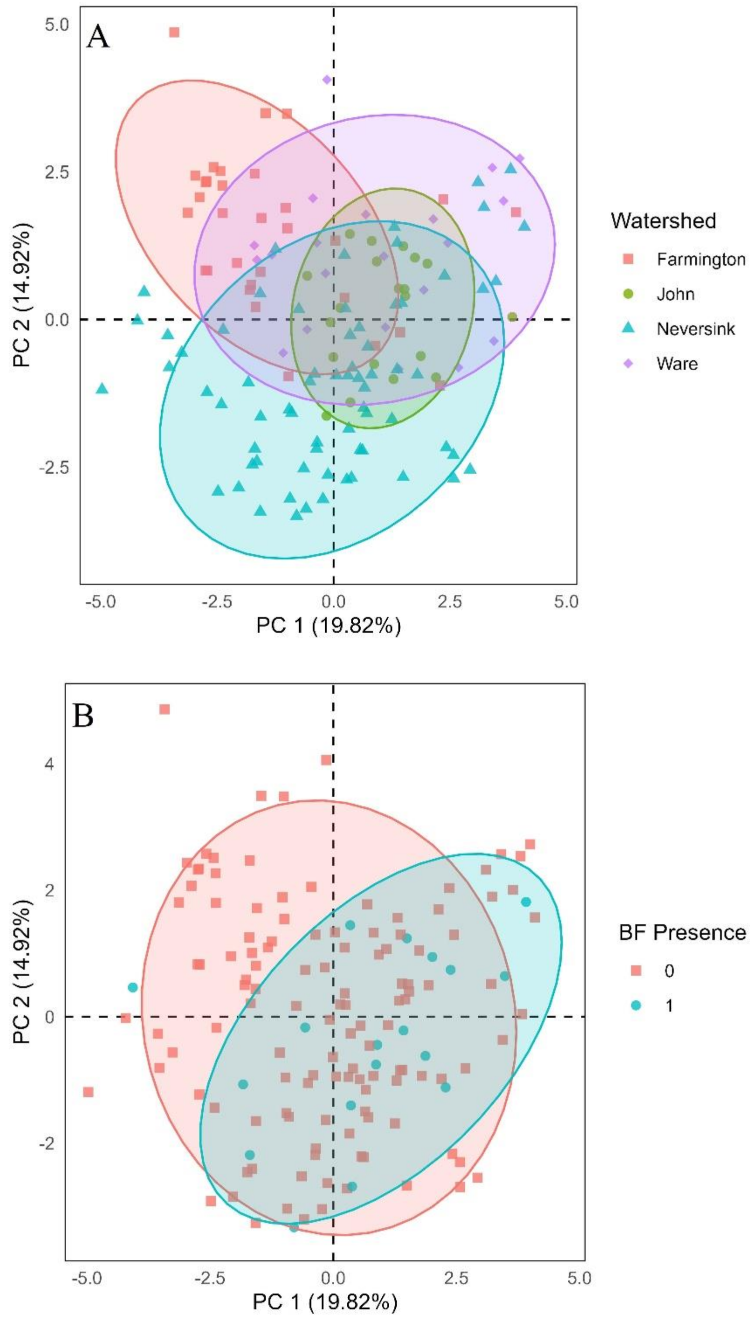

Figure 2.5. Principal component analysis 1 (PCA1) showing different groupings of 141 sites from four HUC10 watersheds (John's, Ware, Farmington, Neversink) using PC1 and PC2. **(A)** Plot of principal components showing site habitat differences between 4 watersheds that contain Brook Floater. The ellipses represent 90% confidence intervals for each watershed. This plot demonstrates the distribution of site habitat within each watershed. **(B)** Plots of principal components showing the same PCA. Ellipses represent 90% confidence intervals around Brook Floater site presence. These plots demonstrate the distribution of site habitat within sites containing Brook Floater.

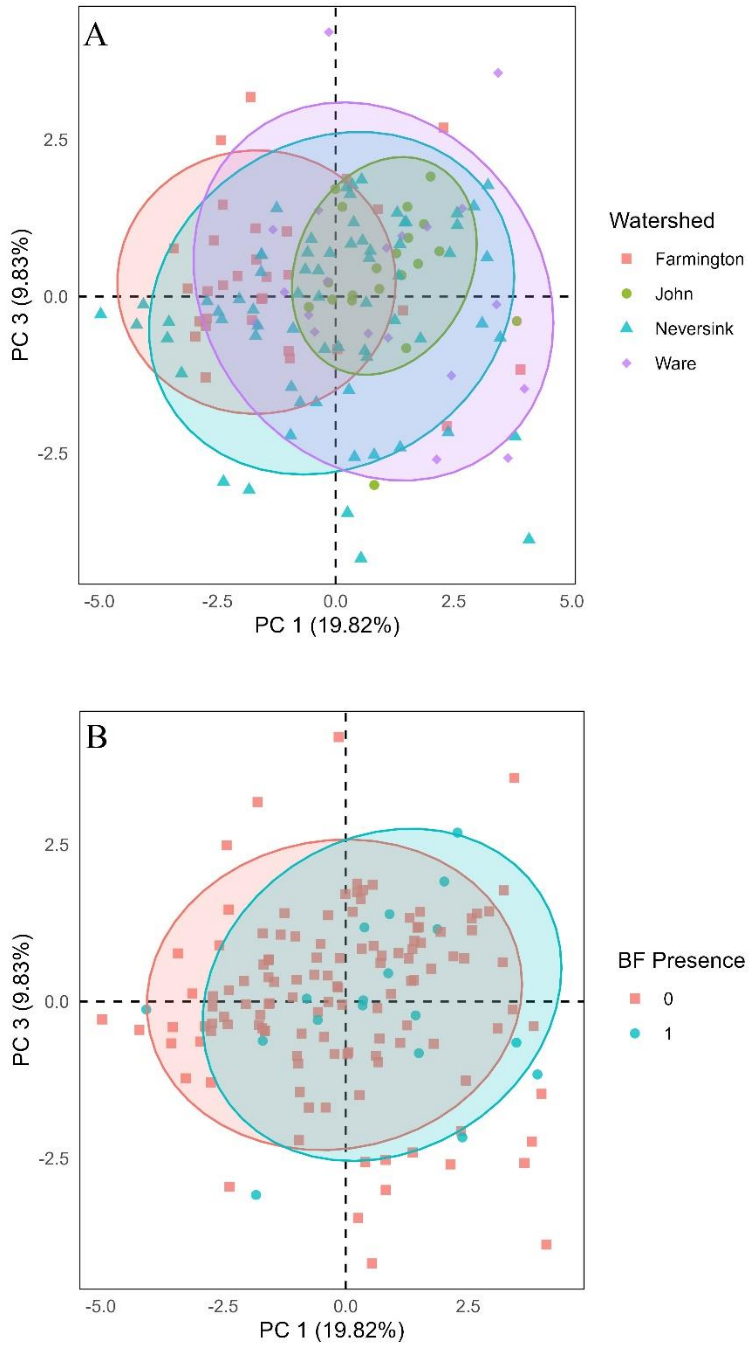

Figure 2.6. Principal component analysis 1 (PCA1) showing different groupings of 141 sites from four HUC10 watersheds (John's, Ware, Farmington, Neversink) using PC1 and PC3. **(A)** Plot of principal components showing site habitat differences between 4 watersheds that contain Brook Floater. The ellipses represent 90% confidence intervals for each watershed. This plot demonstrates the distribution of site habitat within each watershed. **(B)** Plots of principal components showing the same PCA. Ellipses represent 90% confidence intervals around Brook Floater site presence. These plots demonstrate the distribution of site habitat within sites containing Brook Floater.

