

Research Article

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White-tailed deer browse preference for an invasive shrub, Amur honeysuckle (*Lonicera maackii*), depends on woody species composition

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Abstract

Selective browsing by abundant, generalist herbivores on preferred species could allow less-preferred invasive species to flourish. We tested such an effect by examining rates at which white-tailed deer (*Odocoileus virginianus* Zimmermann) consume Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder], an invasive shrub, relative to native woody species across eight forested sites in southwestern Ohio. We tested three hypotheses: (1) deer prefer to browse on *L. maackii* versus other woody plants; (2) *L. maackii* is not a preferred source of browse, but is consumed where preferred foods are scarce; and (3) *L. maackii* provides an important food resource for deer in early spring when other foods are scarce. We used counts of browsed and unbrowsed twigs of each species to calculate, for each site, both the proportion of each species' twigs browsed and the degree to which deer selectively favor each species ("electivity") during early to mid-growing season. Across the eight sites, electivity of *L. maackii* correlated with the proportion of its twigs browsed, and both measures were negatively associated with the density of *L. maackii* twigs. *Lonicera maackii* electivity was negative at most sites, indicating it is generally not preferred, undermining hypothesis 1. The hypothesis that deer consume *L. maackii* when more-preferred foods are depleted was not supported, as there was no negative relationship between *L. maackii* browse and the density of twigs of more-preferred species. We found a negative relationship between the proportion of *L. maackii* twigs browsed and the density of *L. maackii* among sites, which supports the third hypothesis. This finding, combined with seasonal patterns of deer browse on *L. maackii*, indicates that this invasive shrub is an important source of browse for deer during early spring, regardless of its abundance.

Introduction

Selective browsing by herbivores can alter the species composition of plant communities and influence the success of exotic plant species. Higher preference by herbivores for introduced species has been hypothesized to prevent invasion (the biotic resistance hypothesis, or BRH). The enemy release hypothesis (ERH) conversely attributes the success of invasives to the lack of native predators or pathogens. For invasive plants, this could mean less herbivory (e.g., lower preference) from both generalist and specialist herbivores (Colautti et al. 2004). (Box 1)

Herbivory by wild ungulates is now recognized as a strong component of ecological change (Augustine and McNaughton 1998; Kie and Lehmkuhl 2001; Riggs et al. 2000). Many wild ungulate populations, including deer in North America and Europe, are now elevated above historical levels (Côté et al. 2004). Deer populations increased primarily through extirpation of natural predators, restrictions on hunting, and the spread of human-influenced landscapes. The concern for browse impacts has reversed the management of deer populations from sustaining game populations to managing overabundance.

The white-tailed deer (*Odocoileus virginianus* Zimmermann, henceforth referred to as "deer") is a generalist ungulate abundant in many parts of the eastern and midwestern United States, with foraging patterns that impact forest composition (Bradshaw and Waller 2016; Côté 2004; Horsley et al. 2003; Kraft et al. 2004; McCabe and McCabe 1997; McCullough 1979, 1997; McShea 2012). Human-modified landscapes have increased deer populations by providing supplemental browse from ornamentals, crops, and increased habitat edges (McShea 2012). Plants of greater palatability decline even at deer densities below levels at which deer are limited by plant productivity (McShea 2012). This allows less palatable plants, such as ferns or grasses, to flourish and further inhibit the establishment of tree seedlings and native herbs (e.g., Horsley et al. 2003). By indirectly preventing the

Management Implications

Based on previous findings, white-tailed deer browse heavily on an invasive shrub, *Lonicera maackii* (Amur honeysuckle), in some forests. We tested whether this is due to high preference by deer for *L. maackii*, low availability of preferred browse, or *L. maackii* serving as an important browse in early spring before native woody plants have leafed out. By comparing browse intensity on, and preference for, *L. maackii* across sites with different woody understories, we found support for the third hypothesis. Specifically, the proportion of *L. maackii* twigs browsed by deer was greater where abundance of this shrub was lower, suggesting deer browse it preferentially, but mainly during a brief period of the year.

Our findings could inform management decisions concerning *L. maackii* and other invasive shrubs that leaf out early and are browsed preferentially in that season, when other resources are at low availability. In areas with low invasive shrub density and high deer populations, deer browse may be sufficient to curb the growth of the invasives. But in heavily invaded areas, management should focus on reducing deer populations *before* reducing invasive shrubs, in order to facilitate growth of native woody species. We did find a negative relationship between *L. maackii* density and deer browse on a less-preferred species, black cherry (*Prunus serotina* Ehrh.). Removal of invasive shrubs as a source of browse or possible cover could result in higher browse on such less-preferred species.

establishment of preferred species, deer can alter forest regeneration and succession (Côté et al. 2004; Horsley et al. 2003).

