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Beaver (Castor Canadensis) Impacts on Herbaceous and Woody Vegetation in Southeastern Georgia

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BEAVER (CASTOR CANADENSIS) IMPACTS ON HERBACEOUS AND WOODY VEGETATION IN SOUTHEASTERN GEORGIA

by

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(Under the direction of Bruce A. Schulte)

ABSTRACT

North American beavers are considered ecosystem engineers. Their activities can quickly and drastically alter habitat properties and perhaps permit highly aggressive colonizing plants, notably non-native species, to invade and potentially dominate. This study examined if beavers in southeastern Georgia have an effect on the terrestrial plant community. Sampling areas included beaver modified (N=9) and nearby but relatively non-impacted riparian habitat (N=9) in a matched pairs design. Vegetation surveys were performed in spring and summer. Species richness was calculated for herbs, vines, woody seedlings, and woody vegetation. Richness of herbaceous vegetation was higher at distances closer to shore while richness of large woody vegetation increased with distance from shore. Woody vegetation also was more abundant in beaver sites. Composition was not different between the two site types. The presence of exotic species was rare and did not differ by site type. This study provides evidence that beavers may play an important role in determining the vegetative structure of their community.

Index words: Castor canadensis, beaver, herbaceous, vegetation, exotics, ecosystem engineers, non-native

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1
INTRODUCTION

Plant communities change over time through a process termed ecological succession, which includes altering species composition or the structure of a community (Cowles, 1910; Clements, 1916; Clements, 1936). Ecological changes through time can be classified as allogenic or autogenic (Barbour et al., 1999). Allogenic changes are caused by external forces not affected by biotic factors. The changes are the result of the physical environment, for example, when the temperature decreases as elevation increases. Autogenic changes are the direct result of a biotic influence in the community. These changes can be inhibitory to other organisms, such as when tree roots uptake water and nutrients from the soil, potentially reducing the ability of nearby vegetation to grow. Autogenic changes also can be facilitative, such as when organisms benefit from nitrogen fixers in the soil. The focus of this study was on autogenic changes, specifically those caused by the North American beaver (*Castor canadensis*).

Beavers were once abundant and widely distributed throughout North America. Population numbers were estimated at 60-400 million, occupying the majority of waterways in North America, from as far north as the arctic tundra to the deserts of northern Mexico (Jenkins & Busher, 1979). As a consequence of unregulated trapping and habitat loss, beaver populations declined drastically and only small populations existed east of the Mississippi River by 1850 (Johnson & Chance, 1974). In Georgia, beaver were virtually eliminated, so a restoration program began in the 1940's and lasted approximately 10 years. Georgia was considered one of the leaders in beaver restoration. By the 1980's, due to low demand, low price, and a lack of trappers, beaver populations had become reestablished in much of their former geographic range, estimated at 6-12 million (Naiman et al., 1986). Beaver ponds have positive impact on the landscape by maintaining the water table during drought, acting as a filtration system, and being used for irrigation and flood control (Schulte & Müller-Schwarze, 1999). Unfortunately, beavers are known for their negative impacts, which are all costly to the landowner: plugging culverts, girdling and destroying valuable trees, eating crops, and damaging farm ponds by burrowing into them. From an ecological standpoint, Georgia considers the beaver to be one of the most important animals in the state due to the critical habitat they create for waterfowl and migratory birds ("Beaver Management", 2003). In southeast Georgia, research on the beaver, while minimal in the past, has come to a standstill. There are no current population estimates, nor are there any plans for future studies on beaver by the Department of Natural Resources in Georgia (personal conversation, Greg Waters, DNR).

Beavers are considered ecosystem engineers, defined as organisms that control resource availability to other organisms either directly or indirectly by changing the biotic or abiotic materials in a community (Jones et al., 1994). The physical engineering of ecosystems includes the physical modification, maintenance, or creation of habitats (Jones et al., 1994). The extent of impact by an ecosystem engineer can be generally based on five criteria. They include the life span of an individual, the density and distribution of the population, how long the population has been present, the durability of the structure and how many organisms depend upon it. Autogenic engineers, like the beaver, will change the environment through physical structures that they construct. Beavers build dams in streams and rivers creating a wetland from a more freely flowing river system. They fell trees then transport the wood back to their ponds (Jenkins, 1980). The felling of trees can create large openings in the forest canopy resulting in increased sunlight, and therefore, concomitant changes in temperature and space. Water is important to this animal for many reasons. Water allows escape from predators and felled trees can be transported easier via water, requiring less energy. Beaver also feed in the water, though not exclusively. Beavers use wood not only for construction but also as forage. They feed upon the stems, bark, and leaves of a tree in addition to the herbaceous vegetation they consume. The activities of beavers alter three main abiotic components that affect plant community structure, namely water availability, light accessibility, and temperature (Barbour et al., 1999).

Beavers also are central place foragers in that they typically feed on plants obtained on land after bringing them back to the water. As a means of selecting woody vegetation for food and construction, beavers first cut trees nearest the water's edge, moving farther distances from the shore as the wood supply nearest the water decreases (Jenkins, 1980). As beavers move further from the shore they exhibit greater selectivity in tree size, usually opting for the smaller size tree. This is thought to maximize the amount of energy per unit feeding time as well as reduce time to predation risk. This also suggests that beavers would have less of an impact on abiotic components such as light availability and temperature as distance from the shore increases because smaller diameter trees with relatively small canopies would be cut. A study conducted in the boreal forests of Ontario (Donker & Fryxell, 1999) supported this hypothesis of central place foraging in beavers. The authors also found that preferred species abundance increased as distance from shore increased. Those species that are not preferred had higher abundance closer to shore. In addition, the highest plant species richness occurred at an intermediate distance. Even for preferred foods such as aspen (*Populus* sp.), beaver harvest more individuals closer to shore and select smaller trees (less than 4.5 cm in diameter) as distance from shore increases (Basey et al., 1988). Another study suggests that habitat quality is a factor in beaver food selection, stating that in a poor quality habitat distance is not a critical factor in species selection by beavers (Gallant et al., 2004). The size-distance relation of beaver foraging has been examined mainly in the northern and western United States. None of these studies measured the potential impact of beaver foraging behavior on the structure of the surrounding plant community.

Tree felling by beaver may allow greater light to penetrate than those areas without beaver, thereby permitting regeneration of shade intolerant species (Pastor & Naiman, 1992). The resultant gaps can be large when close to shore because this is where beavers will selects larger trees (Jenkins, 1980). Conversely, gaps may be rather small as distance from shore increases due to smaller trees being selected. Tree canopy can dictate forest composition by controlling abiotic factors such as light, moisture, and temperature. These factors can prevent some species from establishing and facilitate others. In a study conducted in a Brazilian neotropical savanna (Hoffman, 1996), most of the seedlings of woody species counted under three levels of canopy density showed increased establishment in sites with overstory cover, regardless if canopy density was high or intermediate. Two possible explanations are offered by Hoffman (1996). First, soil temperature and moisture loss are reduced by tree cover, which can have a large effect on herbaceous plant richness and composition (Wright et al., 2003). Second, canopy cover reduces the density of the herbaceous layer and this indirectly reduces competition for seedlings. In a similar fashion, canopy gaps created by beaver may alter community composition and structure by reducing seedling recruitment or germination rates because of decreased canopy density. Conversely, canopy gaps may increase seedling survival as a result of the increased light. However, these effects may only be observable where beavers forage the most, which is generally closer to shore.

Beaver activity also may create less immediate, but substantial, long-term, changes in the ecosystem (Naiman et al., 1988). Naiman et al (1986) found that dams built by beavers retain a considerable amount of sediments. Dam construction also results in water retention and the subsequent expansion of submerged habitat. Flooding of soil increases the amount of available forms of nitrogen to that soil. A beaver pond with its slow flow can accumulate organic matter, which demands high oxygen levels from water that is already poorly aerated. These changes in the physical and chemical environment of soil can have a dramatic influence on the competitive ability of plants (Pollock et al., 1998). Species that are adapted to dry conditions will be stressed and have a reduced competitive ability during a flood, whereas those plants that are adapted to wet conditions will have a competitive advantage (Pollock et al., 1998). While aquatic biomass is positively associated with beaver impounded water, the physical and chemical changes to water also influence species diversity and composition in the surrounding terrestrial environment (Fryxell, 2001).

Aquatic and terrestrial organisms can benefit from the habitat alterations made by beaver. Wetlands occupied by beaver have significantly more bird diversity and density compared to vacated or potential beaver habitat (Grover & Baldassarre, 1995). In South Carolina, reptile richness and diversity are greater at beaver modified patches when compared to non-impounded streams (Metts et al., 2001). Beaver modified patches contribute up to 25% of total herbaceous plant richness in riparian zones in the Adirondacks of New York State (Wright et al., 2002). Some plant species can inhabit both forested and riparian habitat yet others are unique to one or the other. Therefore, even if the activity of beavers as ecosystem engineers does not increase species richness, it may still provide an exclusive environment for certain species. If these certain species were native to the area, then this would be a positive beaver impact.

Regularly disturbed habitats, including many riparian corridors, are subject to invasion by non-native species (Hobbs & Huenneke, 1992; Pollock et al., 1998). Vujnovic et al. (2002) showed that the diversity of exotic vascular plants increased positively with disturbance. Exotic plants may be able to compete effectively with native species because they are released from density dependent control factors such as parasites, predators, and competitors (Gordon, 1998). In physically disturbed sites, where light penetration is increased, invading exotic plants tend to have high colonization ability and mature quickly (Lake & Leishman, 2004). Physically disturbed sites that decrease the amount of shade generally have a decrease in leaf litter and an increase in bare soil, which is favorable for initial establishment of exotic species (Vujnovic et al., 2002). Invasive plants usually have strong vegetative growth, grow faster, and live longer than the native vegetation with which they compete (Blair & Wolfe, 2004). They also have abundant seed production, high seed germination rate, long-lived seeds, and rapid maturation to a sexually reproductive (seed-producing) stage (Baker, 1974; summarized in Williams & Meffe, 1998). Hence, they can replace native vegetation relatively quickly. This disrupts the natural balance of the ecosystem leading to habitat degradation and reducing native biological diversity (Wilcove et al., 1998). Four of Georgia's top ten invasive plant species are trees: Chinese privet (*Ligustrum sinense*), Chinese tallow tree (*Triadica sebifera*), autumn olive (*Elaeagnus umbellata*), and mimosa (*Albizia julibrissin*) (Murphy, 2005). If beavers use such invaders for food or construction, then this may reduce the number of mature stems and will consequently reduce colonization of non-native plants. In this case, beaver activity would have a positive impact on community structure and function. Conversely, beavers may facilitate the dispersal of exotic plants by transporting seeds or accelerating vegetative regrowth. Exotic plant colonization also may be increased by light gaps created by felled trees. In such cases, beavers would have a negative impact on community structure and function. This study will begin to evaluate if the presence of beavers increases exotic species abundance in a given habitat.

Research on the North American beaver has concentrated in the northern latitudes of North America, where beavers exert variable impacts by season. In the fall, beavers cache large amounts of woody vegetation and fortify dams, clearing tracts of forest, while in winter they harvest virtually no fresh plants (Schulte & Müller-Schwarze, 1999). In the southeast, the lack of extreme seasonality allows beavers to rely less on woody vegetation for food, especially as a winter cache (Roberts & Arner, 1984). The reduced seasonality suggests that beaver in the south would have a steady habitat impact that was more evenly spread across time and species (i.e., woody and herbaceous). Since beavers in southeastern United States consume herbaceous material all year (Roberts & Arner, 1984), they rely less on woody species and therefore, may apply regular, low levels of disturbance. I would predict that beavers would affect the community structure less in the south due to a lesser wood demand. Therefore, a null hypothesis for this study is that beaver will not impact their habitat to a measurable extent when compared to those areas lacking this mammal.

The goal of my study was to determine if beavers have an effect on community structure and on the presence of exotic plants. I compared beaver occupied and unoccupied locations and examined changes in community structure at distances from the shore within the typical foraging range of beavers. The objectives of this study were to (1) determine the richness, abundance, and diversity of herbaceous and woody vegetation as well as collecting canopy cover measurements, and (2) assess relative abundance of non-native to native vegetation in beaver impacted and nearby, but relatively non-impacted riparian habitats.

CHAPTER 2
METHODS

Study Area

This study was performed in Bulloch County, Georgia. Bulloch County is located in southeastern coastal plain region, which is characterized by low relief and sandy substrates with varying topography (Quarterman & Keever, 1962, Hoover & Parker, 1991). Sandy substrates tend to be susceptible to moisture variability on a temporal and spatial sale. Hoover and Parker (1991) described seven community types in the Coastal Plains. This study was conducted in two of these communities, mainly river swamp hardwood forests and lowland hardwood forests. In general, the principal trees in hardwood forests of river swamps are water tupelo (*Nyssa aquatica*), willows (*Salix* spp.), sweetgum (*Liquidambar styraciflua*), and water oak (*Quercus nigra*). The dominant trees in lowland hardwood forest generally are elms (*Ulmus* spp.), river birch (*Betula nigra*), water oak, red maple (*Acer rubrum*), and sour gum (*Nyssa sylvatica*) (Hoover & Parker, 1991).

To find beaver sites, I surveyed 122.5 kilometers of river systems, consisting mostly of Little Lotts Creek, Lotts Creek, and Mill Creek in Bulloch County. I did this by foot until the creeks became too wide, at which point I used a canoe. I focused on surveying first- through fourth-order streams based on where beaver occupancy has been observed the most (Naiman et al., 1986). First-order streams are the smallest streams with year round flow and have no tributaries and fourth-order streams are two third-order streams combined (Mackie, 2004). This provided me with an estimate of active beaver sites, not how many individual beavers were present.

As I traveled the waterways, I recorded the location of beaver activity by using a handheld global positioning system (GPS). Evidence of beaver activity included lodges, dams, trails, and foraging signs. Active sites were categorized as having fresh beaver chew, defined as wood that was clean cut (not gray or brown) and may still have been discharging sap. Active sites also contained a dam that had the current trees added to it, or twigs that had green leaves attached. These locations were mapped using geographic information system (GIS).

After surveying portions of the creeks in Bulloch County, I identified nine active beaver sites at which I performed vegetation surveys (four on Mill Creek, three on Little Lotts Creek, and two on Lotts Creek). Sampling areas included beaver modified habitat (N=9) and nearby but relatively non-impacted riparian habitat (N=9) in a matched pairs design (Figure 1) (see Appendix I for site descriptions and directions). The control and beaver-modified sites had comparable habitat by having visually similar gradients, stream width, and vegetation types. To determine if the control site was to be located upstream or downstream from the beaver site I considered various factors. If the river became too wide, the bank gradient too steep, or I was denied access from private landowners, then the control site was in the opposite direction. Nonetheless, I made certain to keep a relatively equal number of upstream and downstream control sites. Four control sites were chosen upstream from the matched beaver site, four were chosen downstream, and one was located on a parallel stream to the beaver site. The control site was located at least 20 m from the last physical evidence of beaver presence. This provided adequate distance to assure that there is no influence of beaver in the control site (Jenkins, 1980). Beavers rarely forage greater than 60 m from water (Donker & Fryxell, 1999). However, personal observation indicated that all beaver activity was observed within 20 m from the water's edge and 20 m was the common maximum in a study on arctic beaver as well (Aleksiuk 1970).

Data Collection

To determine richness and abundance of herbaceous and woody vegetation I first performed a species area curve to determine that nine transects would be needed to record an accurate measure of all the species present (see Appendix II for the results of the species area curve). In a 100 m X 20 m area, nine transects were placed perpendicular to the shoreline; the 50 m mark was positioned in the area of greatest beaver activity, specifically the dam, lodge, or feeding site (Figure 2). The first transect was the most upstream from the 50 m mark and the ninth transect was the farthest downstream. Transects were chosen using a random numbers table using numbers that were between 1 and 100 and had to be at least 5 m apart to avoid sampling overlap. The middle point of the sampling area was at 50 m so, for example, if a 63 was chosen then the next transect would be 13 m downstream from the middle. To measure herbaceous and woody seedlings vegetation (stems < 1 m tall) I used 1 m X 1 m plots and to measure woody vegetation (stems > 1 m tall) I used 5 m X 5 m plots along nine transects. Most of the woody vegetation was either much smaller or taller than one meter so the one meter value was chosen as a convenient separator. All plots were either flagged, GPS coordinates recorded, or both for re-locating in the future. Each transect started at the water line and ran perpendicular to the shore. The start of each quadrat was at 5 m, 10 m, 15 m, and 20 m and went out to the north side of the transect. For example, the 5 m plot, measuring 25 m^2, started at 5 m and went to 10 m. The 1 m^2 plot started at 5 m and ended at 6 m.

Measurements in this method were taken also at 10 m, 15 m, and 20 m. Dead trees, standing or fallen, were not common and therefore not counted.

Vegetation surveys were performed at each beaver-modified site and non-modified site for two seasons. The first sampling season occurred between May 22 and July 11, 2004. The second sampling season took place between August 9 and September 5, 2004. The purpose of two sampling periods was to collect plants that flower at different times to aid in identification. There was virtually no difference in sampling plots between the two seasons, but when there was a difference in the number of species or individuals counted, then the higher number was used for analysis. Beaver-modified and non-modified sites were sampled no longer than two days apart to control for time variation. Woody and herbaceous vegetation was counted and identified to species level in the field whenever possible either through my own knowledge or by learning their identity after collection. Unknown species were collected and identified by Dr. Donald Drapalik (Georgia Southern University) and by making comparisons with herbarium specimens. Those that were not flowering were identified to genus or family level. Vouchers were collected and were deposited at the Georgia Southern University herbarium (GAS) (see Appendix III for the list of plant vouchers). All species were classified as native or non-native to Georgia. Those species that were labeled as non-native were always identified to the species level. Because beavers may change the type of vegetation present I classified plant species by shade tolerance and wetland indicator (adapted from U.S. Fish & Wildlife, 1988).

I measured canopy opening in beaver-modified and non-modified sites. Measurements were taken for both sampling seasons with no noticeable difference. One measurement was taken along each transect at 10 m from the shoreline using a densiometer (Forestry Suppliers Inc., Spherical Crown Densiometer, Concave – Model C).

Statistical Analyses

To compare species diversity of the beaver impacted and non-impacted sites I used the Simpson's Index, $I = \sum n_i(n_i-1) / N(N-1)$. I chose this index because it considers not only the number of individual species (n_i) and the total number of individuals (N), it also takes into account the proportion of the total that occurs in each species (Brower et al., 1990). In doing so, the Simpson's Index provides an unbiased estimator of species and has the smallest standard deviation among diversity indices (Lande, 1996).

Statistical analyses were performed using JMP 3.1 statistical software (SAS Institute, 1994). Means are presented with one standard error in text and figures. All data were first tested for normal distribution and equal variance. A split-plot design was used to compare beaver-modified and control sites with distance from shore as the second factor and diversity, abundance and richness as the dependent variables. Within this analysis, there is a whole plot calculation with the degrees of freedom being 1 and 8 and a subplot calculation with degrees of freedom of 3 and 48. With the split-plot design, the F values must be calculated by hand because JMP will not compute the F-statistic. Therefore, the P values for these variables are derived from a statistical table and hence not presented as exact values. Exotic species richness between beaver-modified and control sites was compared using analysis of variance (ANOVA).

When assumptions for ANOVA were not met, the data were analyzed using nonparametric tests (Sokal & Rohlf, 1995). Mann-Whitney U-test was used to determine if tree species composition differed by site type and Principle Components Analysis was performed to explain the most variation (Dytham, 1999). This method creates a set of compound axes from the data using a mass of variables. Pair-wise comparisons were performed for tree species that had a high abundance difference to determine if there was significant site type effect. Two-way replicated ANOVA was used to test differences in canopy cover in the two site types. The Wilcoxon signed ranks test was used to compare exotic species abundance by site type.