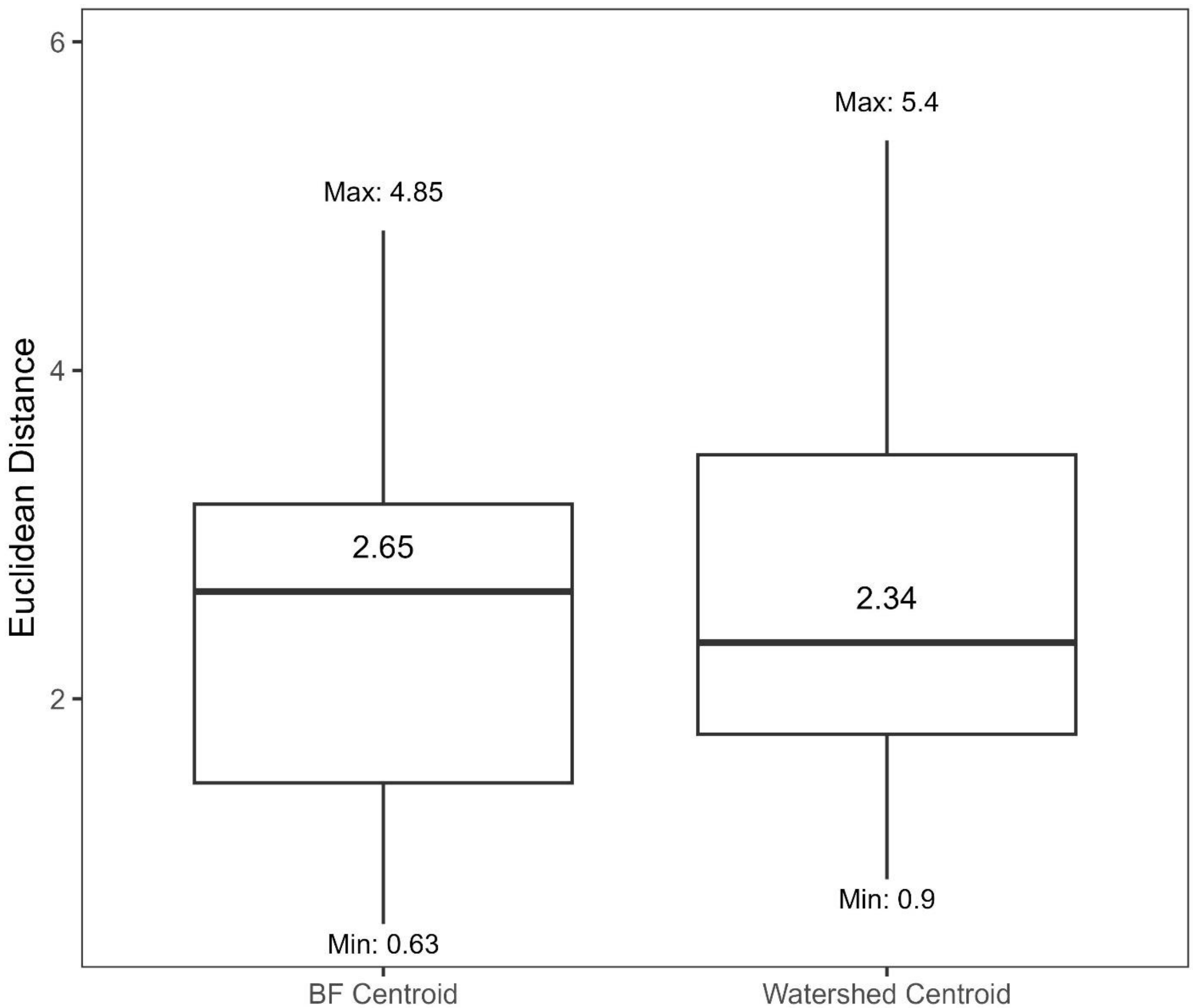

Figure 2.7. Box and whisker plot of the Euclidean distance measurements of 18 sites from 4 watersheds (John's, Ware, Farmington, Neversink). Each site had a distance measured to the centroid of sites with Brook Floater and to the centroid of each site's respective watershed. Tails of the box represent the range of data within 1.5 times the IQR from the quartiles. Distances were calculated using PC1, PC2, and PC3 from PCA1.

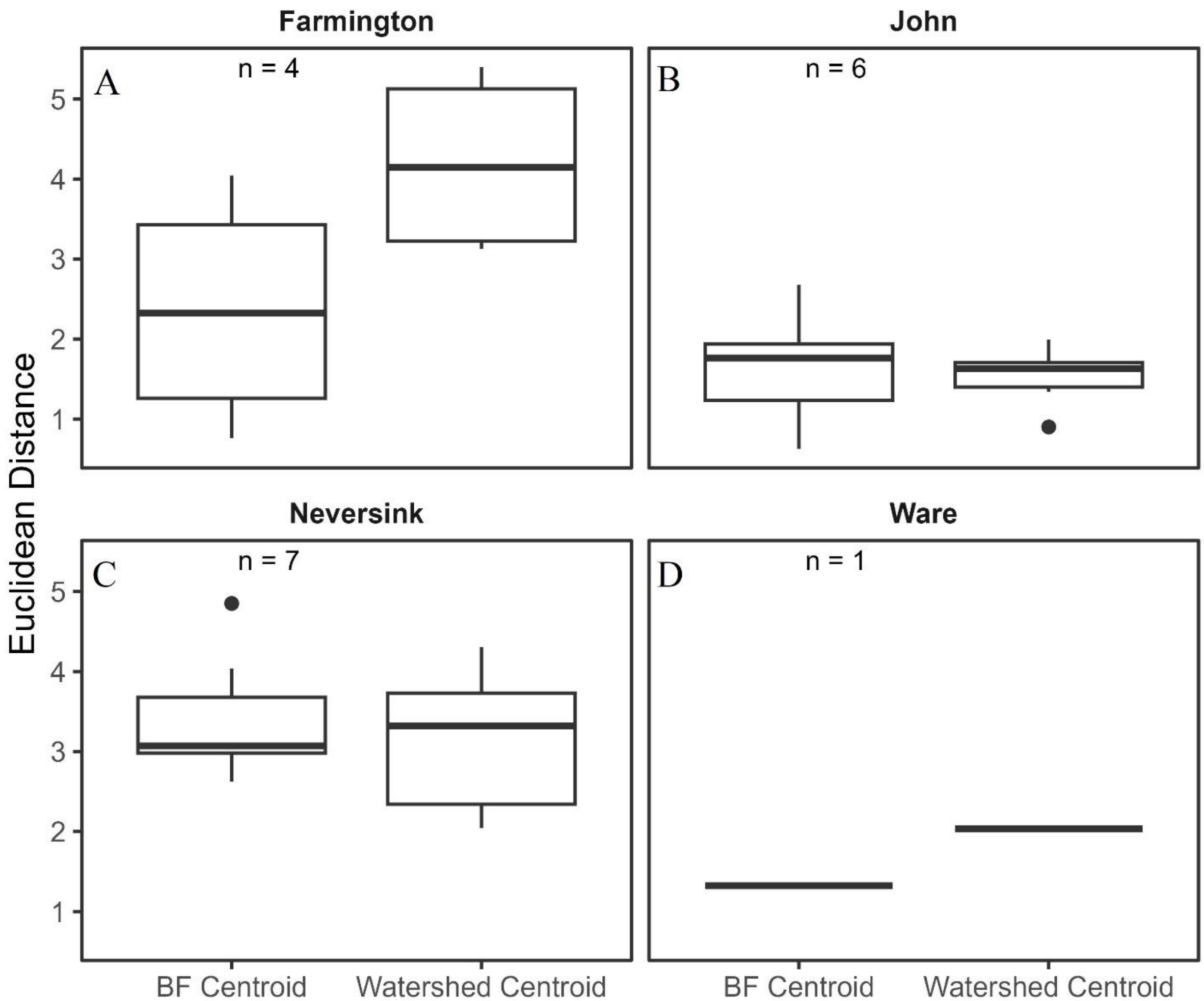

Figure 2.8. Box and whisker plots of the Euclidean distance of 18 sites from 4 watersheds (Farmington (A), John (B), Neversink (C), Ware (D)). In this analysis, the 18 sites are separated into their respective watershed to visualize the distance between their respective watershed centroids and then to the Brook Floater centroid. On each plot, n = number of Brook Floater occupied sites in that watershed. Tails of the box represent the range of data within 1.5 times the IQR from the quartiles. Distances were calculated using PC1, PC2, and PC3 from PCA1.

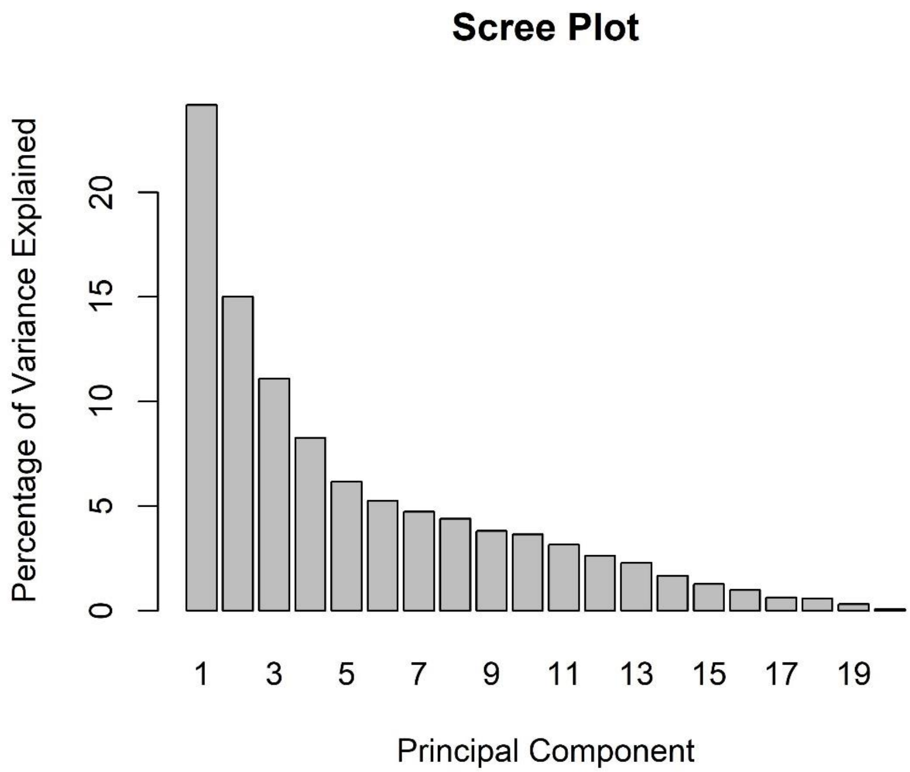

Figure 2.9. Scree plot of 20 principal components describing the variance explained of 68 sites between South Carolina and sites where Brook Floater were present from 4 HUC10 watersheds (Neversink, Ware, Farmington, John's) in PCA2.

