Impact by North American Beaver *(Castor canadensis)* on Forest Plant Composition in the Wilds, a Surface-Mined Landscape in Southeastern Ohio

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ABSTRACT. The impacts of *Castor canadensis* Kuhl (American beaver) on local ecosystems through foraging and dam construction activities have been well documented. Here we examined beaver foraging activity in the Wilds, an ecosystem in southeastern Ohio that was most recently subjected to surface mining betwen the late 1960s and the middle 1980s. Our objective was to make detailed observations of recent and past foraging patterns with the aim of better assessing the impact beaver might have on the recovery of forests in this altered landscape. One active site, a site downstream of the active impoundment and two recently abandoned beaver dam sites were chosen as study sites. At all sites, terrestrial foraging by beaver was generally concentrated within 20 m of water's edge and declined sharply beyond 40 m. Foraging activity was concentrated on, but did not seem to be limiting, the dominant standing species. Thus, there was little indication that foraging activity might be directly altering the nature of forest development in this community. However, other less direct impacts such as consequences arising from damming activities may well yet yield important and long-term effects in this recovering ecosystem.

OHIO J SCI 108(2): 9-15, 2008

INTRODUCTION

Unlike other major North American herbivores, *Castor canadensis* Kuhl (American beaver) have the ability to harvest mature trees. The high degree of selectivity in foraging in combination with the creation of light gaps through canopy openings and subsequent impacts on tree recruitment patterns, suggest beaver foraging could potentially exert an important influence on the structure and diversity of woody plant communities (Aldous 1938, Johnston and Naiman 1990, Fryxell and Doucet 1991). While there have been many studies oriented towards describing foraging preferences and other foraging patterns (Hall 1960, Brenner 1962, Nixon and Ely 1969, Northcott 1971, Jenkins 1979, 1980, Belovsky 1984, McGinley and Whitman 1985, Breck et al. 2003), a small number of studies have focused on assessing the overarching effects of beaver herbivory on forest communities (Pollock et al. 1995, Barnes and Dibble 1988, Johnston and Naiman 1990, Donkor and Fryxell 1999, 2000). Generally, studies suggesting that beaver have the potential to alter plant community structure through impacts on species diversity have been primarily conducted at active beaver impoundments. However, Donkor and Fryxell (1999, 2000) also found the effects on species diversity patterns at an abandoned dam site of three years. By contrast, Barnes and Mallik (2001) found no significant changes in the plant community structure over a longer period of abandonment (12+ years). To our knowledge, no studies have assessed the impact of beaver on an ecosystem recovering from habitat alteration as extreme as surface-mining. In ecosystems in which the recovery of hardwoods is a goal, assessing the short- and long-term effects of beaver foraging on woody plants and forest development could potentially hold important implications for management planning.

The specific objective of this study was to describe the nature and intensity of tree selection at both active and abandoned impoundments. Based on these observations, we aimed to assess the potential impact of beaver foraging on forest development and recovery.

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STUDY SITE

The study was conducted within the Wilds, a conservation research and education facility located on 4,050-ha of reclaimed surface-mined land in southeastern Ohio (81 deg. 42 min. 57.86 sec. W, 39 deg. 50 min. 48.29 sec. N, elevation 910 ft). Study sites were located in the largely forested northern section of the property. Signs such as the presence of dammed streams, lodges, and indications of heavy vegetation browsing were plentiful, suggesting that beaver foraging might be yielding important impacts on forest structure and development. Concern about recreational trail flooding and alterations of forest succession patterns were partial motivations for the study. Because hunting and kill-trapping are prohibited on the property, beaver face reduced mortality relative to other locations in the region. The forest cover is mixed, primarily consisting of maples (*Acer*), European black alder (*Alnus glutinosa*), black locust (*Robinia pseudo-acacia*), tree-of-heaven (*Ailanthus altissima*), autumn-olive (*Elaeagnus umbellata*), sycamore (*Platanus occidentalis*), and red oak (*Quercus rubra*).

METHODS

Beaver feed on a variety of herbaceous vegetation, including grasses, forbs, ferns, shrubs and trees (Northcott 1971, Barnes and Mallik 2001). Harvesting of woody plants, however, is highly selective and consistent with optimal "central place" foraging around the water-based colony where foraging activity is concentrated near the edge of the pond (Aldous 1938, Schoener 1979, Fryxell and Doucet 1991, Basey and Jenkins 1995, Donkor and Fryxell 2000, Barnes and Mallik 2001). Other investigators have reported beaver-favored species to include *Acer rubrum* L. (red maple), *Alnus incana* L. (speckled alder), *Acer saccharum* Marsh. (sugar maple), *Betula alleghaniensis* Britt. (yellow birch), *Corylus cornuta* Marsh. (California hazel), *Salix bebbiana* Sarg. (bebb willow), and *Populus tremuloides* Michx. (quaking aspen) (Belovsky 1984, Donkor and Fryxell 1999). Tree species observed to be selected by beaver at the Wilds include sugar maple, *Salix nigra* Marsh. (black willow), *Elaeagnus umbellata* Thunb. (autumn-olive), *Liquidambar styraciflua* L. (sweetgum), and *Alnus glutinosa* L. (European black alder).