CHAPTER 3
RESULTS

Community Structure

Species Richness

Beaver sites and their matched control sites were statistically shown to have very few differences between them, contrary as to what was expected. Beaver sites had 4.5 ± 0.47 (average ± SE) herbaceous species and control sites contained 4.9 ± 0.91 species. A difference in herbaceous species richness was evident when distance from shore was analyzed ($F=3.90$, $df=3,48$, $P<0.025$) (Table 1; Figure 3). Herbaceous richness for both site types was greatest at the 5 m distance (5.6 ± 0.74) compared to the three more distant sampling points (10 m: 4.6 ± 0.76, 15 m: 4.3 ± 0.47, 20 m: 4.4 ± 0.79), although Tukey pairwise comparisons showed no significant differences. There was no interaction between distance and site type (beaver and control) ($F=2.27$, $df=3,48$, $P>0.1$)

The richness of small woody vegetation in 1 m^2 plots did not significantly differ by site type ($F=4.13$, $df=1,8$, $P>0.1$) (Figure 4). Beaver sites contained 5.1 ± 0.57 species of small woody individuals while control sites had 4.8 ± 0.66 species. There also was no difference in richness at varying distance from shore ($F=1.58$, $df=3,48$, $P>0.25$) and no interaction between site type and distance ($F=1.63$, $df=3,48$, $P>0.25$).

There were 6 ± 0.4 large (stems > 1 m tall) woody species in beaver sites and 5.4 ± 0.6 woody species in control sites at each of the four distances for the 25 m^2 plots. There was no significant interaction between site type and distance from shore ($F=0.14$, $df=3,48$, $P>0.75$). The richness of woody species was not different by site type but did significantly increase as distance to shore increased ($F=159.7$, $df=3,48$, $P<0.001$) from 5 ± 0.47 at 5 to 10 m from shore to 6.3 ± 0.52 at 15 to 20 m from shore (Figure 5).

Vine richness was higher closer to shore ($F=3.05$, $df=3,48$, $P<0.05$) but did not differ between site type with beaver sites having an overall average of 2.4 ± 0.33 and control sites having 2.3 ± 0.31 species (Figure 6). Again, there was no significant interaction between site type and distance from shore ($F=1.30$, $df=3,48$, $P>0.5$).

Species Abundance

Some differences between beaver and control sites were evident based upon species abundance. Herbaceous plant abundance was determined to have an average of 48 ± 10 individuals per beaver site and 82 ± 29 individuals per control site. This vegetation category was calculated as being no different between beaver-modified and control sites as a whole ($F=1.08$, $df=1,8$, $P>0.5$) as well as by distance from the water's edge ($F=1.24$, $df=3,48$, $P>0.5$) (Figure 7). This apparent difference by site type (based on the mean values) resulted from extreme values for three sites (2 control and 1 beaver). When these outliers were removed from analysis the differences became less dramatic with beaver sites having an average of 42 ± 8.9 individuals and control sites having 46 ± 9.8 (Figure 8). The trends stayed relatively the same for the other vegetation types with or without these same sites.

Small woody abundance was greater in beaver-modified sites, which contained 34 ± 5.0 individuals compared to 21 ± 3.3 at control sites (Figure 9). The interaction between site type and distance from shore for this size class was significant ($F=5.26$, $df=3,48$, $P<0.005$). Beaver sites appeared to show a decrease in woody abundance as distance from shore increased while control sites stayed the same over the first three distances with a slight increase at 20m. Of particular interest was the convergence on abundance for the two site types that occurred at the 20 m distance; the region lying on the typical foraging maximum for beavers in my study sites based on preliminary observations.

Large woody species were more abundant in beaver-modified sites than control sites ($F=7.35$, $df=1,8$, $P<0.05$) (Figure 10). Beaver sites had 33 ± 4.3 individuals per site and control sites had 27 ± 2.2. This size class also became more abundant as distance to shore increased ($F=66.2$, $df=3,48$, $P<0.001$). Beaver sites had an average of 20 ± 5.1 individuals per site at 5 to 10 m from shore to 46 ± 3.5 individuals at 15 to 20 m from shore. However, the interaction between site type and distance from shore was not significant ($F=1.43$, $df=3,48$, $P>0.1$).

Species Diversity

Beaver and control sites did not differ widely when species diversity was compared. Diversity of herbaceous species had a significant interaction between site type and distance from shore ($F=4.34$, $df=3,48$, $P<0.01$). While a significance difference by distance from shore also was present ($F=4.54$, $df=3,48$, $P<0.01$), no such difference existed by site type ($F=0.05$, $df=1,8$, $P>0.75$). Herbaceous vegetation in beaver sites had an overall diversity of 0.59 ± 0.05 and control sites had 0.57 ± 0.08 (Figure 11). When looking at herbaceous plant diversity by distance at 5 m, beaver sites had 0.65 ± 0.04 and control sites had 0.53 ± 0.09. At 10 m, beaver sites had 0.59 ± 0.03 and control sites had 0.65 ± 0.05; at 15 m, beaver sites had 0.57 ± 0.07 and control sites had 0.56 ± 0.08; and at 20 m, beaver sites had 0.57 ± 0.04 and control sites had 0.56 ± 0.09. Clearly, the significant interaction results from diversity differences at 5 m and 10 m from shore, the distances at which beaver activity would be expected to be greatest. Small woody vegetation had an average diversity of 0.65 ± 0.05 in beaver sites and 0.65 ± 0.07 in control sites. For this size class of woody species, there was no interaction between site type and distance from shore (F=0.49, df=3,48, P>0.5). In addition, small woody species diversity did not differ by site type (F=3.75, df=1,8, P>0.1) or distance from shore (F=0.27, df=3,48, P>0.75) (Figure 12). The diversity of large woody vegetation in beaver sites had an average of 0.73 ± 0.03 while control sites had an average of 0.71 ± 0.04. Large woody species diversity was calculated as having no significant interaction between site type and distance from shore (F=0.40, df=3,48, P>0.5), and no difference by site type (F=0.16, df=1,8, P>0.5). Diversity did differ by distance to shore with the only trend being control sites showing a marked increase as distance from shore increased, especially at the 15 m distance, but the rest of the differences were in no discernible pattern (F= 65.58, df= 3,48, P= <0.001) (Figure 13).

Species Composition

Species composition did not differ between beaver and control sites. When all vegetation types were included, 46 species (62%) were found in both site types, 8 species (12%) occurred only in beaver-modified sites and 18 species (26%) occurred only in control sites. Those species that did occur in both site types had varying levels of abundance.

Species composition of trees was not significantly different between the two site types (Mann-Whitney, df=20, P=0.70) (Figure 14). The most abundant large woody species, measured in 25 m^2 plots, in beaver sites at each distance to shore (listed from most abundant to less abundant) were *Acer rubrum, Liquidambar styraciflua, Nyssa* *sylvatica, Pinus taeda* and *Quercus nigra*. The species that were most abundant in control sites were *Nyssa sylvatica, Acer rubrum, Liquidambar styraciflua, Quercus nigra*, and *Magnolia virginica*. Those tree species that had the largest differences in relative abundance were *A. rubrum* with 22% in beaver sites and 14% in control sites, *N. sylvatica* with 11% in beaver sites and 22% in control sites, and *Fraxinus caroliniana* with 6% in beaver sites and 1% in control sites. Principal Components Analysis showed that high negative eigenvalues on principle component 1 were attributed to the occurrence of *A. rubrum* and *Fraxinus caroliniana* while high positive eigenvalues were attributed to the occurrence of *Liriodendron tulipifera* and *Persea borbonia* (Figure 15, Table 3). When species were grouped by site type there was no indication that species composition was explained by beaver-modified or control site. The top seven tree species showed no difference between beaver-modified and control sites after performing pair-wise comparisons (for all t-tests, $P > 0.08$). Most of the sites (15/18) had two tree species that composed 50% or more of the diversity. However, they were not the same species each time.

Canopy Cover

Canopy cover did not vary between beaver-modified and control when measured at the 10 m from shore location (2-way replicated ANOVA, $F=0.06$, $df=1,144$, $P=0.80$) (Figure 16). Beaver sites had an average of $78 \pm 2.1\%$ canopy cover and control sites had $73 \pm 5.9\%$ canopy cover. This suggests that beavers did not open the tree canopy significantly by felling trees at this distance from shore as supported by the similarity in abundance of large woody individuals at the 10 m distance from shore (Fig. 10).

Exotic Species

Exotic species richness did not differ between beaver-modified and control sites (F=0.55, df=8,16, P=0.47) (Figure 17) nor did exotic species abundance (Wilcoxon signed ranks test, df=8, P=0.61). Richness was relatively low with sites having zero to a maximum of three exotic species (Figure 17). Because of the low species abundance diversity indices were not descriptive and thus were not calculated. Generally, when a beaver-modified site was invaded by an exotic, then the matched control was as well. The two most common exotic invasive plants in this study were Chinese privet (*Ligustrum sinense*), which fell into both size classes of woody species, and Japanese honeysuckle (*Lonicera japonica*), which was categorized as a vine. Other exotic species present in some sites were alligator weed (*Alternanthera philoxeroides*), bracken fern (*Pteridium aquilinum*) and St. John's wort (*Hypericum* sp).

CHAPTER 4
DISCUSSION

The purpose of this study was to determine if beavers alter the structure and composition of the community in which they inhabit. If beavers change the community to the level that has been observed and studied in northern latitudes (Jenkins, 1980; Jones et al., 1994; Naiman et al., 1988; Schulte & Müller-Schwarze, 1999), then one could expect that they would have the same effect in southern latitudes. Beaver-modified sites would have different structure and composition of herbaceous and woody plant species compared to similar locations without beavers. Beaver-modified sites also would be expected to have a higher degree of canopy openings than control sites. However, in this study, when richness, abundance, and diversity of all vegetation types were compared between sites occupied by beaver and those sites that were not, there was only a difference in abundance of woody vegetation. In addition, this study found that there was no difference in canopy cover at a 10 m distance from the shore between site types. Furthermore, if beavers felled more trees closer to shore than further, as suggested by central place foraging theory (Jenkins, 1980), then one would expect to see structure and compositional differences in the plant communities at varying distances from the waterline. In this study, differences were detected by distance from shore, but not in the expected direction when differences between site types occurred.

Beavers have been found to drastically alter the physical habitat and thus change the vegetative community (Barnes & Dibble, 1988; Naiman et al., 1988; Johnston & Naiman, 1990; Pollock et al., 1998; Schulte & Müller-Schwarze, 1999). This study contradicts these past findings by indicating that beaver sites are not very different from those sites without beaver presence. When herbaceous vegetation in beaver-modified and control sites was compared there was no difference between the two site types. While the mean values for both richness and abundance for herbaceous vegetation look visually different they were not statistically different because of high variability among the study sites. When outlier sites were accounted for, the mean values were quite similar between beaver and control sites. Woody vegetation was generally more abundant in beaver sites possibly indicating a selection preference for sites with abundant woody vegetation by the animal. Beavers may thin the trees in the area they occupy only slightly because beavers in the south may not utilize wood to the extent that beavers do in the north. Alternatively, if beaver selected sites have much denser vegetation than surrounding areas, beavers may significantly reduce density from initial levels but not below that of surrounding areas. This study showed that beavers did not significantly impact the canopy cover in beaver sites when compared to control sites, but discerning between the above two scenarios is not directly possible with the current data. Measuring the extent and type of trees cut by beaver could provide data to examine these competing hypotheses. Woody vegetation of smaller stems had a trend towards being more abundant closer to shore while those of large stems occurred significantly higher further from shore. However, when the composition of large woody vegetation was compared there were no differences between the two site types, and there was also no difference in the number of wetland-adapted plants compared to upland plants. While beavers may impact their habitat by affecting where vegetation types grow in relation to distance from shore, they may not affect what species inhabit the area.

Herbaceous plant species richness and composition can be greatly affected by soil moisture (Wright et al., 2003), or more specifically moisture variability (Pollock et al., 1998). Wetlands are typically characterized as having fluctuating water levels (Mitsch & Gosselink, 1993). The beaver sites used in this study, however, were consistently saturated throughout the sampling period indicating a lack of variability. The highest richness occurred at 10 m from the waterline at control sites and 20 m at beaver-modified sites. The herbaceous species primarily found at these distances (*Clethra alnifolia, Lyonia lucida, Polygonum* spp*., Hydrocotyle* spp.) are adapted to living in wet conditions (Taylor, 1998). This indicates that beaver-modified sites have higher water levels, characteristic of flooding, perhaps allowing for these species to expand their range from shore.

Large woody species had higher richness and abundance further from shore. This is consistent with previous research on beavers as central place foragers (Jenkins, 1980). Prey items (trees) that are closer to the central place, or beaver pond, are consumed before prey at further distances. Beavers will travel further distances from shore for prey until the energy gain no longer exceeds the expense. Trees are heavy and require energy to transport and beavers are more vulnerable to predators when on land. Thus, it would be predicted that there would be more, larger trees at further distances from shore. The two most abundant species observed at distances greater from shore were *Acer rubrum* and *Liquidambar styraciflua*. *Acer rubrum*, while found in dry locations, is characteristic of swampy sites; it is an effective pioneer, and has rapid growth (Harlow et al., 1996). In addition, its seedlings are very tolerant of flooding. *Liquidambar styraciflua* can occur in a variety of sites but does best in moist alluvial soils and aggressively pioneers disturbed sites (Harlow et al., 1996). Both of these species are trees that would be expected to grow best in the environment that beavers create.

To maximize their energy gain beavers will also fell smaller trees before larger trees (Jenkins, 1980). The lack of difference in canopy cover measured at 10 m is further evidence to support this previous study in beaver foraging behavior. Therefore, it is possible that beavers are leaving the large, canopy filling trees and removing those smaller trees that may not have reached the upper canopy yet. Two of the more abundant tree species in both beaver and control sites were *Nyssa sylvatica, L. styraciflua*, both of which are usually present in the overstory greater than 50% of the time in the Coastal Plain region (Quarterman & Keever, 1962). *Quercus nigra, Q. laurifolia,* and *Pinus taeda* were also high in abundance and they are characterized as being present in the overstory 61-80%. The tree composition of this study resembles later successional stages described for this region. Pines are succeeded by hardwoods, which then show an increase in shared dominance of the overstory (Quarterman & Keever, 1962). Woody vegetation can become established regardless of the density of overstory cover (Hoffman, 1996). The tree that was most abundant in beaver sites, *Acer rubrum*, is shade tolerant and is a prolific sprouter. The seedlings are more tolerant than mature trees and can live in the understory for many years. The woody seedlings that were most abundant close to shore were the same species as those large trees further from shore and composing the canopy. It is also possible that woody seedlings are better competitors than herbaceous vegetation. This could be an explanation as to why there was no difference in canopy cover, yet there was a higher abundance of woody seedlings closer to shore.

The second objective of this study was to assess the relative abundance of non-native to native vegetation. The results of this study indicated that beaver-modified sites had no greater chance of containing exotics than control sites, and overall exotic species were rare in both locations. Exotic plant species are thought to exhibit increased growth in their introduced range instead of allocating energy to other attributes such as herbivore defense (Blossey & Notzold, 1995; Maron & Vila, 2001; Wolfe, 2002). Invasions from exotic species have also been positively correlated with resource enrichment (Huenneke et al., 1990). One resource essential to plant growth, nitrogen, has been found to be in greater abundance in the water around embankments as a result of beaver disturbance (Pastor & Naiman, 1992). The second most abundant exotic species in this study was Japanese honeysuckle (*Lonicera japonica*). This species can grow rapidly by nutrient enrichment not only because it is an exotic but also because it is a vine. This is because vines allocate little investment in structural support and this allows them to put more energy towards rapid growth. Diversity of exotic invaders can increase with the magnitude of the disturbance (Vujnovic, 2002). While beavers are known to create a disturbance, and it could be hypothesized that invasions will increase with this animal, the values for richness and abundance of exotics for this study were very low and thus conclusions cannot be decisively stated.

The two most common exotic invasive plants in this study were Chinese privet (*Ligustrum sinense*) and Japanese honeysuckle (*Lonicera japonica*). These species are numbers two and three of the top 10 pest plants in Georgia (Murphy, 2005). Chinese privet prefers moist habitats and Japanese honeysuckle commonly invades right-of-ways; both are shade tolerant (Miller, 2003). Chinese privet provides valuable browse for white-tailed deer (*Odocoileus virginianus*) (Stromayer et al., 1998) and, through personal observation, also is used by beaver. While the extent of use is unknown, beavers do transport this species to the water. The richness and abundance of exotics in this study was relatively small so the species that were present may have recently invaded the area and the effects have yet to create a measurable impact. In this study, beavers do not appear to facilitate the colonization of exotic plant species, but beavers may assist the range expansion of exotic plants.

Forest composition should change over time if the probability of an attack on a particular plant exceeds the probability of replacement (Fryxell, 2001). Studies have shown that beaver maintain ecosystems in an early stage of succession (Pastor & Naiman, 1992). Early successional species have high reproductive rates and beavers in the south eat a greater variety of food than the north (Roberts & Arner, 1984). Therefore, the probability of attack in southern beaver habitats may not exceed the probability of replacement; hence, species composition between beaver-modified and control sites could be expected to be similar. The sites for this study were generally abundant in *A. rubrum, L. styraciflua, P.taeda,* and *Quercus* spp. Past studies have shown that of all these species are utilized by beavers (Jenkins, 1975; Roberts & Arner, 1984; Gallant et al., 2004). However, the level of selectivity varies greatly by location. Jenkins (1975) found that pines had a greater frequency of uncut stems than those cut, while oaks and maples had generally equal frequency with moderate oscillations. In the study by Gallant et al. (2004) the selectivity of most conifer trees were low while *A. rubrum* had moderate to high selectivity by beaver. Conversely, *A. rubrum* was found to be avoided and can potentially be used as a deterrent to beaver (Müller-Schwarze et al., 1994). However, because the current study did not look specifically at cut stems direct comparisons with the literature on utilization cannot be made, but my own observations indicated that the species mentioned were used by beaver. The only other study conducted in the southern United States (Roberts & Arner, 1984) found that wood was 53% of the yearly total of beaver consumption. Thus, if beaver density is low and consumable wood is high then there may not be many measurable differences between those areas with and without beavers.

A second explanation for composition not being different between site types may be that the beaver sites were relatively new. This study was focused on active beaver sites but did not take into account the age of individual sites. In addition, beaver density in this area is probably low, meaning that there is not much pressure being exerted on the abiotic environment. Assuming that all stream length surveyed was habitable to beaver, then the density would be 0.07 colonies/km. This is a high estimate of habitable area, so if only half of the stream kilometers surveyed (61.25 km) were habitable, then site density would be 0.15 colonies/km. This number is still very low when compared to other studies where the average density was approximately 0.6-0.7 colonies/km (Müller-Schwarze & Schulte, 1999). Similarly, Snodgrass (1997) found much lower rates of water impoundment by beavers in the Upper Coastal Plain of South Carolina compared to similar study in Minnesota. It may be possible that as the age of beaver-modified sites and density of beavers increases, the composition will gradually change to more mesic, non-preferred foraging species and further differentiate from control sites.

While beaver-modified and control sites contained very similar species, one species of vine, partridgeberry (*Mitchella repens*), was exclusive to beaver-modified sites. This particular species requires moist soil and shade, and it is usually associated with conifer trees (Taylor, 1998). Loblolly pine (*Pinus taeda*) does best on land that has plenty of moisture (Harlow et al., 1996) and was more frequent at beaver sites. In this study, partridgeberry was located under loblolly pines (personal observation). When a disturbance occurs with nutrient enrichment, the vegetation has traits that are associated with maximum allocation to growth, such as climbing or vine growth forms (Lake & Leishman, 2004). This study found that there was no difference in community composition, yet there was evidence to support that beavers may play a role in creating a unique habitat.

Succession can be divided into two different types: allogenic and autogenic (Barbour et al., 1999). The North American beaver is an organism that causes autogenic succession through its activities as an ecosystem engineer (Jones et al., 1994). In the past, beavers have been generalized as having the same impact regardless of region. The current study provides evidence that this generalization may not be correct. There are few published reports on community effects of beavers in the southern United States (Snodgrass, 1997; Wright et al., 2002). These studies showed that the level of activity and therefore impact of beaver in this region does differ from northern regions of North America. For example, a study conducted in South Carolina found that beavers impounded fewer streams than in their northern counterpart (Snodgrass, 1997). Snodgrass showed that the North American beaver does significantly affect certain factors of the vegetative community in southeastern regions of the United States by altering abundance and diversity at varying distances from shore. Yet, the presence of beavers did not result in a difference in species composition compared to nearby areas devoid of current beaver presence. The tree species present, which were relatively the same at both types of sites, resembled the characteristic species present in late successional stages of the Coastal Plain region. The sandy, well-drained soils of the southern Coastal Plain have been hypothesized to result in quick recovery of the riparian forest (Snodgrass, 1997), whereas in northern regions, such as New York State, no areas disturbed by beaver returned to forest even after beaver left the area (Remillard et al., 1987). This suggests that biotic influences alone will not dictate what happens to a community.

