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Beavers cut, but do not prefer, an invasive shrub, Amur honeysuckle (*Lonicera maackii*)

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Abstract The North American beaver is a keystone riparian obligate which creates and maintains riparian areas by building dams. Invasive shrubs are common in riparian zones in the eastern U.S., but it is not known if beavers promote or inhibit these invasions. In southwest Ohio, we investigated beaver preference for Amur honeysuckle (*Lonicera maackii*), a prevalent riparian invader, compared to other woody species. At each of eight sites, we identified woody stems greater than 2.5 cm diameter on two 120 × 2 m transects parallel to the water's edge and six, 25 m secondary transects perpendicular to these, recording diameter, distance to the water's edge, and whether cut by beaver. The roles of plant genus, diameter, and distance to water in determining which stems were cut by beaver were determined by binomial generalized regression. Beaver preference for each genus and each site was quantified with an electivity index, which utilizes the proportion of stems cut compared to available stems. Probability of stem cutting depended on genus, diameter, and distance; stems closer to water and with smaller diameter had a higher probability of being cut. Although *L. maackii* comprised 41% of cut stems, it was low preference for beaver at six of eight sites. Beaver electivity for *L. maackii* was negatively associated with the density of small diameter stems of preferred taxa (*Salix, Ligustrum*, *Pyrus*, *Carya* and *Acer negundo*). These findings indicate that beaver do not hinder *L. maackii*. Another non-native shrub, *Elaeagnus umbellata*, had high electivities, suggesting beavers may impede its invasion.

Keywords *Castor canadensis* · Electivity · Exotic species · Riparian areas

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Introduction

Through heavy grazing or browsing, herbivores can change the composition of palatable and unpalatable plant species in an area (Tierson et al. 1966; Marquis 1981). Selective feeding on a non-native plant species could prevent invasion, consistent with the biotic resistance hypothesis (BRH), which states that ecosystems with higher biodiversity are more resistant to invasion than those with lower biodiversity (Elton 1958). In contrast, if the herbivore avoids or has low preference for the non-native species, that could

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promote invasion, as predicted by the enemy release hypothesis (ERH) (Maron and Vila 2001).

North American Beavers, *Castor canadensis*, have been observed consuming and using invasive woody species in riparian areas in the southwest United States. On the Rio Grande River in the Chihuahuan Desert, beaver had a high preference for the invasive Russian olive (*Elaeagnus angustifolia*) (Barela and Frey 2016). In areas with high cottonwood densities in eastern Montana, beaver cut 80% of the cottonwood trees while rarely cutting Russian olive or Salt Cedar (*Tamarisk* sp.). The growth rates of both of these invasives were higher in sites where beaver greatly reduced cottonwood canopy cover, suggesting beaver facilitated their ecological release (Lesica and Miles 2004). Additional evidence for beaver facilitation of tamarisk invasion comes from Grand Canyon National Park, where tamarisk is abundant in sites where beavers were abundant (Mortenson et al. 2008).

Although beavers were largely extirpated from the eastern U.S. before 1900, they have now repopulated most of their former range (Baker and Hill 2003). Beaver were abundant in Ohio until their extermination in 1830 (Chapman 1949) and disappeared from the Cincinnati area by 1805 (Hedeen 1985). Beaver re-established in parts of northwestern and eastern Ohio in the early 1930's (Chapman 1949). Beaver reappeared in the Cincinnati area in 1984 (Hedeen 1985) and the overall Ohio beaver population has been growing since the 1980s. Only one study in the eastern deciduous forest examined beaver use of non-native woody plants. In the Appalachian Mountains of North Carolina, Rossell et al. (2014) found that the nonnative shrub, Chinese privet (*Ligustrum sinense*), was one of the species 'moderately selected' by beaver, with a lower percentage cut than musclewood (*Carpinus carolina*), sweetgum (*Liquidambar styraciflua*), and tag alder (*Alnus serrulata*). No information has been published on interactions between beaver and other invasive shrubs, including Amur honeysuckle (*Lonicera maackii*), a prevalent invader in many Midwestern forests.

Lonicera maackii (Rupr.) Herder (Caprifoliaceae) is a shrub from east Asia that was introduced in North America in 1898 for horticulture and erosion control and is now regulated as an invasive species in eight states (Luken and Thieret 1996; McNeish and McEwan 2016; EDDMaps 2017). Studies have shown that *L. maackii* reduces plant species richness and abundance in invaded ecosystems and can greatly reduce herbaceous plant fitness (literature reviewed by McNeish and McEwan 2016). *Lonicera maackii* is also positively associated with riparian urbanization (Pennington et al. 2010; White et al. 2014). However, *L. maackii* density was lower in bottomlands compared to west and east facing slopes at a site in southwestern Ohio, (Gayek and Quigley 2001), a pattern the authors hypothesized was due to continuous canopy cover in the bottomland.