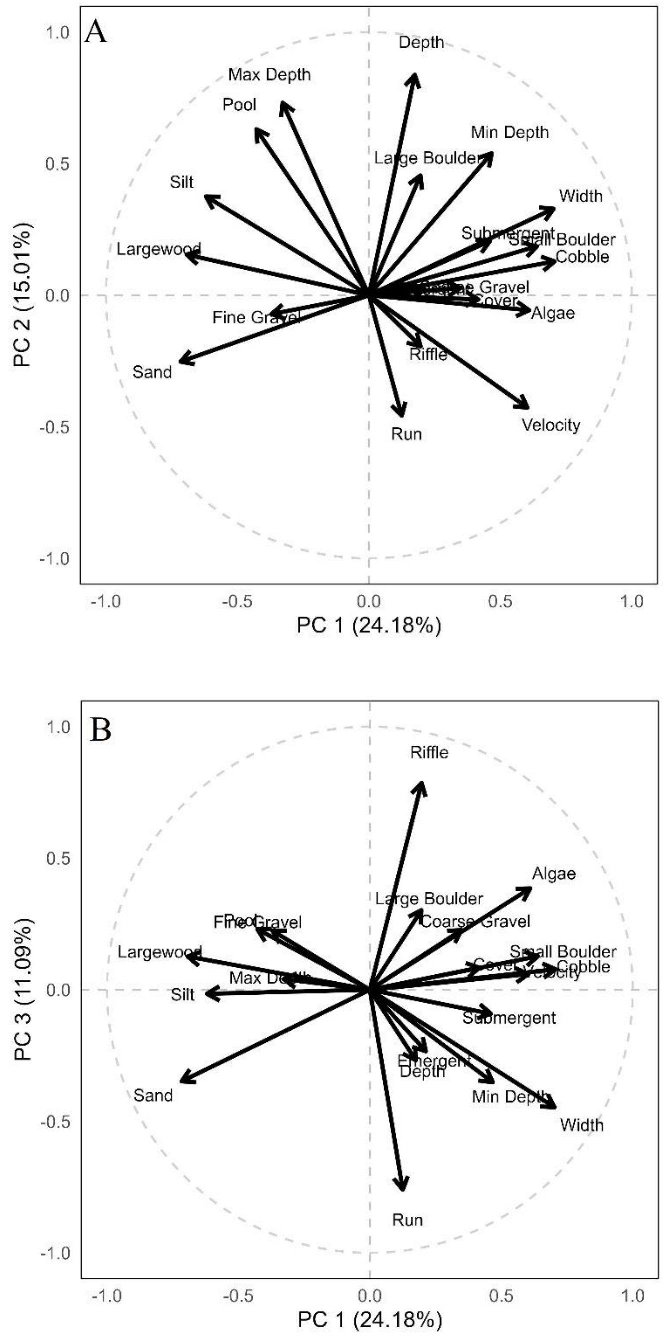

Figure 2.10. PCA2 was performed on 68 sites from four HUC10 watersheds (John's, Ware, Farmington, Neversink) and five HUC10 watersheds from target watersheds in South Carolina and Georgia. PC1 versus PC2 (A) and PC1 versus PC3 (B) show the strength (arrow distance) and effect (positive or negative) an original habitat variable has on a principal component.

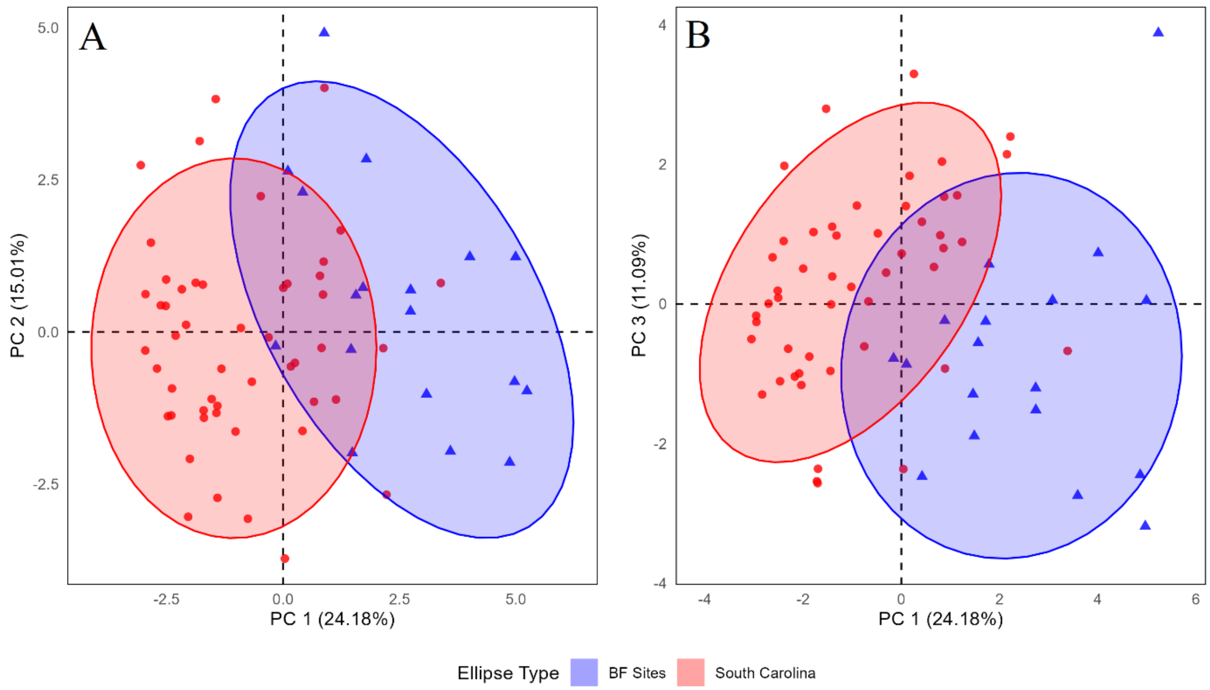

Figure 2.11. PCA2 was performed on 50 sites from South Carolina, and 18 sites where Brook Floater were present in the other five watersheds. **(A/B)** Plot of principal components showing the relationship between habitats of South Carolina and sites in other watersheds containing Brook Floater. The ellipses represent 90% confidence intervals for each watershed.

CHAPTER 3

HABITAT AND LANDSCAPE VARIABLES AFFECTING *CORBICULA FLUMINEA* PRESENCE IN THE UPPER SAVANNAH RIVER DRAINAGE

Introduction

Less than 1% of the Earth is covered by freshwater ecosystems, yet these ecosystems contain nearly 10% of all species found on Earth (Balian et al., 2008). These ecosystems are critically important to humans, who rely on them for water supply, recreation and tourism, flood control, and food production. The greatest threat to freshwater ecosystems is habitat destruction, specifically the altering of flow patterns, pollution from runoff, and land-use change (Sala et al., 2000). Habitat degradation also affects freshwater ecosystems indirectly by increasing the amount of biotic exchange that takes place (Strayer 2010). Biotic exchange, and proliferation of invasive species may displace native species and can disrupt ecosystem function in the invaded habitat. Human activities, specifically land-use changes like agriculture, urbanization, and the creation of reservoirs have led to an increase in biotic exchange and fragmented habitats, further endangering freshwater ecosystems (Vörösmarty et al., 2010).

Invasive species have had severe negative impacts on the North American economy. It is estimated that between 1960 and 2017, invasive species have cost the North American economy at least $1.26 trillion (Crystal-Ornelas et al., 2021). Environmental impacts caused by invasive species are often difficult to measure and quantify. However, invasive species are known to negatively impact native species abundance (Bradley et al., 2019), species richness (Mollot et al., 2017), and ecosystem function (Rong et al., 2021). Additionally, species introductions may be the leading cause of biodiversity loss and native species endangerment in North America (Pimentel et al., 2005).

Aquatic invasive species (AIS) invade new habitats through vectors such as shipping ballast water (Holeck *et al.*, 2004), aquarium releases, water gardens, deliberate stocking, bait buckets, and horticulture (Hobbs *et al.*, 1989; Keller & Lodge, 2007). Certain life history traits improve the likelihood that a species will be a successful AIS; such as a high reproductive capacity and rates, smaller body size, asexual reproduction, broad physical habitat tolerances, and early maturation improve the success of invasive species (Kolar & Lodge, 2001). Invasive species have the potential to disrupt the entire food web, creating a trophic cascade that affects the entire ecosystem (Strayer, 2010). For instance, Zebra Mussel (*Dreissena polymorpha*) are a highly invasive species of freshwater bivalve that often have large ecological impacts where they have invaded and established populations (Karatayev et al., 2015). Zebra Mussel have a high reproductive capacity, free-swimming planktonic larvae, and are highly efficient suspension feeders, which likely attributes to their success as invaders. Considered an “ecosystem engineer”, this species can control available resources for other organisms (Karatayev et al., 2007). In the Hudson River, shortly after their arrival in 1991 native freshwater mussel (Unionida) densities were reduced by an estimated 56%, likely due to the competition for food resources and the negative environmental conditions created by Zebra Mussel fouling (Strayer & Smith, 1996). In western Lake Erie, the species introduction was associated with a near total loss of native freshwater mussels in deep water samples (Schloesser & Nalepa, 1994), which is likely due to the negative effects associated with high rates of shell attachment (Schloesser et al., 1996). Understanding how invasive species affect ecosystems is important for the future of conservation, but it can also be beneficial for management to understand how invasive species spread across landscapes and reach new habitats.

Variation in biotic and abiotic conditions seen in different communities and ecosystems can influence the likelihood of invasion by non-native species. Elton (1958) first described the concept of biotic resistance, which suggests that ecosystems with a greater number of species are less susceptible to invasions because of the amount of competition for limited resources between species, making it more difficult to invade. MacArthur (1965) expanded on this idea with the explanation of “species packing”, where species in a community will optimize each of their niche spaces and create a self-organized community. The more species are packed into a community, the fewer niches are available to exploit. A community lacking structural and functional diversity of species to occupy available niches are likely more invadable than a community with high species richness (Elton, 1958).

The Basket Clam (*Corbicula fluminea*, O.F. Müller, 1774) is a freshwater bivalve native to southeast Asia but has been found in North America, South America, Europe, and some countries of North Africa (Clavero et al. 2012; Crespo *et al*. 2015). In North America, the species first appeared in Seattle, WA in 1938, and quickly expanded across the country. It can now be found in 44 of the 50 states. Their dispersal is likely facilitated by activities related to trade, including global shipping, construction of shipping canals, and building of reservoirs (Karatayev et al., 2007). On a more local scale, *C. fluminea* disperse through attachment on fishing gear and boat hulls, bait-bucket transfers, the pet trade, and the use as a food resource (Ferreira-Rodríguez et al., 2019).