The current study investigated whether the North American beaver altered plant community structure by influencing plant richness, diversity, abundance or composition. There are many factors that contribute to the establishment and changes of a plant community. The species of plants that will grow will differ between regions because of such abiotic factors as temperature, rainfall, topography, and latitude (Terbourgh, 1992). Within a community, species of vegetation can be determined by the nutrients in the soil, the amount of space and light available, density of the vegetation, and the composition of herbivores (Terbourgh, 1992; Barbour et al., 1999). In the Coastal Plains of Georgia sandy soils are characteristic, which make drainage and distance from the water table crucial to this community (Quarterman & Keever, 1962). The current study provides some evidence that beavers may play an important role in determining the vegetative structure of their community, yet beavers in the Coastal Plains of Georgia appear to have a different type and lesser extent of impact compared to beavers in more northerly regions of North America.

The results of the current study have stimulated additional hypotheses for investigation. The variable of canopy cover should be further examined perhaps by collecting measurements at various distances from shore rather than just one as done herein. In addition, ground cover measurements also would be valuable in conjunction with the canopy cover measures. As previously stated, collecting data on cut and uncut woody trees would give a more direct measure of beaver impact and selection on large woody vegetation (such data would not be possible for small woody or herbaceous vegetation unless beavers were observed directly as done by Fryxell and Doucet (1993) in Canada). To further distinguish the influence beavers have on their habitat, relevant abiotic variables could be measured, such as temperature, soil moisture, and soil nutrients. Because many factors can affect a given habitat it is important to determine how much influence can be attributed directly or indirectly to herbivores such as the beavers.

REFERENCES

Aleksiuk, M. (1970). The seasonal food regime of Arctic beavers. *Ecology*, 51, 264-270.

Baker, H.G. (1974). The evolution of weeds. *Annual Review of Ecology and Systematics*, 5, 1-24.

Barbour, M.G, Burk, J.H., Pitts, W.D., Gilliam, F.S., & Schwartz, M.W. (1999). *Terrestrial plant ecology* (3rd ed.). New York: Addison Wesley Longman, Inc.

Barnes, W.J., & Dibble, E. (1988). The effects of beaver in riverbank forest succession. *Canadian Journal of Botany*, 66, 40-44.

Basey, J.M., Jenkins, S.H., & Busher, P.E. (1988). Optimal central place foraging by beavers: tree size selection in relation to defensive chemicals of quaking aspen. *Oecologia*, 76, 278-282.

Blair, A.C., & Wolfe, L.M. (2004). The evolution of an invasive plant: and experimental study with *Silene latifolia*. *Ecology*, 85, 3035-3042.

Blossey, B., & Notzold, R. (1995). Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology*, 83, 887-889.

Brower, J.E., Zar, J.H., & von Ende, C.N. (1990). *Field and laboratory methods for general ecology* (4th ed.). New York: WCB/McGraw-Hill.

Clements, F.E. (1916). Plant succession: an analysis of the development of vegetation. Washington, D.C.: Carnegie Institution of Washington Publication 242.

Clements, F.E. (1936). Nature and structure of the climax. *The Journal of Ecology*, 24, 252-284.

Cowles, H.C. (1910). The causes of vegetational cycles. *Annals of the Association of American Geographers,* 1, 3-20.

Donker, N.T., & Fryxell, J.M. (1999). Impact of beaver foraging on structure of lowland boreal forests of Algonquin Provincial Park, Ontario. *Forest Ecology and Management,* 118, 83-92.

Dytham C. (1999). *Choosing and using statistics, a biologist's guide*. Oxford: Blackwell Science, Ltd.

Fryxell, J.M. (2001). Habitat suitability and source-sink dynamics of beaver. *Journal of Animal Ecology*, 70, 310-316.

Fryxell, J.M., & Doucet, C.M. (1993). Diet choice and the functional response of beavers. *Ecology*, 74, 1297-1306.

Gallant, D., Berube, C.H., Tremblay, E., & Vasseur, L. (2004). An extensive study of the foraging ecology of beavers (*Castor canadensis*) in relation to habitat quality. *Canadian Journal of Zoology*, 82, 922-933.

Georgia Department of Natural Resources, Wildlife Resources Division. Beaver management and control in Georgia. June 23, 2003. http://georgiawildlife.dnr.state.ga.us/content/displaycontent.asp?txtDocument=227&txtPage=1/

Gordon, D.R. (1998). Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. *Ecological Applications*, 8, 975-989.

Grover, A.M., & Baldassarre, G.A. (1995). Bird species richness within beaver ponds in south-central New York. *Wetlands*, 15, 108-118.

Harlow, W.M., Harrar, E.S., Hardin, J.W., & White, F.M. (1996). *Textbook of dendrology*. New York: McGraw-Hill, Inc.

Hobbs, R.J., & Huenneke, L.F. (1992). Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology*, 6, 324-337.

Hoffman, W.A. (1996). The effects of fire and cover on seedling establishment in a neotropical savanna. *Journal of Ecology*, 84, 383-393.

Hoover, S.R., & Parker, A.J. (1991). Spatial components of biotic diversity in landscapes of Georgia, USA. *Landscape Ecology*, 5, 125-136.

Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A., & Vitousek, P.M. (1990). Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology*, 71, 478-491.

Jenkins, S.H. (1975). Food selection by beavers: A multidimensional contingency table analysis. *Oecologia*, 21, 157-173.

Jenkins, S.H. (1980). A size distance relation in food selection by beavers. *Ecology*, 61, 740-746.

Jenkins, S.H., & Busher, P.E. (1979). *Castor canadensis*. Mammalian Species, 120, 8pp.

Johnson, D.R., & Chance, D.H. (1974). Pre-settlement overharvest of upper Columbia River beaver populations. *Canadian Journal of Zoology*, 52, 1519-1521.

Johnston, C.A., & Naiman, R.J. (1990). Browse selection by beaver: effects on riparian forest composition. *Canadian Journal of Forest Research*, 20, 1036-1043.

Jones, C.G., Lawton, J.H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69, 373-386.

Lake, J.C., & Leishman, M.R. (2004). Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biological Conservation*, 117, 215-226.

Lande, R. (1996). Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*, 76, 5-13.

Mackie, G. (2004). *Applied Aquatic Ecosystem Concepts* (2^{nd} ed.). Dubuque, Iowa: Kendall/Hunt Publishing Company.

Maron, J.L., & Vila, M. (2001). When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos*, 95, 361-373.

Metts, B.S., Lanham, J.D., & Russell, K.R. (2001). Evaluation of herpetofaunal communities on upland stream and beaver-impounded streams in the upper Piedmont of South Carolina. *American Midland Naturalist* 145, 54-65.

Miller, J.H. (2003). *Nonnative invasive plants of southern forests*. Asheville, North Carolina: United States Department of Agriculture, Forest Service.

Mitsch, W.J., & Gosselink, J.G. (1993). *Wetlands* (2^{nd} ed.). New York: John Wiley & Sons, Inc.

Müller-Schwarze, D., & Schulte, B.A. (1999). Behavioral and ecological characteristics of a "climax" population of beaver (*Castor canadensis*). In: *Beaver Protection, Management, and Utilization in Europe and North America* (PE Busher and RM Dziecidowski, eds.), pp. 161-177. Plenum Press, NY.

Müller-Schwarze, D., Schulte, B.A., Sun, L., Müller-Schwarze, A., & Müller-Schwarze, C. (1994). Red maple (*Acer rubrum*) inhibits feeding by beaver (*Castor canadensis*). *Journal of Chemical Ecology*, 20, 2021-2034.

Murphy, T.R. (2005). Proposed exotic pest plant species for Georgia. *Georgia Exotic Pest Plant Council*. Retrieved January, 2005, http://www.gaeppc.org/exotalk1.html.

Naiman, R.J., Melillo, J.M., & Hobbie, J.E. (1986). Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology*, 67, 1254-1269.

Naiman, R.J., Johnston, C.A., & Kelley, J.C. (1988). Alteration of North American streams by beaver. *Bioscience*, 38, 753-762.

Pastor, J., & Naiman, R.J. (1992). Selective foraging and ecosystem processes in boreal forests. *The American Naturalist*, 139, 690-705.

Pollock, M.M., Naiman, R.J., & Hansley, T.A. (1998). Plant species richness in riparian wetlands – a test of biodiversity theory. *Ecology*, 79, 94-105.

Quarterman, E., & Keever, C. (1962). Southern mixed hardwood forest: climax in the southeastern Coastal Plain, USA. *Ecology*, 32, 167-185.

Remillard, M., Gruendling, G.K., & Bogucki, D.J. (1987). Disturbance by beaver (*Castor canadensis* KUHL) and increased landscape heterogeneity. In M.G. Turner (ed.) Landscape Heterogen-eity and Disturbance, Ecological Studies, 64, 103-122. New York: Springer-Verlag.

Roberts, T.H., & Arner, D.H. (1984). Food habits of beaver in east-central Mississippi. *Journal of Wildlife Management*, 48, 1414-1419.

SAS Institute, Inc. (1994). Cary, North Carolina.

Schulte, B.A., & Müller-Schwarze, D. (1999). Understanding North American beaver behavior as an aid to management. In: *Beaver Protection, Management, and Utilization in Europe and North America* (PE Busher and RM Dziecidowski, eds.), pp. 109-127. Plenum Press, NY.

Snodgrass, J.W. (1997). Temporal and spatial dynamics of beaver-created patches as influenced by management practices in a south-eastern North American landscape. *Journal of Applied Ecology*, 34, 1043-1056.

Sokal, R.R., & Rohlf, F.J. (1995). *Biometry* (3rd ed.). New York: W.H. Freeman and Company.

Stromayer, K.A., Warren, R.J., Johnson, A.S., Hale, P.E., Rogers, C.L., & Tucker, C.L. (1998). Chinese privet and the feeding ecology of white-tailed deer: the role of an exotic plant. *Journal of Wildlife Management*, 62, 1321-1329.

Taylor, W.K. (1998). *Florida wildflowers in their natural communities*. Gainesville, Florida: University Press of Florida.

Terborgh, J. (1992). *Diversity and the tropical rainforest*. New York: Scientific American Library.

US Fish & Wildlife Service. (1988). *National list of vascular plant species that occur in wetlands*. US Fish & Wildlife Service Biological Report 88.

Vujnovic, K., Wein, R.W., & Dale, M.R.T. (2002). Predicting plant species diversity in response to disturbance magnitude in grassland remnants of central Alberta. *Canadian Journal of Botany*, 80, 504-511.

Wilcove, D.S., Rothstein, J., Dubrow, A.P., & Losos, E. (1998). Quantifying threats to imperiled species in the United States. *BioScience*, 48, 607-615.

Williams, J.D., & Meffe, G.K. (1998). Status and trends of the nation's biological resources: nonindigenous species. U.S. Department of the Interior, U.S. Geologic Survey, pp. 117-129.

Wolfe, L.M. (2002). Why alien invaders succeed: support for the escape-from-enemy hypothesis. *The American Naturalist*, 160, 705-711.

Wright, J.P., Jones, C.G., & Flecker, A.S. (2002). An ecosystem engineer, the beaver, increases species richness at the landscape level. *Oecologia*, 132, 96-101.

Wright, J.P., Flecker, A.S., & Jones, C.G. (2003). Local vs. landscape controls on plant species richness in beaver meadows. *Ecology*, 84, 3162-3173.

Table 1. An example of a split-plot design for richness of herbaceous vegetation. There were two site types, beaver and control, and four distances (5, 10, 15 and 20 m) from shore. A total of nine matched sites were examined in Bulloch County, Georgia during the spring and summer 2004.

Whole Plot

Variable	**df**	**MS**	**F**
Site type	1	0.77	0.32
Error	8	2.40	

Subplot

Variable	**df**	**MS**	**F**
Distance	3	0.39	3.90
Distance*Site type	3	0.23	2.27
Error	48	0.10	

Table 2. Wetland classification of herbaceous and woody vegetation as per U.S. Fish & Wildlife Service (1988).

Wetland Type	Description	# of Species at Beaver Sites	# of Species at Control Sites
Obligate Wetland	Occurs almost always under natural conditions in wetlands	3[a]	6[a]
Facultative Wetland	Usually occurs in wetlands, but occasionally found in non-wetlands	10[c]	11[d]
Facultative	Equally likely to occur in wetlands or non-wetlands	8[e]	8[e]
Facultative Upland	Usually occurs in non-wetlands, but occasionally found on wetlands	3[f]	5[g]
Obligate Upland	Occurs in wetlands in another region, but occurs almost always under natural conditions in non-wetlands in the regions specified	0	0

[a] Osmunda cinamonea, Woodwardia areolata, Taxodium distichum

[b] Iris virginiana, Osmunda cinamonea, Woodwardia areolata, Taxodium distichum, Cephalanthus occidentalis, Salix nigra

[c] Acer rubrum, Alnus serrulata, Arundinaria gigantea, Clethra alnifolia, Ilex coracea, Ilex glabra, Liriodendron tulipifera, Lyonia lucida, Persea borbonia, Quercus laurifolia

[d] Acer rubrum, Alnus serrulata, Arundinaria gigantea, Betula nigra, Clethra alnifolia, Impatiens capensis , Ilex opaca, Liriodendron tulipifera, Lyonia lucida, Persea borbonia, Quercus laurifolia

[e] Ligustrum sinesense, Parthencissus quinquefolia, Quercus nigra, Rubus trivialis, Smilax glauca, Smilax rotundifolia, Vitis rotundifolia, Pinus taeda

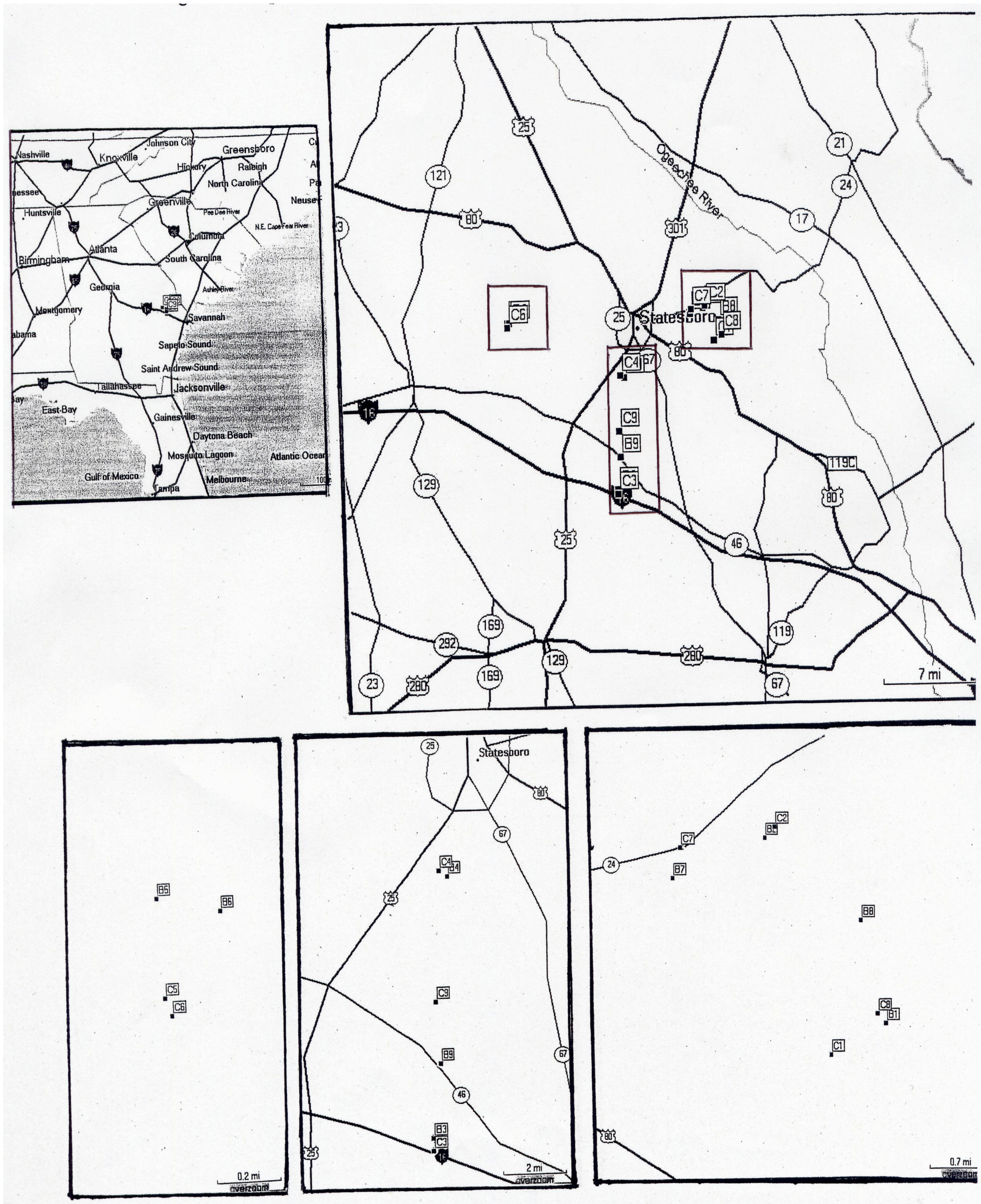
[f] Fraxinus caroliniana, Pteridium aquifolia, Smilax smallii

[g] Fraxinus caroliniana, Prunus serotina, Pteridium aquifolia, Smilax smallii, Solanum carolinense

Table 3. Principle Components Analysis of large woody vegetation of beaver-modified and control sites in Bulloch County, Georgia. Principle components indicate the amount of variability accounted for by woody vegetation.

Variable	PC1	PC2
Eigenvalue	3.1508	2.7564
Percent	15.0037	13.1257
CumPercent	15.0037	28.1294
Acer rubrum	-0.2524	0.0353
Alnus serrulata	0.2752	0.4017
Fraxinus caroliniana	-0.2304	0.1271
Ligustrum sinense	0.1912	-0.0659
Liquidambar styraciflua	0.116	0.1237
Liriodendron tulipifera	0.3828	-0.1352
Magnolia virginica	-0.1146	-0.265
Myrica cerifera	-0.1447	-0.1549
Nyssa sylvatica	-0.1892	-0.1093
Persea borbonia	0.4412	0.1485
Pinus taeda	-0.0292	-0.0982
Platanus americana	0.3604	0.2161
Quercus laurifolia	-0.1266	0.387
Quercus nigra	0.1727	0.0722
Taxodium distichum	-0.2703	0.0949
Betula nigra	-0.1437	0.1755
Cephalanthos occidentalis	-0.1049	0.3917
Ilex opaca	-0.1812	0.4134
Magnolia grandiflora	0.0204	0.0089
Prunus serotina	0.0088	-0.1898
Salix nigra	0.1781	-0.2085

Figure 1. Map of study sites in Bulloch County, Georgia.



