

Beaver herbivory on aquatic plants

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Abstract Herbivores have strong impacts on marine and terrestrial plant communities, but their impact is less well studied in benthic freshwater systems. For example, North American beavers (*Castor canadensis*) eat both woody and non-woody plants and focus almost exclusively on the latter in summer months, yet their impacts on non-woody plants are generally attributed to ecosystem engineering rather than herbivory. Here, we excluded beavers from areas of two beaver wetlands for over 2 years and demonstrated that beaver herbivory reduced aquatic plant biomass by 60%, plant litter by 75%, and dramatically shifted plant species composition. The perennial forb lizard's tail (*Saururus cernuus*) comprised less than 5% of plant biomass in areas open to beaver grazing but greater than 50% of plant biomass in beaver exclusions. This shift was likely due to direct herbivory, as beavers preferentially consumed lizard's tail over other plants in a field feeding assay. Beaver herbivory also reduced the

abundance of the invasive aquatic plant *Myriophyllum aquaticum* by nearly 90%, consistent with recent evidence that native generalist herbivores provide biotic resistance against exotic plant invasions. Beaver herbivory also had indirect effects on plant interactions in this community. The palatable plant lizard's tail was 3 times more frequent and 10 times more abundant inside woolgrass (*Scirpus cyperinus*) tussocks than in spatially paired locations lacking tussocks. When the protective foliage of the woolgrass was removed without exclusion cages, beavers consumed nearly half of the lizard's tail leaves within 2 weeks. In contrast, leaf abundance increased by 73–93% in the treatments retaining woolgrass or protected by a cage. Thus, woolgrass tussocks were as effective as cages at excluding beaver foraging and provided lizard's tail plants an associational refuge from beaver herbivory. These results suggest that beaver herbivory has strong direct and indirect impacts on populations and communities of herbaceous aquatic plants and extends the consequences of beaver activities beyond ecosystem engineering.

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Introduction

Herbivory has been intensively studied in terrestrial and marine ecosystems, and ecologists have long appreciated the diverse impacts that herbivores have on plant community structure and ecosystem function (John et al. 1992; Rosenthal and Berenbaum 1992). By selectively consuming palatable plants and avoiding

low preference plants, herbivores commonly reduce plant standing stock, directly and indirectly alter community composition, and ultimately influence detrital accumulation, geochemical cycling, and other ecosystem processes (Lubchenco and Gaines 1981; Huntly 1991; Hay and Kicklighter 2001, 2002). The effects of herbivory on freshwater plant communities, however, have been largely ignored until more recently (Lodge et al. 1998).

Vertebrate herbivores in particular often have strong impacts on marine and terrestrial plant communities (Crawley 1989; Hay and Steinberg 1992), but their roles in freshwater communities generally have been overlooked, perhaps in part because of historical depletion by European settlers. For example, after being nearly extirpated by European colonists, North American beavers (*Castor canadensis*) are now thriving over much of their historical range and fundamentally modifying hydrologic regimes (Naiman et al. 1988), plant and animal communities (Martinsen et al. 1998; Wright et al. 2002, 2003; Pollock et al. 2003), and elemental cycling (Naiman et al. 1994). Beavers are best known as ecosystem engineers (sensu Jones et al. 1994) with the propensity to alter landscapes by felling trees, constructing dams, and digging canals (Muller-Schwarze and Sun 2003). Beavers, however, eat both woody and non-woody plants, often spending the majority of their time foraging for herbaceous plants, particularly in the summer (Tevis 1950; Jenkins 1980; Svendsen 1980; Doucet and Fryxell 1993). Despite these well-known foraging patterns, beaver impacts on herbaceous aquatic plant communities are generally attributed to the indirect effects of ecosystem engineering, including changes in water depth, sediment composition, and flood plain geomorphology (Naiman et al. 1988; Ray et al. 2001; Wright et al. 2002, 2003). Few studies have experimentally examined the direct effects of herbivory by this common and widespread aquatic herbivore.

Although beavers could directly influence aquatic plant communities by selectively foraging on palatable plants, plant neighborhoods composed of different species are likely to generate different preference hierarchies and ultimately influence patterns of impact (Atsatt and O'Dowd 1976; Milchunas and Noy-Meir 2002). Moderately acceptable plants may be ignored until more palatable neighbors have been selectively removed (Atsatt and O'Dowd 1976), whereas high preference plants may gain refuges from herbivory by associating with less palatable plants that physically or chemically deter herbivores (Tahvanainen and Root 1972; Hay 1986). Beavers, for example, are known to successively remove palatable trees from wetlands

until only the least palatable species remain (Barnes and Mallik 2001), whereas many freshwater wetlands are dominated by tussock-forming sedges and rushes that can harbor diverse floral communities (e.g., Ervin and Wetzel 2002), a pattern that has been hypothesized to result from sedge tussocks providing an associational defense and protecting palatable plants from vertebrate herbivores (Levine 2000). Thus, plant community composition may modify the effects of beaver herbivory for particular species at different spatial scales. Furthermore, selective feeding by beavers is also particularly important for contemporary patterns of wetland plant community structure as the widespread invasion of aquatic habitats by non-native plants (Galatowitsch et al. 1999) is generally thought to reflect herbivore feeding preferences for native over exotic plants (Keane and Crawley 2002), though experimental evidence is equivocal or even opposite to this pattern (Parker and Hay 2005; Parker et al. 2006a).