C. fluminea possess many of the same life history traits as other AIS, including high reproductive rates, affinity to human mediated dispersal methods, and are a habitat generalist. *C.*

fluminea can reproduce asexually (Strayer, 1999) and can produce 35,000 offspring per breeding season (McMahon, 2002), allowing them to establish new populations from only one individual. Outside of human intervention, *C. fluminea* can disperse passively with water current through the release of juveniles, surviving the gut biome of fish, and by attaching to the legs of waterfowl and shorebirds (McMahon, 1982). Once released from an adult, larval *C. fluminea* have a short time window (100 hours) where they persist in the water column by “swimming” with an organ called the velum (Mackie & Claudi, 2010). This stage allows juveniles to disperse greater distances. During this time juveniles can also attach to human or wildlife vectors, which is most likely the method for short-distance upstream dispersal (Pernecker et al., 2021). Further, *C. fluminea* have a high filtration rate, can feed on a variety of algae, and can efficiently incorporate nutrients into somatic and reproductive growth (McMahon, 2002). These dispersal and foraging characteristics of *C. fluminea* likely improve its success when invading new freshwater ecosystems (Pigneur et al., 2012). Across their range, *C. fluminea* are considered habitat generalists, occurring in a wide range of lentic and lotic conditions across a multitude of substrate classes (Schmidlin & Baur, 2007; Patrick et al., 2017; Kelley et al., 2022). In the southeastern United States, *C. fluminea* densities have been linked to agricultural land use, including the amount of agriculture in the watershed, increased water temperature, and increased nitrogen pollution (Ferreira-Rodríguez et al., 2022).

Early detection and prevention are important and more cost-effective solutions to invasive *C. fluminea* than removal or sustained management (Coughlan et al., 2020). However, monitoring aquatic environments to prevent the spread of invasive species often lags behind the establishment of new populations (Beric & Macisaac, 2015). Our goal is to understand the habitat and landscape variables that affect *C. fluminea* dispersal and presence in the upper

Savannah River watershed in Georgia and South Carolina. To accomplish this, we will quantify how habitat and landscape variables of forested, agriculture, and developed watersheds relate to the presence of *C. fluminea*. Based on previous literature, we expect *C. fluminea* will be positively associated with sites composed of mostly sandy habitat, due to the species preference for sand dominated river habitats (Schmidlin & Baur, 2007). We also expect *C. fluminea* to be positively associated with the amount of agricultural land cover (Ferreira-Rodríguez et al., 2022) and the distance downstream of a reservoir. *C. fluminea* have been associated with reservoirs receiving recreational pressure and seen in higher abundances downstream of dams; therefore, we expect to see the same association in our study (Karatayev et al., 2005; Robb-Chavez et al., 2022). Understanding the habitat and landscape variables that affect *C. fluminea* dispersal may allow more effective monitoring and prioritization of habitats for preventative measures.

Methods

Study Area

The upper Savannah River basin begins in the Blueridge region of North Carolina, South Carolina, and Georgia. The Savannah River forms at the convergence of the Seneca and Tugaloo rivers. This portion of the Savannah River drainage is home to five of the largest reservoirs in South Carolina, including Lake Hartwell (227 km^2) and Lake Keowee (75 km^2) (Wachob et al., 2009). The study area spanned five Hydrologic Unit Code 10 (HUC10) watersheds in the upper Savannah River drainage: the Chattooga, Chauga, Coneross, Lower Tugaloo, and Little River watersheds (Figure 3.1). The north-western portion of the study area is dominated by forested land cover of the Chattahoochee-Oconee National Forest in Georgia, and the Francis Marion and Sumter National Forests in South Carolina. In the south-eastern portion of the study area near the

Hartwell and Keowee reservoirs, higher densities of agriculture land cover and development are present (Figure 3.1). While larger reservoirs like Lake Keowee and Lake Hartwell extend beyond the study area, our focus is on the smaller, localized reservoirs specific to the study area. Across the 5 watersheds, 35 reservoirs larger than 0.05 km^2 were present, with the largest being 1.00 km^2 in the Coneross watershed (Figure 3.1).

Site Surveys

We selected study sites and conducted surveys using the methods of the Brook Floater Rapid Assessment Protocol (Sterrett et al., 2018); 10 sites were sampled in each of five HUC10 watersheds. Briefly, 50 sites were randomly selected from a pool of all possible bridge crossings within a HUC10 watershed using the U.S. Census Bureau's "Transportation" layer (USGS, 2021) and the United States Geological Survey (USGS) National Hydrography Dataset (NHD, 2023). Within each of the five watersheds, 40 bridge crossings were randomly chosen, and randomly split into 20 priority sites and 20 replacement sites. Our goal was to sample 10 priority sites; if there were not enough suitable priority sites to reach the goal of 10, then replacement sites were randomly chosen to sample until 10 sampled sites was achieved. We considered sites suitable for sampling if they met criteria of the rapid assessment protocol (Sterrett et al. 2018), including < 1m in depth and ≥ 3 m in width, legally and safely accessible from the bridge, and safe to traverse. Sites that did not meet suitability criteria were replaced with a randomly chosen replacement site that did meet the survey criteria. Upon arrival at a site, 100 meters was measured in the upstream direction from the road crossing, then another randomly chosen distance between 0-100 meters was measured to mark the start of the survey site. This protocol was designed to avoid the scour pools or other habitat bias associated with bridge crossings (Sterrett et al. 2018).

We adopted the survey methodology of Sterrett et al. (2018), which was originally designed for use of surveying native freshwater mussels (Bivalvia: Unionida). This protocol uses longitudinal transects (i.e., lanes) running the length of the stream reach to designate the search area boundary for each observer. The number of lanes is equal to the number of observers ($n \geq 3$). The width of each lane is equal to the stream width divided by the number of observers, where lane width is a minimum of 1 meter and a maximum of 3 meters. Surveys were standardized to a total of 2 person hours, and surveyors were trained to maintain a survey search rate of 10 m^2 per minute. Surveyors started the search at the bottom (downstream) transect and moved in the upstream direction searching the benthos of their respective lane until the 2 person hours limit was reached, at which point the surveyors would be at the most upstream transect. Each observer used snorkeling or view buckets to scan the stream substrate within their lane and documented the presence of either shell or live *C. fluminea*.

Habitat surveys were also performed in accordance with the protocol described by Sterrett et al. (2018). Habitat variables at each site were assessed as means of lane-specific habitat characteristics, or data collected at the reach level. Stream depth variation at a site was a measure of the coefficient of variation between all measurements of depth at a site. Depth measurements were taken from five locations in each lane (start, 25%, 50%, 75%, end). Similarly, the dominant substrate was measured at five equidistant locations (start, 25%, 50%, 75%, end) along each lane. Surveyors classified the substrate into a substrate size class as characterized by the National Rivers and Streams Assessment 2013-2014 (USEPA, 2013). Large woody debris is the counted number of large wood pieces (>10 cm in diameter and 1.5m long) within each lane. If a lane contained large wood in the form of snags, log jams, or root wads, they were counted as one large wood. Large wood was measured by a surveyor once per lane and averaged for the site. Canopy cover was estimated using a modified spherical densiometer counting the number of 17 intersections covered by canopy vegetation. This measurement was taken at the middle of the reach along both banks and is the average of readings in upstream, downstream, river-right, and river-left directions taken at each bank. Mesohabitat description encompassed a characterization of the mesohabitat for the entire searched area (% riffle, run, pool). This measurement was the approximate proportion of each mesohabitat searched during the survey. Lane level habitat values were averaged across lanes, except for substrate classes, where we calculated the frequency of occurrence of each substrate type as the dominant substrate.

Spatial Data

We classified land cover data for each site at a spatial resolution of 10 m within a 3 km buffer of the site and within a delineated catchment of a site. We calculated the percentage of land use of four land cover classes at a spatial resolution of 10m, including water (combining open water, woody wetlands, and emergent herbaceous wetlands), agriculture (combining pasture/hay, cultivated crops, and grassland/herbaceous), forest (combining deciduous forest, evergreen forest, and mixed forest) and developed landscape (combining developed open space, developed low intensity, developed medium intensity, developed high intensity, and barren land). We calculated the percentage of each land cover within a site’s catchment and the land cover percentage in a 3 km buffer surrounding each site.

We used the USGS NHD to measure each site's relationship to reservoirs within the HUC10 watershed using two metrics: the distance to the nearest reservoir (river km) and a binary indicator denoting whether there were any reservoirs present upstream. To be considered in the analysis, reservoirs must have been larger than 0.05 km^2. This minimum reservoir size was chosen to exclude smaller farm ponds used primarily for fish production (e.g., 8-12 acres or 0.03-0.05 km^2; Steeby & Avery 2002) or livestock watering as we were largely interested in evaluating recreational use. Furthermore, Karateyev and others (Karateyev *et al.* 2005) evaluated reservoirs across Texas and found that *C. fluminea* were uncommon in reservoirs smaller than 0.10 km2. However, the majority of reservoirs within our study system were smaller than this, and we chose 0.05 km2 as a representative cut-off considering likely recreation use and availability. All spatial analyses were conducted in ArcGIS Pro (Version 3.0.3, ESRI, Redlands, California). In total, we had 26 descriptor variables, that included six landscape-level from GIS layers, 18 site-level variables measured directly in the sampling sites during May-September of 2023, and two that were based on a site's position in the watershed relative to reservoirs (Table 3.2).

Statistical Analysis

We used binomial logistic regression models to evaluate the effects that site specific habitat and landscape variables have on the presence of *C. fluminea*. We developed multiple competing hypotheses for each dominant landscape category (i.e., % agriculture, % developed, % forested), and included variables shown to be affected by these land use patterns (Jacobson et al., 2001) (Table 3.1). For example, % agriculture and % developed landscapes in a watershed increases fine sediment in streams. Therefore, we included the proportion of sand or fine sediments as a predictor variable in models explaining *C. fluminea* presence during agriculture or developed land use dominant cases, but not forested land use. From this, a set of 10 candidate models was constructed using *a priori* hypotheses associated with developed, agricultural, or forested landscapes (Table 3.3). A Pearson correlation coefficient of $r = 0.5$ was used as a threshold to limit the inclusion of two correlated variables in any single model (Figure 3.2). All models were ranked using Akaike's Information Criterion (Burnham & Anderson, 2004) values corrected for small sample size (AICc) to determine which model and characteristics most influenced *C. fluminea* presence at a site. We chose to only interpret models with the lowest ΔAIC values and a cumulative AIC weight of 95%. Parameter estimates on the logit scale were back transformed to the probability scale by exponentiating coefficient estimates. An alpha level of 0.05 was used as the level of significance in all statistical tests, which were performed in the R statistical programming language (R Core Team, 2024).