Alterations in the riparian plant community due to *L. maackii* invasion can have impacts on both the terrestrial and aquatic environment. *Lonicera maackii* has been found to negatively correlate with native tree seedlings and sapling densities within urban or disturbed riparian zones (White et al. 2014). A study conducted by McNeish et al. (2015) in western Ohio found where *L. maackii* has been removed from a stream reach, there is significantly greater in-stream light availability and terrestrial organic matter input. Beavers could be facilitating *L. maackii* invasion by cutting the native woody competitors (as found in some studies with other invasive species (Lesica and Miles 2004; Mortenson et al. 2008)) or could hinder the invasion by removing *L. maackii* and facilitating native plant species.

To determine whether *L. maackii* invasion is being facilitated or hindered, we investigated whether North American beavers use *L. maackii* preferentially compared to other woody species. We also investigated what factors were associated with differences in preference for this invasive shrub among sites. To address these objectives, we surveyed woody stems along transects at eight sites in southwest Ohio, calculated an electivity (preference) index for each genus in each site, and related electivity for *L. maackii* to the site characteristics of canopy openness, beaver residency time, and density of preferred stems.

Methods

Study sites

Eight sites in southwest Ohio (Fig. 1; Table 1) were selected for this study. Sites were located in the southern tip of the beech-maple-basswood region of eastern deciduous forest (Dyer 2006) in secondary forest stands within a matrix of row-crop agriculture

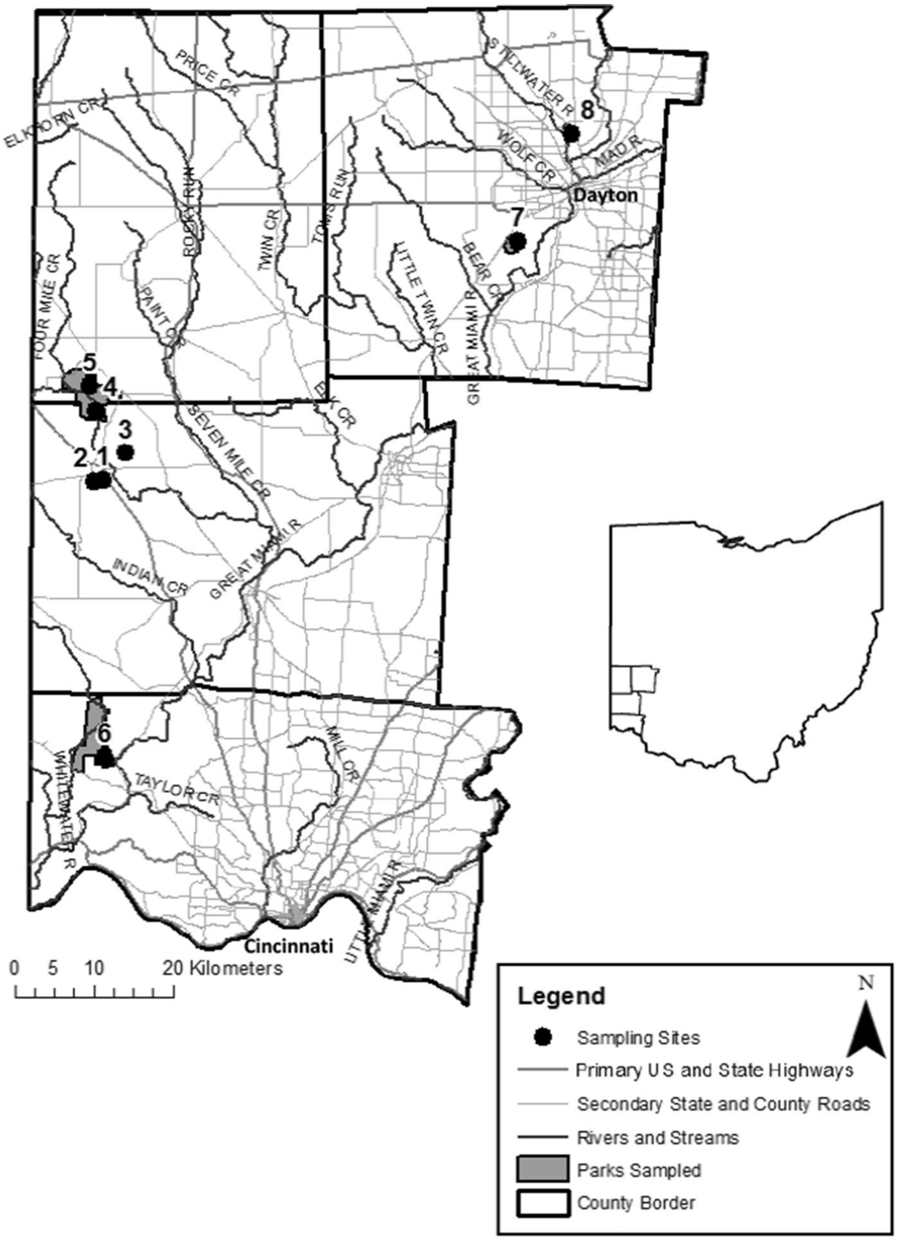

Fig. 1 Locations of study sites in southwest Ohio. Road and stream data obtained from Ohio Department of Transportation