Here, we used a series of field experiments to ask whether beaver herbivory affected: (1) the standing stock and species composition of wetland plants and associated plant litter in two beaver wetlands, (2) the abundance of an invasive exotic plant, and (3) associational patterns of herbivory among co-occurring plant species. We also used a field feeding assay to determine if patterns of field impact reflected beaver feeding preferences among different plant species.

Materials and methods

Site description

Fieldwork was conducted in three beaver wetlands located in the Chattahoochee River National Recreation Area (CRNRA) near Atlanta, Georgia, USA. Beavers were common along the river despite its location within a metropolitan area of roughly 5,000,000 humans, though human disturbances (maintaining utility easements, hiking, bicycling, dogs, etc.) occasionally disturbed areas and caused beavers to move among wetlands or to avoid use of specific areas within a wetland. The Johnson Ferry wetland (33° 54.7' N, 84° 24.3' W) is approximately 5 km north of the Gumby Swamp wetland (33° 54.6' N, 84° 27.0' W), which is approximately 1 km north of the Cochran Shoals wetland (33° 54.3' N, 84° 26.8' W). All three wetlands are in separate watersheds draining into the northern bank of the Chattahoochee River. Beaver activity at all three wetlands was conspicuous at the outset of the experiment, including active lodge and dam building, uprooted macrophytes, torn and chewed woody vegetation,

beaver tracks, active beaver runs, and direct observations of beavers foraging in the vicinity of our treatments. Although we also observed other potential herbivores at sites, including one swamp rabbit (*Sylvilagus aquaticus* Bachman), mallards (*Anas platyrhynchos* L.), and two American snapping turtles (*Chelydra serpentina* L.), these observations were rare and there was no evidence (e.g., tracks in the vicinity of torn vegetation) to suggest their impact approached that of beavers. The vast majority of herbivory appeared to be due to beaver grazing.

Beaver exclusion

Beaver impacts on wetland macrophytes were evaluated experimentally by excluding beavers and monitoring changes in plant species composition and aboveground biomass over 13–28 months. In late March, 2003, we established three treatments in each of six spatial blocks at each wetland: (1) an open treatment allowing herbivore access, (2) a three-sided cage control allowing herbivore access but controlling for the presence of caging materials, and (3) a four-sided cage excluding herbivores. Each block consisted of three 1.22×1.22 -m plots arranged in an L-shape. Treatments were randomly assigned to the three plots, with the stipulation that the open treatment had to have at least three open sides and thus occupy either end of the L-shape. Exclusion cage treatments were constructed of 91-cm-tall wire fencing (5.1×7.6 cm mesh galvanized steel “rabbit fence”) affixed to four 1.22-m steel rebar posts. The cage control was a similarly constructed three-sided cage that shared one wall with the cage treatment. The open treatment abutted one side of the cage or cage control treatment and was delineated with steel rebar posts but had no mesh fencing. Plots were oriented randomly with respect to the main axis of each beaver wetland (and thus potential gradients in flow or wind direction) and were at similar depths across treatments ($P = 0.882$) within each wetland, but were in significantly deeper water at Gumby Swamp (45 ± 2 cm, mean \pm SE) than Cochran Shoals (31 ± 1 cm) and Johnson Ferry (25 ± 2 cm, $P < 0.001$, two-way blocked ANOVA).

To assess whether vegetation varied across treatments at the outset of the experiment, we placed a 1.0-m^2 quadrat atop each treatment and recorded the frequency with which each species of plant occurred within each of eighty-one $10 \times 10\text{-cm}^2$ gridded squares in the quadrat. For the three–four dominant species in each wetland (their summed frequencies accounted for >90% of the total summed frequency of all species), we

assessed whether their frequency of occurrence varied among treatments at the initiation of the experiment.

In April 2003, we noticed that beaver activity at Cochran Shoals was highly concentrated in particular areas of the marsh, and that some plots were in areas that were not visited by beavers. To increase the spatial coverage of our cages and capture the impacts of beavers where they were actually foraging, on 16 April we established four additional blocks (constructed as before) at haphazard locations within marsh areas having clear signs of beaver activity. Similarly, on 23 June 2003, we established four additional blocks in areas of apparent beaver activity at Gumby Swamp. Because cage placement was not random throughout the wetland, this design limits our inferences about beaver impacts to areas of the wetlands in which beavers were present and foraging.