Results

Watershed Characteristics

We found *C. fluminea* at 20 of the 50 sites sampled (Table 4). The presence of *C. fluminea* varied across watersheds, ranging from no occurrences in the Chattooga watershed to eight occurrences in the Coneross watershed. A summary of land cover, reservoir presence, and prevalence of *C. fluminea* for each watershed can be found in Table 3.4. The Chattooga watershed had the highest amount of forest land cover at nearly 90% and the lowest amount of agriculture (2.6%) and developed (6.9%) land cover. The Coneross watershed had the highest amount of developed (22%) land cover because of the towns of Seneca, Westminster, and Walhalla. The Lower Tugaloo watershed had the highest amount of agriculture (29.4%) land cover. The number of sites with a reservoir present upstream ranged from eight sites in the Coneross to only one site in the Chattooga watershed. The Chauga and Little watersheds had the highest number of reservoirs that met the 0.05 km^2 criterion, while the Chattooga had the lowest number of reservoirs.

Model Selection and Parameter Estimation

Models associated with developed landscapes ranked as the top three models with a cumulative AICc weight of 0.949 (Table 3.5), with the top model (Developed 1) having an AICc weight of 0.715. All three top models for developed habitat contained the predictor of upstream reservoir presence (Table 3.6). The best performing models from predictors of forested (Forested 3) and agricultural landscapes (Agriculture 3) had AIC weights of 0.036 and <0.001, respectively.

Upstream reservoir presence was a significant predictor of *C. fluminea* presence in three of the four best fitting models, and significantly increased the likelihood of *C.fluminea* being present at a site (Table 3.6). Using predictions of *C. fluminea* presence in the top model (Developed 1) when other variables were held at the mean value, the probability that *C. fluminea* were present at a site was 0.62 when a reservoir is present upstream and 0.13 when there was not a reservoir upstream (Figure 3.3).

In the top-performing model (Developed 1), the proportion of developed land cover surrounding a site was a significant positive predictor of *C. fluminea* presence (Table 3.6). In contrast, developed land cover within the catchment (Developed 2) was not a significant predictor. As the proportion of developed land cover within the 3km buffer increased, the likelihood of *C. fluminea* presence also increased. This effect was more pronounced at sites with an upstream reservoir, which consistently had higher probabilities of *C. fluminea* presence compared to those without (Figure 3.4).

Habitat predictor variables did not appear significant in top performing models; however, some habitat variables were significant in lower ranked (AICc) models. The percentage of sand at a site was a significant predictor in two models, Agriculture 1 (logit-scale estimate = 2.412 ± 1.160 SE, $z = 2.078$, $p = 0.037$) and Agriculture 3 (logit-scale estimate = 2.519 ± 1.085 std. error, $z = 2.321$, $p = 0.020$). The percentage of the site composed of riffle habitat was a significant predictor in three models, Forest 1 (logit-scale estimate = -0.063 ± 0.026 std. error, $z = -2.401$, $p = 0.0164$), Forest 2 (logit-scale estimate = -0.066 ± 0.027 std. error, $z = -2.424$, $p = 0.0154$), and Forest 3 (logit-scale estimate = -0.058 ± 0.024 std. error, $z = -2.441$, $p = 0.0147$).

Discussion

We used an information theoretic approach to evaluate multiple competing hypotheses of landscape influence (agriculture, forest, developed) and site level habitat to best predict *C. fluminea* presence in the upper Savannah River watershed in South Carolina and Georgia, USA. We found *C. fluminea* presence was predicted best by landscape variables associated with developed environments, further supporting that anthropogenic activity may act as a vector to *C. fluminea* dispersal. Specifically, upstream reservoir presence and the % developed landscape within 3 km of a site were the best predictors of *C. fluminea* presence.

Our results partially aligned with the initial hypothesis related to the presence of *C. fluminea* and certain habitat and landscape variables. Despite previous literature stating that *C. fluminea* abundance was related to the amount of agriculture land cover within a watershed, our results saw no significance related to the amount of agriculture within a site's catchment, or in the surrounding area. Instead, *C. fluminea* presence was associated more with the amount of developed land cover surrounding a site. On the contrary, the proportion of a site composed of sandy substrates was a significant predictor, though not in top performing models. As predicted, *C. fluminea* presence was highly associated with reservoirs. Our findings suggest that landscape variables related to developed environments play an important role in determining *C. fluminea* presence, while site-level habitat characteristics such as substrate composition were less influential.

Newly constructed reservoirs generally have lower species diversity than their original lotic systems, resulting in species-poor environments with open niches that invasive species like *C. fluminea* can exploit (Havel et al., 2015). This may cause reservoirs to be more invadable, because as younger ecosystems with less established communities of zooplankton and benthic macroinvertebrates (Wetzel, 1990), reservoirs lead to more open niches available for invaders. In our study area, the initial introductions of *C. fluminea* may have been facilitated by human recreational activities, including boating, swimming, and fishing, and is likely spread to nearby reservoirs in the same manner (Havel et al., 2015). Other species like Zebra Mussels in the Great Lakes region were found to be dispersing across a landscape by sticking to the hulls and motors of boats (Johnson & Carlton, 1996). Once established, *C. fluminea* disperses downstream (Pernecker et al., 2021), aided by its free-swimming juvenile stage that lasts for approximately 100 hours (Mackie & Claudi, 2010). This life stage provides sufficient time for larvae to reach the outflow of reservoirs and be carried further downstream. The ability to reach new reservoirs through the passive attachment on human-mediated vectors, coupled with the ability to spread downstream through natural dispersal mechanisms could be why *C. fluminea* presence is so strongly associated with upstream reservoir presence.

Freshwater ecosystems are heavily affected by changing land use (Sala et al., 2000), and land cover in the catchment of a site may affect many different habitat parameters (Jacobson et al. 2001). Most importantly, land cover can influence sediment loads, which in turn may impact benthic organisms, water flow, and critical habitat along and within the streams (Allan, 2004). Despite this, we did not find a significant effect of catchment land cover on the presence of *C. fluminea*. We saw a positive association with the amount of developed land cover surrounding a site and the presence of *C. fluminea*, which is contrary to Kelley et al. (2022) who found *C. fluminea* densities were negatively associated with the amount of urban land cover. It is plausible that environmental correlates of an initial invasion are independent from those that optimize population growth, thus explaining differences in trends discovered by Kelley et al. (2022) and in the upper Savannah River basin. We did not measure *C. Fluminea* density or abundance and are uncertain if these measures would have held the same pattern in our basins. Nevertheless, it does appear that in the upper Savannah basin, the introduction of *C. fluminea* is strongly related to the proximity of developed land as a potential proxy of human activity, even if landscape mediated changes in habitat were not involved.

Successful aquatic invaders may tolerate a wide range of habitats. For instance, *C. fluminea* can withstand a range of flow conditions in lentic and lotic systems such as slow-moving sandy rivers (Schmidlin & Baur, 2007), rivers with larger substrate (Kelley et al., 2022), and in reservoirs (Karatayev et al., 2003; Patrick et al., 2017). Habitat variables measured in this study incorporate many habitat conditions associated with forest, agriculture, and developed watersheds (Table 3.1, Jacobson et al. 2001). However, site level habitat variables were less important than human modified landscapes in predicting *C. fluminea* presence. Predicting preferred habitat for a generalist species may be difficult as habitat associations are likely to vary depending on habitat available within a system.

Humans have long been associated with the accidental or intentional moving of AIS, and sites with a large amount of developed land cover surrounding them are more likely to be visited by humans than if the same site was less developed. Karatayev et al. (2005) related *C. fluminea* presence to landscape characteristics throughout the state of Texas, USA. The authors found that *C. fluminea* were disproportionally present in larger reservoirs compared to smaller ones due to the amount of human activity that these reservoirs received compared to smaller reservoirs. Another study on the Columbia River found that sites with higher abundance of *C. fluminea* were located downstream of a dam compared to lower abundances upstream of the dam (Robb-Chavez et al., 2022). Similarly, the best performing predictive variable in our models was the presence of an upstream reservoir that may serve as an introduction pathway for *C. fluminea*. Reservoirs have been shown to act as a stepping stone for AIS invasions by providing accessible environment for human activities like boating, which increases propagule pressure (Johnson et al., 2008). Also, reservoirs' relatively young age, fluctuating water levels, and lower biotic resistance make them vulnerable to invasion by AIS (Havel et al., 2005).

Monitoring for *C. fluminea*, especially in the southeastern United States where benthic and aquatic diversity is especially high, is necessary to disentangle the complex relationships and impacts that invasive species have on native populations and biodiversity. For example, in habitats with only sandy substrate, *C. fluminea* may actually provide hard structure that some macroinvertebrate species prefer (Werner & Rothhaupt, 2007). Conversely, freshwater mussel growth appears to be negatively affected by higher densities of *C. fluminea* (Ferreira-Rodríguez et al., 2018; Haag et al., 2021), perhaps due to competition for food. *C. fluminea* can occupy a large tropic niche that often overlaps with the feeding strategies of native freshwater mussel species (Modesto et al., 2021). As we still do not fully understand how *C. fluminea* impacts ecosystems, improving ways to efficiently detect new occurrences of *C. fluminea* by prioritizing locations where introductions are most likely to occur may lead to increased monitoring efficiency and more rapid detections. Future research could focus on examining reservoirs based on the type of human pressure it receives, such as either boating, fishing, or swimming. This could allow managers to better understand the pathways through which invasive species are spread or introduced. Future studies could explore the factors that influence invasions, such as reservoir size, water quality, and connectivity to other systems so we can refine our understanding of these invasion factors and develop management strategies aimed at reducing the impact and spread of *C. fluminea*.

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Tables and Figures

Table 3.1. Hypothesized pathways for how major land-use types (Landscape influences) could experience different factors that cause changes in stream habitat and result in decreases (-) or increases (+) of several potential predictor variables used in the candidate model set for predicting the probability of *C. fluminea* site presence.