Whether deer may limit (BRH) or promote (ERH) invasion depends on their preference for each introduced species. A meta-analysis found a general trend for native herbivores to prefer invasive over native plant species (Parker et al. 2006). Deer, however, appear to browse less on invasive plants than native species within the same genus (Schierenbeck et al. 1994). Eschtruth and Battles (2008) found positive relationships between deer density and the abundances of three invasive species, garlic mustard [*Alliaria petiolata* (M. Bieb.) Cavara & Grande], Japanese stiltgrass [*Microstegium vimineum* (Trin.) A. Camus], and Japanese barberry (*Berberis thunbergii* DC.), and suggested this was due to competitive release due to deer browse on native species. Similarly, Knight et al. (2009) attributed greater cover of *M. vimineum* and *A. petiolata* in deer access versus enclosure plots to lower preference by deer. Averill et al. (2016) found that deer did not consistently favor native species over invasive species, but some invasive species, including Morrow's honeysuckle (*Lonicera morrowii* A. Gray), were highly preferred.

The preference of deer for individual species also shifts seasonally (Smith 2013). During the winter, deer browse on leafless twigs, which are less nutritious than leafy twigs (Martinod and Gorchoy 2017; Mattson 1980). Leafy twigs have more nitrogen (%N), indicating higher crude protein, which is an important nutrient for deer during the spring and summer (Berteaux et al. 1998; Dostaler et al. 2011). Certain species of nonnative plants exhibit extended leaf phenology (ELP)—leafing out earlier in spring and retaining leaves later in the fall (Smith 2013). Early expansion of leaves during the springtime could thus reduce starvation of pregnant does and result in stronger fawns (Moen 1978; Perkins et al 1998).

The invasive shrub, Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder, Caprifoliaceae], exhibits ELP (McEwan et al. 2009; Wilfong et al. 2009) and is an important component of the deer diet (Martinod and Gorchoy 2017). In the Miami University Natural Areas (MUNA) in southwestern Ohio, *L. maackii* was estimated to comprise 14% to 47% of annual deer diet, based on measurements of deer browse and estimated deer food consumption from the literature (Martinod and Gorchoy 2017). Consistent with the hypothesis that ELP species are important for spring browse (Smith 2013), Martinod and Gorchoy (2017) found browse on *L. maackii* was highest during early spring, but was also high in late summer. Additionally, the %N of leafy *L. maackii* twigs was higher than winter twigs of common woody species (Martinod and Gorchoy 2017). Whether the high percentage of deer diet in MUNA composed of *L. maackii* is due to its relatively high nutritional value before native woody plants leaf out in the spring, the high abundance of *L. maackii* at these sites, or depletion of higher-quality browse due to chronic high deer density, is not known.

We tested three hypotheses for the substantial deer browse on *L. maackii*: (1) deer prefer to browse on *L. maackii* versus other woody plants; (2) *L. maackii* is not preferred, but is consumed where preferred foods are unavailable; and (3) *L. maackii* serves as an important food resource for deer during early spring, a season of scarcity. To test these hypotheses, we recorded proportions of twigs browsed for each woody species in each of eight sites and used these proportions to calculate deer preference using an index of electivity. The prediction from hypothesis 1 is that *L. maackii* has a positive electivity (is preferred) at all sites. Higher electivity where more-preferred species are less abundant would support hypothesis 2. Having a higher proportion of *L. maackii* twigs browsed where it is less abundant would support hypothesis 3. This last prediction is based on the reasoning that *L. maackii* will not be browsed beyond the quantity needed to satiate deer during a brief period (early spring), leading to lower percentage browse proportions in areas of higher *L. maackii* density.

Materials and Methods

Study Species

Lonicera maackii is one of several Eurasian bush honeysuckle species invasive in the United States (Webster et al. 2006). It is native to East Asia and was introduced for landscaping and erosion control in 1898 (Luken and Thieret 1996). *Lonicera maackii* escaped from cultivation across the central and eastern United States and is currently regulated in eight of those states (EDDMapS 2017).

Characteristics of *L. maackii* that contribute to invasiveness have been reviewed by McNeish and McEwan (2016). Of specific relevance to this study, *L. maackii* exhibits ELP—earlier leaf out in spring (McEwan et al. 2009) and retention of leaves later in the fall (Wilfong et al. 2009)—compared with native deciduous species.

Insect herbivory on *L. maackii* is low, with damage steadily accumulating throughout the growing season (Lieurance and Cipollini 2011). However, deer browse on *L. maackii* is high, at least in some sites in southwestern Ohio; Guiden et al. (2015) found that 60% of branches showed evidence of browse during a 3-mo period from late fall to early winter, and Martinod and Gorchoy (2017) found 22% to 32% of *L. maackii* twigs were browsed in a 1-yr span.