and development. *Lonicera maackii* is a very common understory shrub in these forest stands. The predominant soil series within this region of Ohio is Bennington–Cardington–Centerburg, which are fine textured soils formed in glacial till with low lime content and range from poorly to moderately well drained (ODNR 2018). The Climate Normals (1981–2010) for a point close to the center of the study area, Eaton, Ohio, are an annual temperature of 10.7 °C and annual precipitation of 1042 mm (U.S. Climate Data 2019). All sites were spaced at least 1 km apart, following methods in Small et al. (2016), in order to avoid sampling the same beaver colony twice. For a site to be suitable for this study it had to be forested, have woody stems recently cut by beaver, and have *L. maackii* present.

Table 1 The location, time that beavers have been present, management entity, aquatic system, and transect type (see "Methods" section) at each site

Location	Beaver residency time (years)	Mgt entity	System	Transect type
Peffer Park (PEPK)	0.25	Miami Natural Areas	Stream	A
Hueston North (HUNO)	20	Ohio Department of Natural Resources	Stream	A
Acton Lake (ACLA)	15	Ohio Department of Natural Resources	Lake	B
Bachelor Pond (BAWO)	5	Miami Natural Areas	Pond	B
Oxford Landfill (OXLA)	2.75	Oxford Department of Service and Engineering	Stream	C
Miami Whitewater (MIWI)	5	Great Parks of Hamilton County	Stream	A
Possum Creek MetroPark (POCR)	16	Five Rivers MetroParks	Pond	B
Wegerzyn Gardens MetroPark (WEGA)	4	Five Rivers MetroParks	Beaver channel	A

Factors influencing stem cutting

Field methods

At each site, we sampled woody stems in fall (15 October–30 November, 2018) and spring (25–31 March, 2019) using modifications of the transect method used by Barela and Frey (2016), Gerwing et al. (2013), and Gallant et al. (2004). Only woody stems greater than 2.5 cm in diameter were considered (Jenkins 1975).

Beaver cutting of woody stems is influenced by diameter and distance from water as well as plant taxon, so to avoid these factors confounding our preference calculation, we included them in our analyses. Beavers are central place foragers that become more selective the farther away they move from their dam (Jenkins 1980; Gallant et al. 2004). Beavers rarely forage farther than 50 m from the water's edge even if the colony has inhabited the site for a relatively long period of time (Stoffyn-Egli and Willison 2011). They also have been shown to have a stem size preference. A study conducted by Raffel et al. (2009) found that beavers selected (overall—for building material and food) medium-sized stems (2.0–6.9 cm) at all distances from the water's edge.

At each site we marked off either one (240 m) or two (120 m) primary transects and six secondary transects (each 25 m); all transects were 2 m wide. The configuration of transects at a site depended on the waterway and forest characteristics. If the site was a stream with a forested riparian zone greater than 25 m wide on both banks, we had one 120 m primary transect on each bank, parallel to the water's edge, and located 0.5 m into the forest vegetation. The primary transects were centered in the area of highest woody stem cutting so that 60 m was upstream and 60 m downstream. We then placed three 25 m secondary transects perpendicular to each primary transects, one at its center and the others 40 m upstream and downstream (transect type A). If the site was a stream with a forested riparian zone greater than 25 m on only one bank, the two 120 m primary transects were established as above, but all six secondary transects were on the side with the greater than 25 m wide forested riparian zone (type B). If the site was a pond or lake, we established a single curved 240 m primary transect parallel to the water's edge, 0.5 m into the beginning of the riparian vegetation, centered in the area of highest woody stem cutting. The six 25 m secondary transects were perpendicular to the primary transect (type C).

During the fall 2018 woody vegetation survey, all woody stems $\geq$ 2.5 cm in diameter were identified, measured for diameter at 30 cm or, if less than 30 cm, at the highest height possible (Gallant et al. 2004), and scored as cut, browsed, or uncut. "Cut" stems were cut completely through by beavers, whereas "browsed" stems had cut marks made by beavers but not cut all the way through. The wood of the cut stem also had to be light tan to gray brown in color, to exclude stems that had been cut well before (> ~ 1 year) the census. We measured the distance the stem was to the water's edge to the nearest 0.1 m. In spring 2019, we resurveyed the stems that were not cut in the fall survey, and scored these as cut, browsed, or uncut. Species were identified with field guides and cut woody stems were identified using a bark photo collection we created from uncut stems. We distinguished between native and non-native taxa in our dataset using the U.S. Department of Agriculture's PLANTS database, plants.sc.egov.usda.gov. For data analysis, we grouped all species by genus because in some genera, species identification was difficult and in others, individual species were uncommon. *Acer negundo* was analyzed separately from other *Acer* species because there was a higher proportion of *A. negundo* stems cut compared to other *Acer* stems.