In the fall of 2003, the local municipality removed beavers from the Johnson Ferry wetland. In subsequent visits to this wetland, there were no signs of beaver activity. Thus, we considered the Johnson Ferry wetland a “control” site where beavers had been experimentally removed but other herbivores may have been present (e.g., rabbits, waterfowl, and turtles). To determine whether plant communities at this site were altered due to grazing from herbivores other than beavers, we analyzed among-treatment differences in the final frequency of the most abundant plant species in our treatments at this wetland.

In late July 2004, after 13–15 months of intact treatments, we harvested all aboveground plant biomass from one-half of each treatment at both Cochran Shoals and Gumby Swamp, with the harvested side from each treatment being randomly selected. We harvested only half of each plot to minimize disturbance to the plant communities in this National Park. Plants were clipped at the sediment surface, shaken to remove excess water, sorted to species, and weighed to the nearest gram. We also collected and weighed the accumulated leaf litter on the sediment surface in each treatment. We analyzed the final aboveground plant biomass for all plants combined, for those species that were abundant, and for the total leaf litter in each treatment with a two-way randomized block ANOVA. Data were square root transformed where necessary to meet ANOVA assumptions. Additionally, we randomly selected five of the ten blocks in each wetland to be left intact so as to monitor longer term changes to the plant community.

By 30 October 2005, after treatments had been in place for about 28 months, the Gumby Swamp wetland had been heavily invaded by the exotic South American plant *Myriophyllum aquaticum*. Four of the five

remaining blocks in this wetland were in areas showing signs of beaver activity; the fifth block was excluded because it was in an area where beavers had never foraged. Using methodologies similar to the 14-month duration experiment, we harvested one-half of the plant biomass from each these four blocks to determine beaver impact on a newly colonizing, invasive species nearly 2.5 years after establishment of the beaver-exclusion treatments. Beavers had abandoned the Cochran Shoals wetland by this time, so treatments in that wetland were not assessed.

Indirect effects of sedge tussocks on lizard's tail (*Saururus cernuus*)

By early June, 2003, the perennial forb lizard's tail (*Saururus cernuus*) was abundant within the exclusion cages but not the open treatments at the Cochran Shoals wetland (this species was not present at Gumby Swamp). Lizard's tail appeared rare throughout the rest of the wetland, but it did occur within tussocks of the woolgrass sedge, *Scirpus cyperinus* (L.) Kunth. We hypothesized that sedge tussocks might impede beaver foraging and provide lizard's tail an associational refuge from herbivory (e.g., Hay 1986). To determine whether lizard's tail was positively correlated with the presence of sedge tussocks, we counted the number of lizard's tail shoots emerging from each of 50 individual sedges located haphazardly throughout the wetland; these sedges constituted 50 of the approximately 70 total sedge patches in that wetland, with roughly ten of the unused patches being small and located along the wetland–upland border. The sedges we assessed thus constituted the vast majority of sedges within the wetland. We paired observations from within sedges with counts from 50 equal-sized areas adjacent to each sedge tussock but lacking a sedge. To obtain equal-sized areas adjacent to each tussock, we used a ring that we adjusted to the diameter of each tussock of interest. Locations of control plots were selected using a random compass direction and were placed within 20 cm of the tussock edge. We analyzed whether the occurrence and the density of lizard's tail shoots differed within vs. outside of sedge tussocks with a Fisher's exact test and a paired *t*-test, respectively.

To experimentally determine whether lizard's tail gained an associational refuge from beavers by growing within sedge tussocks, we conducted a crossed, factorial experiment excluding beavers and manipulating the presence of sedge foliage. We identified 60 sedges of roughly similar size containing at least one lizard's tail plant and counted the total number of leaves on lizard's tail shoots within each tussock as a measure of lizard's

tail abundance. We then clipped and removed the aboveground sedge foliage from 30 randomly selected sedge tussocks (clipping treatment), leaving the lizard's tail shoots intact. We placed standard tomato plant cages reinforced with 16-gauge galvanized wire (giving a mesh size of approximately 6.0×10.0 cm) around 15 of the clipped sedges and 15 of the unclipped sedges (caging treatment). We trimmed sedges every few days as they grew back. Thus, our crossed factorial design had the following treatments: (1) no clipping, no cage = ambient herbivory or control; (2) no clipping, cage; (3) clipping, no cage; (4) clipping, cage. This design allowed us to test the effects of beaver herbivory on lizard's tail in the presence and absence of sedge foliage and with or without cages excluding beavers.

After 2 weeks we counted the number of leaves remaining on lizard's tail shoots within each treatment and used the percent loss in leaf number as a measure of beaver impact. Data were analyzed with a two-way ANOVA followed by Tukey post hoc tests. Four replicates (7% of the total, one from each treatment) were excluded from the analysis because two cages had been pushed over and treatments grazed by beavers, and two open treatments appeared to have been trampled by humans.