Study Sites

Eight sites in southwestern Ohio were selected based on low-to-moderate abundances of *L. maackii*, high densities of other woody understory plants, and (where information was available) high deer abundances (Figure 1; Table 1). Of the sites with lower *L. maackii* density, some had not yet been extensively invaded and others had abundance of this shrub reduced by management.

We selected sites with ≥ 7.7 deer km⁻², the density considered to be the ecological carrying capacity for an eastern broadleaf deciduous forest and often used for park management (Horsley et al. 2003; Ristau et al. 2012). Our reason for using sites with high deer densities was to get a better indication of which species are preferred where browse is more intensive. Three sites had deer densities estimated by aerial infrared survey (AIS) (Great Parks of Hamilton County 2013; Cincinnati Park Board 2014) (Table 1). AISs have low bias, but consistently underestimate deer populations by approximately 30% (Beaver et al. 2014; DeCalesta 2013). We also calculated deer harvest density for sites that provided counts of deer harvested fall 2016 to winter 2017 (all but HW) by dividing this count by the area of management units where hunting was carried out; this is expected to correlate with density during the 2016 field season (Table 1). At one site (TM), an indicator of deer density, browse on red oak (*Quercus rubra* L.) sentinel seedlings, was estimated to be 44%; red oak browse damage >15% was considered to reflect deer density >7.7 deer km⁻² (Van Clef 2008).

The tree canopy at these sites was dominated by sugar maple (*Acer saccharum* Marshall); this species had the highest stand density and frequency at all sites and the highest basal area at seven of the sites (based on point-quarter sampling of trees >10 cm in diameter at breast height; Wright 2017). At the other site, HW,

northern red oak (*Quercus rubra* L.) had greater basal area than *A. saccharum*. At most sites, the genus *Quercus* (mostly *Q. rubra*, white oak [*Quercus alba* L.], bur oak [*Quercus macrocarpa* Michx.], and chinquapin oak [*Quercus muehlenbergii* Engelm.]) was second in importance (based on relative density, frequency, and basal area summed by genus). At DW and MWE *Carya* spp. (shagbark hickory [*Carya ovata* (Mill.) K. Koch] and bitternut hickory [*Carya cordiformis* (Wangenh.) K. Koch]) were of secondary importance. At MWW, American beech (*Fagus grandifolia* Ehrh.) was of secondary importance, and this species was present at most sites, as were *Fraxinus* spp. (Wright 2017).

Understory Woody Species Composition

In summer 2016 we quantified the twig density of *L. maackii* and other woody plant species in the browse layer in each site. We defined the browse layer (twigs accessible to deer) as 0.3 to 1.7 m; the minimum was based on Frelich and Lorimer (1985) and the maximum on Martinod and Gorchov’s (2017) finding that minimal deer browse on *L. maackii* occurred above 1.7 m. Using a geographic information system, we located four 100-m parallel transects, 50 m apart, in an interior forest area (Figure 2). The starting point of the first transect was a randomly selected point between 100 and 120 m from the forest edge. The direction of this transect was randomly generated, constrained within a 179° range centered on the direction away from the forest edge. The three parallel transects were located on the side of the first transect that faced the forest interior.

We sampled twigs in plots at 10-m intervals along each transect (N = 44 plots site⁻¹). Plot sizes varied depending upon the frequency of woody species at each site (Table 1). At four sites, plots were 2 by 1 m. At three sites, woody species were sparse, so plots were extended to 4 by 1 m. At one site where *L. maackii* was scarce, plots were increased to 6 by 1 m. To assess twig abundance and percent of twigs browsed, we counted in each plot both the total number of twigs, and the number of twigs browsed by deer, for each woody species (Supplementary Table A.1). To ensure that only current-year browse was counted, we scored only new-growth twigs—twigs that leafed out during the spring 2016. Deer browse was distinguished by the shredded appearance of twigs (Swift and Gross 2008). All twig counts were done July 19 to August 12, 2016, enabling us to encompass browse that occurred from the beginning through the middle part of that growing season.