Statistical analysis

To determine whether beaver cutting of woody stems was influenced by genus or other factors, we conducted binomial generalized regression (logistic regression) (Gerwing et al. 2013) using R 3.4.3 (R Core Team 2017), the lme4 package (Bates et al. 2015), and used the car package (Fox and Weisberg 2011) to produce an analysis of deviance table with Type III Wald chi-square tests. The response variable was stem cut (1) or uncut (0), fixed factors were the distance the woody stem was from the water's edge, the diameter of the woody stem, the genus identity, and the interaction of diameter and distance, while site was included as a random factor. Because genera present only at a few sites could potentially skew results, we conducted a second logistic regression using only stems of genera that were recorded at five or more sites. A third logistic regression included only *L. maackii* stems; genus was not included as a factor in this analysis.

Electivities

In order to determine which genus beavers were choosing to use, we calculated Vanderploeg and Scavia's (1979) electivity index for each woody genus available at each site during the fall sampling period. Electivity is a measure of preference based on the proportion of a food item that is consumed compared to that food item's abundance in the community. To calculate electivity, we used the formula (Eqs. 1, 2) from Vanderploeg and Scavia (1979):

$$E_i = \left(W_i - \frac{1}{n}\right) \Big/ \left(W_i + \frac{1}{n}\right) \quad (1)$$

$$W_i = \frac{r_i}{p_i} \Big/ \sum_i^n \frac{r_i}{p_i} \quad (2)$$

In these equations, r_i is the proportion of stems cut which belongs to genus i, p_i is the proportion of stems available which belongs to genus i, and n is the number of genera available at that site. W_i is the selectivity coefficient. E_i values between 0 and 1 indicate the genus is preferably cut, while E_i between − 1 and 0 indicates beavers tend to avoid that genus. E_i = 0 indicates beavers neither avoid nor preferentially cut that genus.

Differences in *L. maackii* electivity among sites

Anticipating that beaver preference for *L. maackii* might differ among sites, we quantified site characteristics that might account for these differences such as beaver residency time at a site, canopy openness, and density of preferred stems. Beavers residency time at a site has been shown to change the overall vegetation structure of the site over time. A study conducted in Alberta, Canada, found that sites with the longest history of beaver activity had wide meadows surrounding ponds and dams and the oldest of these sites had all forest cover removed within their 48 m transect (Martell et al. 2006). The residency time of beavers at each of our sites was based on notes of the land managers and expressed as the number of years beavers were present at that location as of October 2018.

Canopy openness can influence beaver selectivity by shaping forest vegetation structure and can be used as a measure of forest invasibility for non-native species such as *Lonicera maackii*, as forests with higher canopy cover had lower cover of *L. maackii* (Hutchinson and Vankat 1997). We measured the canopy openness at each site during August 2018 using a spherical densitometer Model C (Strickler 1959), utilizing methods found in Lemmon (1956). Spherical densitometers are comparable to more sophisticated measures such as hemispherical photography in their effectiveness at measuring light environments in forested ecosystems (Englund et al. 2000). We took these measurements at a height of 1.2 m at the middle and each end of each secondary transect, for a total of 18 samples at each site; and calculated the average canopy openness value for each site.

Beaver are also considered selective generalist herbivores because of their known preference for some species of woody plants over others (Jenkins 1975; Jenkins 1979; Gallant et al. 2004). Because of this preference, for each site we calculated the density of "preferred stems" as the number of stems belonging to those genera that were consistently preferred ($E_i > 0$ at all sites where they were recorded), and with diameter 25–69 mm (these were cut at the highest proportion), divided by the total sampled area (780 m^2).

In order to determine which environmental factors or site characteristics were influencing *L. maackii* electivity among the 8 sites, we conducted linear regressions of *L. maackii* electivity on each of these factors: residency time of the beaver, average canopy openness, and density of preferred stems. All data were analyzed using R 3.4.3 (R Core Team 2017).

Results

A total of 2344 stems comprised of 32 genera were censused over the eight study sites in Fall 2018 (Table S1). Of these, 1837 (78%) were uncut and re-censused in Spring 2019. *Lonicera maackii* accounted for 41% of cut stems in Fall 2018, followed by *Elaeagnus umbellata* which accounted for ~ 20%, and *A. negundo* which accounted for ~ 10% (Fig. 2).