Field Sampling

One active and two recently abandoned beaver dam sites were chosen as primary study sites. At the active site, we elected to make addition observations downstream of the impoundment as a means of assessing the degree to which there were spatial gradients in current foraging activity (which would be expected based on predictions of central place foraging theory). The four study sites were selected after conducting an extensive walking inspection of the area as well as by reviewing aerial photographs. All field measurements in this study were made between 15 July and 8 August 2004.

Evidence of current use (that is active impoundments) included the presence of saplings bearing fresh cone-shaped tree cut marks as well as the presence of well-maintained dams and lodges. In addition, the presence of branches with freshly peeled bark was also regarded as an indication of recent beaver activity. Evidence of previous use included the presence of decaying stumps cut by beaver and the presence of poorly maintained lodges and dams.

The species and diameter of living woody plants as well as plants cut by beaver were recorded along 2 x 40 m transects (Donkor and Fryxell 1999, 2000, Fryxell 2001, Breck et al. 2003). We limited transect length to 40 m after investigation of the study area indicated that beaver rarely harvested plants beyond that distance. Two transects were established at the active impoundment, the downstream site, and at one of the abandoned impoundments. Three transects were established at the other abandoned impoundment. Each of the nine total transects were further divided into four 2 x 10 m subplots in order to facilitate comparisons of foraging impact as a function of distance to water (Donkor and Fryxell 2000). Transects were placed at least 20 m apart starting at waters edge and were oriented perpendicular to the edge of the water (Donkor and Fryxell 1999, 2000, Barnes and Mallik 2001, Fryxell 2001).

Diameters of beaver-cut stumps and uncut trees ≥1 cm were recorded within each subplot. Diameter measurements were taken at 30 cm above the ground (Barnes and Mallik 2001). In cases in which plants were cut below 30 cm, then diameter measurements were taken at the point cutting was initiated. Some stumps had decayed to such a degree that species identification was impossible and were therefore excluded from inclusion in the analyses.

We followed the methods established by Donkor and Fryxell (1999, 2000) to estimate feeding activity and sapling recruitment. In most cases, bark characteristics were sufficient to allow for species identification. Following Donkor and Fryxell we defined recruitment rate of each tree species as the number of stems in the 1-4 cm diameter size class per subplot. Tree diversity was estimated using a simple count of species number (that is species richness). Stem density was estimated as the number of stems / m^2 observed in each 20 m^2 area subplot. Basal area estimates were based on circumference measurements taken at 0.3 m above the ground. Given there was only one downstream site in our study, species diversity, stem density, and basal area data were pooled across the two active impoundment and abandoned sites in order to facilitate cross site-type comparisons.

RESULTS

Forest Vegetation Patterns

Adjacent to the active impoundments, tree species diversity was low; ranging from three to four species across the entire 40 m transect distance (Fig. 1). Stem diversity was low near the pond (< 0.50 stems / m^2) but increased as function of distance from waters edge; peaking between 20.1 – 30 m at 2.25 stems / m^2. Basal area diversity followed a similar pattern and declined sharply between 30.1 – 40 m. Sweetgum and autumn-olive had the highest stem densities (87% and 5% respectively). Sweetgum had the highest basal area (60%). Black locust and sycamore also had high basal areas (14% and 15% respectively). Ninety-two percent and 89% of the total stems and total basal area of uncut woody plants were represented by these species (Table 1).

Observations at the downstream site indicated species richness was higher, peaking at seven species in the second subplot (10.1 – 20 m from the water's edge, Fig. 2). Stem diversity also peaked between 10.1 – 20 m at 0.85 stems /m^2. Basal area diversity followed the same pattern observed at the active impoundments, but did not decline as sharply between 30.1 – 40 m (Fig. 2). Sweetgum (54%) and autumn-olive (34%) had the highest stem densities. American beech and black locust also constituted high proportions, constituting 3% of the total stems each. Red oak, sweetgum, and white pine had the highest basal area (43%, 25%, and 11% respectively). These species accounted for 94% of the total stems and 79% of the total basal area of uncut woody plants (Table 2).

At the abandoned impoundments, species richness increased with distance, peaking in the 20.1-30 m distance class and then declined. Stem density was slightly higher beyond 30.1 m than it was within 10 m of the water's edge. Between 10.1 – 30 m stem density declined sharply. Basal area declined between 10.1 – 20 m but then rose sharply. Basal area at distances 20.1 – 30 m and 30.1 – 40 m was higher than the basal area within 10 m of the shore (Fig. 3).

Autumn-olive and tree-of-heaven had the highest stem densities at the two abandoned sites (58% and 26% respectively). The bulk of the basal area consisted of sycamore (32%), tree-of-heaven (27%), and silver maple (21%). Eighty-four percent and 80% of the total stems and total basal area of uncut woody plants were represented by these species (Table 3).