Field feeding assays

We conducted a cafeteria-style (i.e., multiple choice) field feeding assay to determine patterns of feeding preference among five of the most common plant species from the Gumby Swamp and Cochran Shoals wetlands. We collected the upright stems and foliage of *Sparganium americanum*, hereafter bur-reed, lizard's tail, woolgrass sedge, *Polygonum densiflorum*, and *M. aquaticum* from both wetlands and placed approximately three to six intact stems from each plant species in 13 separate blocks into the sediment in approximately 5–10 cm of water along one shoreline of the Gumby Swamp wetland. After 48 h we visually scored the remaining total foliage of each species into the categories: 0, 25, 50, 75, or 100% foliage remaining.

Results

Beaver exclusion

At all sites where we erected cages, initial frequencies of plant cover were similar among treatments. At Cochran Shoals, there were no differences in the initial frequency of bur-reed, ($P = 0.402$), lizard's tail ($P = 0.402$), or *Ludwigia palustris* ($P = 0.455$) across

the beaver exclusion cage, cage control, or open treatments. At Gumby Swamp, these contrasts were: bur-reed ($P = 0.268$), *L. palustris* ($P = 0.263$), and smartweed (*Polygonum densiflorum*) ($P = 0.303$). At Johnson Ferry, these contrasts were: *Spirogyra* sp. ($P = 0.927$), *Potamogeton diversifolius* ($P = 0.467$), and *L. palustris* ($P = 0.643$). Thus, starting conditions did not differ across treatments within a wetland. When we erected four additional blocks of cages in areas of beaver activity at Cochran Shoals and Gumby Swamp in April and June, respectively, we also detected no initial among-treatment differences in plant frequency ($P = 0.499$, 0.958, 0.249, and 0.095 for bur-reed, lizard's tail, *L. palustris*, and *Polygonum* spp. respectively at Cochran Shoals; $P = 0.290$, 0.648, and 0.213 for bur-reed, *Polygonum densiflorum*, and *Juncus effusus*, respectively, at Gumby Swamp).

At Johnson Ferry, where beavers had been removed but other potential herbivores remained, more than 1 year of caging produced no significant, among-treatment differences in the abundance of freshwater plants [for species comprising >90% of the total plant cover: *Ludwigia palustris* ($P = 0.462$), *Polygonum* spp. ($P = 0.146$), *Sagittaria latifolia* ($P = 0.117$), *Leersia oryzoides* ($P = 0.116$), or *Juncus accuminatus* ($P = 0.121$)]. There also were no visual indications that biomass differed across the treatments.

By contrast, at both Cochran Shoals and Gumby Swamp where there were consistent signs of beaver activity (Fig. 1a), aboveground plant biomass was noticeably greater inside versus outside the exclusion cages (Fig. 1b). At these sites, excluding beavers resulted in a 2.9-fold increase in aboveground plant biomass compared to open plots where beavers could graze (Fig. 2). Plant mass did not differ between open area and cage control treatments (Fig. 2), suggesting that cages did not introduce substantial artifacts affecting plant growth and that beavers grazed within cage controls. Significant block and site effects (Fig. 2)

indicated spatial patchiness of aboveground plant biomass both within and across wetlands (i.e., there was more plant biomass inside certain blocks and at Cochran Shoals versus Gumby Swamp), though the lack of a significant site \times exclusion cage interaction term ($P = 0.702$, Fig. 2) indicated that grazing effects on total aboveground plant biomass were consistent between the two wetlands.

Two abundant plant species were strongly affected by beavers. Bur-reed was one of the only plant species that was present in our exclusion cages at both wetlands. At Gumby Swamp it was ninefold more abundant inside the exclusion plots than in the open plots, but at Cochran Shoals bur-reed was not significantly affected by excluding beavers (Fig. 3a). This pattern produced a significant site \times exclusion cage interaction term ($F_{2,45} = 4.00$, $P = 0.025$), indicating that this effect varied between wetlands. If wetlands were pooled, bur-reed was 1.7-fold more abundant inside the exclusion cages versus the open plots (exclusion effect: $F_{1,45} = 3.42$, $P = 0.042$). Lizard's tail was the second species strongly affected by beavers; at Cochran Shoals it was 180-fold more abundant inside exclusion cages versus the open plots where it was nearly absent (Fig. 3b). Lizard's tail did not occur at Gumby Swamp. The remaining species at each wetland were either too patchily distributed or too scarce to show consistent effects of grazing.

The exclusion of beaver also affected litter accumulation. Across both wetlands, leaf litter accumulation was fivefold greater inside the exclusion cages than in the open plots (Fig. 4). There was no site \times cage interaction (Fig. 4), indicating that the effects of beaver exclusion on litter accumulation were similar between wetlands.