Factors influencing stem cutting

Fall 2018

For all stems in the dataset, the significant predictors in determining whether a stem was cut or uncut were genus, distance to the water's edge, and stem diameter, but the interaction between distance and diameter was not significant, based on logistic regression (Table 2). The probability of beavers cutting stems was highest near the water's edge and decreased the farther away the stem was from the water (Fig. 3). There was also higher probability of a stem being cut if its basal diameter was 25–59.9 mm, with lower probabilities at greater diameters (Fig. 4).

To explore whether these findings were influenced by infrequent genera, we restricted the logistic regression to genera recorded at $\geq$ 5 sites. As in the previous model, the significant predictors in determining whether a stem was cut or uncut were genus, distance to the water's edge, and stem diameter, but not the interaction between distance and diameter (results reported in Deardorff 2019).

For the analysis of only *L. maackii* stems, the significant predictors in determining whether a stem was cut or uncut were distance, diameter, and the interaction between distance and diameter (Table 3). The probability of a stem being cut was higher closer to the water's edge and for smaller diameter stems. The interaction reflected a stronger negative relationship between the proportion of stems cut and stem diameter for stems closer to the water's edge (Fig. 5).

Only 41 stems were browsed in the fall census. These consisted of 13 genera, primarily *Acer*, *Fraxinus*, and *Lonicera*. The diameter of browsed stems ranged from 27 to 1197 mm, with most > 70 mm.

Spring 2019

Only 14 stems were cut and 9 browsed in the Spring 2019 census of stems not cut or browsed in Fall 2018. More than half of the cut or browsed stems were between 25 and 39 mm in diameter and half were *L. maackii*.

Electivities

Electivities ranged from avoidance to strong preference, with *Lonicera* having low to intermediate values among the frequently encountered genera (Fig. 6). *Gleditsia* had the lowest electivities (− 1), meaning that it was largely avoided by beaver, whereas *Acer negundo* was the most highly preferred taxon, with a mean electivity ~ 0.5. Despite *L. maackii* accounting for a plurality of cut stems, electivities revealed it was not preferred at six of the eight sites (Fig. 6, Table S1). *L. maackii* electivity ranged from complete avoidance (-1) at Hueston North to slight preference (0.11) at Miami Whitewater Forest and Acton Lake.

The genera *Salix, Ligustrum*, *Pyrus*, *Carya* and the species *Acer negundo* were preferred in all sites in which they were found (Fig. 6, Table S1), and

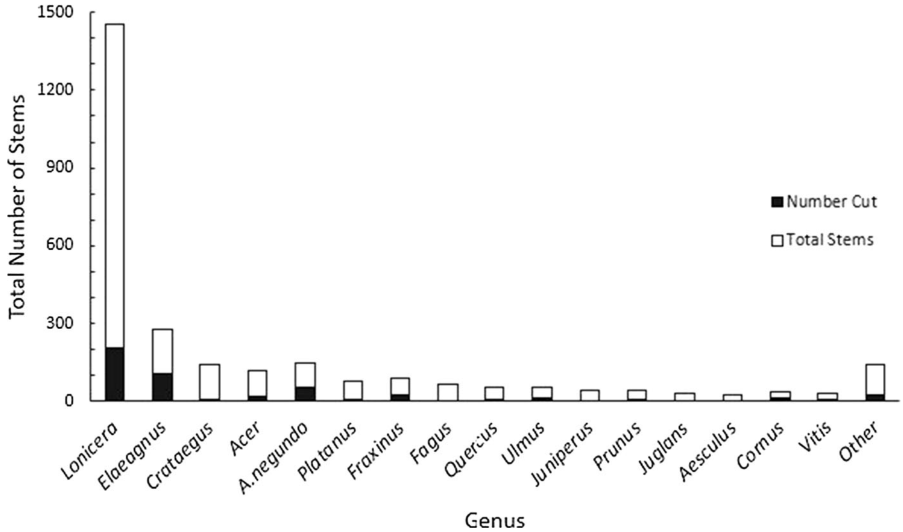

Fig. 2 Stacked barplot of total number of stems (white) and number of cut stems (black) belonging to each genus. 'Other' represents all other genera, each of which were rare at the study sites

Table 2 Analysis of deviance table (Type III Wald chi-square tests) for generalized binomial regression on whether a stem was cut or uncut using stems from all genera

	χ^2	*df*	*p*
Intercept	20.0255	1	< 0.001
Genus	291.4137	24	< 0.001
Distance to water's edge	11.6996	1	< 0.001
Diameter	46.7808	1	< 0.001
Distance to water: diameter	0.0007	1	0.979

therefore comprise the genera for "preferred stems" used in a later linear regression. Additionally, the genera *Fraxinus* and *Elaeagnus*, had mean electivities (among sites) > 0 (Fig. 6).