Foraging Activity

At the active impoundments, 55% (21 cut of 38 available) of the all woody plants within 10 m of the shore were harvested. At 10.1-20m, 68 stems were available of which 38% were harvested. At 20.1-30 m, 129 stems were available of which 28% were harvested. At 30.1 – 40 m, beavers only harvested 20% of woody plants (15 cut, 74 available). Cutting activity was concentrated within 20 m of the water's edge around the beaver pond. Forty-eight percent (47 cut, 106 available) of stems were cut at 0 – 20 m while 37% (36 cut, 129 available) of stems were cut between 20.1 – 30 m. Only 15% of all cut stems were cut between 30.1 – 40.

Of six available woody plant species, only autumn-olive and sweetgum were selected. Foraging on these species was concentrated within 20 m of the water's edge. Within 10 m of waters edge 62% (13 cut, 21 available) of autumn-olive stems were cut while 90% (9 cut, 10 available) were harvested between 10.1 – 20 m (Fig. 4). Seventy-seven percent (10 cut, 13 available) of sweetgum stems were harvested within 10 m of waters edge and 34% (17 cut, 50 available) were cut at distances between 10.1 – 20 m. No autumn-olive was harvested further than 20.1 m from the shoreline. At distances of 20.1 – 30 m and 30.1 – 40 m, 29% (36 cut, 126 available) and 21% (15 cut, 71 available) of sweetgum stems were harvested (Fig. 4).

Downstream of the impoundment, cutting activity was also concentrated close to waters edge. Sixty-three percent of cut stems were within 10 m of the shore and 89% of cut stems were within 20 m of the water's edge. Within 10 m of the shoreline 45% (24 cut, 53 available) of all stems were harvested. At distances 10.1 – 20 m and 20.1 – 30 m 22% (10 cut, 45 available) and 11% (four cut, 36 available) of all stems were selected. Unlike cutting around the beaver pond, no woody plants were cut past 30 m (Fig. 4).

Of 10 available species, four were cut (Fig. 4). Herbivory was concentrated on autumn-olive and sweetgum although tulip tree and sycamore were taken at least once. Autumn-olive was only selected within 10 m of the shore with 14% (one cut, seven available) being cut. It was available at the other distances: 10 stems available each at distances 10.1 – 20 m and 20.1 – 30 m and 12 stems available beyond 30 m. Fifty percent (23 cut, 46 available) of cut sweetgum was within 10 m of shore. At distances 10.1 – 20 m and 20.1 – 30 m 32% (nine cut, 28 available) and 15% (three cut, 20 available) were harvested. Only one sweetgum, which was

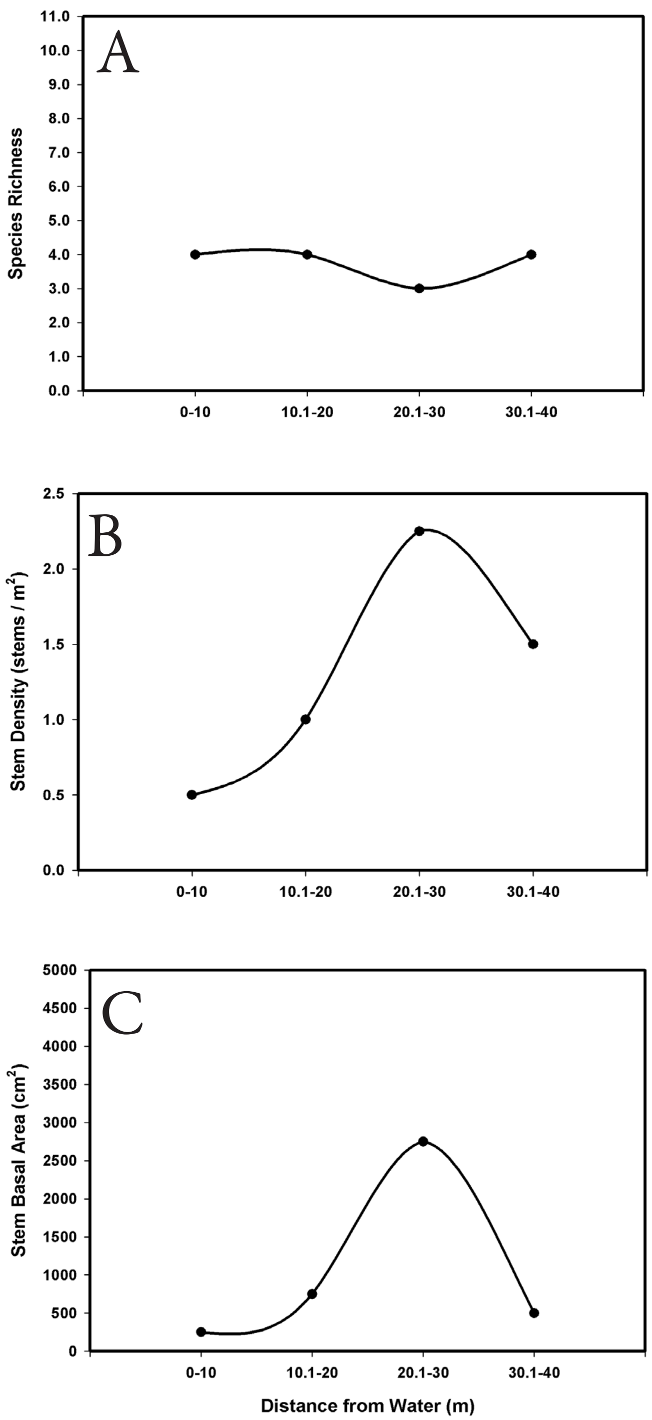

Figure 1. Relationship between distance from water and species richness (A), stem density (B), and basal area (C) around the active impoundment.