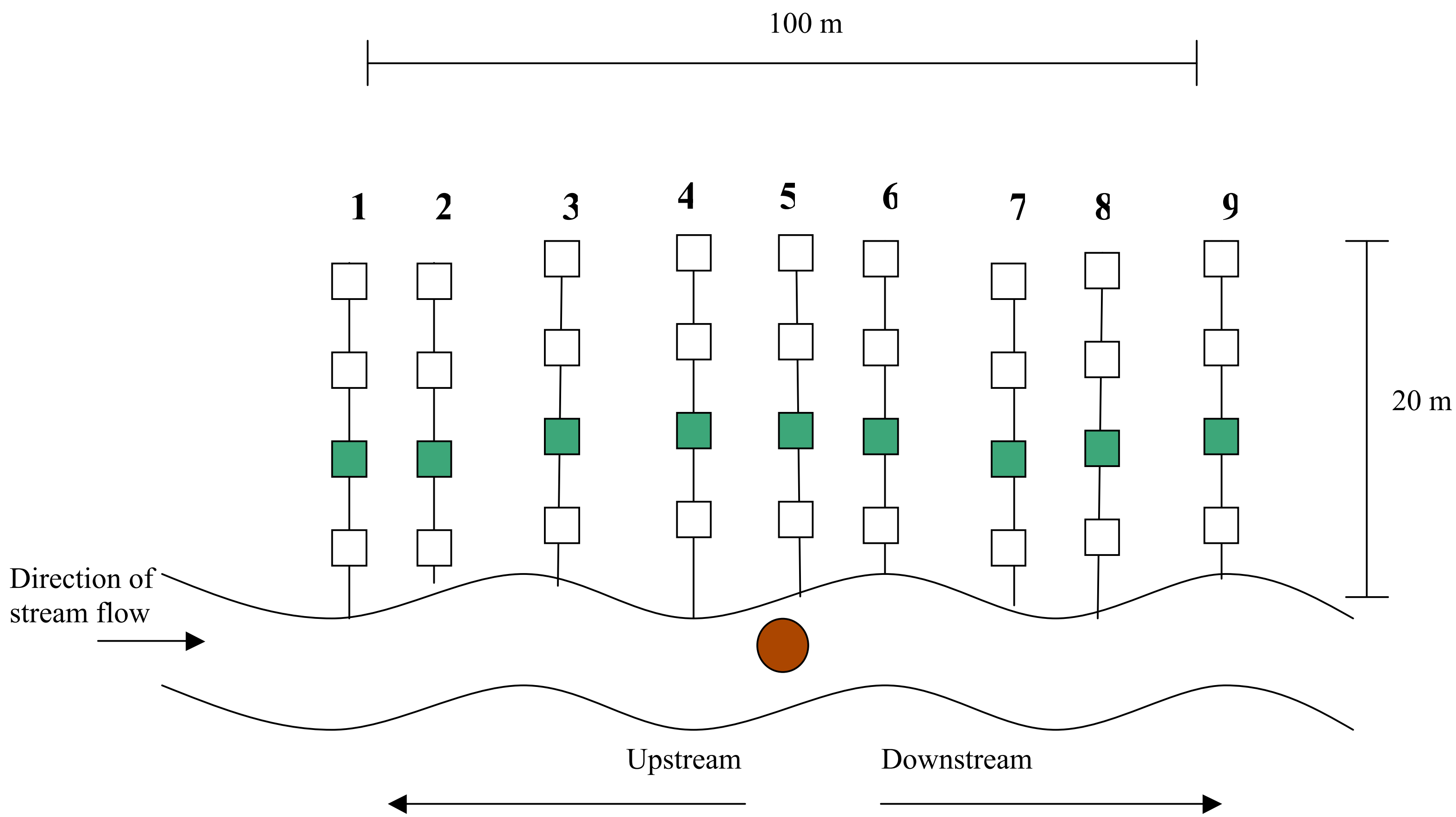


Figure 2. Diagram of vegetation survey method. Includes transects 1-9 and plots at 5 m, 10 m, 15 m, and 20 m indicated by the squares. Canopy cover measurements were taken at the 10 m distance from shore (the shaded squares) along each transect. Transect 5 represents the site of highest activity. Transects were placed at random, but at least 5 m apart. The circle represents the beaver lodge or the presence of the dam.

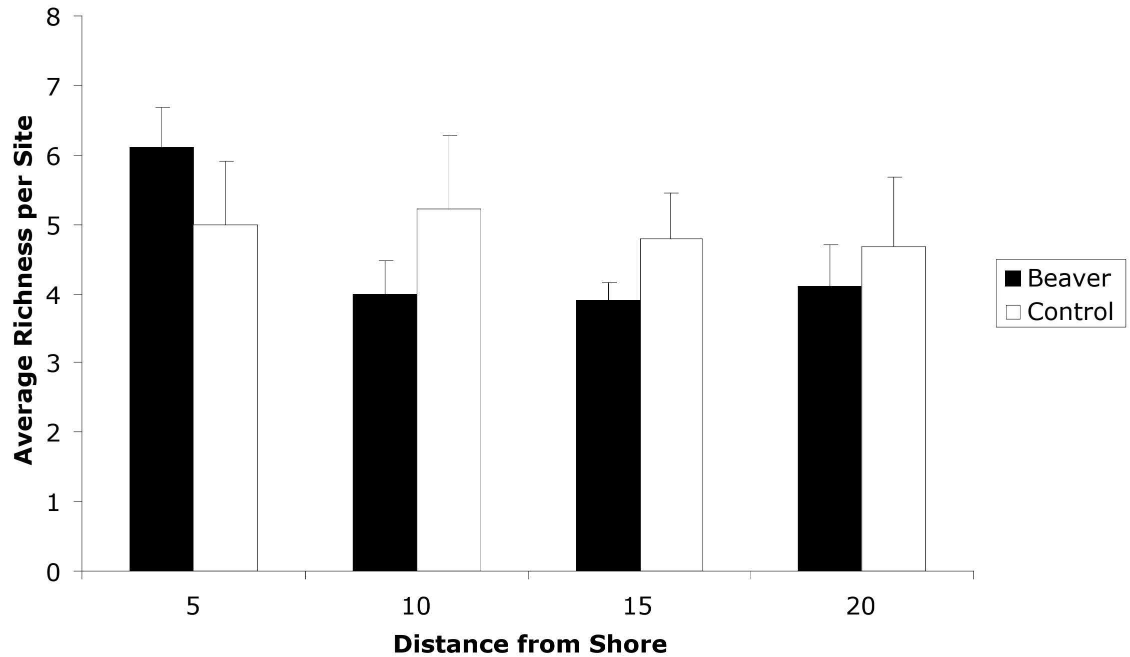


Figure 3. Average herbaceous vegetation richness measured at four distances from shore in beaver-modified (n=9) and control sites (n=9). Sites were sampled in Bulloch County, Georgia in 2004. Beaver sites had 4.5 ± 0.5 (average ± SE) species per distance and control sites contained 4.9 ± 0.9 species.

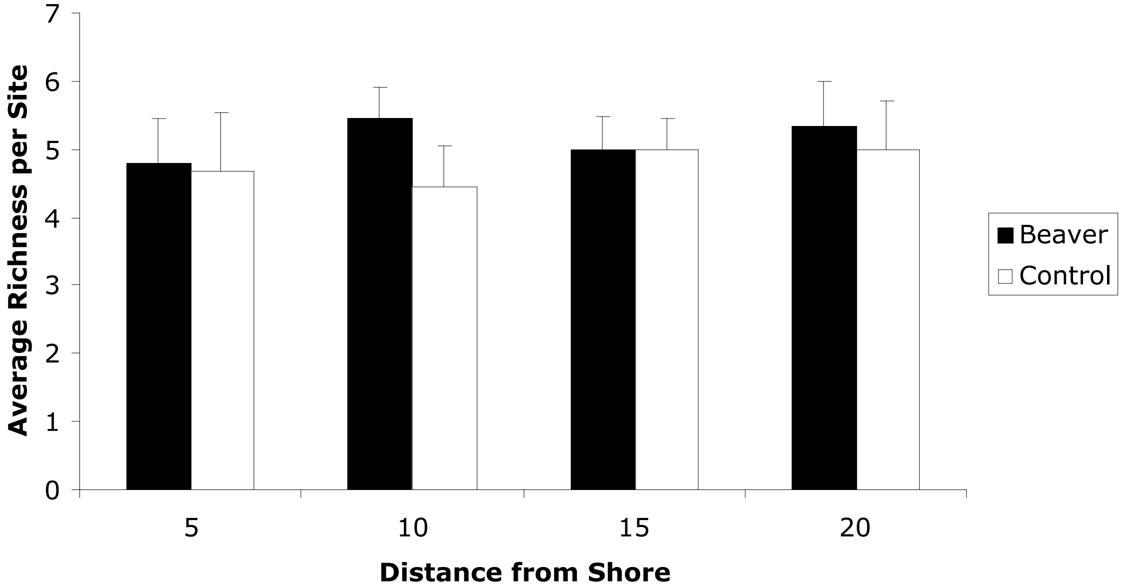


Figure 4. Average woody richness in 1 m^2 plots measured at four distances from shore in beaver-modified (n=9) and control sites (n=9). Sites were sampled in Bulloch County, Georgia in 2004. Beaver sites contained 5 ± 0.6 species per distance and control sites had 5 ± 0.7 species.

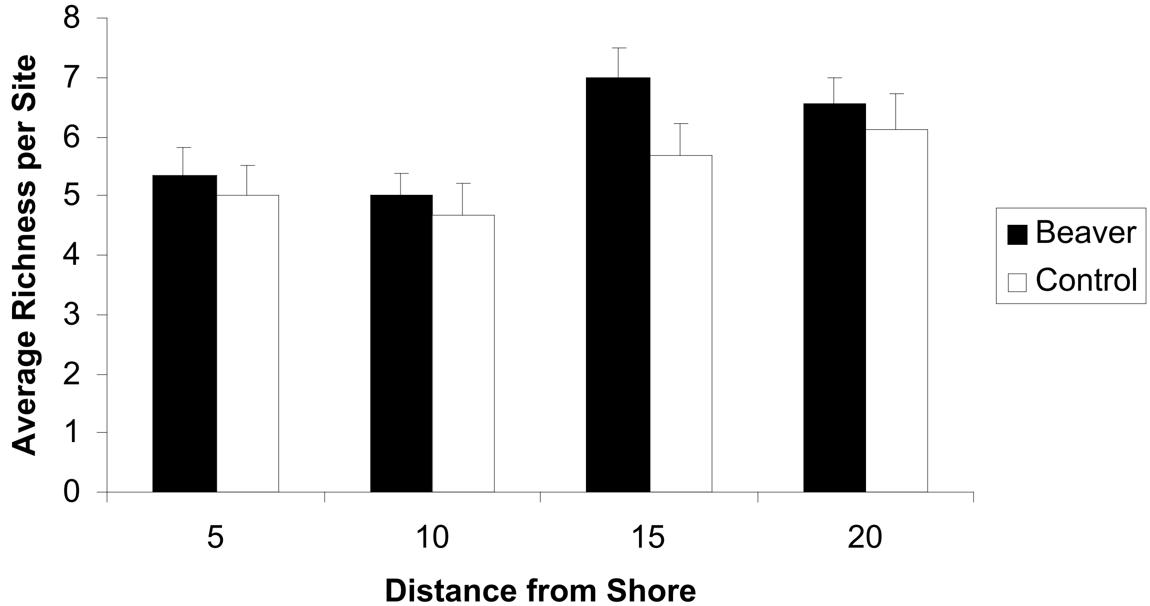


Figure 5. Average woody richness in 25 m^2 plots measured at four distances from shore in beaver-modified (n=9) and control sites (n=9). Sites were sampled in Bulloch County, Georgia in 2004. Beaver sites contained 6 ± 0.4 species per distance and control sites had 5.4 ± 0.6 species.

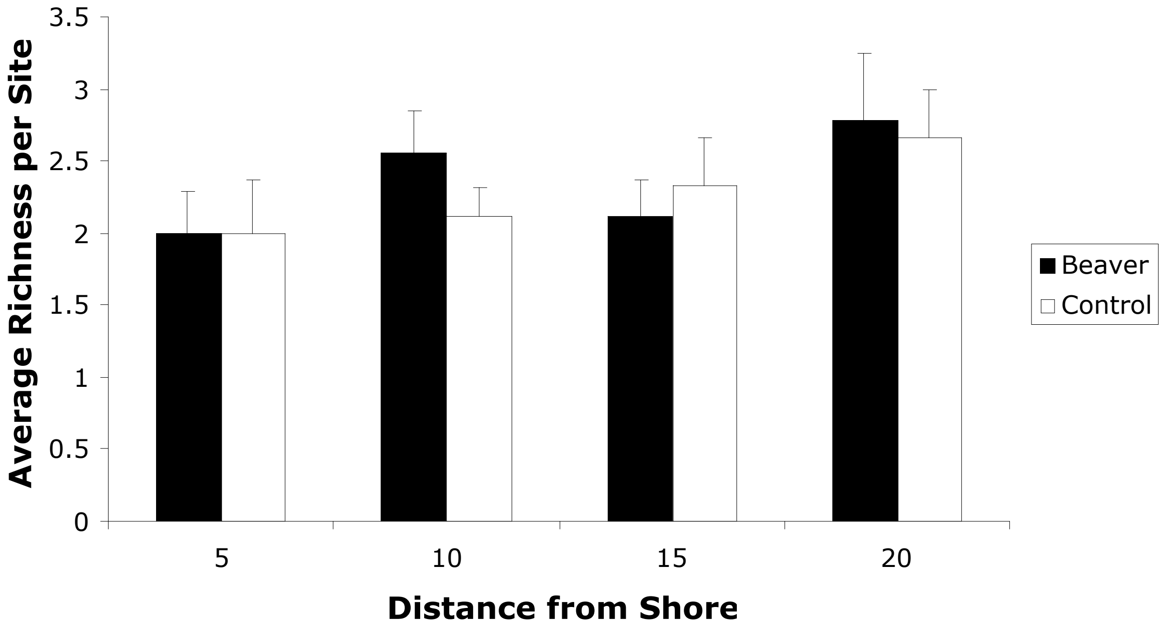


Figure 6. Average vine richness measured at four distances from shore in beaver-modified (n=9) and control sites (n=9). Sites were sampled in Bulloch County, Georgia in 2004. Beaver sites had an average of 2.4 ± 0.3 and control sites had 2.3 ± 0.31 species.

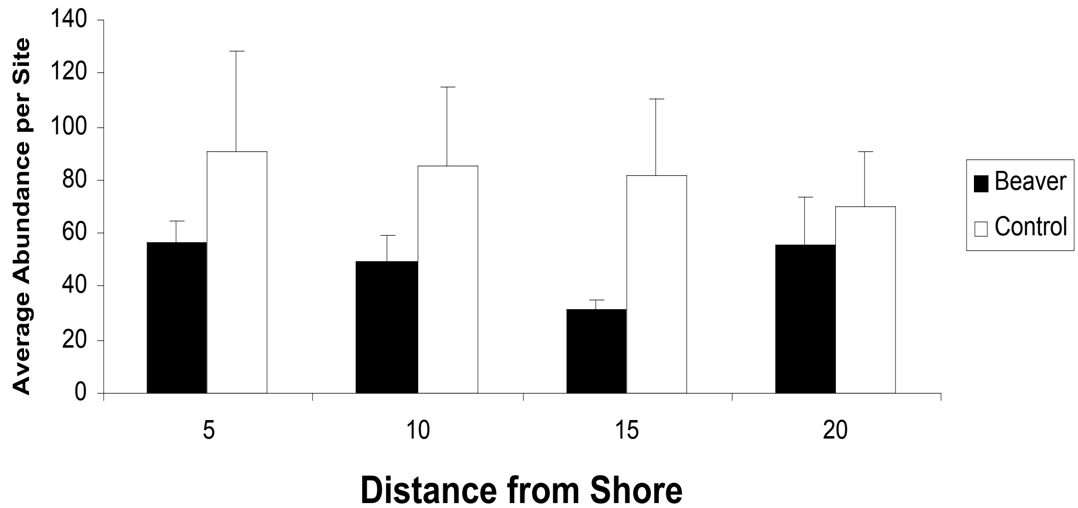


Figure 7. Average herbaceous vegetation abundance measured at four distances from shore in beaver-modified (n=9) and control sites (n=9). Sites were sampled in Bulloch County, Georgia in 2004. Beaver sites had an average of 48 ± 10 individuals and control sites had 82 ± 29 individuals. This apparent difference by site type (based on the mean values) resulted from extreme values for three sites (2 control and 1 beaver), see Fig. 8.

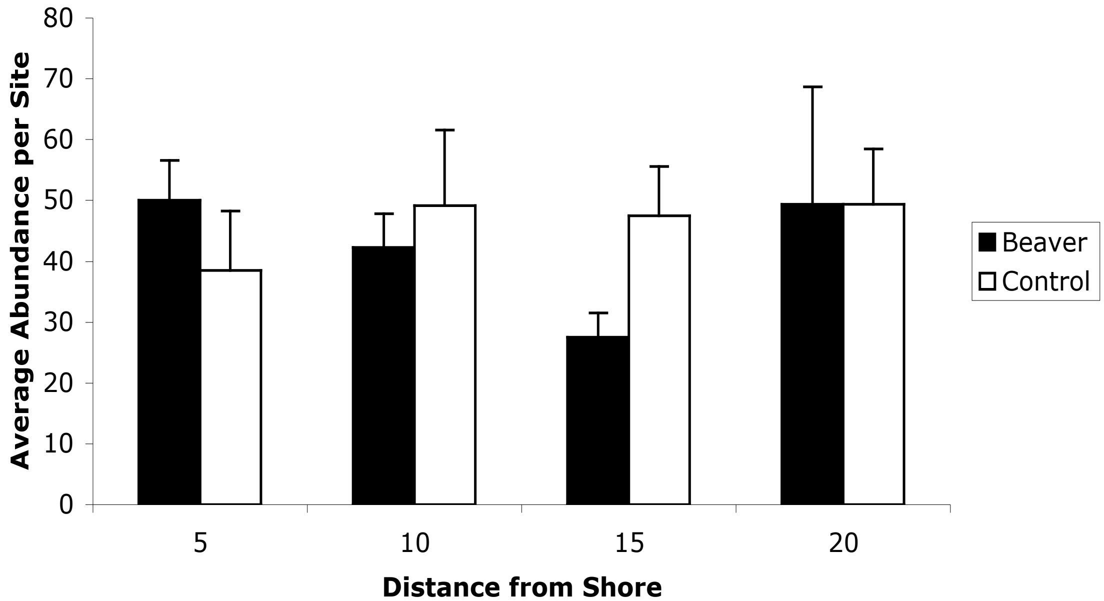


Figure 8. Average abundance for herbaceous vegetation when the outlier sites (2 beaver and 1 control) were removed from analysis. The differences became less dramatic with beaver sites having an average of 42 ± 8.9 individuals and control sites having 46 ± 9.8.

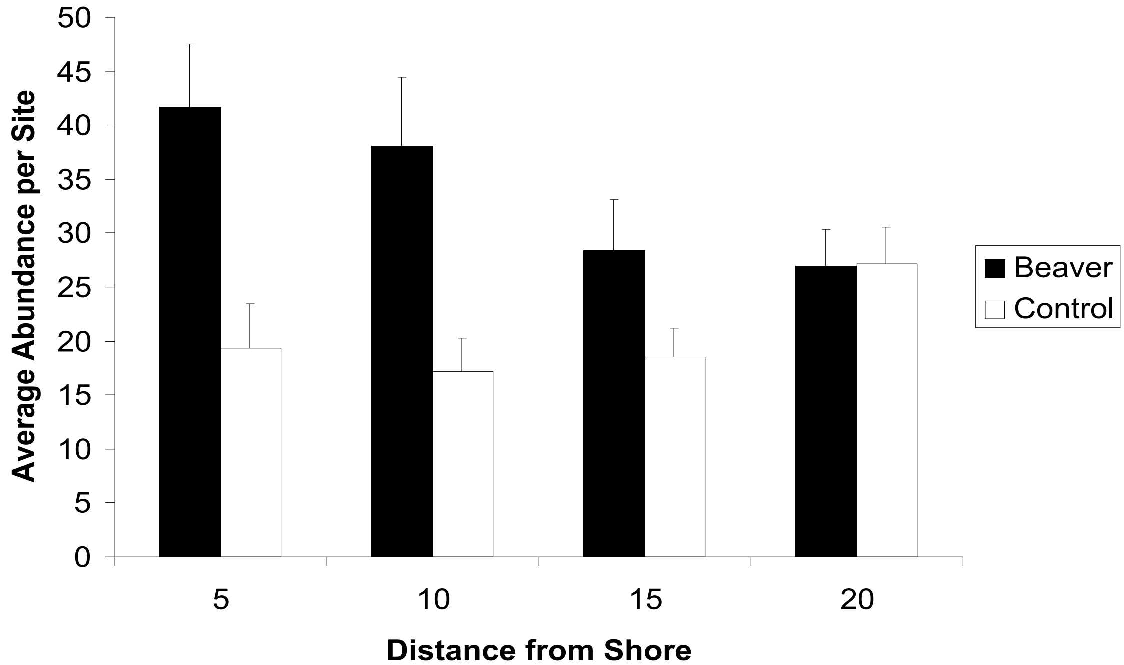


Figure 9. Average woody abundance in 1 m^2 plots measured at four distances from shore in beaver-modified (n=9) and control sites (n=9). Sites were sampled in Bulloch County, Georgia in 2004. Beaver sites have an average of 34 ± 5 individuals and control sites have 21 ± 3.3.