Differences in *L. maackii*electivity among sites

Among sites, beaver electivity for *Lonicera maackii* showed a negative trend with density of preferred stems, based on linear regression ($p = 0.071$, $r^2 = 0.3514$; Fig. 7). *Lonicera maackii* electivity did not depend on average canopy openness ($p = 0.158$, $r^2 = 0.1861$) or beaver residency time ($p = 0.1559$, $r^2 = 0.1889$).

Discussion

Beaver cutting of *L. maackii* v other woody plants andimplications for invasion

Though *Lonicera maackii* made up the largest proportion of cut stems in the fall census, it was not preferred by beaver at most sites. Because beavers are not cutting it preferentially compared to other native woody species, they do not, in general, hinder *L. maackii* invasion. However, beaver preference for specific size classes and stem selection closer to the water's edge could add mortality pressure to *L. maackii* stems depending on site condition. Overall, it is likely beaver facilitate *L. maackii* invasion by selectively cutting other woody genera and releasing it from competition.

We think beavers cut *L. maackii* stems primarily as building material in lodges and dams rather than a food source. In spring 2018 we observed cut *L. maackii* branches that appeared to have been dragged towards the water's edge; these stems still had leaves and none of the bark had been stripped off. Both the dam at Peffer Park and lodge at Bachelor Pond contained many *L. maackii* stems of various sizes.

Native taxa such as *Acer negundo*, *Salix*, *Fraxinus*, and *Carya* had mean electivities that were above zero indicating that they were predominantly preferred at most sites. *Acer* and *Salix* have been found to be

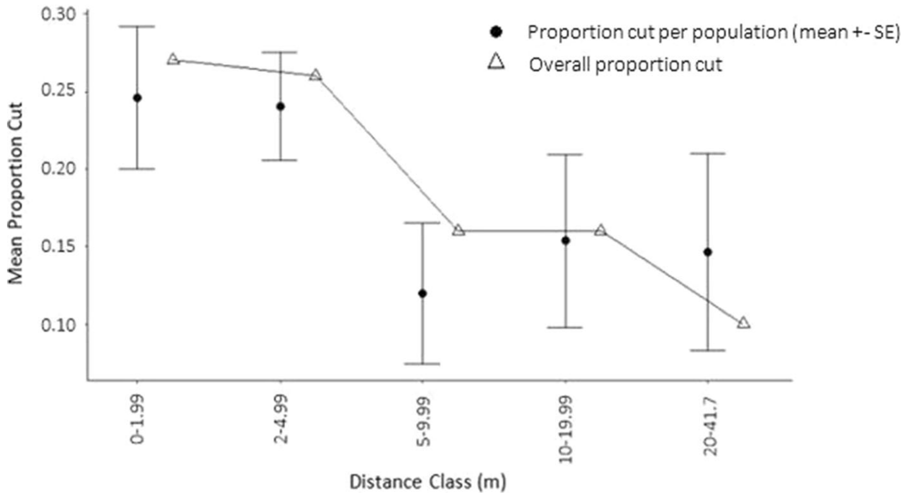

Fig. 3 For each distance class, the mean (± SE) proportion of stems cut for the 8 sites and the overall proportion of stems cut out of all stems (the latter represented by connected triangles). Distance refers to how far the stem was from the water's edge

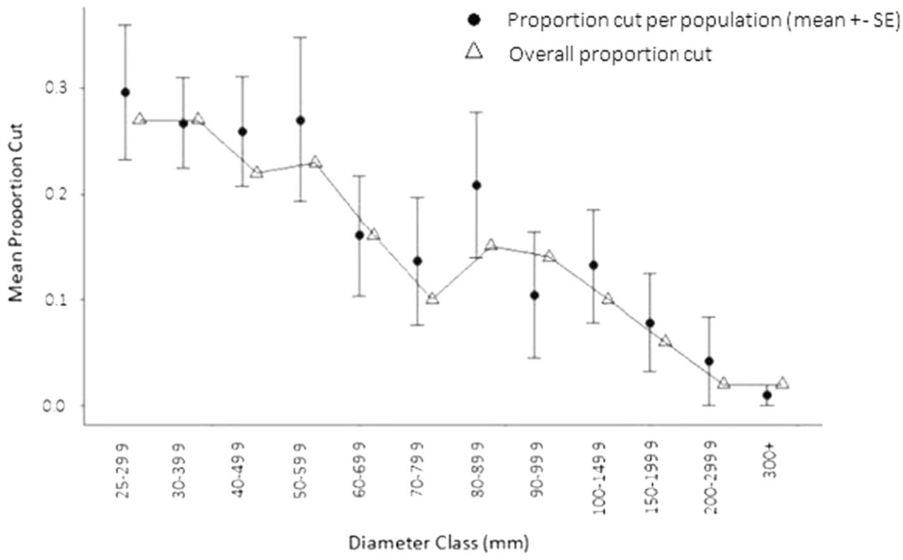

Fig. 4 For each diameter class, the mean (± SE) proportion of stems cut for the 8 sites and the overall proportion of stems cut out of all stems (the latter represented by connected triangles)