Table 1

Species composition of standing woody plants with a diameter ≥1 cm adjacent to the active impoundment

Species	Stem (%)	Basal area (%)
Liquidambar styraciflua L. (sweetgum)	87.2	60.1
Elaeagnus umbellate Thunb. (autumn olive)	5.2	0.5
Robinia pseudoacacia L. (black locust)	3.3	13.6
Ailanthus altissima P. Mill. (tree-of-heaven)	3.3	7.8
Fraxinus pennsylvanica Marsh. (green ash)	0.5	3.3
Platanus occidentalis L. (American sycamore)	0.5	14.7

Note: Total standing stems = 211, total basal area of standing woody plants = 4984.4 cm^2. Both transects measured 2 m x 40 m.

Table 2

Species composition of standing woody plants with a diameter ≥1 cm downstream of the active impoundment

Species	Stem (%)	Basal area (%)
Liquidambar styraciflua L. (sweetgum)	53.6	24.5
Elaeagnus umbellate Thunb. (autumn olive)	33.9	6.1
Fraxinus pennsylvanica Marsh. (green ash)	2.7	1.1
Robinia pseudoacacia L. (black locust)	2.7	4.5
Quercus rubra L. (red oak)	1.8	43.1
Ulmus rubra Muhl. (slippery elm)	1.8	4.2
Liriodendron tulipfera L. (tuliptree)	0.9	0.0
Pinus strobes L. (eastern white pine)	0.9	10.6
Platanus occidentalis L. (American sycamore)	0.9	2.6
Ailanthus altissima P. Mill. (tree-of-heaven)	0.9	3.3

Note: Total standing stems = 112, total basal area of standing woody plants = 4961.0 cm^2. Both transects measured 2 m x 40 m.

not cut, was observed at 30.1 – 40 m. Of the two tulip trees, both found between 10.1 – 20 m, one was harvested. Though sample size was obviously limited, all of the sycamores (one cut, one available) between 20.1 – 30 m were cut while the only other sycamore, at 10.1 – 20 m, remained standing (Fig. 4).

At the abandoned impoundments, as was observed at the active impoundment and downstream of the active impoundment, cutting activity was concentrated within 20 m of the water's edge at the abandoned sites. Sixty-six percent of cut stems were found within 20 m of the shore while only 2% of all cut stems were between 30.1 – 40 m. Thirty-six percent (39 cut, 109 available) of stems within 10 m of the shore and 26% (19 cut, 73 available) of stems between 10.1 – 20 m were harvested. No stems were cut between 20.1 – 30 m.