After 2.5 years of beaver exclusion, beavers still significantly suppressed total plant abundance, and they also strongly suppressed the abundance of an exotic plant that colonized the Gumby wetland largely after

Fig. 1 **a** Beaver foraging at one of our sites. **b** View of one experimental block showing three-sided cage control, cage, and open treatment at Cochran Shoals wetland. Note presence of lizard's tail, *Saururus cernuus*, inside the cage treatment, but torn and uprooted vegetation outside of protected area



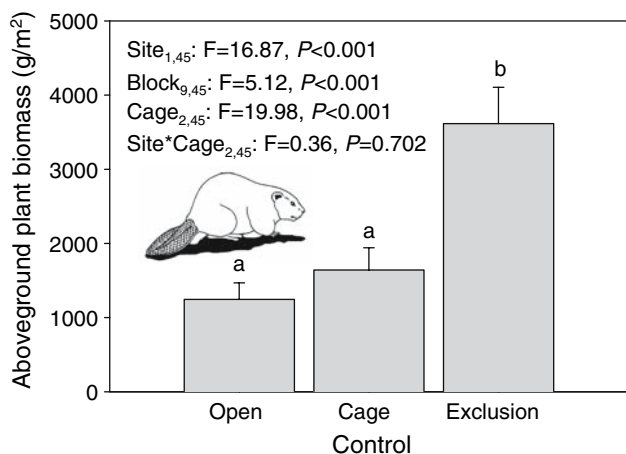


Fig. 2 Final aboveground fresh plant biomass per m² in each treatment type across both sites (Cochran Shoals and Gumby Swamp) after 13–15 months. Different letters above bars indicate means that were significantly different ($P < 0.05$, Tukey’s post hoc test)

the initial 13–15 month experiment ended. Total aboveground plant biomass was eightfold higher in the exclusion cages ($10,933 \text{ g/m}^2 \pm 8028$, $n = 4$) versus open treatments ($1,345 \pm 671 \text{ g/m}^2$, $n = 4$, $P = 0.050$, Friedman’s test) in the four blocks left at Gumby Swamp, with little evidence of a cage artifact in the cage control treatments ($1,939 \pm 1,211 \text{ g/m}^2$, $n = 4$). About 95% of the difference in total plant biomass was due to the exotic plant *M. aquaticum*, which was 7.9-fold more abundant in the cage ($10,275 \pm 8,243 \text{ g/m}^2$, $n = 4$) versus open treatments ($1,300 \pm 692 \text{ g/m}^2$, $n = 4$, $P = 0.039$, Friedman’s test), again with little evidence of a cage artifact ($1,879 \pm 1,234 \text{ g/m}^2$, $n = 4$).

Indirect effects of sedge tussocks on lizard’s tail

At the Cochran Shoals swamp, shoots of lizard’s tail occurred in 76% of sedge tussocks, but only 28% of the equal sized, adjacent areas lacking sedges (Fisher’s exact test $P < 0.001$, $n = 50$). Additionally, shoot density of lizard’s tail was tenfold higher inside than outside of sedge tussocks (6.7 ± 1.5 lizard’s tail shoots per sedge tussock, mean \pm SE vs. 0.64 ± 0.18 , respectively; $n = 50$, paired t -test $P < 0.001$). In the experiment crossing the presence of sedge foliage with a protective cage, leaf abundance of lizard’s tail declined by 43% in areas where sedges were clipped but not caged and thus exposed to beaver feeding ($P < 0.001$, Fig. 5). In contrast, leaf abundance of lizard’s tail increased by statistically similar amounts in the three treatments where lizard’s tail was surrounded by a sedge tussock (77%), a cage (73%), or both (93%, Fig. 5). Thus, sedge tussocks were as effective as cages at excluding beaver foraging.