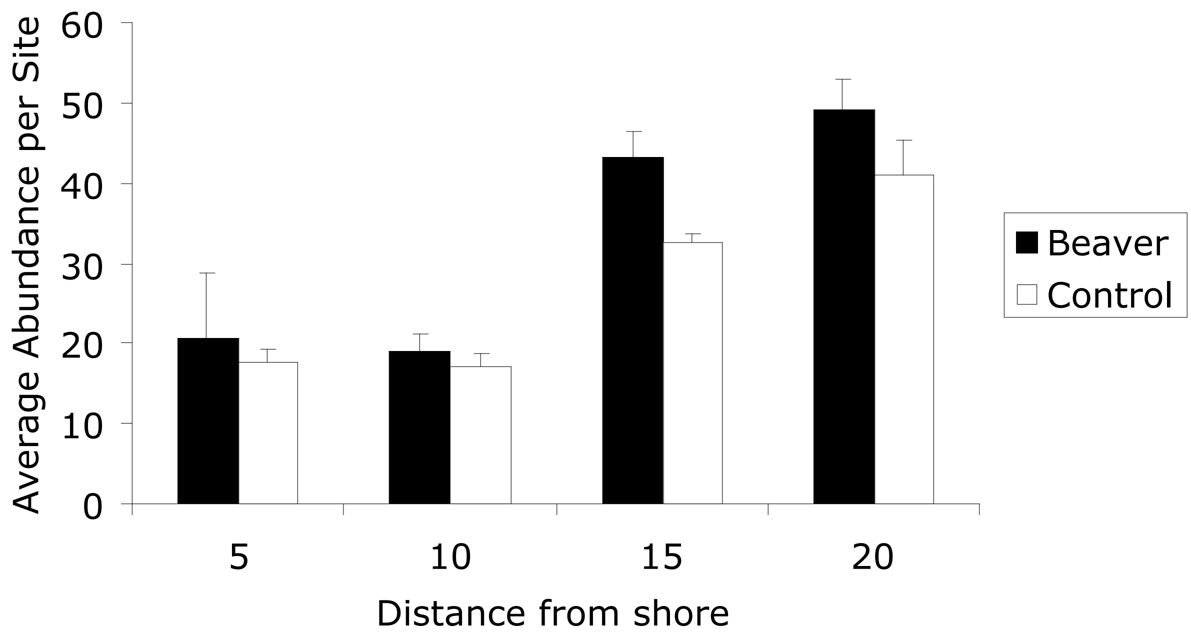


Figure 10. Average large woody vegetation abundance measured in 25 m^2 plots at four distances from shore in beaver-modified (n=9) and control sites (n=9). Sites were sampled in Bulloch County, Georgia in 2004. Average abundance for beaver sites was 33 ± 4.3 and 27 ± 2.2 for control sites.

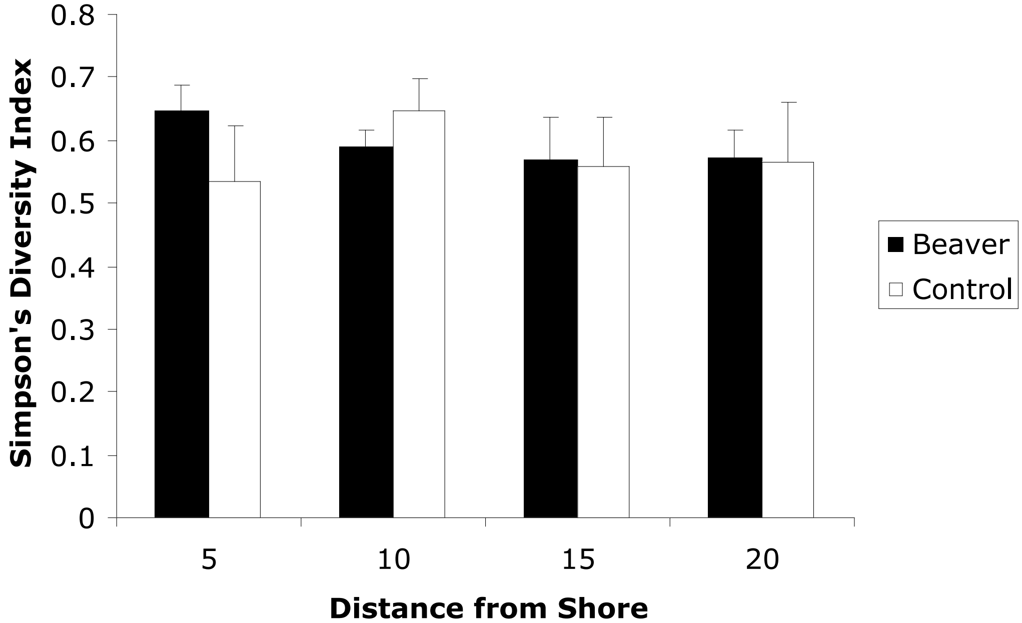


Figure 11. Diversity of herbaceous vegetation measured at four distances from shore in beaver-modified (n=9) and control sites (n=9). Sites were sampled in Bulloch County, Georgia in 2004. Average for beaver sites was 0.59 ± 0.05 and 0.58 ± 0.08 for control sites.

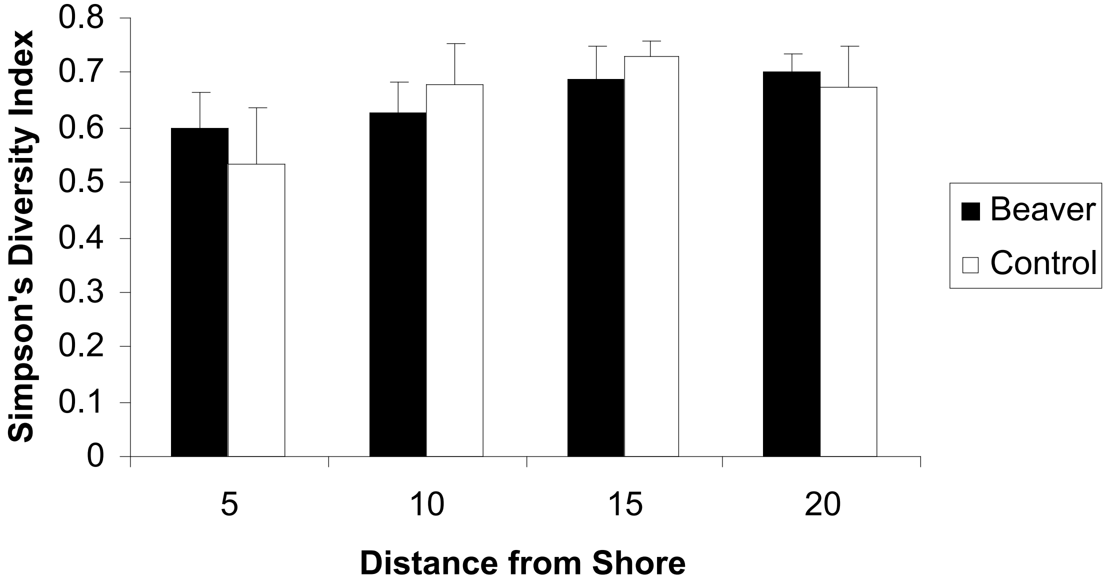


Figure 12. Diversity for small woody vegetation measured at four distances from shore in beaver-modified (n=9) and control sites (n=9). Sites were sampled in Bulloch County, Georgia in 2004. Average diversity for beaver sites was 0.65 ± 0.05 and 0.65 ± 0.07 for control sites.

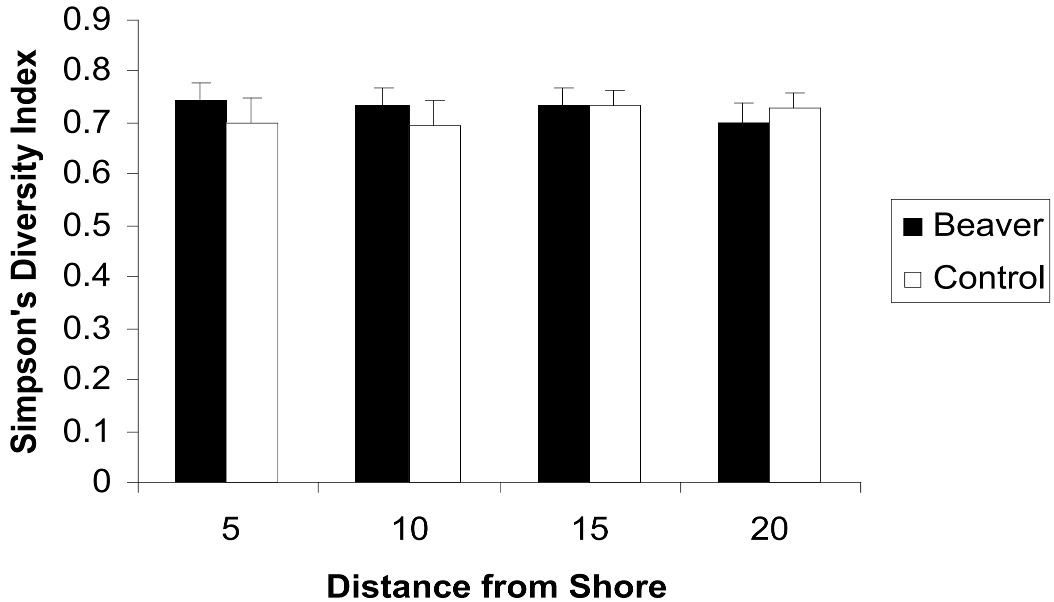


Figure 13. Diversity of large woody vegetation measured at four distances from shore in beaver-modified (n=9) and control sites (n=9). Sites were sampled in Bulloch County, Georgia in 2004. Average diversity for beaver sites was 0.73 ± 0.03 and 0.71 ± 0.04 for control sites.

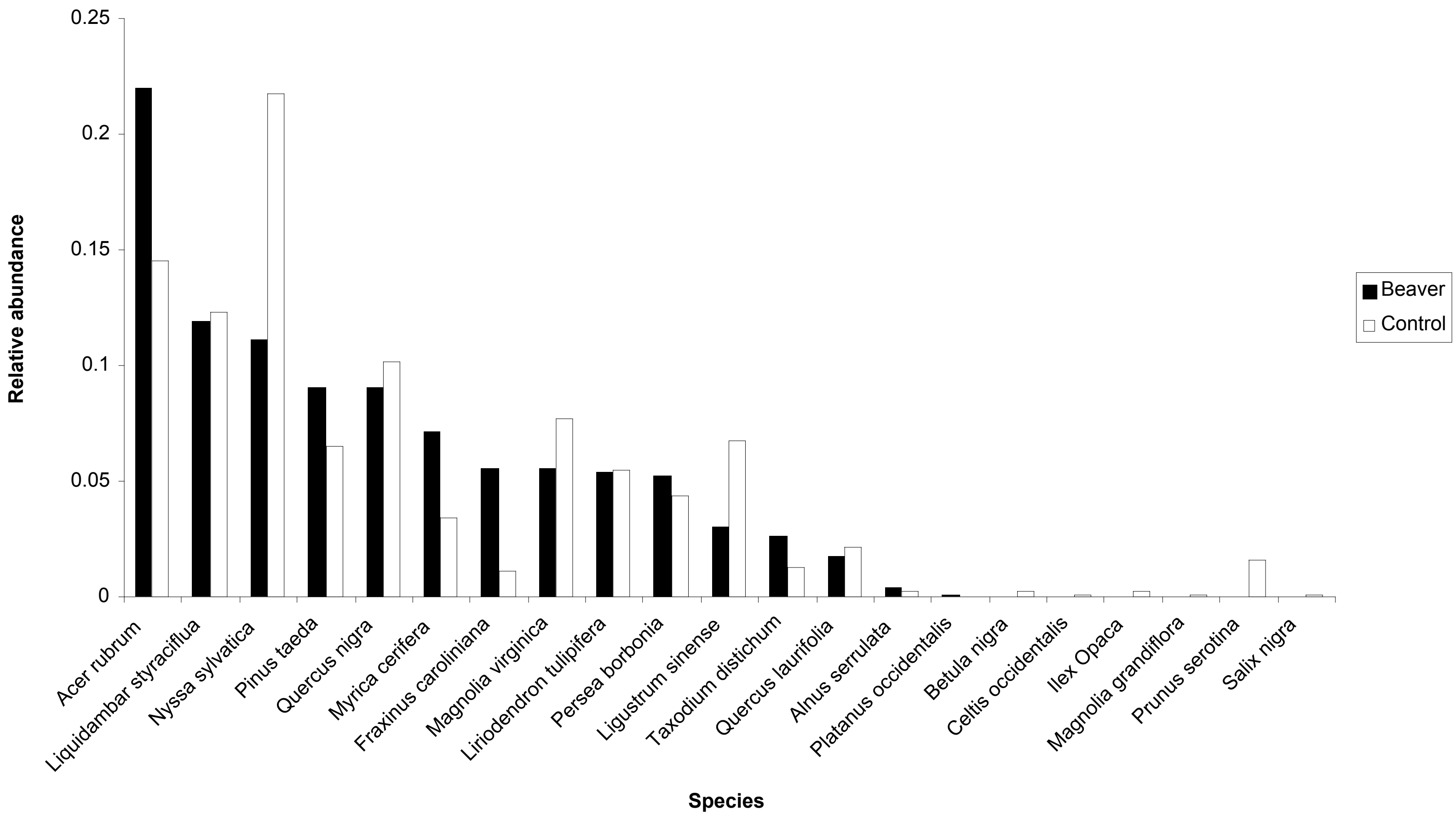


Figure 14. The relative abundance of all large woody vegetation measured in 25 m^2 plots for beaver-modified (n=9) and control (n=9) sites. Sites were sampled in Bulloch County, Georgia in 2004.

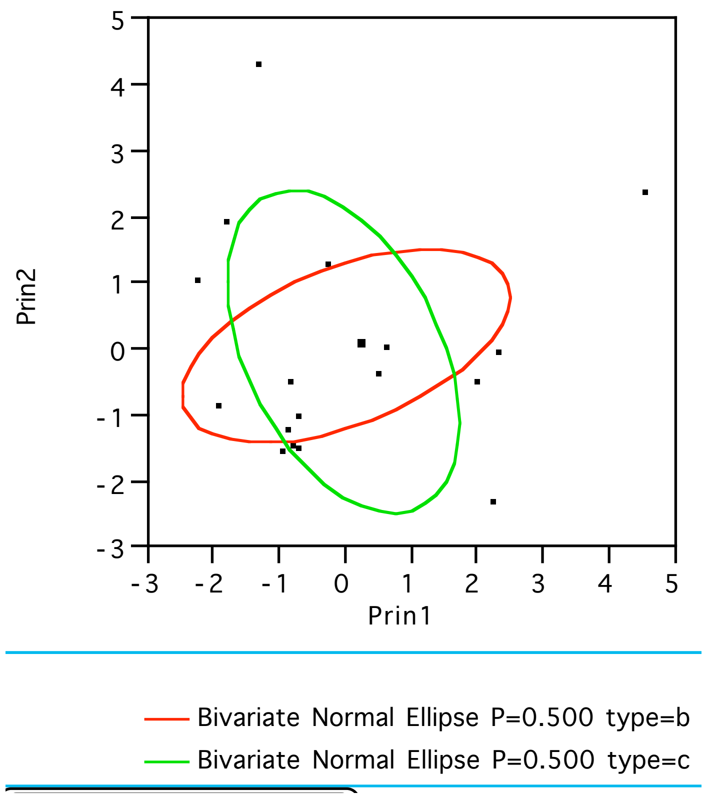


Figure 15. Principle Components Analysis performed on large woody vegetation with site type the grouping variable. Red group indicates beaver-modified and green group indicates controls. Principle component 1 has the highest positive values for the genus *Liriodendron* and *Persea* and the highest negative values for *Acer* and *Fraxinus* (see Table 3 for eigenvalues).

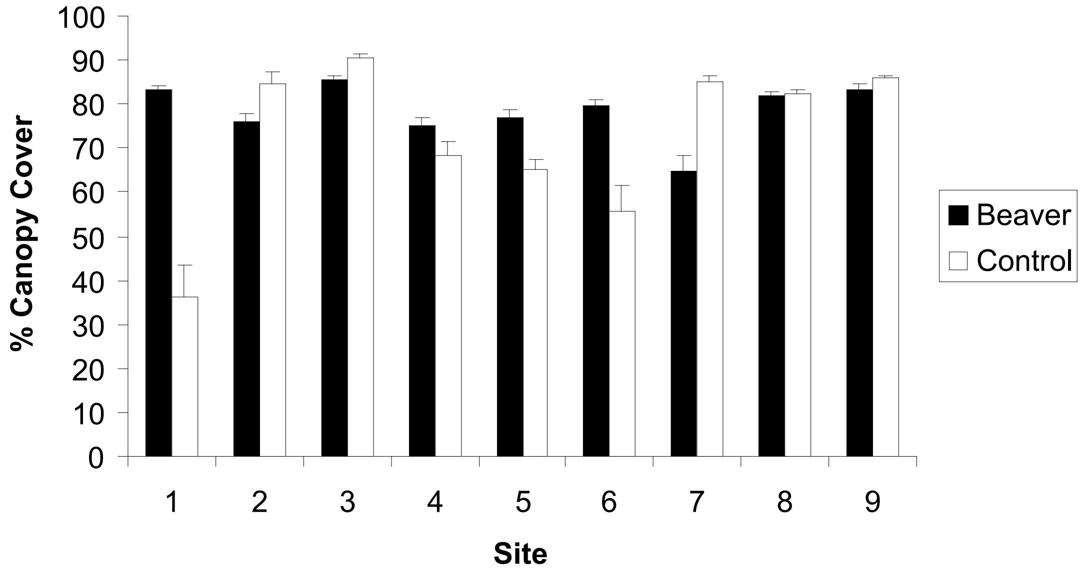


Figure 16. Canopy cover measurements for matched beaver-modified and control sites (n=9) measured at 10 m from the water's edge. Nine measurements were averaged for each site. Sites were sampled in Bulloch County, Georgia in 2004.

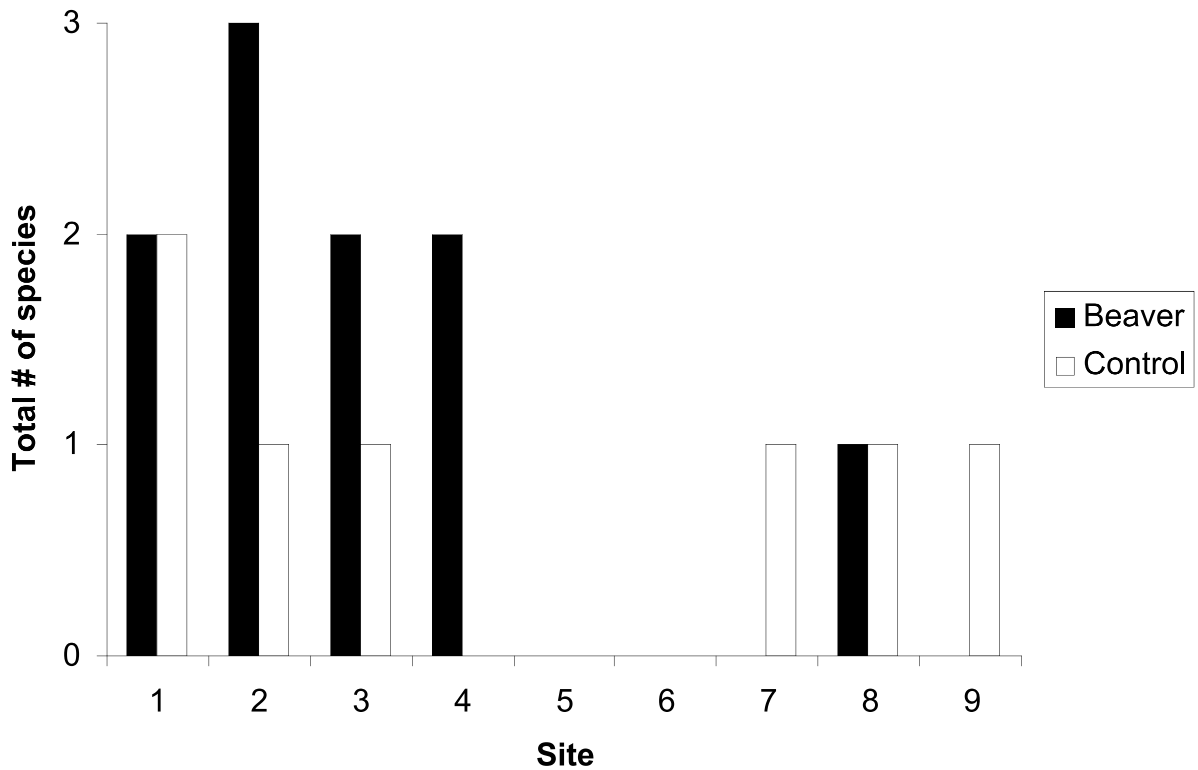


Figure 17. The number of exotic plant species, herbaceous and woody, per site for beaver-modified and control (n=9). Most prevalent was Chinese privet with Japanese honeysuckle being the next most abundant.