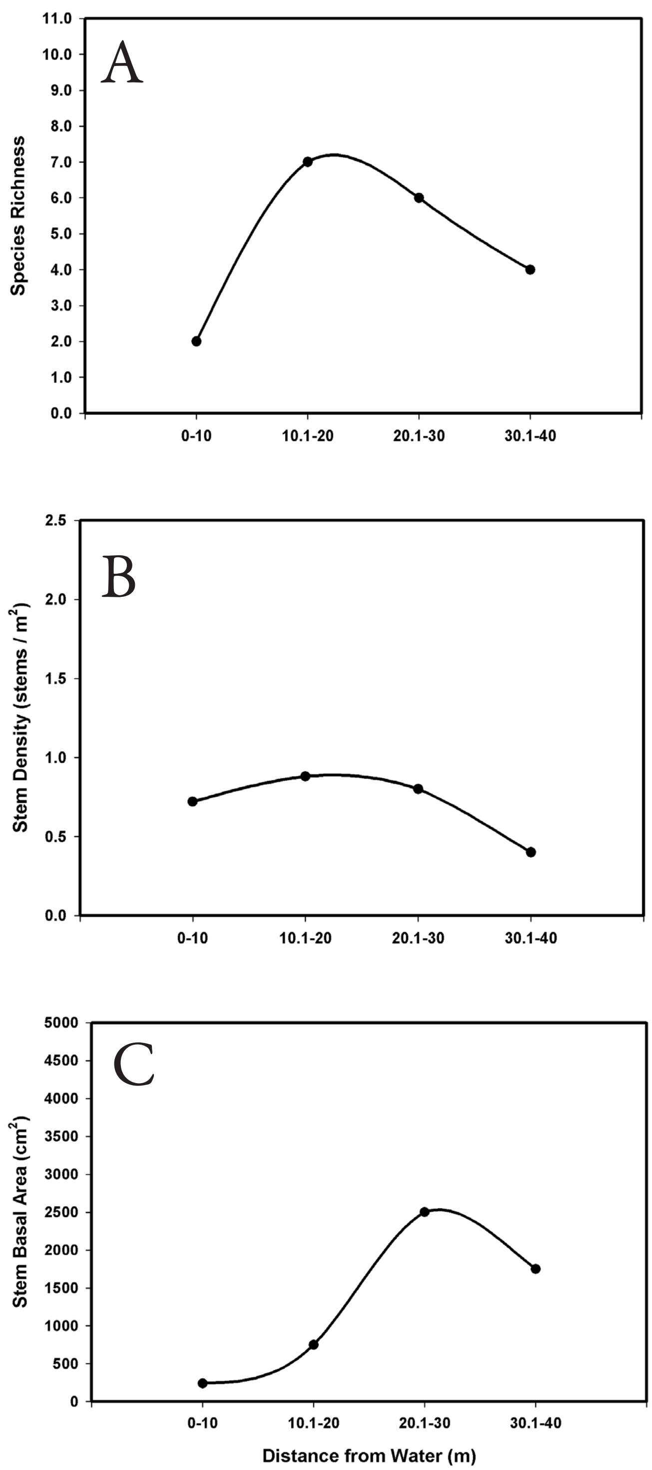

FIGURE 2. Relationship between distance from water and species richness (A), stem density (B), and basal area (C) downstream of the active impoundment.

Of 15 available woody plant species, all hardwoods, only autumn-olive and black locust were selected. Foraging of these species was concentrated within 20 m of the water's edge. Forty-one percent (36 cut, 87 available) of autumn-olive stems were cut within 10 m of the shore (Fig. 4). Between 10.1 – 20 m 39% (19 cut, 49 available) were cut. No autumn-olive was cut between 20.1 – 30 m. Between 30.1 – 40 m only 2% (one cut, 42 available) of stems were harvested. For black locust stems, 57% (four cut, seven available) were cut within 10 m of the shore. One uncut plant was observed between 10.1 – 20 m. No black locust was observed at distances 20.1 – 30 m and 30.1 – 40 m (Fig. 4).

Sapling Recruitment

Sapling recruitment of autumn-olive was negatively associated with distance from water's edge at the active impoundments (seven saplings within 10 m and one sapling at each interval from 10.1 – 40 m). Sweetgum sapling recruitment was positively associated with distance up to 30 m (five saplings within 10 m, 30 between 10.1 – 20 m, and 83 between 20.1 – 30 m), but declined between 30.1 – 40 m (49 saplings; Fig. 5).

Downstream of the impoundment recruitment of autumn-olive was positively associated with distance (six saplings within 10 m, seven between 10.1 – 20 m, and nine between 20.1 – 30 m), but declined between 30.1 – 40 m (seven saplings). Sweetgum recruitment was negatively associated with distance (22 saplings within 10 m, 19 between 10.1 – 20 m, and 13 between 20.1 – 30 m). No sweetgum saplings were found between 30.1 – 40 m (Fig. 5). There were not enough woody plant saplings of other tree species to discern any patterns either at or downstream of the active impoundment.

At the abandoned impoundments, recruitment of autumn-olive was negatively associated with distance (46 saplings within 10 m, 25 between 10.1 – 20 m, and 16 between 20.1 – 30m), but increased between 30.1 – 40 m (33 saplings, Fig. 5). Sapling recruitment of tree-of-heaven increased with distance (eight saplings within 10 m and between 10.1 – 20 m, 9 between 20.1 – 30 m, and 12 between 30.1 – 40 m, Fig. 5).

DISCUSSION

Herbivory by beavers has been reported to be highly selective (Aldous 1938, Fryxell and Doucet 1991, Barnes and Mallik 2001). In this study, foraging was largely concentrated on sweetgum and autumn-olive. Given the mining history of this site and what we assume to be its significant impacts on patterns of forest development, we were not surprised to see distinct patterns of herbivory.

Beaver foraging patterns have been described as generally consistent with central place foraging theory (Schoener 1979, Basey and Jenkins 1995, Donkor and Fryxell 2000, Barnes and Mallik 2001). Time spent searching for food is reduced and energy is conserved if beaver forage near the lodge or den (Anderson 1978). Indeed, several studies have found that beaver rarely harvested woody plants more than 60 m from the water's edge (McGinley and Whitman 1985, Basey et al. 1988, Donkor and Fryxell 1999, 2000). At the Wilds, foraging by beaver declined sharply over 40 m from water's edge. A similar spatial pattern was documented by Barnes and Mallik (2001). Indeed, foraging activity at all three sites was generally concentrated near water's edge. At the active beaver impoundment, the largest percentage of harvested stems was observed at distances 20.1 – 30 m from water whereas downstream of the active impoundment and at the abandoned impoundment, the greatest percentage of cut stems was within 10 m of water's edge.