Landscape influences	Factor	Cause	Effect on stream habitat	Variables affected
Agriculture	Plowing and deforestation	Soil erosion	Increased sediment load, embeddedness, width - to-depth ratio, decrease in channel cross sectional area, large wood recruitment	(+) fine sediments (sand, fine gravel) (-) riffle/run/pool complexity (-) large wood
	Livestock access to stream	Livestock trampling of stream bank	Bank erosion, increased sediment load, habitat degradation	(-) canopy cover (-) vegetation (+) increased fine sediments
Forest	Riparian preservation	Undisturbed vegetation along stream bank	Improved bank stability, large wood recruitment, decreased embeddedness	(+) riffle/run/pool complexity (+) canopy cover (+) cobble (+) large wood
Developed	Impervious surface	Increased runoff	Increased flows during flooding, channelization, decreased large wood	(-) variation in depth (-) large wood
	Development encroachment	Riparian buffer removal	Increased sedimentation, reduction in habitat complexity, decreased vegetation, large wood	(-) canopy cover (-) riffle/run/pool complexity (-) large wood (+) fine sediments (sand, fine gravel)

Table 3.2. Summary table describing all potential predictor variables analyzed to find their effect on *C. fluminea* site presence. Within the table, the variable term represents the term used in the analysis, the range of actual values observed in the study, and a description of each term including the type of data and general information.

Variable Term	Range	Description
% developed catchment	1-34%	Proportion of developed land cover within the catchment of a site
% developed surrounding	2-42%	Proportion of developed land cover in a 3km buffer surrounding a site
% agriculture catchment	0-66%	Proportion of agriculture land cover within the catchment of a site
% agriculture surrounding	0-53%	Proportion of agriculture land cover in a 3km buffer surrounding a site
% forest catchment	13-98%	Proportion of forest land cover within the catchment of a site
% forest surrounding	24-98%	Proportion of forest land cover in a 3km buffer surrounding a site
Reservoir distance	0.29-32.51 km	Distance (kilometers) to the nearest reservoir in the upstream or downstream reservoir using the river network
Upstream reservoir presence	0 or 1	Presence (1) or absence (0) of a reservoir upstream using river network, reservoir must be > $0.05km^2$
Variation in depth	0.18-0.77	Coefficient of variation in depth, calculated as the ratio of standard deviation to mean
Canopy cover	0.38-17.00	Average amount of overhead cover, 0 being none and 17 being full coverage
Sand	0.00-1.00	Proportion of a site's substrate composed of sandy substrate
Cobble	0.00-1.00	Proportion of a site's substrate composed of cobble
Fine gravel	0.00-0.53	Proportion of a site's substrate composed of fine gravel
Riffle	0.00-0.80	Proportion of a site's mesohabitat composed of riffle
Pool	0.00-0.85	Proportion of a site's mesohabitat composed of pool
Large woody debris	0.00-15.33	Average number of large wood per site

Table 3.3. *A priori* models used to predict *C. fluminea* site presence by combining habitat and landscape variables.

Agriculture 1	catchment agriculture density + sand + stream depth variation
Agriculture 2	3km agriculture density + sand + fine gravel + canopy cover
Agriculture 3	sand + fine gravel
Forested 1	catchment forest density + cobble + riffle + pool
Forested 2	3km forest density + riffle + canopy cover + large woody debris
Forested 3	cobble + riffle
Developed 1	3km developed density + upstream reservoir + closest reservoir distance + canopy cover
Developed 2	catchment developed density + upstream reservoir + closest reservoir distance
Developed 3	upstream reservoir + sand
Developed 4	canopy cover + cobble + stream depth variation

Table 3.4. Attributes of 5 HUC10 watersheds.

Watershed	**# of sites with *C. flluminea* present**	**% Developed**	**% Forest**	**% Agriculture**	**# Sites w/ Reservoir Upstream**	**# Reservoirs ≥ 0.05km^2**
Chauga	4	7.5	86.7	5.1	6	6
Little	5	15.5	67.2	8.3	3	6
Coneross	8	21.9	53.0	21.9	8	5
Chattooga	0	6.9	89.8	2.6	1	2
Tugaloo	3	13.1	47.6	29.4	3	5

Table 3.5. Results from logistic regression models to predict *Corbicula fluminea* presence at a site. The AICc table contains all models for all 3 habitats. Models were created using a specific set of habitat and landscape variables (see Table 1) collected that represented characteristics of a specific habitat type. AICc = Akaike information criterion corrected for small sample size, K = the number of parameters in a model. ΔAICc, AICc weight (AICcWT), and cumulative weight (Cum.Wt) are also shown.

Model	K	AICc	ΔAICc	AICcWT	Cum.Wt
Developed 1	5	52.406	0.000	0.716	0.716
Developed 3	5	55.923	3.517	0.123	0.839
Developed 2	4	56.152	3.745	0.110	0.949
Forested 3	3	58.387	5.980	0.036	0.985
Forested 2	5	61.289	8.883	0.008	0.993
Forested 1	5	62.238	9.831	0.005	0.999
Developed 4	4	65.351	12.944	0.001	0.999
Agriculture 3	3	67.710	15.304	< 0.001	0.999
Agriculture 1	4	68.992	16.585	< 0.001	0.999
Agriculture 2	6	73.100	20.693	< 0.001	1.000

Table 3.6. Best fitting models, model statistics, and parameter estimates for logistic regression models of habitat and landscape variables affecting *Corbicula fluminea* presence. Parameter estimates provided on the scale of the model using the logit link. AICc = Akaike information criterion corrected for small sample size, K = the number of parameters in a model. AICc weight (AICcWT) is also shown.

Model Name		AICc	AICcWT	*k*
Developed 1		52.41	0.716	5
Parameter	Estimate	Standard error	z value	p value
Intercept	0.12	1.73	0.07	0.944
Upstream reservoir presence	2.36	0.89	2.65	0.008
Closest reservoir distance	-0.11	0.07	-1.55	0.121
3km mean developed	11.07	5.15	2.15	0.032
Canopy Cover	-0.18	0.12	-1.46	0.144
Developed 3		55.92	0.123	3
Parameter	Estimate	Standard error	z value	p value
Intercept	-1.11	1.06	-1.04	0.296
Upstream reservoir presence	1.93	0.74	2.62	0.009
Closest reservoir distance	-0.11	0.08	-1.31	0.189
Sand	0.91	1.30	0.70	0.486
Developed 2		56.15	0.110	4
Parameter	Estimate	Standard error	z value	p value
Intercept	-0.89	0.96	-0.92	0.356
Upstream reservoir presence	1.89	0.73	2.57	0.010
Closest reservoir distance	-0.12	0.08	-1.60	0.109
Catchment mean developed	2.63	5.23	0.50	0.615

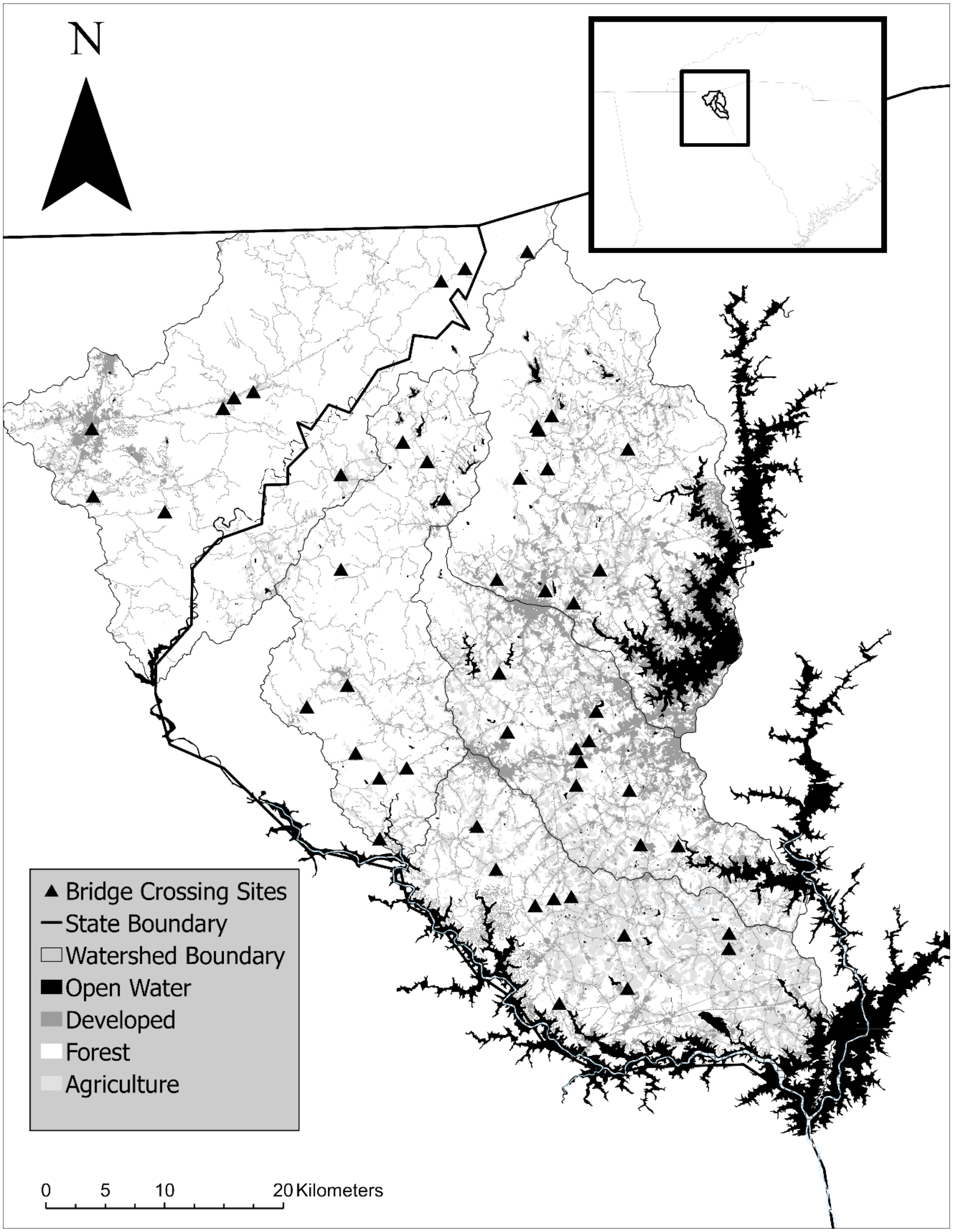

Figure 3.1. Map detailing the boundaries of the five HUC10 watersheds used in the study. The northern region of the study area is dominated by forest, while the southern regions contain more of an agriculture and developed landscape.