Appendix 1. Directions and Descriptions of Study Sites

Study sites are active beaver sites that were found by surveying three river systems in southeast Georgia. Once streams from first to third order were surveyed there were nine active beaver sites for this study. Control sites were located by traveling upstream, downstream, or adjacent from the beaver site. The direction was dependent upon where there were no signs of beaver as well as having comparable habitat to the beaver site. Transect 5 was centered at the area with the highest beaver activity, in this case a lodge or dam. Transect 1 was always placed at the furthest point upstream from transect 5 and transect 9 was always placed at the furthest point downstream. Transects were placed at least 5 m apart to avoid re-sampling and the total area between transects 1 and 9 was 100 m. GPS coordinates listed for each site is at transect 5.

Site 1

Beaver Site **N**32°26.134 W81°40.394

Directions: From 301 bypass turn right onto Rt. 24. Turn right onto Five Chop Road and turn left onto Burkhalter Road. Site is downstream from the first bridge. The middle point of the sampling area is approximately 50 m from the bridge.

Description: This site contains a large amount of small trees but they are tall enough to provide abundant cover. The most abundant tree species are *Liquidambar styraciflu*a with 16% relative abundance and *Magnolia virginiana* with 9%. There is a beaver dam and fresh chew present. A very large dam is located upstream from the bridge as well, but the shoreline is unclear.

Control Site **N**32°25.845 W81°40.971

Directions: From 301 bypass turn right onto Rt. 24. Turn right onto Five Chop Road, then turn right onto Burkhalter Road. Site is downstream from the first bridge. The middle of the sampling area is approximately 50 m from the bridge.

Description: There are very few large trees close to shore at this site. Large trees become more abundant at distances greater than 20m. The trees of highest relative abundance are *Nyssa sylvatica* at 10% and *Acer rubrum* at 9%. This site has an abundant herbaceous and woody vine layer.

Site 2

Beaver Site N32°17.811 W81°48.406

Directions: Go south on Old Register Road, turns into Sinkhole Road. Turn left onto Aden Lanier. At fork in the road, veer to the left onto Jim Waters. The beaver site is upstream from the bridge with the beginning of the sampling area being approximately 100 m from the bridge.

Description: This site is large tree dominated with *Quercus nigra* and *Liriodendron tulipifera* having relative abundances of 12% and 10%. There was a low abundance of undergrowth. The beaver lodge is close to shore, in the middle of the creek. Fresh beaver chew can be located at the shore.

Control site N32°17.539 W81°48.404

Directions: At the fork in the road, veer to the right onto Aden Lanier. Control site is downstream from the bridge. The middle of the sampling area is approximately 50 m from the bridge.

Description: Present at this site are moderate to large trees and relatively a thick overstory cover. The trees with the highest relative abundance for this site were *Nyssa sylvatica*, which had 7%, and *Acer rubrum*, which had 6%. The shoreline is overgrown with vines.

Site 3

Beaver Site N32°17.611 W81°41.743

Directions: From 301 bypass, take a right onto Rt. 24. Pass Mill Creek Park. Turn right onto Homer Bunch Road. Beaver site it upstream from the bridge (there is another dam downstream as well). The middle of the sampling area is approximately 50 m from the bridge.

Description: There is an abundant tree layer at this site, therefore dense canopy cover is present. Those trees with the highest relative abundance were *Acer rubrum* with 28% and *Liquidambar styraciflua* at 12%. There is a beaver lodge present and visible from the shore.

Control Site N32°27.706 W81°41.622

Directions: Upstream from beaver site. The middle of the sampling area is approximately 50 m upstream from the beginning of the beaver site sampling area.

Description: This site contained an abundant tree later so as a result there is heavy canopy cover. *Liriodendron tulipifera* had the highest relative abundance with 17% and *Liquidambar styraciflua* was the second most abundant with 9%.

Site 4

Beaver Site N32°23.866 W81°47.826

Directions: From 301 bypass, turn onto Old Register Road away from campus. At Langston Chapel Road turn left. At first culvert, beaver site is downstream. Can't see dam until you are off of the road. Active beaver area is approximately 20 m from the road.

Description: This site has an abundant overstory and mid-story layer. *Myrica cerifera* had the highest relative abundance of 22% and *Acer rubrum* was the second highest at 16%.

Control Site N32°24.012 W81°48.092

Directions: From the corner of Old Register Road and Langston Chapel Road, go north on Old Register. At first culvert, control site is upstream. Half of area is abundant overstory with large *Nyssa* and half is open with thick understory and shrub layer. Control site is approximately 50 m from the road.

Description: This site contains tall, mature trees that provide overhead canopy cover. *Nyssa sylvativa* and *Prunus serotina* are the most abundant trees with relative abundances of 29% and 8%.

Site 5

Beaver Site N32°26.990 W81°56.634

Directions: From 301 bypass, turn onto West Side Road. Make a left onto Henry Blitch Road. Follow road until it dead ends, then turn left. Before the bridge, at the church, turn left. At second gate is the Mathews property. Drive to shed, follow foot trail to beaver site.

Description: This site contains an abundant middle story layer with small trees and tall shrubs. The trees with the highest relative abundance were *Acer rubrum* at 26%and *Peresa borbonia* at 17%. A beaver dam is close to shore with plentiful fresh beaver chew in the water and close to shore. There is also a very long, large, fortified dam.

Control Site N32°26.760 W81°56.598

Directions: Downstream from Mathews property. Must be walked.

Description: There were not many large trees at this site and there were standing dead trees present. There appeared to be more trees at distances greater than 20 m from shore. *Acer rubrum* had the highest relative abundance with 7% and *Magnolia virginiana* was the next abundant with 4%. This site had a very tall and thick herbaceous layer (waist high).

Site 6

Beaver Site N32°26.844 W81°56.668

Directions: From 301 bypass, turn onto West Side Road. Make a left onto Henry Blitch Road. Follow road until it dead ends, then turn left. Before the bridge, at the church, turn left. At second gate is the Mathews property. Drive to shed, follow foot trail to beaver site.

Description: *Nyssa sylvatica* was the most abundant with a relative abundance of 34% and *Acer rubrum* was the second most abundant with 20%. This provides heavy canopy cover. There is a very long dam constructed and abundant beaver chew in the surrounding area. The area appeared to be frequently flooded, thus minimizing the herbaceous layer.

Control Site N32°26.718 W81°56.577

Directions: Downstream from Mathews property, further downsteam from Mathews control site 1. Must be walked.

Description: There were not many large trees at this site and there were also many standing dead trees. Large trees appeared to be more plentiful when distance from shore was greater than 20 m. The most abundant trees for this site included *Nyssa sylvatica* and *Acer rubrum* whose relative abundances were 9% and 3%. This site also contained a very tall and thick herbaceous layer (waist high)

Site 7

Beaver Site N32°27.286 W81°42.797

Directions: From 301 bypass turn right onto Rt. 24. Pass Mill Creek Park. Beaver site is downstream from the bridge with the middle of the sampling area being approximately 100 m from the bridge.

Description: This site contains very little underbrush. The tree with the highest relative abundance is *Liquidambar styraciflua* at 23%. *Pinus taeda* is plentiful with a relative abundance of 13%. Beavers have eaten the pine and there are some heavily fed areas. There are two possible lodges though neither is definite. Fresh chew is present as well as feeding sites in the water.

Control Site N32°27.534 W81°42.704

Directions: From the 301 bypass turn right onto Rt. 24. Pass Mill Creek Park. Control site is upstream from the bridge with the middle of the sampling area located approximately 50 m from the bridge.

Description: This site contains an abundant middle-story canopy layer with few herbaceous vegetation. *Quercus nigra* was the tree with the highest relative abundance of 21% and *Liquidambar styraciflua* was the second highest with 17%.

Site 8

Beaver Site N32°26.932 W81°40.633

Directions: From the 301 bypass, turn right onto Rt. 24. At fork in the road, veer to the left onto Zettwell Rd. Beaver site is downstream from the bridge with the middle of the sampling area being approximately 50 m from the road.

Description: This site has tall, large trees with high amounts of canopy cover. It is heavily invaded by *Ligustrum sinense*, which has the highest relative abundance of 18%. The tree with the next highest abundance is *Acer rubrum* at 12%. A dam and fresh chew is present. A visible feeding site is located downstream from dam (*L. sinense* found eaten in water).

Control Site N32°26.145 W81°40.417

Directions: From the 301 bypass, turn onto Rt. 24. At the fork in the road, veer right onto Zettwell Road. Turn right onto Edenfield Lane, then turn right onto Burkhalter Road. Control site is upstream from the bridge. The beginning of the sampling area is approximately 100 m from the road.

Descriptions: There was a dense middle and overstory canopy layer at this site. Those trees with the highest relative abundance for this site include *Quercus nigra* with 20%, *Liquidambar styraciflua* with 16%, and *Pinus taeda* with 16%.

Site 9

Beaver Site N32°19.556 W81°48.147

Directions: Go south on Old Register Road. Turn left onto Rt. 46. Beaver site is downstream from the bridge. The middle of the sampling area is approximately 50 m from the bridge.

Description: There are abundant trees providing overstory cover. These trees include *Acer rubrum* with the relative abundance of 22% and *Fraxinus caroliniana* at 9%. A beaver dam and fresh chew is present but the lodge is not visible from site due to its distance from shore. There is another dam and more chew upstream from the bridge but it’s more flooded with no clear shoreline.

Control Site N32°20.968 W81°48.266

Directions: From Old Register Road (before you get to Rt. 46) turn left onto Oliver Road. Control site is upstream from the bridge. The sampling area begins at approximately 100 m from the road.

Description: This site was mostly a woody area with abundant overstory cover. *Ligustrum sinense* has heavily invaded this site having a relative abundance of 19%. *Persea borbonia* was the second most abundant with 8%

Common name	Species name	Code
Red maple	Acer rubrum	AR
Alligator weed	Alternanthera philoxeroides	AP
Hazel alder	Alnus serrulata	AS
Peppervine	Ampelopsis arborea	AA
Water hyssop	Bacopa sp.	BA
River birch	Betula nigra	BN
American beautybush	Callicarpa americana	CA
Switch cane	Arundinaria gigantea	AG
Buttonbush	Cepalanthus occidentalis	CO
Sweet pepperbush	Clethra alnifolia	CL
Flat sedge	Cyperus sp.	CY
Dog fennel	Eupatorium sp.	EU
Carolina ash	Fraxinus caroliniana	FC
Pennywort	Hydrocotyle sp.	HC
St.Johns wort	Hypericum sp.	HP
Large gallberry	Ilex coriacea	IC
Inkberry	Ilex glabra	IG
American holly	Ilex opaca	IO
Jewelweed	Impatiens capensis	IM
Virginia sweetspire	Itea virginica	IV
Chinese privet	Ligustrum sinense	LS
Sweetgum	Liquidambar styraciflua	LQ
Yellow poplar	Liriodendron tulipifera	LT
Fetterbush	Lyonia lucida	LL
Southern magnolia	Magnolia grandiflora	MG
Sweet bay	Magnolia virginiana	MV
	Malvaceae	MA
Mint	Mentha	ME
Partridge berry	Mitchella repens	MR
Wax myrtle	Myrica cerifera	MC
Black gum	Nyssa sylvatica	NS
Cinnamon fern	Osmunda cinnamomea	OC
Royal fern	Osmunda regalis	OR
Switch grass	Panicum sp.	PN
Redbay	Persea borbonia	PB
Loblolly pine	Pinus taeda	PT
American sycamore	Platanus occidentalis	PO
Smartweeds	Polygonum sp.	PG
Jumpseed	Polygonum virginica	PV
Grass	Polypodum sp.	PP
Black cherry	Prunus serotina	PS
Bracken fern	Pteridium aquilinum	PA
Laurel oak	Quercus laurifolia	QL
Water oak	Quercus nigra	QN
Blackberry	Rubus betulifolia	RB
Southern dewberry	Rubus trivialis	RT
Black willow	Salix nigra	SN
Carolina horsenettle	Solanum carolinense	SC
Whitebeam	Sorbus	SB
Spleenwort	Asplenium trichomanes	AT
Bald cypress	Taxodium distichum	TD

Common name	Species name	Code
Poison ivy	Toxidendron radicans	TR
Blueberry	Vaccinium	VE
Possumhaw vibernum	Vibernum nudum	VN
Netted chain fern	Woodwardia areolata	WA
Virginia chain fern	Woodwardia virginica	WR
	Unknown 1	U1

Site 1: Beaver

Transect	AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
	Species																									
1	2							10													2	9		1		5
2										3											3	2		1		3
3										2											6	3	2	1		5
4																					7	8		2		1
5										5											4	5				9
6	2																				1	5				1
7	2																				0	3				2
8	3			2						4											0	15	3			3
9	9			5																		4				
sum	18	0	0	7	0	0	0	10	0	14	0	0	0	0	0	0	0	0	0	0	23	54	5	5	0	29
percent	5.4	0	0	2.1	0	0	0	3	0	4.2	0	0	0	0	0	0	0	0	0	0	7	16	1.5	2	0	8.8

Site 1: Control

Transect	AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1								3		6												2				
2																		1				5				
3	1			4																						
4				1																		1				
5	1			3															6							
6								1		12								1			1	2	1	1		
7	11									1												2				
8	9			3		2								2								2				
9	5			4															7			1				
sum	27	0	0	15	0	2	0	4	0	19	0	0	0	2	0	0	0	2	13	0	1	15	1	1	0	0
percent	9.3	0	0	5.2	0	0.7	0	1.4	0	6.6	0	0	0	0.7	0	0	0	1	4	0	0	5	0.3	0	0	0

Site 1: Beaver

Transect	MA	ME	MR	MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT
	Species																							
1				4														2						
2				1														2						
3					8													3						
4				2	1													1						
5					1													0		1				
6				4														12		0				
7				1														5		2				
8				4						6								0		0				
9										6		3					5			1				
sum	0	0	0	16	10	0	0	0	0	12	0	3	0	0	0	0	5	25	0	4	0	0	0	0
percent	0	0	0	4.8	3	0	0	0	0	3.6	0	0.9	0	0	0	0	1.5	7.6	0	1.2	0	0	0	0

Site 1: Control

Transect	MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	MA	ME	MR	SC	SB	AT
1		4				2								1	1									
2		2																						
3		6															2							
4		7																						
5		10									8													
6						2									4		5							
7															1		8							
8																	10			4				
9	2													1	2									
sum	2	29	0	0	0	4	0	0	0	0	8	0	0	2	8	0	25	0	0	4	0	0	0	0
percent	0.7	10	0	0	0	1.4	0	0	0	0	2.76	0	0	0.7	2.8	0	8.6	0	0	1.4	0	0	0	0

Site 1: Beaver

Transect	TD	TR	VE	VN	WA	WR	U1	
	Species							
1					1	0		
2					1	2		
3					8	0		
4		1	11		10	0		
5		4	0		5	0		
6		11	0		7	0		
7		5	5		2	0		
8		2	0		10	0		
9		3	0		3			
sum	0	26	16	0	47	2	0	331
percent	0	7.9	4.8	0	14	0.6	0	

Site 1: Control

Transect	TD	TR	VE	VN	WA	WR	U1	
1	2				27			
2		2			22			
3		4			20			
4	1	1	1		10			
5					5			
6		3						
7	1				2			
8	2							
9	3							
sum	9	10	1	0	86	0	0	290
percent	3.1	3.4	0.3	0	30	0	0	

Site 2: Beaver

	Species																								
Transect :	AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1	8									11												7	1			4
2										8						5							1			
3																										
4	4			4						4						9						4	3			
5	1									8						15							1			
6	4															1					1	1	7			
7										2						2					2	1	2			
8	4															4					1		6			6
9	7															4					1	1	8			
sum	28	0	0	4	0	0	0	0	0	33	0	0	0	0	0	40	0	0	0	0	5	14	29	0	0	10
percent	7.8	0	0	1.1	0	0	0	0	0	9.2	0	0	0	0	0	11	0	0	0	0	1	4	8.1	0	0	2.8

Site 2: Control

Transect	AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1	2												3	32												
2		12		4								2	1	40								3				
3	1			10									3								1	4				
4	5		3	5																	2	1				
5	5			6						5		13									2					
6	5			6					1	6		5										3				
7	3											6										2				
8	3		2	9						9		7						1				1				
9	5			16						14		3	1	9							3	3				3
sum	29	12	5	56	0	0	0	0	1	34	0	36	8	81	0	0	0	1	0	0	8	17	0	0	0	3
percent	5.8	2.4	1	11	0	0	0	0	0.2	6.8	0	7.2	1.6	16	0	0	0	0	0	0	2	3	0	0	0	1

Site 2: Beaver

Transect	Species MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA	ME	MR
1	5					2									3									
2		4					1								6									
3																								
4	3		1			3	5								7									
5		2				3	2						6		6									
6	2	3				6									5									
7	1					5	1								3									
8		7													3									
9		1													2									
sum	11	17	1	0	0	19	9	0	0	0	0	0	6	0	35	0	0	0	0	0	0	0	0	0
percent	3.1	4.7	0.3	0	0	5.3	2.5	0	0	0	0	0	1.7	0	9.7	0	0	0	0	0	0	0	0	0

Site 2: Control

Transect	MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA	ME	MR
1		7							12															
2		1			10									6			3		4					
3		1			47									2			14							
4		9				1			7					2			3							
5		3							12					1			4							
6		5												1			3							
7		2							4					3			2							
8		6												3										
9		3							1					1										
sum	0	37	0	0	57	1	0	0	36	0	0	0	0	19	0	0	29	0	4	0	0	0	0	0
percent	0	7.4	0	0	11	0.2	0	0	7.2	0	0	0	0	3.8	0	0	5.8	0	0.8	0	0	0	0	0

Site 2: Beaver

Transect	Species TD	TR	VE	VN	WA	WR	U1	
1								
2								
3					9	2		
4					3			
5		1	4					
6								
7		1			5			
8					2			
9		1			8	3		
sum	0	3	4	0	27	5	0	359
percent	0	0.8	1.1	0	7.5	1.39	0	

Site 2: Control

Transect	TD	TR	VE	VN	WA	WR	U1	
1	2				2			
2				1				
3					11			
4					9			
5	2							
6	4				2			
7	2	8	1					
8	2	5	2					
9	1							
sum	13	13	3	1	24	0	0	499
percent	2.6	2.6	0.6	0.2	4.8	0	0	

Site 3: Beaver

	Species																									
Transect	AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1	27																					2				
2	8		1									1										2				
3	10			5																		4				
4	19			2								2										6				
5	4			6																		6				
6	9																					8		1		
7	11																					7				
8	9														2							3		4		
9	10													7								6				4
sum	107	0	1	13	0	0	0	0	0	0	0	3	0	7	2	0	0	0	0	0	0	44	0	5	0	4
percent	39	0	0.4	4.8	0	0	0	0	0	0	0	1.1	0	2.6	0.7	0	0	0	0	0	0	16	0	2	0	1.5

Site 3: Control

Transect	AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1	2																				2		34			
2	2			7						2												2	2			7
3	4			2						1											5	1	1			3
4	1			6						4											6	6	3			
5																					4	2	2			
6	1																				2	8	2			
7																							10			
8	4											8											2			
9												9		3							1	11	4			
sum	14	0	0	15	0	0	0	0	0	7	0	17	0	3	0	0	0	0	0	0	20	30	60	0	0	10
percent	4.2	0	0	4.5	0	0	0	0	0	2.1	0	5.1	0	0.9	0	0	0	0	0	0	6	9	18	0	0	3