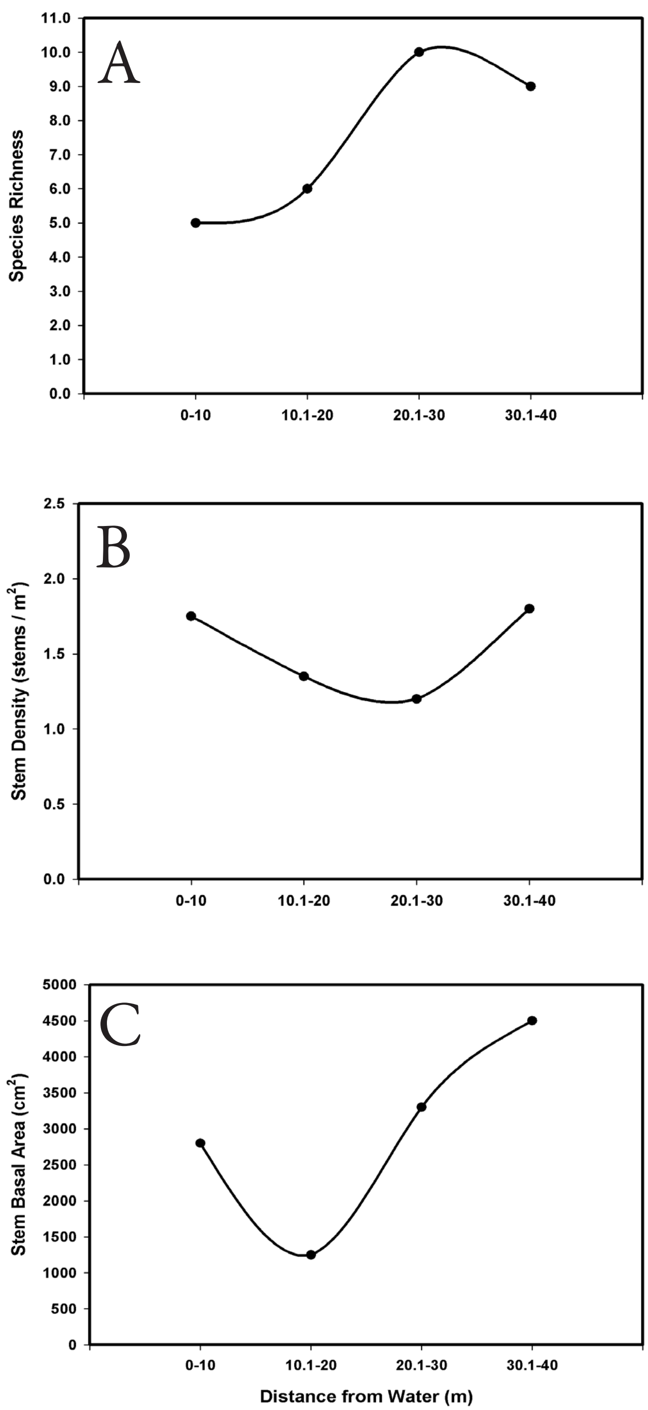

Figure 3. Relationship between distance from water and species richness (A), stem density (B), and basal area (C) around the active abandoned impoundments.

In their field studies, Jenkins (1980) and Belovsky (1984) suggest that beaver foraging behavior is strongly influenced by the risk of predation. Predation has often been cited as a driving mechanism behind foraging patterns that conform to central place expectations. Barnes and Mallik (2001) reported intense foraging activity within 20 m of the water's edge in areas with high *Canis lupus* Linnaeus (gray wolf) population numbers, while studies in areas without wolves reported longer foraging ranges (Bradt 1947, Hodgdon and Hunt 1953, Belovsky 1984, Johnston and Naiman 1990, Donkor and Fryxell 1999, 2000).

At the Wilds, beaver could be predated on by *Canis latrans* Say (eastern coyote). The fact that foraging activity was concentrated within 20 m from the water's edge (and thus near the safety of the water) is consistent with suggestions that predation pressure could be limiting the nature and magnitude of beaver foraging impact. However, it should be noted that the density of highly selected tree species (autumn olive and sweetgum) appears to have been higher relative to other species near the water's edge, thus complicating comparison and interpretation.

To what extent does foraging by beaver appear to be altering future forest composition at the Wilds? If it were the case that future stand composition was being significantly altered by beaver harvesting, it would be expected that recruitment of preferred species should appear to vary more as a function harvesting intensity

Table 3

Species composition of standing woody plants with a diamete ≥1 cm at both abandoned impoundments

Species	Stem (%)	Basal area (%)
Elaeagnus umbellate Thunb. (autumn olive)	58.1	9.0
Ailanthus altissima P. Mill. (tree-of-heaven)	25.7	26.6
Lindera benzoin L. (northern spicebush)	2.9	0.1
Platanus occidentalis L. (American sycamore)	2.5	32.4
Acer saccharinum L. (silver maple)	2.1	20.7
Quercus rubra L. (red oak)	1.7	0.1
Robinia pseudoacacia L. (black locust)	1.7	4.0
Fraxinus pennsylvanica Marsh. (green ash)	1.2	0.0
Acer negundo L. (box elder)	0.8	6.8
Carya spp. Nutt. (hickory species)	0.8	0.1
Ulmus rubra Muhl. (slippery elm)	0.8	0.3
Fagus grandifolia Ehrh. (American beech)	0.4	0.0
Carya alba L. (mockernut hickory)	0.4	0.0
Sassafras albidum Nutt. (sassafras)	0.4	0.0
Prunus serotina Ehrh. (black cherry)	0.4	0.0