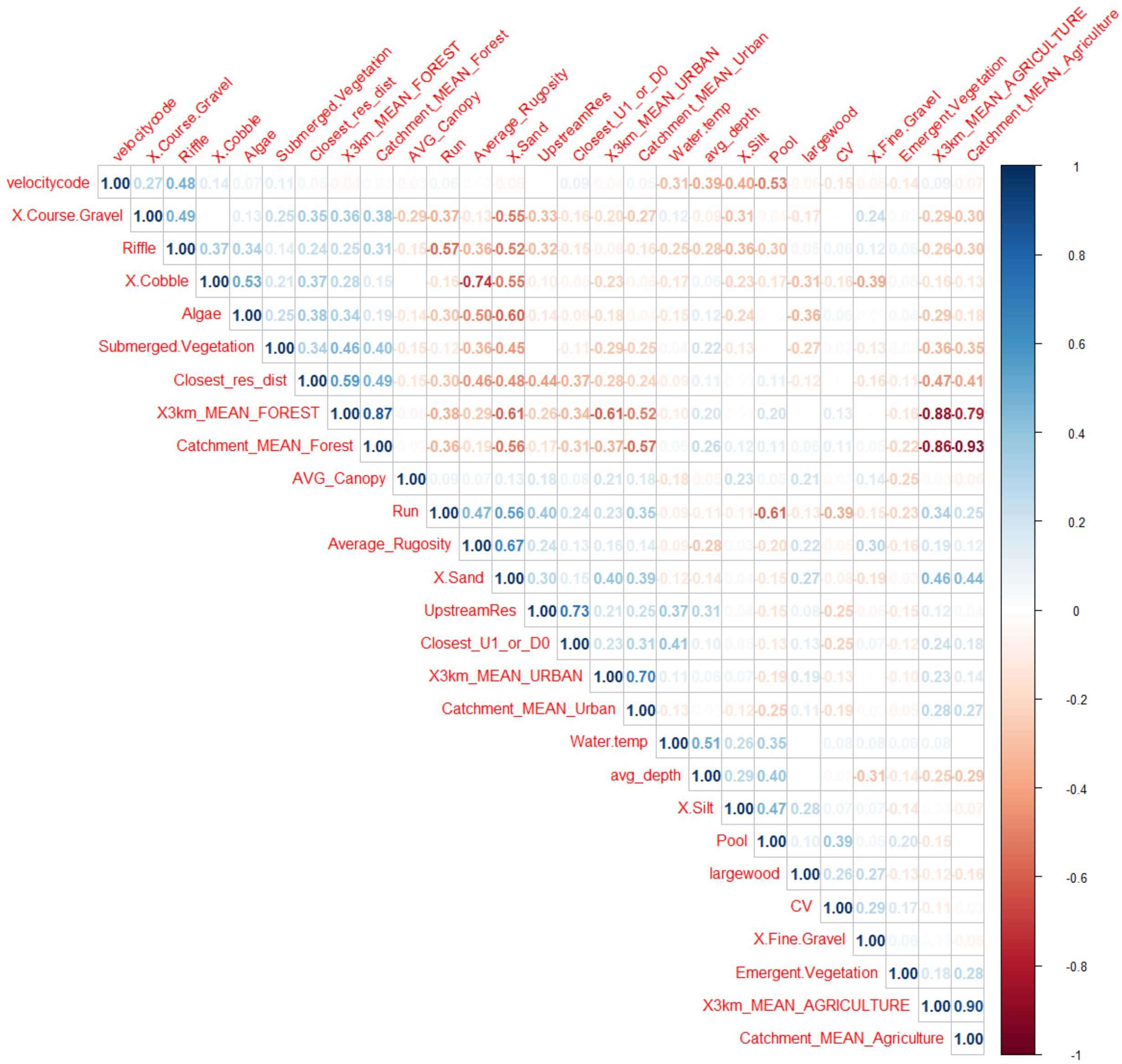

Figure 3.2. Correlation matrix of all predictor variables that we considered using in final models for *C. fluminea* presence. A correlation level of 0.5 was chosen to eliminate redundancy within models. Predictor variables with a value of 0.5 or greater were not used in the same model.

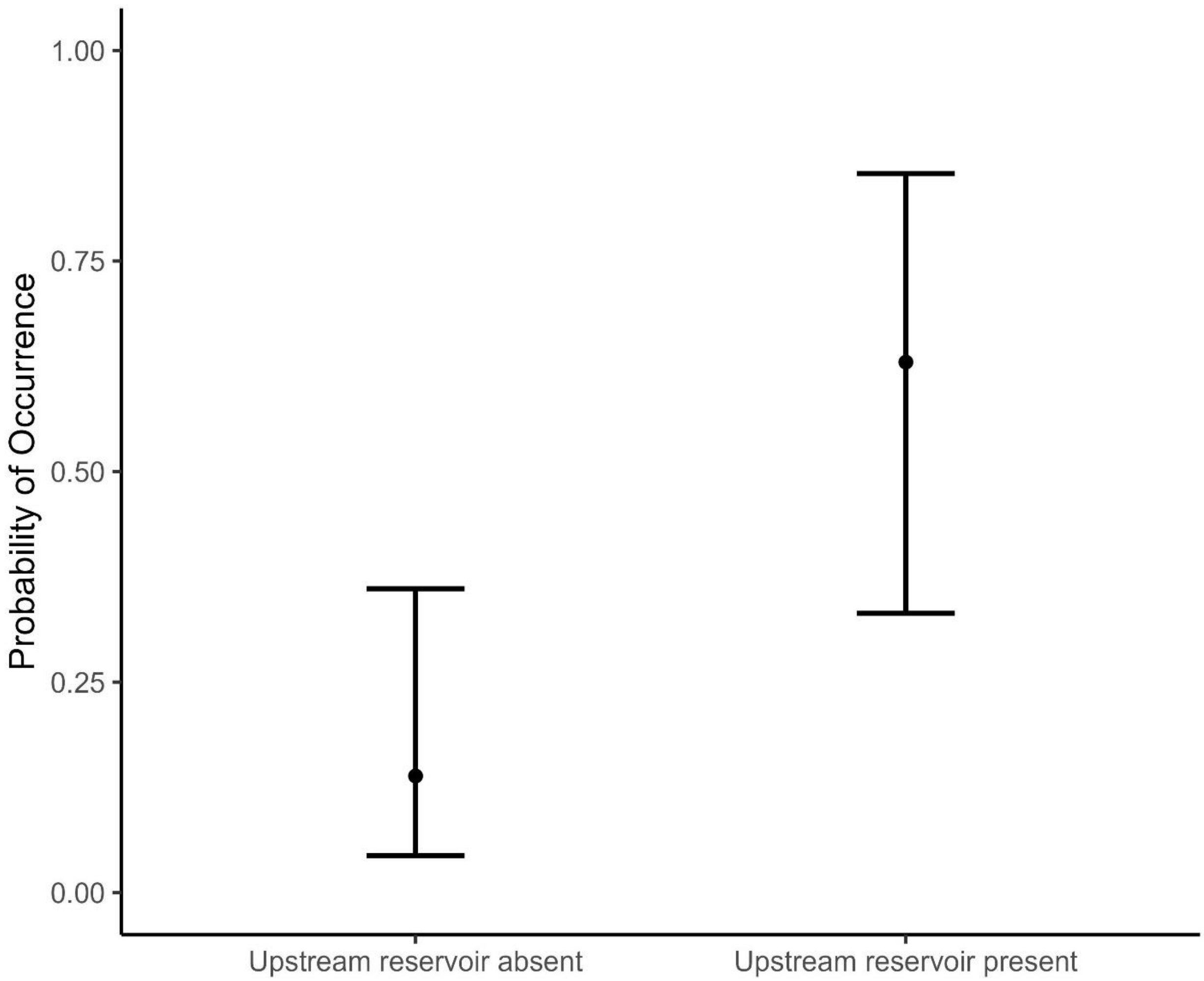

Figure 3.3. Probability of site *C. fluminea* presence using predicted effects of upstream reservoir from Developed 1 model with the mean value of other predictor variables (±95% confidence limits).