Site 3: Beaver

Transect	**Species** MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA	ME	MR
1		4					1							1										
2	3										29													
3						1	2				8			1	1									
4	2				2		1				24				1		5							
5		2					3							1	7									
6						1	3				1				12									
7		2					3								8									
8		2					2								5									
9	1	3			1		2				5			6										
sum	6	13	0	0	3	2	17	0	0	0	67	0	0	9	34	0	5	0	0	0	0	0	0	0
percent	2.2	4.8	0	0	1.1	0.7	6.3	0	0	0	24.6	0	0	3.3	13	0	1.8	0	0	0	0	0	0	0

Site 3: Control

Transect	MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA	ME	MR
1															1									
2	1								1									1						
3	3						1																	
4	1						2								1									
5	3						1								1						4			
6	4						7								2						1			
7	2						4								2					15	1			
8	1					1						2			1									
9	2						5					1												
sum	17	0	0	0	0	1	20	0	1	0	0	3	0	0	8	0	0	1	0	15	6	0	0	0
percent	5.1	0	0	0	0	0.3	6	0	0.3	0	0	0.9	0	0	2.4	0	0	0.3	0	4.5	2	0	0	0

Site 3: Beaver

Transect	TD	TR	VE	VN	WA	WR	U1	
	Species							
1			5	1	4			
2	1		4					
3				5	1			
4	1							
5			2					
6			1					
7			5					
8			3		2			
9						2		
sum	2	0	20	6	7	2	0	272
percent	0.7	0	7.4	2.2	2.6	0.74	0	

Site 3: Control

Transect	TD	TR	VE	VN	WA	WR	U1	
1					16			
2					7			
3					20			
4		4			13			
5					8			
6		1			6			
7		2			1			
8		15						
9		3			2			
sum	0	25	0	0	73	0	0	332
percent	0	7.5	0	0	22	0	0	

Site 4: Beaver

Transect	**Species** AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1	11												4								1			2		
2	7												5								2			2		
3	3												3								1					3
4	16			2									4											7		
5	14									3			6								1			3		
6	8									4			6								2			2		1
7	7			4						4			2	8							1					1
8	4			4						5											2			3		
9	4																				1					
sum	74	0	0	10	0	0	0	0	0	16	0	0	30	8	0	0	0	0	0	0	11	0	0	19	0	5
percent	19	0	0	2.6	0	0	0	0	0	4.2	0	0	7.9	2.1	0	0	0	0	0	0	3	0	0	5	0	1.3

Site 4: Control

Transect	AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1										6			1													
2										5		1														
3	3									8		6	9													4
4	2									6																
5	2									5			2													
6										11	1															
7	2									6																
8	3									7		6												1		
9	7									6		4	1											3		
sum	19	0	0	0	0	0	0	0	0	60	1	17	13	0	0	0	0	0	0	0	0	0	0	4	0	4
percent	7.7	0	0	0	0	0	0	0	0	24	0	6.9	5.2	0	0	0	0	0	0	0	0	0	0	2	0	1.6

Site 4: Beaver

Transcect	Species MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA	ME	MR
1	5																							
2	5																2							
3	11																							
4	10	2					1																	
5	2	1					1										2							
6	22	1															5							
7	15						1										9							
8	13						5										11							
9	17						1								1	3	7							
sum	100	4	0	0	0	0	9	0	0	0	0	0	0	0	1	3	36	0	0	0	0	0	0	0
percent	26	1	0	0	0	0	2.4	0	0	0	0	0	0	0	0.3	0.8	9.4	0	0	0	0	0	0	0

Site 4: Control

Transect	MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA	ME	MR
1		10					2																	
2		8																						
3	4	6					1																	
4		15					1																	
5		13																						
6		15					2										3							
7		5										3			2									
8		1										8			6	1	4							
9		4										10			3									
sum	4	77	0	0	0	0	6	0	0	0	0	21	0	0	11	1	7	0	0	0	0	0	0	0
percent	1.6	31	0	0	0	0	2.4	0	0	0	0	8.5	0	0	4.4	0.4	2.8	0	0	0	0	0	0	0

Site 4: Beaver

	Species							
Transect	TD	TR	VE	VN	WA	WR	U1	
1	3				4			
2		6			12			
3	1	5			24			
4	1	1			1			
5		7			5			
6		31			11			
7		4			3			
8		3						
9		8						
sum	5	65	0	0	60	0	0	382
percent	1.3	17	0	0	16	0	0	

Site 4: Control

Transect	TD	TR	VE	VN	WA	WR	U1	
1	1							
2								
3		1						
4								
5								
6		1						
7	2	4			4			
8						9		
9								
sum	3	6	0	0	4	9	0	248
percent	1.2	2.4	0	0	1.6	3.63	0	

Site 5: Beaver

	Species																									
Transect :	AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1	34												4										9			
2	50										4	1											8	4		
3	14																						4	31		
4	7																							20		
5	11																						1	24		
6			6							3												2		18		
7	1																1					8		6		
8	4									5																
9																	13									
sum	121	0	6	0	0	0	0	0	0	8	4	1	4	0	0	0	14	0	0	0	0	10	22	##	0	0
percent	35	0	1.7	0	0	0	0	0	0	2.3	1	0.3	1.2	0	0	0	4	0	0	0	0	3	6.4	30	0	0

Site 5: Control

Transect	AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1	10												4	6												6
2	18				17									59						4						5
3	7				17								3	13						6						5
4	16				42						5			24					6							3
5	2				16						2			24					11							
6	2				18								1	15					34							5
7	4				43																					3
8					23									24					11							6
9	2				22									27					17							5
sum	61	0	0	0	198	0	0	0	0	0	7	0	8	192	0	0	0	0	79	10	0	0	0	0	0	38
percent	6.7	0	0	0	22	0	0	0	0	0	1	0	0.9	21	0	0	0	0	9	1	0	0	0	0	0	4.2

Site 5: Beaver

Transcect	MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA	ME	MR
	Species																							
1						1			8						1									
2						3			6															
3		3				4									1									
4		3				3		1							2		1							
5		3		1		4									1		1							
6						7									1									
7						9									1									
8				3		28									1									
9				2		22									7									
sum	0	9	0	6	0	81	0	1	14	0	0	0	0	0	15	0	2	0	0	0	0	0	0	0
percent	0	2.6	0	1.7	0	24	0	0.3	4.1	0	0	0	0	0	4.4	0	0.6	0	0	0	0	0	0	0

Site 5: Control

Transect	MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA	ME	MR
1	1	3							13													3		
2		1	2	2					9															
3		1	8							22														
4		4							52															
5	2	1	2						80															
6									21															
7		2							20													2		
8		1							34															
9		5					1		12															
sum	3	18	12	2	0	0	1	0	241	22	0	0	0	0	0	0	0	0	0	0	0	5	0	0
percent	0.3	2	1.3	0.2	0	0	0.1	0	27	2.4	0	0	0	0	0	0	0	0	0	0	0	0.6	0	0

Site 5: Beaver

	Species							
Transect	TD	TR	VE	VN	WA	WR	U1	
1					3			
2					12			
3					11			
4					7			
5								
6								
7								
8					8			
9			3					
sum	0	0	3	0	41	0	0	344
percent	0	0	0.9	0	12	0	0	

Site 5: Control

Transect	TD	TR	VE	VN	WA	WR	U1	
1					3			
2								
3					1			
4								
5								
6								
7			4					
8								
9								
sum	0	0	4	0	4	0	0	905
percent	0	0	0.4	0	0.4	0	0	

Site 6: Beaver

Transect #	Species AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1																								20		4
2	2																							28		7
3	7																									5
4	8																						1			
5	14																						1			7
6	16																						4			1
7	14																						2			
8	10																						1			11
9	16																									
sum	87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	48	0	35
percent	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.5	14	0	9.9

Site 6: Control

Transect	AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1	3				38																				4	
2	3				58							3													3	
3	6				150																				2	
4	6				59							10												6		
5	6				30									8											2	18
6	7				12									44										6	3	
7	3				34									36											5	5
8	1				75									55											7	
9					9									49											2	5
sum	35	0	0	0	465	0	0	0	0	0	0	13	0	192	0	0	0	0	0	0	0	0	0	12	28	28
percent	3	0	0	0	40	0	0	0	0	0	0	1.1	0	17	0	0	0	0	0	0	0	0	0	1	2.4	2.4

Site 6: Beaver

Transect	Species MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA	ME	MR
1		8	2												3									
2		1			30						3				1									
3		23									23				3									
4		26									13				2									
5		35									5													
6		3									1													
7		16									4													
8		28																						
9		11									11													
sum	0	151	2	0	30	0	0	0	0	0	60	0	0	0	9	0	0	0	0	0	0	0	0	0
percent	0	43	0.6	0	8.5	0	0	0	0	0	16.9	0	0	0	2.5	0	0	0	0	0	0	0	0	0

Site 6: Control

Transect	MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA	ME	MR
1		22		3																				
2		1								44														
3		3								26														
4	6	8								15														
5	3	11								50														
6	2	8		6			2			50														
7		9		5			1																	
8		22																						
9		15		1																				
sum	11	99	0	15	0	0	3	0	0	185	0	0	0	0	0	0	0	0	0	0	0	0	0	
percent	0.9	8.5	0	1.3	0	0	0.3	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	

Site 6: Beaver

Transcect	TD	TR	VE	VN	WA	WR	U1	
	Species							
1								
2						2		
3								
4								
5				1				
6				3		3		
7								
8								
9					2			
sum	0	0	0	4	2	5	0	355
percent	0	0	0	1.1	0.6	1.41	0	

Site 6: Control

Transect	TD	TR	VE	VN	WA	WR	U1	
1							16	
2								
3								
4							3	
5							12	
6					5		5	
7							7	
8							9	
9							15	
sum	0	0	0	0	5	0	67	1158
percent	0	0	0	0	0.4	0	5.8	

Site 7: Beaver

Transect	Species AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1										3		1		6								18				
2	4									9				10								44				
3	6									9		3		11								2				
4	4									12		1		35								55				
5	5									2		2	5									9				
6	3									6		10	10									4				
7	4									1		4	2	27								1				
8	1									7			3	10								5				
9																						24				3
sum	27	0	0	0	0	0	0	0	0	49	0	21	20	99	0	0	0	0	0	0	0	162	0	0	0	3
percent	4	0	0	0	0	0	0	0	0	7.3	0	3.1	3	15	0	0	0	0	0	0	0	24	0	0	0	0.4

Site 7: Control

Transect	AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1	1																				1	5				
2	3						2															9				
3	4						6														5	4				
4	7																				1	6				
5	4																					6				
6	7						3															6				
7	2						1														3	3				
8	5						1														3	7				
9	5						1															1				
sum	38	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	13	47	0	0	0	0
percent	16	0	0	0	0	0	5.7	0	0	0	0	0	0	0	0	0	0	0	0	0	5	19	0	0	0	0

Site 7: Beaver

Transect	Species MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA	ME	MR
1							6										5							
2							9				2													
3							17				1						2							
4							21				34						1							
5							7				43				1									
6							6				15				1									
7							3				37						6							
8							19				34				1									
9							3				22				2									
sum	0	0	0	0	0	0	91	0	0	0	188	0	0	0	5	0	14	0	0	0	0	0	0	0
percent	0	0	0	0	0	0	13	0	0	0	27.9	0	0	0	0.7	0	2.1	0	0	0	0	0	0	0

Site 7: Control

Transect	MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA	ME	MR
1	3														7		2							
2															6		2							
3		1													6									
4															6									
5															10		4							
6		1													8		2							
7															6									
8															8		1							
9	2						1								3		6							
sum	5	2	0	0	0	0	1	0	0	0	0	0	0	0	60	0	17	0	0	0	0	0	0	0
percent	2	0.8	0	0	0	0	0.4	0	0	0	0	0	0	0	25	0	7	0	0	0	0	0	0	0

Site 7: Beaver

Transect	Species TD	TR	VE	VN	WA	WR	U1	
1								
2								
3	4	4						
4	2							
5	3		1					
6	3		2					
7	1							
8								
9	3							
sum	16	4	3	0	0	0	0	675
percent	2.4	0.6	0.4	0	0	0	0	

Site 7: Control

Transect	TD	TR	VE	VN	WA	WR	U1	
1			2					
2		4	1					
3			4					
4		3	3					
5		13	22					
6			7					
7		1	12					
8			5					
9		1	7					
sum	0	22	63	0	0	0	0	244
percent	0	9	26	0	0	0	0	

Site 8: Beaver

Transect	**Species** AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1	5			1																	12					8
2	6			1																	15			7		4
3	4																				10			3		2
4	2			1																	13					
5	3																				5					
6	9																				4					
7	9																				8					
8	6																				9					
9	13																				8					
sum	57	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	84	0	0	10	0	14
percent	14	0	0	0.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	2	0	3.4

Site 8: Control

Transect	AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1																						1				
2	3							2														10				
3	3																					1				
4	3																					4				
5																						7			1	
6	7																					5				
7	1																					5				
8	1																					1				
9	1																					5			1	
sum	19	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	39	0	0	2	0
percent	7.8	0	0	0	0	0	0	0.8	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0.8	0

Site 8: Beaver

Transcect	MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA		MR
	Species																							
1		3															3							
2	2	2															1							
3	9	1							37							3								
4	11	2																						
5		3															1							
6		4															1							
7		6				4											1							
8		5																						
9	2	2																						
sum	24	28	0	0	0	4	0	0	37	0	0	0	0	0	0	3	7	0	0	0	0	0	0	0
percent	5.9	6.8	0	0	0	1	0	0	9	0	0	0	0	0	0	0.7	1.7	0	0	0	0	0	0	0

Site 8: Control

Transect	MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA	ME	MR
1	2	8				2	6					2												
2	1					2	6								1									
3		7				2	9								9									
4	5	1					11								9									
5		2													3									
6		3					1							8	9									
7	1													6	5		1							
8	2	1					4								10									
9							2					1			3		2							
sum	11	22	0	0	0	6	39	0	0	0	0	3	0	14	49	0	3	0	0	0	0	0	0	0
percent	4.5	9	0	0	0	2.5	16	0	0	0	0	1.2	0	5.7	20	0	1.2	0	0	0	0	0	0	0

Site 8: Beaver

Transect	Species: TD	TR	VE	VN	WA	WR	U1	
1				8	11			
2				8	5			
3					15			
4				5	24			
5		10		7	15			
6		10			9			
7		4		4	14			
8		1		4	21	1		
9		2			18			
sum	0	27	0	36	132	1	0	410
percent	0	6.6	0	8.8	32	0.24	0	

Site 8: Control

Transect	TD	TR	VE	VN	WA	WR	U1	
1					4	1		
2								
3								
4			1					
5								
6			3					
7		11						
8		14						
9		1						
sum	0	26	4	0	4	1	0	244
percent	0	11	1.6	0	1.6	0.41	0	

Site 9: Beaver

	Species																									
Transect :	AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1	17									5		1	4	24												
2	4												3	11												
3	3									2			6	34												
4	8												2	11												
5	6												2	17								1				
6	14												5	14												
7	10												9													
8	36									1			14	21												
9	17												2	21								1				
sum	115	0	0	0	0	0	0	0	0	8	0	1	47	153	0	0	0	0	0	0	0	2	0	0	0	0
percent	29	0	0	0	0	0	0	0	0	2	0	0.2	12	38	0	0	0	0	0	0	0	0	0	0	0	0

Site 9: Control

Transect	AR	AP	AS	AA	BA	BN	CA	AG	CO	CL	CY	EU	FC	HC	HP	IC	IG	IO	IM	IV	LS	LQ	LT	LL	MG	MV
1																					15			19		
2																					11			44		
3	2																				16	3		2		
4	3																				13			14		
5	5																				10		2	34		
6	1																				12		4	23		
7	2																				9	4		19		
8	6																				6	1	1	21		2
9	1																				8	1		13		1
sum	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	9	7	##	0	3
percent	3.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	2	1.3	36	0	0.6

Site 9: Beaver

	Species																							
Transect	MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA	ME	MR
1		3									42			1										
2											24			2										
3		14												2										
4											4													
5											2			3										
6											8													
7											4				3									
8											11													
9											2													
sum	0	17	0	0	0	0	0	0	0	0	97	0	0	8	3	0	0	0	0	0	0	0	0	0
percent	0	4.2	0	0	0	0	0	0	0	0	24.1	0	0	2	0.7	0	0	0	0	0	0	0	0	0

Site 9: Control

Transect	MC	NS	OC	OR	PN	PB	PT	PO	PG	PV	PP	PS	PA	QL	QN	RB	RT	SN	SC	SB	AT	MA	ME	MR
1						3									1		1							
2						4											2							
3														1	2									
4						3								2			1							
5						7			6															
6						6											5							
7		2				9			9								11							3
8						3								1	1		1							
9						4								1			3							
sum	0	2	0	0	0	39	0	0	15	0	0	0	0	5	4	0	24	0	0	0	0	0	0	3
percent	0	0.4	0	0	0	7.5	0	0	2.9	0	0	0	0	1	0.8	0	4.6	0	0	0	0	0	0	1

Site 9: Beaver

	Species							
Transect	TD	TR	VE	VN	WA	WR	U1	
1	11	1						
2	1				5			
3	3	7						
4	2	13						
5	1	10						
6	2							
7	4							
8	3							
9	4							
sum	31	31	0	0	5	0	0	403
percent	7.7	7.7	0	0	1.2	0	0	

Site 9: Control

Transect	TD	TR	VE	VN	WA	WR	U1	
1					4			
2					9			
3		5			8			
4					14			
5					5			
6		1			14			
7					17			
8					12			
9	3				8			
sum	3	6	0	0	91	0	0	520
percent	0.6	1.2	0	0	18	0	0	

Appendix 2. Species Area Curve.

A species area curve was performed prior to collecting data to determine the number of transects needed for sufficient sampling. This method is commonly used to determine the number of replicates needed as well as the size of the sampling plot (Brower et al., 1997). The cumulative number of species sampled is plotted against the area sampled. When the line of the graph plateaus then a sufficient number of replicates has been acquired.

The species area curve for this study was conducted at beaver site 3, N32°17.811 W81°48.406. Directions to this site are as followed: go south on Old Register Road, turns into Sinkhole Road. Turn left onto Aden Lanier. At fork in the road, veer to the left onto Jim Waters. The beaver site is upstream from the bridge with the beginning of the sampling area being approximately 100 m from the bridge.

Sampling consisted of two plot sizes: 1 m^2 and 25 m^2. Herbaceous and small sized woody (stems < 1 m tall) vegetation types were collected together in the 1 m^2 plots and large sized woody (stems > 1 m tall) vegetation was collected in the 25 m^2 plots. The results of the species area curve determined that there would be nine sampling plots per distance needed. As a result, nine transects were used for sampling at four distances from the waterline: 5 m, 10 m, 15 m, and 20 m.

Distance from shore: 5 m
Plot size: 1 m²

Sample #	Cumulative Area Sampled (m²)	# of Species	# of New Species	Cumulative # of New Species
1	1	4	4	4
2	2	6	4	8
3	3	3	3	11
4	4	2	0	11
5	5	4	3	14
6	6	4	2	16
7	7	2	0	16
8	8	4	1	17
9	9	6	0	17

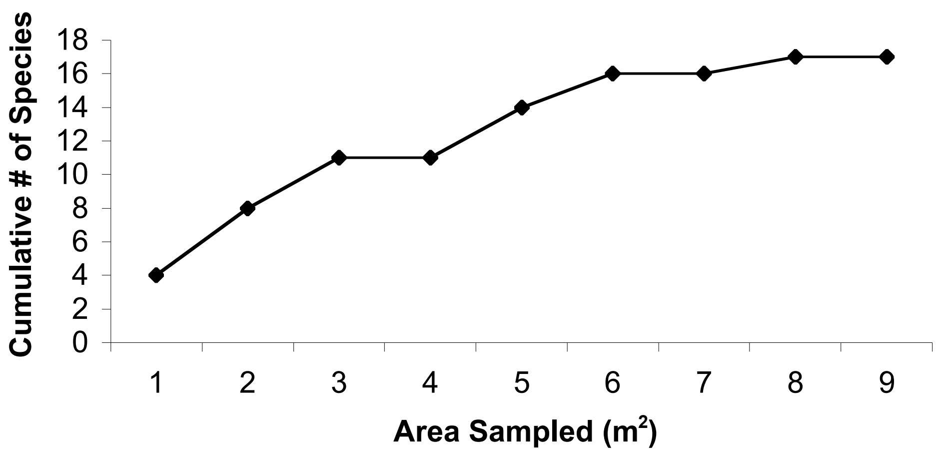


Figure 66. Species area curve at 5 m from shore measured in 1 m² plots.