Note: Total standing stems = 241, total basal area of standing woody plants = 11849.628 cm^2. All transects measured 2 m x 40 m.

rather than density of mature conspecifics. Observations for sweetgum at the active impoundment show some consistency with this expectation; however, we did not clearly observe this pattern at other sites suggesting that any impact of beaver foraging on sweetgum density would likely be limited. In addition, we cannot preclude the possibility that some other factor(s) are responsible for the recruitment patterns of sweetgum at these sites. Finally, given that no recruits of species other than sweetgum and autumn-olive were observed to be harvested, there is little basis for suggesting that beaver harvesting was likely imparting important impacts on future forest composition (at least without invoking claims that beaver foraging resulted in the complete decimation of recruits drawn from what appeared to be "non-preferred species"). Similarly, Donkor and Fryxell (1999) concluded that beaver foraging did not shift the woody plant community towards non-preferred species.

Nonetheless, foraging may well be exerting important, though perhaps less obvious effects. Beaver cutting could create canopy light gaps, provide space, and free up nutrients. Conceivably, such effects could eventually facilitate the growth of unselected species to establish themselves, thus enhancing forest tree diversity. That being

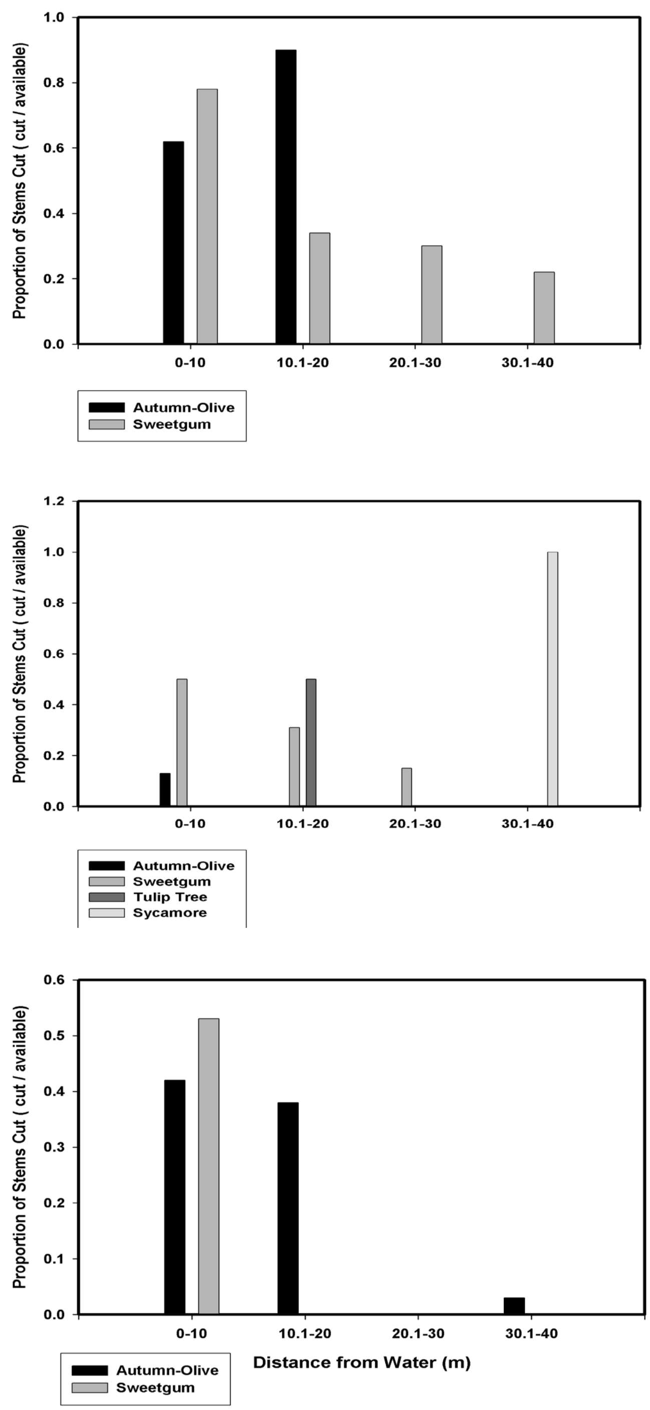

Figure 4. Proportions of tree stems harvested by beaver (*Castor canadensis*) at the active impoundment (A), downstream from the impoundment (B), and at the abandoned impoundment (C).