Table 3 Analysis of deviance table (Type III Wald chi-square tests) for generalized binomial regression on whether a *L. maackii*. stem was cut or uncut

	χ^2	*df*	*p*
Intercept	0.8711	1	0.351
Distance to water's edge	24.3986	1	< 0.001
Diameter	29.6135	1	< 0.001
Distance to water: diameter	10.8096	1	0.001

preferred by beaver (Henry and Bookhout 1970; Jenkins 1979; Gerwing et al. 2013), while *Fraxinus* was found to be neutrally preferred, and *Carya*, depending on the species, was either avoided or neutrally preferred (Raffel et al. 2009). Diet preference by beaver for certain genera are influenced by levels of tannins (Hagerman and Robbins 1993; Bailey et al. 2004) and nutritional quality and digestibility (Doucet and Fryxell 1993). These factors were not, however, quantified in this study.

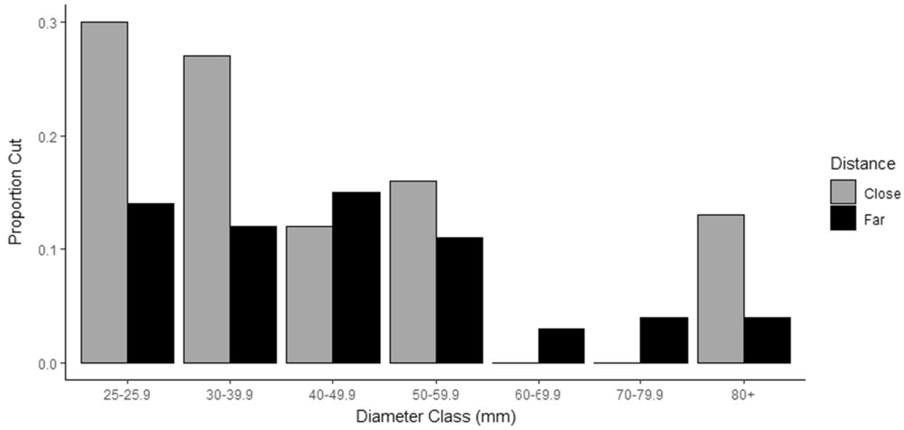

Fig. 5 Proportion of *L. maackii* stems cut for each size class for stems close to the water's edge and stems far from the water's edge. Stems $\leq$ 3.15 m (the median distance) were considered 'close' while stems > 3.15 m were considered 'far'

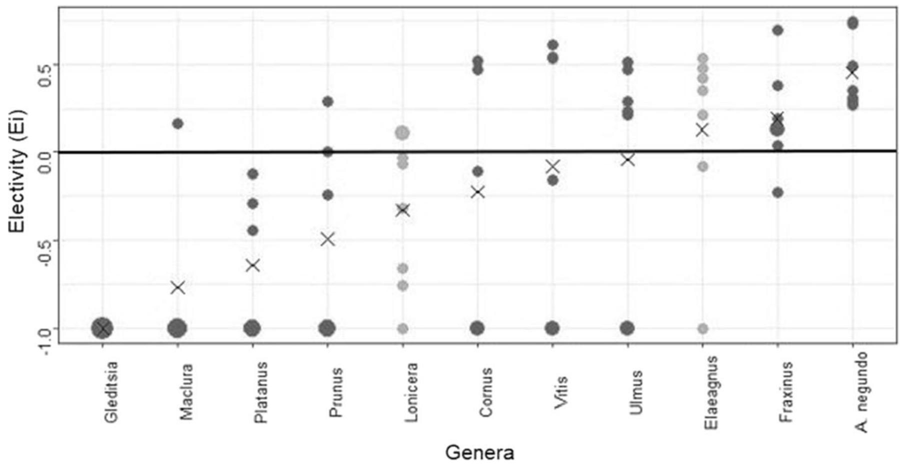

Fig. 6 Electivity values (E_i) for genera recorded at $\geq$ 5 sites. The dark gray points are native genera while the light gray points are invasive genera. The black x's represent the mean electivity for each genus and the black line represents an electivity of 0. The size of the point corresponds with the number of sites that shared the same electivity value for that genus