Distance from shore: 5 m
Plot size: 25 m^2

Sample #	Cumulative Area Sampled (m^2)	# of Species	# of New Species	Cumulative # of New Species
1	5	3	3	3
2	10	4	1	4
3	15	2	1	5
4	20	2	0	5
5	25	2	0	5

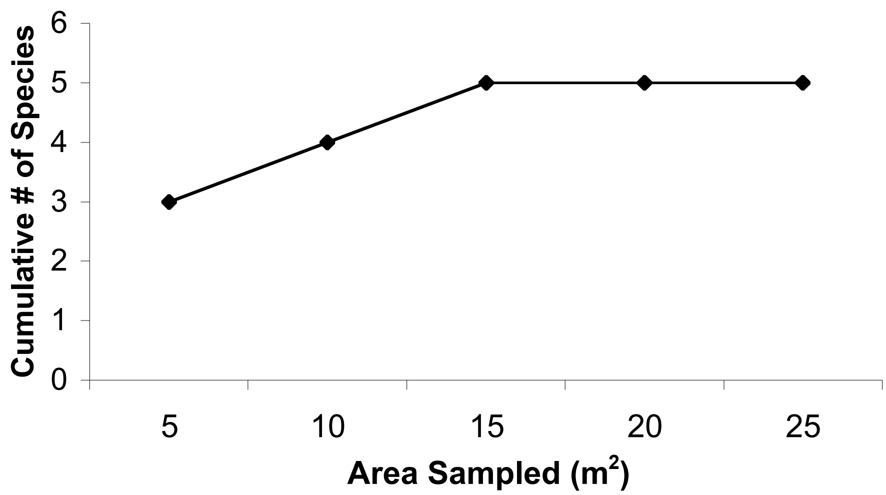


Figure 67. Species area curve at 5 m from shore measured in 25 m^2 plots.

Distance to shore: 10 m
Plot size: 1 m^2

Sample #	Cumulative Area Sampled (m^2)	# of Species	# of New Species	Cumulative # of New Species
1	1	3	3	3
2	2	2	1	4
3	3	2	1	5
4	4	3	1	6
5	5	2	1	7
6	6	3	0	7
7	7	2	1	8
8	8	4	0	8
9	9	5	0	8

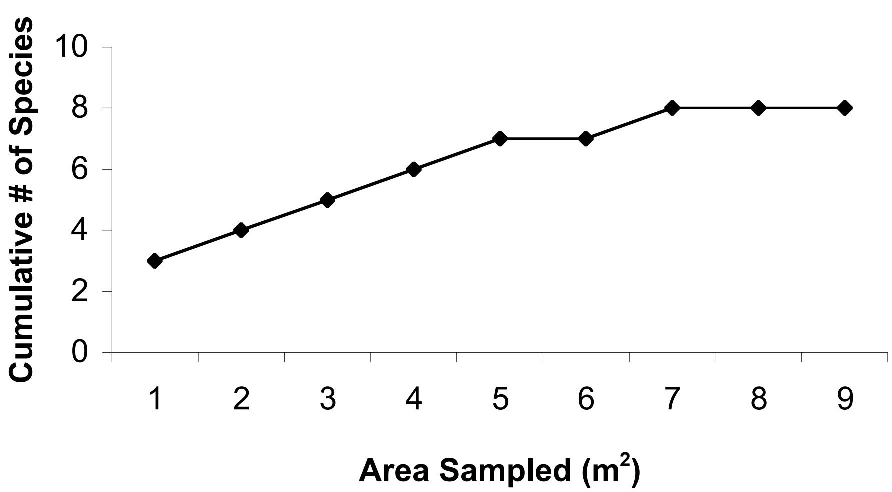


Figure 68. Species area curve at 10 m from shore measured in 1 m^2 plots.

Distance to shore: 10 m
Plot size: 25 m^2

Sample #	Cumulative Area Sampled (m^2)	# of Species	# of New Species	Cumulative # of New Species
1	5	4	4	4
2	10	3	1	5
3	15	3	0	5
4	20	3	0	5

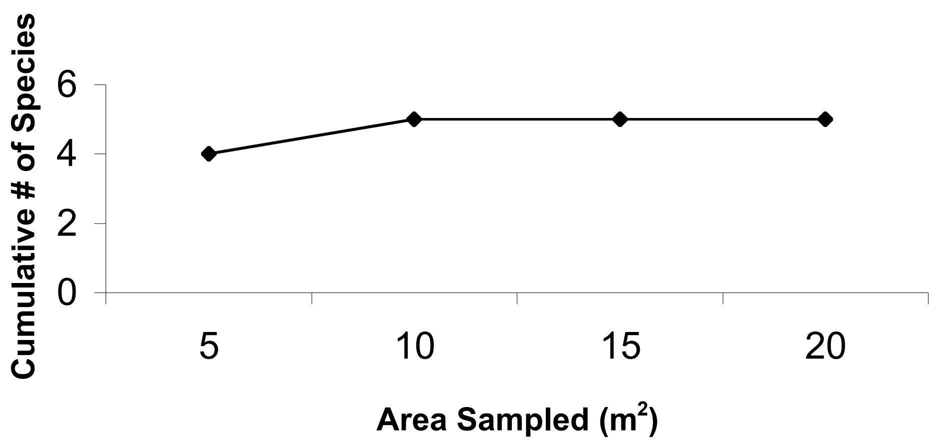


Figure 69. Species area curve at 10 m from shore measured in 25 m^2 plots.

Distance to shore: 15m
Plot size: 1 m^2

Sample #	Cumulative Area Sampled (m^2)	# of Species	# of New Species	Cumulative # of New Species
1	1	4	4	4
2	2	4	1	5
3	3	3	1	6
4	4	3	1	7
5	5	4	1	8
6	6	5	0	8
7	7	3	0	8

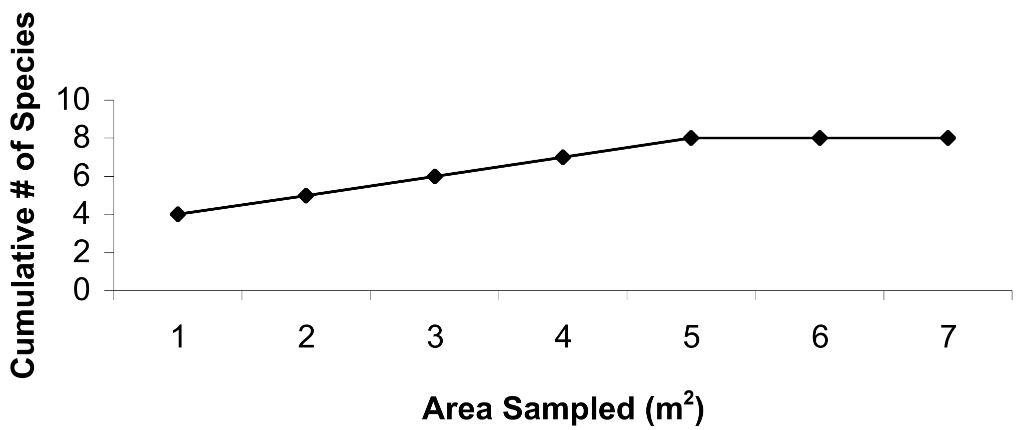


Figure 70. Species area curve at 15 m from shore measured in 1 m^2 plots.

Distance to shore: 15m
Plot size: 25 m^2

Sample #	Cumulative Area Sampled (m^2)	# of Species	# of New Species	Cumulative # of New Species
1	5	3	3	3
2	10	3	1	4
3	15	3	0	4
4	20	4	1	5
5	25	3	1	6
6	30	3	0	6
7	35	4	1	7
8	40	4	0	7
9	45	4	0	7

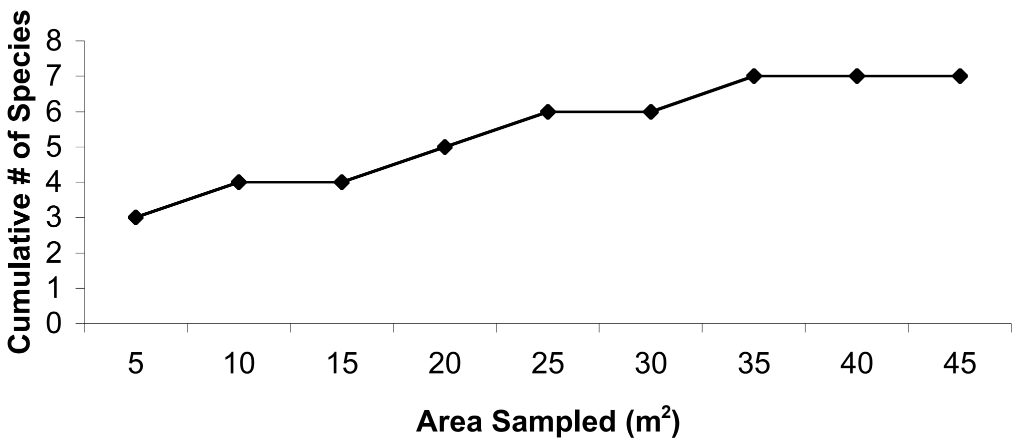


Figure 71. Species area curve at 15 m from shore measured in 25 m^2 plots.

Distance to shore: 20m
Plot size: 1 m^2

Sample #	Cumulative Area Sampled (m^2)	# of Species	# of New Species	Cumulative # of New Species
1	1	4	4	4
2	2	3	2	6
3	3	3	1	7
4	4	2	0	7
5	5	4	2	9
6	6	3	1	10
7	7	4	1	11
8	8	3	0	11
9	9	3	0	11

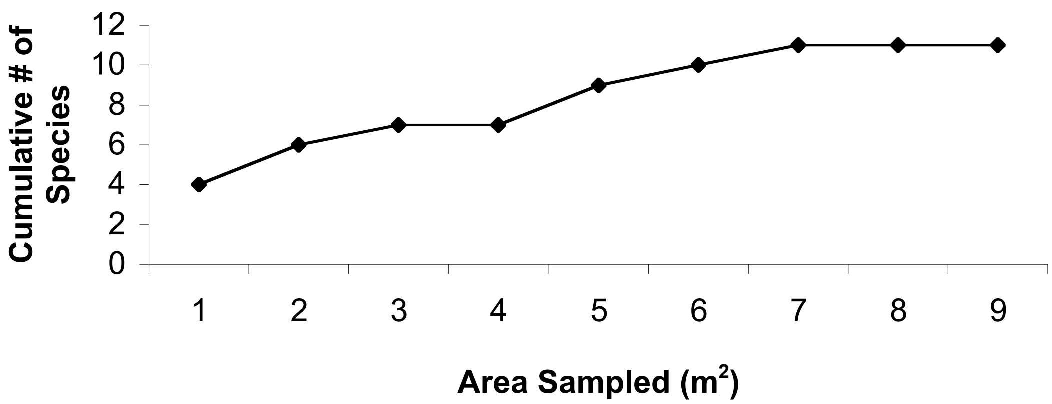


Figure 72. Species area curve at 20 m from shore measured in 1 m^2 plots.

Distance to shore: 20m
Plot size: 25 m^2

Sample #	Cumulative Area Sampled (m^2)	# of Species	# of New Species	Cumulative # of New Species
1	5	3	3	3
2	10	2	1	4
3	15	3	1	5
4	20	0	0	5
5	25	5	2	7
6	30	6	1	8
7	35	5	0	8
8	40	6	1	9
9	45	0	0	9
10	50	0	0	9

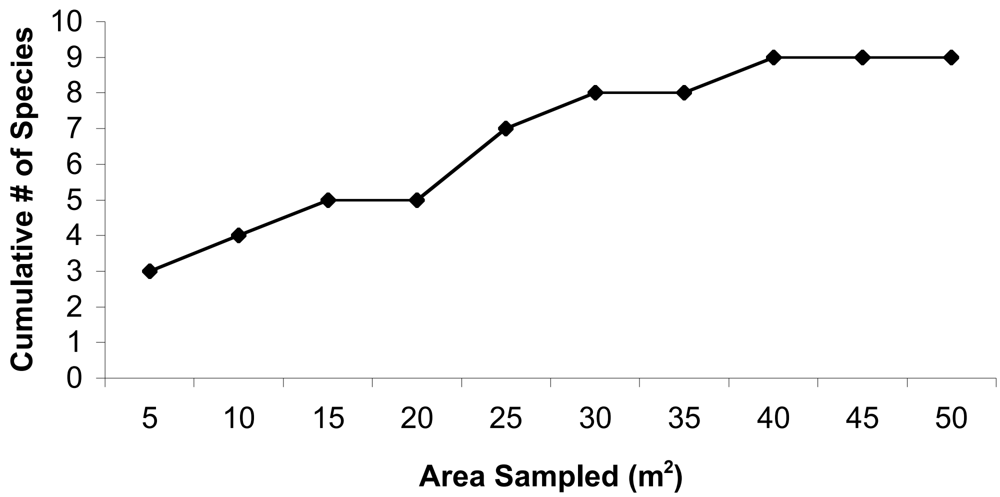


Figure 73. Species area curve at 20 m from shore measured in 25 m^2 plots.

Appendix III. List of Plant Vouchers Collected at Study Sites.

This collection is deposited at the Georgia Southern University herbarium (GAS). All species were collected in Bulloch County, Georgia, USA. Appendix I contains the collection site information.

Collection Site	Site Type	Collection #	Species	Family	Habitat
Site 6	Control	2	*Eupatorium compositifolium*	*Asteraceae or Compositae*	moist soil, moderate sunlight
Site 6	Control	3	*Bacopa* sp	*Scrophulariaceae*	wet, soggy soil with full sunlight
Site 6	Control	4	*Rhynchospora*	*Cypercaeae*	moist soil, moderate sunlight
Site 2	Beaver	5	*Poaceae*	*Poaceae*	moist, shaded soil
Site 8	Beaver	6	*Vibernum nudum*	*Caprifoliaceae*	moist, shaded soil
Site 8	Beaver	7	*Vibernum nudum*	*Caprifoliaceae*	moist, shaded soil
Site 8	Beaver	8	*Clethra alnifolia*	*Clethraceae*	moist, shaded soil
Site 5	Control	9	*Vibernum nudum*	*Caprifoliaceae*	moist, shaded soil
Site 5	Control	10	*Osmunda cinnamomea*	*Osmundaceae*	moist, shaded soil
Site 5	Control	11	*Osmunda regalis*	*Osmundaceae*	moist, shaded soil
Site 5	Control	12	*Cyperus*	*Cypercaeae*	moist, shaded soil
Site 5	Control	13	*Rhynchospora*	*Cypercaeae*	moist, shaded soil
Site 5	Control	14	*Polyganum virginianum*	*Polygonaceae*	wet, soggy soil with full sunlight
Site 5	Control	16	*Poaceae*	*Poaceae*	moist, shaded soil
Site 5	Control	17	*Polyganum virginianum*	*Polygonaceae*	wet, soggy soil with full sunlight
Site 5	Control	18	*Bacopa* sp	*Scrophulariaceae*	wet, soggy soil with full sunlight
Site 5	Control	19	*Malvaceae*	*Malvaeae*	wet, soggy soil with full sunlight
Site 3	Control	20	*Hypericum* sp	*Hypericaceae*	moist, shaded soil
Site 3	Control	22	*Sorbus* sp.	*Rosaceae*	moist, shaded soil
Site 3	Control	23	*Ligustrum sinense*	*Oleaceae*	moist, shaded soil
Site 3	Control	24	*Asplenium*	*Aspleniaceae*	moist, shaded soil
Site 3	Control	26	*Sorbus* sp.	*Rosaceae*	moist, shaded soil
Site 1	Control	27	*Panicum* sp	*Poaceae*	moist soil, moderate-high sunlight
Site 1	Control	28	*Alternanthera philoxeroides*	*Amaranthaceae*	moist soil, moderate-high sunlight
Site 7	Beaver	29	*Pinus taeda*	*Pinaceae*	dry soil, moderate sunlight
Site 9	Control	30	*Quercus nigra*	*Fagaceae*	slightly moist soil, low sunlight
Site 9	Control	31	*Quercus nigra*	*Fagaceae*	slightly moist soil, low sunlight
Site 9	Control	32	*Callicarpa americana*	*Verbebaceae*	slightly moist soil, low sunlight
Site 9	Control	33	*Vaccinium*	*Ericaceae*	slightly moist soil, low sunlight
Site 4	Beaver	34	*Myrica cerifera*	*Myricaceae*	slightly moist soil, moderate sunlight
Site 5	Beaver	35	*Vitis rotundifolia*	*Vitaceae*	slightly moist soil, moderate sunlight

Collection Site	Site Type	Collection #	Species	Family	Habitat
Site 7	Beaver	36	*Liquidambar styraciflua*	*Hamamelidaceae*	moist, shaded soil
Site 1	Control	37	*Ampelopsis arborea*	*Vitaceae*	slightly moist soil, low sunlight
Site 4	Control	38	*Prunus serotina*	*Rosaceae*	dry soil, moderate sunlight
Site 1	Control	39	*Rubus trivialis*	*Rosaceae*	moist soil, moderate-high sunlight
Site 7	Control	40	*Lonicera japonica*	*Caprifoliaceae*	slightly moist soil, low sunlight
Site 1	Beaver	41	*Parthenocissus quinquefolia*	*Vitaceae*	slightly moist soil, moderate sunlight
Site 7	Control	42	*Smilax glauca*	*Liliaceae*	moist, shaded soil
Site 2	Beaver	43	*Vitis rotundifolia*	*Vitaceae*	moist, shaded soil
Site 2	Beaver	44	*Liriodendron tulipifera*	*Magnoliaceae*	dry soil, moderate sunlight
Site 7	Control	45	*Magnolia grandifolia*	*Magnoliaceae*	dry soil, moderate sunlight
Site 5	Beaver	46	*Ilex opaca*	*Cyrillaceae*	dry soil, moderate sunlight
Site 5	Beaver	47	*Acer rubrum*	*Aceraceae*	moist, shaded soil
Site 4	Beaver	48	*Rubus betulifolia*	*Rosaceae*	moist soil, moderate-high sunlight
Site 4	Beaver	49	*Quercus laurifolia*	*Fagaceae*	slightly moist soil, low sunlight
Site 5	Beaver	50	*Smilax smallii*	*Liliaceae*	slightly moist soil, moderate sunlight
Site 4	Beaver	51	*Fraxinus caroliniana*	*Oleaceae*	slightly moist soil, moderate sunlight
Site 5	Beaver	52	*Clethra alnifolia*	*Clethraceae*	moist soil, moderate-high sunlight
Site 2	Control	53	*Ligustrum sinense*	*Oleaceae*	moist, shaded soil
Site 5	Beaver	54	*Lyonia lucida*	*Ericaceae*	moist, shaded soil
Site 5	Beaver	55	*Magnolia virginiana*	*Magnoliaceae*	moist soil, moderate-high sunlight
Site 5	Beaver	56	*Mikania scandens*	*Asteraceae*	moist soil, moderate-high sunlight
Site 6	Beaver	57	*Nyssa sylvatica*	*Nyssaceae*	moist, shaded soil
Site 5	Control	58	*Polyganum sp*	*Polygonaceae*	wet, soggy soil with full sunlight
Site 1	Control	59	*Polyganum sp*	*Polygonaceae*	wet, soggy soil with full sunlight
Site 1	Control	60	*Eupatorium sp*	*Asteraceae or Compositae*	moist soil, moderate-high sunlight
Site 4	Control	61	*Eupatorium sp*	*Asteraceae or Compositae*	moist soil, moderate-high sunlight
Site 1	Control	62	*Hydrocotyle sp*	*Apiaceae*	wet, soggy soil with full sunlight
Site 1	Control	63	*Juncus sp.*	*Juncaceae*	moist soil, moderate-high sunlight
Site 5	Beaver	64	*Persea borbonia*	*Lauraceae*	moist soil, moderate sunlight
Site 4	Beaver	65	*Woodwardia areolata*	*Blechnaceae*	moist, shaded soil
Site 5	Beaver	66	*Woodwardia virginiana*	*Blechnaceae*	moist soil, moderate-high sunlight
Site 2	Beaver	67	*Pteridium aquilinum*	*Pteridaceae*	moist, shaded soil