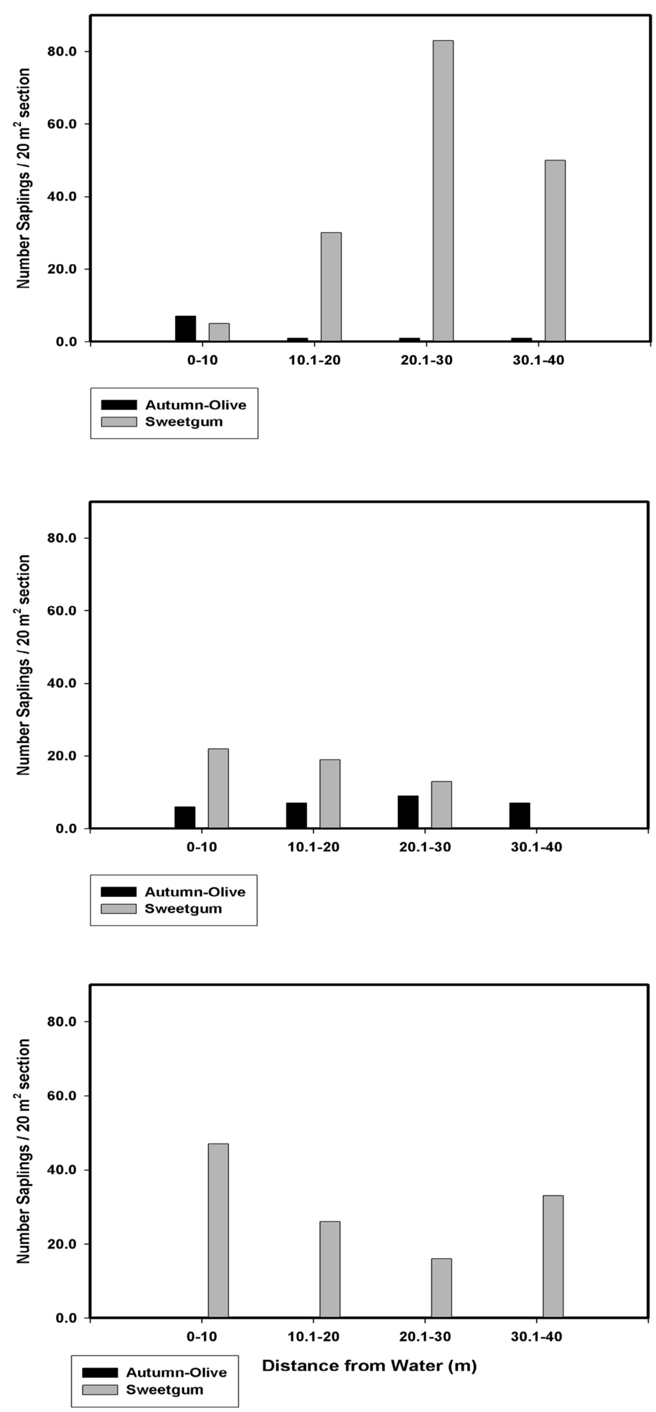

Figure 5. Sapling recruitment of beaver-selected species, by (*Castor canadensis*) at the active impoundment (A), downstream from the impoundment (B), and at the abandoned impoundment (C).

said, at this point the relatively low levels of forest tree diversity we observed would suggest that no such effect has manifested itself as yet. Comparisons with recovering sites not colonized by beaver or with perhaps to beaver exclusion plots would prove very helpful in elucidating any such effects.

Finally, it may be possible that the cumulative affects of damming and flooding by beaver could induce changes in forest succession or diversity in the Wilds. The physical modification of habitat by beaver dam-building produces patches, or discrete communities (Pickett and White 1985). Following their abandonment, dams deteriorate, drain impoundments and create beaver meadows where new sediment enriched through the decay of vegetation is exposed (Wright et al. 2003). Fertile soil, high levels of sunlight, and elevated nitrogen levels characterize beaver meadows (Naiman et al. 1994, Johnston et al. 1995). These factors can allow woody plant species to persist within abandoned beaver-modified habitats that may not be present in the adjacent community, where light and nutrient availability and soil moisture levels differ (Wright et al. 2002). The increased habitat quality and diversity can lead to increased plant species richness. If the stream is not impounded again, seedlings of riparian and eventually upland tree species will grow among the grasses, herbs and shrubs and establish a forest that could differ from the surrounding, unmodified forest community (Snodgrass 1997).

If woody plant species other than what appear to be the dominant sweetgum and autumn-olive for example are able to exploit the beaver meadows of the Wilds, then there could be an increase in species richness. Visual observation of beaver activity throughout the northern section of the Wilds revealed numerous abandoned impoundments. Many of the abandoned dams remain intact and therefore are modifying waterflow and engendering the eventual development of beaver meadows. Evaluation and possible management of these abandoned dams may be determined to be important components of ongoing restoration efforts.

Acknowledgments. Ashley Campbell and Emily Snode contributed significantly to field work. We particularly wish to thank the Wilds for logistic support in the development and execution of this study, as well as facilitating access to a secure study site. Finally, we wish to thank Muskingum College for its award of a summer research fellowship to one of the investigators (B.V.) and enthusiastic commitment to the enhancement of student science education through participation in research.

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