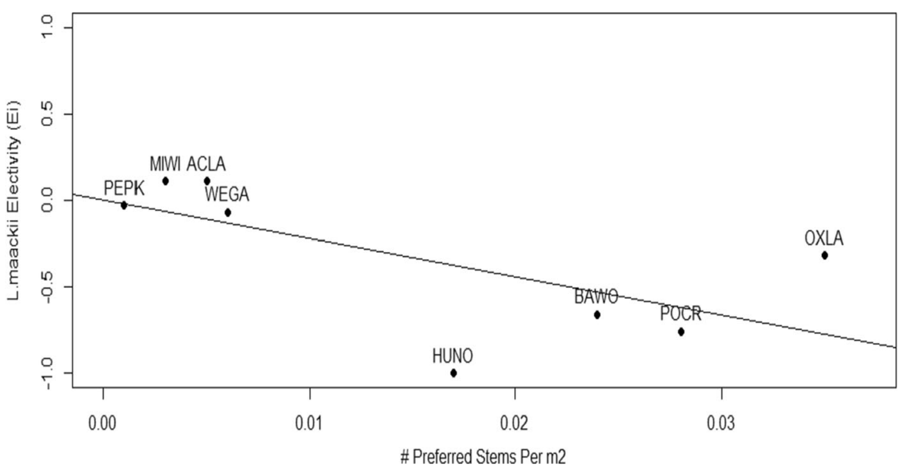

Fig. 7 Regression of *L. maackii* electivity (E_i) on density of preferred stems (p = 0.071, R^2 = 0.351), among the eight sites. Site abbreviations are in Table 1

Another invasive species found within our transects, Autumn olive (*Elaeagnus umbellata*), was preferentially cut by beavers at 5 of 7 sites where it was present. This finding suggests that beavers slow the invasion of *E. umbellata* in riparian areas. Beaver have been shown to have a preference for a congener, *Elaeagnus angustifolia* (Barela and Frey 2016). We found that another invasive shrub, border privet (*Ligustrum obtusifolium*), was preferentially cut in the one study site where it occurred, providing some evidence beaver potentially hinder *L. obtusifolium* invasion. A previous study found beavers had a moderate selection for Chinese privet (*Ligustrum sinense*) (Rossell et al. 2014). Further investigation of more sites with *Ligustrum* present is warranted to determine if beavers deter *Ligustrum* invasion.

Factors influencing differences in *L. maackii* electivity

Our finding that beaver electivity for *L. maackii* tended to be negatively related to the density of preferred stems at a site suggests that beavers first forage for more preferred genera, and only cut *L. maackii* after these preferred resources become sparse. However, beaver electivity for *L. maackii* did not have a significant relationship with residence time. We attribute this surprising result to beaver shifting their lodge and foraging area over time, so that depletion of preferred stems near the current center of activity (where our sampling was centered) is not greater at sites that have been occupied longer.

Such a spatial shift in foraging area over time may explain why we found very few cut stems in the spring 2019 census. The beavers could have exhausted most of the available preferred stems along our transects before the fall census and moved on to other sections of the site. During the spring census we noticed freshly cut stems upstream and downstream of our original transects at most of our sites.

The low number of stems cut in the spring census could also be due to beaver use of cached resources during the interval between censuses. A study conducted in southeastern Ohio found that during winter beavers primarily ate material in caches and bark from previously downed trees along the shoreline, and in early spring herbaceous vegetation made up between 40–50% of the beaver's diet (Svendsen 1980). When we sampled in spring, there was still very little herbaceous vegetation.

Further observations

During the fall census, on a few of the beaver-cut *L. maackii* stems, we observed browse by white-tailed deer on some of the shoots of new growth. After *L. maackii* stems are cut, new shoots grow after about three weeks (McDonnell et al. 2005). If the beavers at our sites cut *L. maackii* in early spring during one of their peak cutting seasons (Jenkins 1979; Brzyski and Schulte 2009), by summer shoots should be large enough to be browsed by deer. White-tailed deer have been shown to browse *L. maackii*, particularly in early spring when other preferred food sources are not abundant and in late summer (Martinod and Gorchov 2017), right before we observed these browsed shoots. In addition to beaver cutting of *L. maackii* stems creating a food source for white-tailed deer, the combined cutting of beaver and browse by deer could potentially hinder overall *L. maackii* plant growth. This latter effect was demonstrated for the interaction between beaver, elk, and willows in Rocky Mountain National Park, Colorado. Willows at sites that had combined herbivory by beaver and elk had a smaller biomass and diameter, were shorter, and had a higher percentage of dead biomass which strongly suppressed standing crop, compared to sites that only had one or no herbivore present (Baker et al. 2005). This interaction between beaver and abundant white-tailed deer at our study sites warrants further investigation into the possibilities of it serving as a natural management of *L. maackii*.

Conclusions

Although *L. maackii* stems accounted for 41% of the total stems that beavers cut, it was overall of low preference compared to other woody stems, resulting in no evidence that beavers hinder invasion of this non-native shrub. Another invasive species, Autumn olive (*Elaeagnus umbellata*), was preferred at 5 of the 6 sites it was found and a third, border privet (*Ligustrum obtusifolium*) was preferred at the one site it was found, which suggests that beavers hinder the invasion of these two species, at least at some sites. Among sites, the marginally significant negative relationship between *L. maackii* electivity and the density of "preferred" stems suggests that beaver use of *L. maackii* is associated with depletion of these higher preference stems.

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