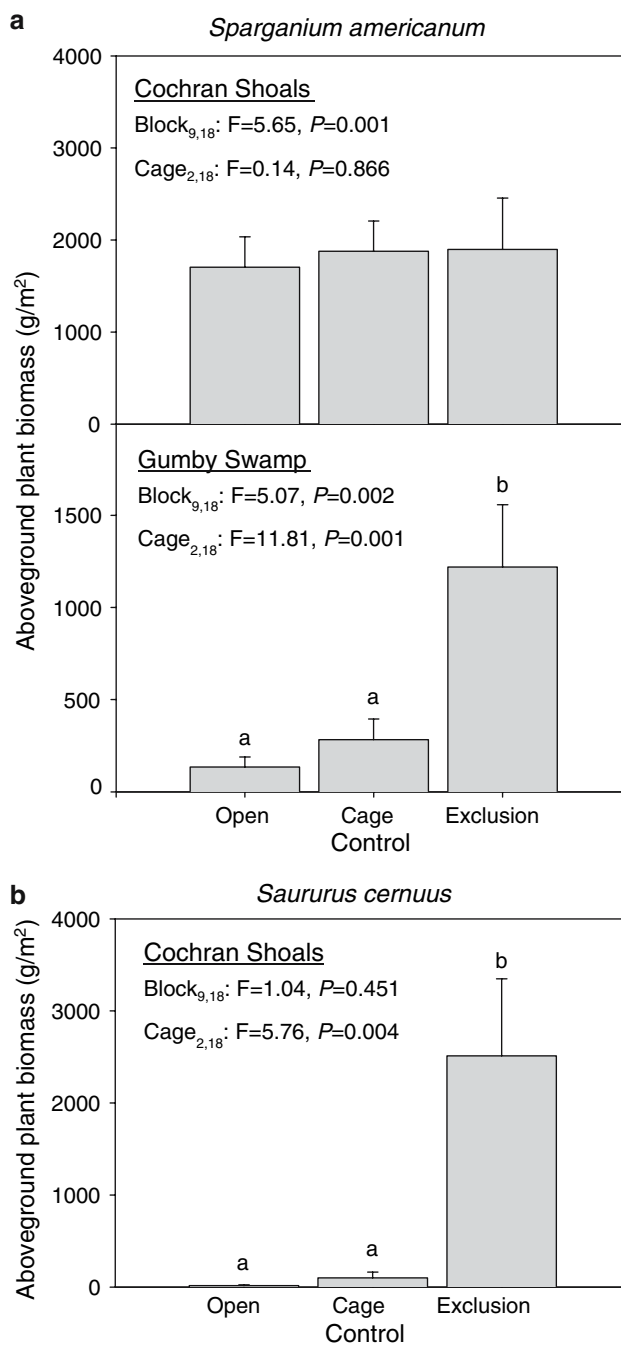


Fig. 3 Final aboveground fresh plant biomass for **a** bur-reed, *Sparganium americanum*, per m² at Cochran Shoals and Gumby Swamp, and **b** lizard’s tail, *Saururus cernuus*, at Cochran Shoals, in each treatment type after 13–15 months. Different letters above bars indicate means that were significantly different ($P < 0.05$, Tukey’s post hoc test)

Field feeding assays

Beavers selectively fed on lizard’s tail in a field feeding assay. Nine of 13 cafeteria-style arrays had evidence of feeding after 48 h, including torn leaves and stems and

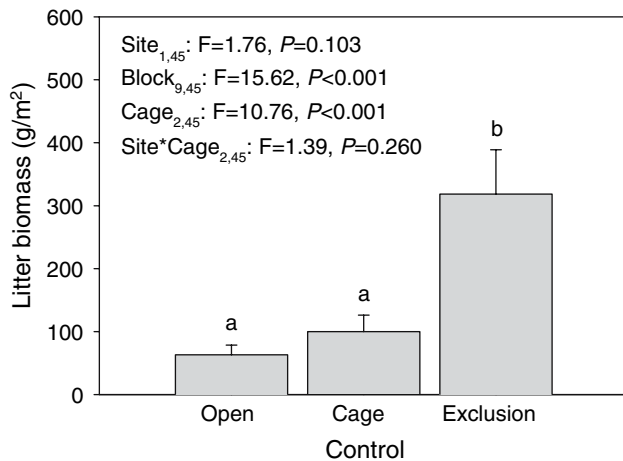


Fig. 4 Final aboveground litter biomass per m² in each treatment type across both sites (Cochran Shoals and Gumby Swamp) after 13–15 months. Different letters above bars indicate means that were significantly different ($P < 0.05$, Tukey's post hoc test)

missing plant portions. Among these nine blocks, beavers removed an estimated mean of $53 \pm 10\%$ of lizard's tail foliage but none of the woolgrass sedge foliage (Fig. 6, $P = 0.002$, Friedman's test). The remaining three species (bur-reed, *P. densiflorum*, and *M. aquaticum*) were of intermediate preference but statistically indistinguishable from any other choices in post-hoc multiple comparison tests (Fig. 6).

Discussion

Beavers are well-known ecosystem engineers that can impact herbaceous plant communities via flooding and other changes to edaphic or hydrologic conditions (Naiman et al. 1988, 1994; Pollock et al. 2003). Although beavers consume large amounts of herbaceous wetland plants in addition to woody species (Tevis 1950; Jenkins 1980; Svendsen 1980; Fryxell and Doucet 1993), the community-level impacts of beaver feeding on aquatic plants have not been quantified. Here, we show dramatic shifts in herbaceous plant species composition and biomass as a function of beaver feeding (Figs. 1, 2). When beavers were excluded by cages, aboveground plant biomass more than doubled (Fig. 2), and the Cochran Shoals site switched from dominance by bur-reed, *Sparganium americanum*, to dominance by lizard's tail, *Saururus cernuus*, (compare Fig. 3a, b). This new dominant in the cages at Cochran Shoals was the species that was most readily eaten in a field feeding assay (Fig. 6). Thus, by selectively consuming high preference aquatic plants, beavers fundamentally shifted both the standing stock and species composition of the herbaceous plants in these wetlands.