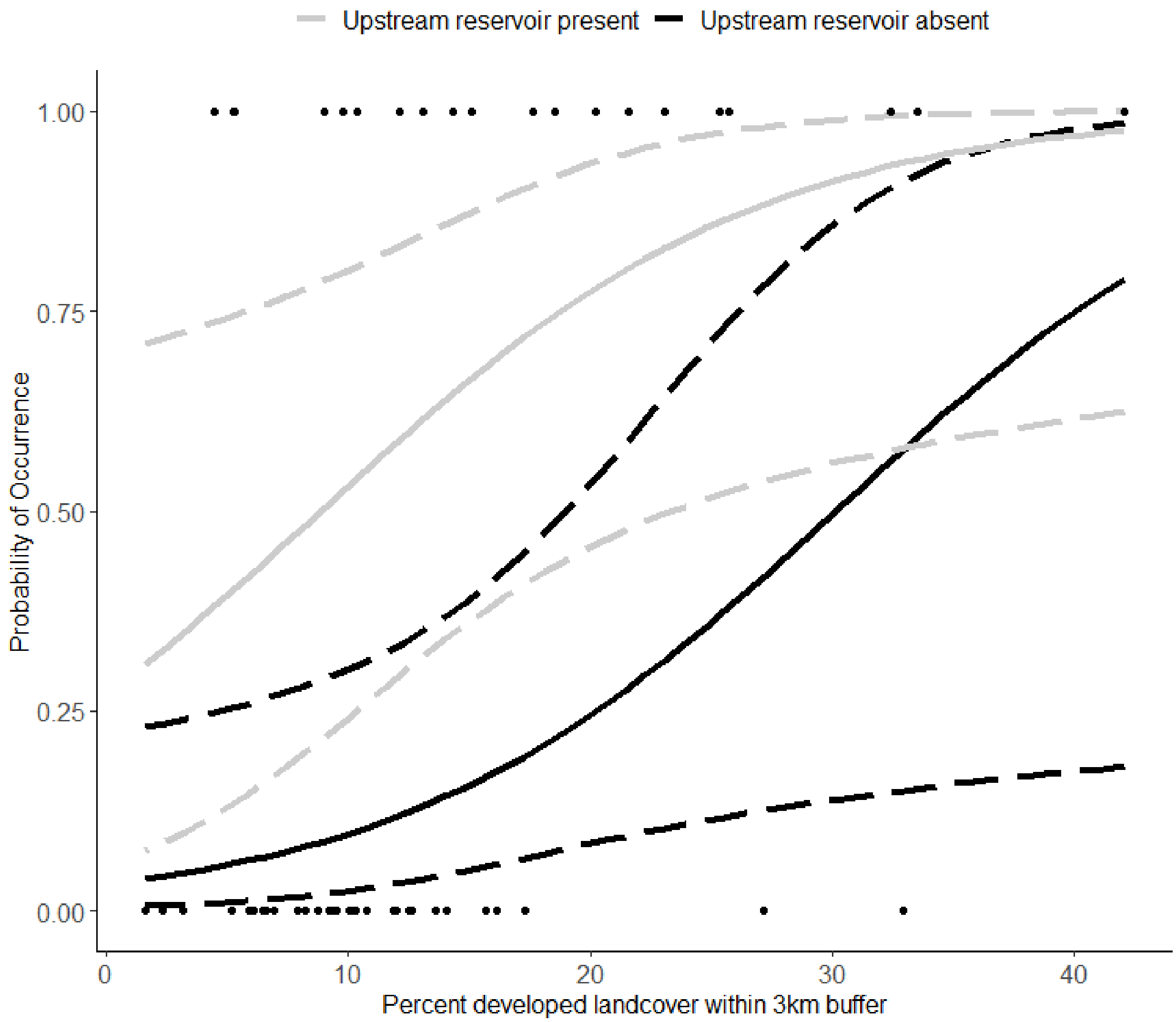

Figure 3.4. Plot of logistic regression showing the probability of *C. fluminea* site presence across a range of developed land cover quantities surrounding a site in a 3km buffer during 2 different scenarios, one where a reservoir is present upstream and when a reservoir is absent upstream. Solid lines show model predictions and dashed lines show 95% confidence bands.

CHAPTER 4

SUMMARY AND MANAGEMENT IMPLICATIONS

Researchers and managers who work with rare mussel species and aquatic invasive species may notice they share a few similarities. One major similarity between the two groups is rarity; the challenge of finding AIS before they become abundant across a landscape mirrors the difficulty of finding rare mussel species during declines. Identifying key habitat correlates of species presence can aid managers and researchers in finding and preventing the spread of AIS, and is also helpful in identifying reintroduction habitats for rare species conservation. In the research presented here, I have evaluated habitat use by the imperiled Brook Floater and the invasive *Corbicula fluminea* towards informing conservation actions for both species. Habitat data in both studies were collected using the same protocol, originally designed to evaluate occurrence and abundance of rare native freshwater mussels.

The protocol identified naive sites that most closely resemble sites that contain Brook Floater. I used an ordination approach (PCA) to compare similarity of sites in multidimensional habitat space. Sites containing Brook Floater were associated with the presence of larger substrate classes like cobble, small boulder, and larger boulder; flow levels consistent with riffles and runs; sites without very deep pools and very shallow sections; and moderate cover and algae. These habitat qualities are consistent with previous findings, with a few key differences. Other studies looking at the substrate of Brook Floater found they preferred sand to be present mixed among the substrate (Marshall & Pulsifer, 2010; Skorupa et al., 2024). It was also found that Brook Floater were absent from areas of riffle (Skorupa et al., 2024). This PCA was meant to capture the variability across all sites and then group sites based on related characteristics among groups. Many unoccupied sites in South Carolina represented habitat far different from occupied Brook Floater sites and contained high proportions of sand. As a result, previously associated habitat characteristics, like sand, may not have emerged as associated habitat characteristics. Other research has successfully implemented a habitat modeling framework of available river habitat to locate appropriate reintroduction sites of a riverine fish (Fisk et al., 2014). The conclusions of this analysis call attention to the protocol's ability to identify trends in a species habitat use, which may be valuable for broader management decisions.

Watershed rankings from the habitat similarity of naïve sites were developed to aid management decisions in selecting watersheds that will provide the most success for Brook Floater reintroduction. Understanding habitat needs of species, and how to assess habitats for potential reintroduction sites is crucial for the conservation of a species through reintroduction (IUCN, 2013). Previous researchers have used similar approaches to quantify mussel habitat at relocation sites of native freshwater mussels (Johnson & Brown, 2000). My approach of looking at habitat similarity of occupied and unoccupied sites may be another useful tool for site selection decisions in data poor systems.

In a seperate analysis of habitat and landscape variables associated with *C. fluminea* presence, I found that streams below reservoirs are more likely to contain *C. fluminea*, and thus reservoirs may be a source of introduction for *Corbicula* into unaffected streams, facilitating further dispersal. Reservoirs play a significant role in shaping the world's aquatic ecosystems (Rosenberg et al., 2000) and have a significant effect on shaping aquatic habitats (Havel, et al., 2005; Thomaz et al., 2015). Reservoir habitats may serve as safe havens for many AIS (Johnson et al., 2008), and recreational use of reservoirs by humans also serve to transport AIS over terrestrial landscapes (Johnson et al., 2001).

Evidence from this analysis also supported specific landscape characteristics as being more associated with *C. fluminea* presence than site habitat variables in my study area. In particular, the protocol successfully identified developed landscape characteristics related to the presence of reservoirs as key predictors of *C. fluminea* presence at a site and the amount of developed land cover surrounding a site. These results follow the patterns seen in other literature. Urban environments often promote invasive species abundance (Riley et al., 2005), and *C. fluminea* abundances have been positively correlated with sites downstream of dams (Robb-Chavez et al., 2022). The results from this study may show that before AIS become established and fully abundant in a watershed, they are more likely to first occur in these locations that have an increased probability of introduction and sustaining AIS populations, like reservoirs and areas with high developed densities. The results also provided evidence to support landscape variables as more associated with *C. fluminea* site presence that site level habitat variables. That could be for two reasons, 1) *C. fluminea* are a generalist species and 2) the protocol did not track abundance. *C. fluminea* are considered a generalist species, so associating them to a singular habitat may prove difficult with a protocol like the one implemented in this study. With a protocol that tracked density, perhaps site habitat characteristics would have proven to be more important for *C. fluminea* presence. Reservoirs represent a pathway for *C. fluminea*, others have found that abundances of this AIS were related to the size of reservoirs in Texas, also hypothesizing that the amount of recreational pressure each reservoir received was to blame for *C. fluminea* numbers (Karatayev et al., 2005). Future research in this area may want to focus on classifying reservoirs by the type of recreational pressure a reservoir receives and associating that to groups or abundances of AIS.

Based on the relationship between certain site and spatial variables and *Corbicula* site presence, managers can use landscape characteristics, in particular the presence of reservoirs and the amount of surrounding developed land cover as indicators for monitoring the spread of *Corbicula.* Management strategies should focus on monitoring reservoirs and in areas with high human activity. Boaters, anglers, and other recreational users should be educated of the life cycles, methods of AIS introduction, and how users may inadvertently spread dangerous invasive species through passive transport. In the upper Savannah River watershed, management should focus on areas that are high-risk and have important ecosystems, like the Chattooga River. The Chattooga River is home to a strong and healthy population of Brook Floater (Krause et al. 2020), but the river is also a popular destination for recreational whitewater rafting users and fishermen (USFS, 2024). Educating the public in these hotspot locations may help in maintaining these important ecosystems, and monitoring boat and fishing use and traffic could prevent AIS invasions into areas where the species does not yet occur.

It is unclear if *C. fluminea* populations are to blame for the lack of native mussel species in the upper Savannah River basin. Though few studies have looked at the interaction between *Corbicula* and Unionids in natural settings, there is evidence that *Corbicula* abundance may reduce growth rates in juvenile mussels deployed in natural systems (Haag et al., 2021). In the literature, habitat destruction is cited most for the decline in local native freshwater mussel abundances, whether that be alterations of flow regimes or damming and the creation of reservoirs (Downing et al., 2010). Reservoirs within the upper Savannah basin may also be the cause of historic declines seen in Brook Floater and other native freshwater mussel populations.

Since 1950, five large reservoirs have been built, eliminating the connectivity between almost all large tributaries in the basin (Wachob et al., 2009). Large reservoirs have been shown to affect mussel populations downstream, with higher species richness and presence of rare mussels increasing with greater distances from reservoirs (Vaughn & Taylor, 1999). The loss of Brook Floater and native freshwater mussels in the upper Savannah is likely due to a degradation of habitat caused by impoundments and land use practices, and not directly caused by the introduction of AIS like *C. fluminea*.

The Brook Floater Rapid Assessment Protocol (Sterrett et al. 2018) used in this study was developed to evaluate occupancy and occurrence of Brook Floater and other mussels in wadeable streams in the Atlantic Slope drainages. It is now being used in Canada and across 10 states as a tool for rapidly collecting data on mussel assemblages and their habitat. I used data collected with the Rapid Assessment Protocol to answer questions beyond the scope of the protocol design. My chapters 2 and 3 are examples of how this rapid approach to assessing stream habitat can be used beyond surveying for individual freshwater bivalve species. The protocol may not only be helpful in tracking occurrences of native freshwater mussels, but may be adaptable to use for other taxa, and captures sufficient habitat data to understand trends in habitat use and similarity across sites in a rapid and repeatable framework. As more agencies and researchers implement this protocol, more data and analyses will become available to inform better protocol design, and for conservation planning for native freshwater mussels in North America.

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