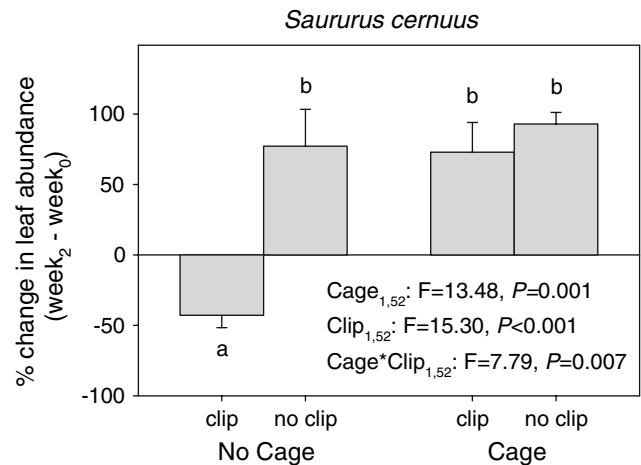


Fig. 5 The percent change in leaf abundance for lizard's tail *Saururus cernuus* plants at Cochran Shoals 2 weeks after we clipped back the surrounding foliage of woolgrass sedge *Scirpus cyperinus* and then left these plants either unprotected from beaver herbivory or protected with a cage. Different letters above bars indicate means that were significantly different ($P < 0.05$, Tukey's post hoc test)

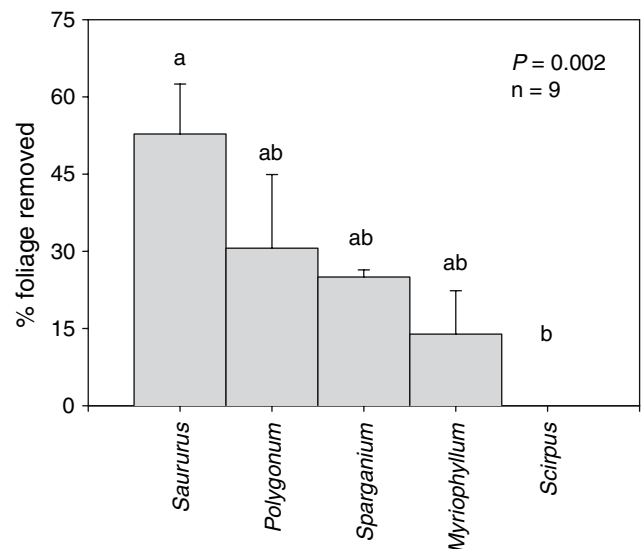


Fig. 6 Average amount of foliage removed by beavers from each plant species presented during a 48-h field feeding assay

Although beavers had strong impacts on particular species, these effects were mediated by the co-occurrence of neighboring plant species. Lizard's tail plants were largely absent from open areas of Cochran Shoals that were available to beavers but were tenfold more abundant when associated with tussocks of the woolgrass sedge *Scirpus cyperinus*. When we removed sedge foliage, lizard's tail plants lost about half their foliage within 2 weeks, while plants protected by either sedge foliage or cages increased their foliage by 73–93%

(Fig. 5). Thus, lizard's tail gained a spatial refuge from herbivory when growing in dense tussocks of this sedge. Similar instances of plant associational refuges have been described in both terrestrial (e.g., Atsatt and O'Dowd 1976; McNaughton 1978; McAuliffe 1986) and marine communities (Wahl and Hay 1995; Hay 1997). The sedge likely protects lizard's tail via physical defenses; *Scirpus* sedges have stout, silica-rich stems that could physically impede beaver foraging. Tussock-forming sedges often facilitate aquatic plant diversity (Ervin and Wetzel 2002; Crain and Bertness 2005; Ervin 2005), and may deter vertebrate herbivores in other systems (Levine 2000), suggesting that sedges can be strong interactors with extended consequences for wetland plant communities. Interestingly, approximately 1 month after we terminated this relatively short-term experiment, beavers essentially clear-cut all of the sedges at Cochran Shoals, leaving behind the clipped sedge vegetation but removing lizard's tail plants. Thus, sedge plants provided a spatial refuge from herbivory, but this refuge was temporally limited to the time period when beavers were unwilling or unable to forage within the sedge foliage.

Although beavers preferentially consumed and nearly eliminated lizard's tail from the wetland where it occurred, this same plant was unpalatable and chemically noxious to the crayfish *Procambarus clarkii* (Kubaneck et al. 2000, 2001). In fact, abundant populations of the crayfish *P. acutus* were observed in all three beaver wetlands, and organic extracts from lizard's tail from Cochran Shoals were chemically repugnant to these crayfish in laboratory feeding assays (J. Parker, unpublished data). It is not uncommon for plant chemical defenses to be effective against one consumer but not another (e.g., Hay 1992; Schupp and Paul 1994), suggesting that the lignoids that render lizard's tail repugnant to crayfish are inadequate defenses against beaver browsing. We also cannot rule out the possibility that some of the observed "herbivory" by beavers may have been related to bioturbation and ecosystem engineering rather than foraging. For example, beavers often clear vegetation and other debris to deepen water channels for predator escape routes and access to foraging areas (Muller-Schwarze and Sun 2003). However, beavers selectively fed on lizard's tail in our field feeding assay (Fig. 6), and quickly fed on lizard's tail foliage when protective sedge tussocks were removed (Fig. 5), both results suggesting that beavers were selectively feeding on, rather than indirectly damaging certain aquatic macrophytes like lizard's tail.

Aquatic macrophytes can have strong direct and indirect effects on ecosystem level processes including

productivity, biogeochemical fluxes, and water flow (Carpenter and Lodge 1986). Here, beavers reduced the total plant standing stock of wetland plant communities (Fig. 2), altered plant species composition (Fig. 3), and concomitantly caused a reduction in plant litter in areas exposed to beaver grazing (Fig. 4). Reductions in litter likely arose because dense stands of plants inside cages died and senesced in situ, whereas treatments exposed to beavers had less standing vegetation to produce litter and may have received more physical disturbance by beavers. Given that leaf litter from both allochthonous and autochthonous sources is an important source of organic matter in freshwater systems (Vannote et al. 1980), this result suggests that beavers could indirectly influence carbon flow, detrital processing, nutrient availability, and ultimately production of higher trophic levels by altering the quality and quantity of carbon sources in beaver wetlands, with potential impacts on processes occurring downstream of beaver impoundments (e.g., Naiman et al. 1994).

Historically, herbivores have been thought to facilitate exotic plant invasions by selectively consuming native over exotic plants (Keane and Crawley 2002). However, beavers reduced the biomass of the exotic aquatic plant *M. aquaticum* by nearly 90% in treatments open to beaver grazing. This result supports recent evidence that exotic plants are often palatable to and suppressed by native herbivores in field settings (Maron and Vila 2001; Parker and Hay 2005; Parker et al. 2006a). Nevertheless, *M. aquaticum* still comprised the majority of the total plant biomass in the open, cage control, and exclusion cage treatments, suggesting that reductions in the abundance of *M. aquaticum* were not associated with recolonization of these plots by native plants. Results in Parker et al. (2006a) were similar; native herbivores reduced the abundance of exotic plants but this was not always accompanied by native plant re-establishment. Thus, exotic plants often thrive in spite of the biotic resistance provided by native consumers, suggesting that factors other than herbivory may explain the success and spread of many exotic plants.

Beaver impacts in this study also had a spatial context at the scale of wetland. Bur-reed was only impacted at a site where the surrounding vegetation did not contain the highly preferred lizard's tail (Fig. 3), suggesting that lizard's tail may have served as an "attractant" plant (Atsatt and O'Dowd 1976) that reduced herbivory on the less-preferred bur-reed (Fig. 6) within this wetland. In contrast, beavers consumed bur-reed at Gumby Swamp, where lizard's tail was absent, and the strong impacts of beavers on

bur-reed at this wetland may have occurred because the alternative food sources at that wetland, primarily soft rush *J. effusus*, dense knotweed *P. densiflorum*, and (later) parrotfeather *M. aquaticum*, were not strongly preferred over bur-reed, as is suggested by the field feeding trial (Fig. 6). Thus, bur-reed may have been targeted at Gumby Swamp because it co-occurred with potentially less palatable neighbors, fulfilling the definition of “associational susceptibility” (Brown and Ewel 1987; White and Whitham 2000), and ignored at Cochran Shoals because of the presence of more palatable neighbors, i.e., associational resistance (Atsatt and O’Dowd 1976). In contrast, other large, mammalian grazers generally emigrate from stands dominated by unpalatable species in an effort to locate better foraging areas (reviewed in Milchunas and Noy-Meir 2002). Beavers, however, are central place foragers essentially tied to their lodge area and contiguous outlying wetlands because of the large construction costs associated with their habitats (Muller-Schwarze and Sun 2003), and in lieu of migrating from wetlands with less than optimal foods, beavers generally increase their consumption of non-preferred foods (Gallant et al. 2004), a pattern that may explain the late season cropping of sedges. Whether the lack of lizard’s tail at the Gumby wetland was the result of edaphic factors, extirpation by beaver, dispersal limitation, or other factors remains unknown. However, the strong effects of beaver on lizard’s tail at Cochran Shoals suggest the potential for beaver to at least periodically extirpate species through foraging.

Herbivory on freshwater plant communities has traditionally been considered insignificant (e.g., Shelford 1918; Rosine 1955; Hutchinson 1975). However, quantitative reviews show that aquatic herbivores remove as much or more of the plant standing stock in freshwater systems as they do in marine and terrestrial systems (Newman 1991; Cyr and Pace 1993; Lodge et al. 1998). Our results confirm these expectations and support a growing number of studies showing that generalist vertebrates, often native herbivores now recovering from early nineteenth century overharvesting (e.g., Srivastava and Jefferies 1996, this study), or non-native herbivores introduced by humans (e.g., Parker et al. 2006b), commonly have strong impacts on aquatic plant communities. These results suggest that although aquatic herbivores are often underappreciated, they are likely becoming more common, widespread, and will have increasingly important effects on the ecology and evolution of freshwater plant communities.

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