From these twig counts we calculated deer preference for *L. maackii* and the other focal woody species at each site using Vanderploeg and Scavia’s (1979) electivity index (E_i) (Supplementary Table A.2). The electivity index calculates an herbivore’s preference for a species based on the relative amount of consumption composed of that species in relationship to its relative frequency, and was considered to be the best of several measures of feeding preference in an analysis by Lechowicz (1982). Electivity rates herbivore preference from a value of -1 (avoidance) to +1 (preference), with 0 indicating a species is browsed in proportion to its abundance. Electivity was calculated using Equation 1.

$$E_i = W_i - \frac{1}{n} / W_i + \frac{1}{n} \tag{1}$$

where W_i is the electivity coefficient (Equation 2),

$$W_i = \frac{r_i}{p_i} / \sum_i^n \frac{r_i}{p_i} \tag{2}$$

where r_i is the ratio of species i consumed divided by total consumption, p_i is the proportional abundance of species i , and n is

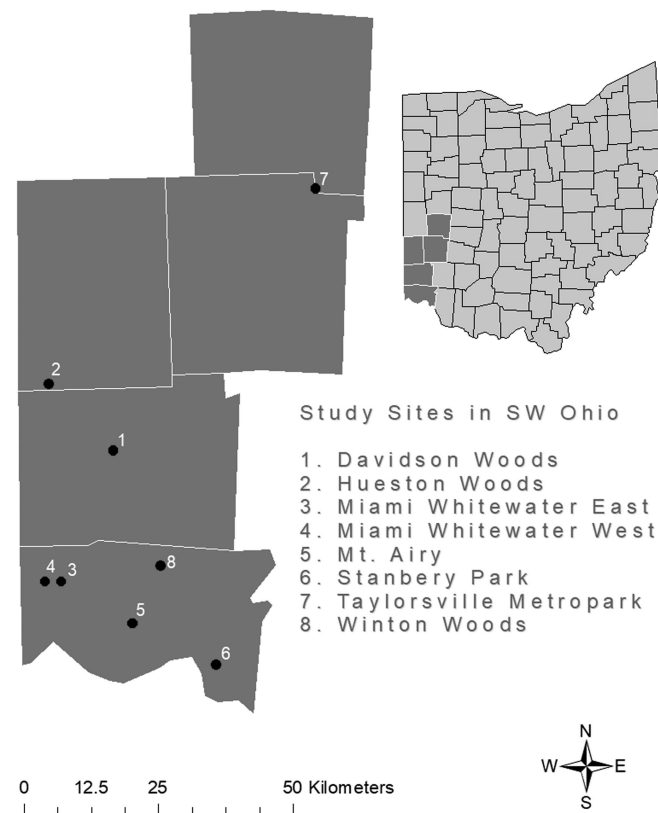


Figure 1. Study site locations in southwestern Ohio.

Table 1. Study sites with abbreviations, park systems (Butler County, State of Ohio, GreatParks of Hamilton County, Cincinnati Metroparks, and Five Rivers Metroparks), contiguous forest size, dimensions of plots for twig counts, twig densities in browse layer (0.3–1.7 m), basal area and density of trees >10-cm diameter at breast height, density of deer harvested fall 2016 to winter 2017 (number killed divided by area hunted), and density from most recent aerial infrared survey (AIS) where available.^a

Site abbreviation	Park system	Forest area km ²	Plot size m	Twig density twigs m ⁻²	L. maackii twig density		Stand basal area m ² ha ⁻¹	Trees no. ha ⁻¹	Deer harvested per km ²		AIS deer km ⁻²
					twigs m ⁻²	twigs m ⁻²			no. km ⁻²	no. km ⁻²	
Davidson Woods	Butler	1.61	2 × 1	54.2 (11.5)	46.7 (10.7)	31.0	512.1	2.36	—	—	
Hueston Woods	Ohio	5.19	2 × 1	11.7 (10.5)	5.3 (5.2)	59.0	581.4	—	—	—	
Miami Whitewater East	Ham.	7.67*	2 × 1	12.5 (8.6)	7.7 (7.8)	37.0	376.1	9.82*	9.65*	9.65*	
Miami Whitewater West	Ham.	7.67*	6 × 1	10.8 (4.6)	0.7 (1.1)	32.0	315.1	9.82*	9.65*	9.65*	
Mt Airy	Cinc.	1.67	4 × 1	12.4 (8.3)	9.7 (7.5)	29.1	343.2	26.34	—	10.87	
Stanbery Park	Cinc.	1.90	4 × 1	26.9 (9.0)	23.1 (5.7)	26.8	380.9	46.30	—	—	
Taylorville Metropark	5 Rivers	1.63	4 × 1	19.0 (16.5)	16.3 (15.1)	26.6	445.3	32.54	—	—	
Winton Woods	Ham.	0.58	2 × 1	17.4 (10.5)	7.9 (6.3)	39.6	466.7	28.08	6.95	6.95	

^aFor twig density and *L. maackii* twig density, SDs based on values from $n = 4$ transects are provided in parentheses. *The two sites in Miami Whitewater Forest (MWE, MWW) are within the same block of contiguous forest and deer management unit, so values for these in their entirety are listed.

the total number of species in the sample (Vanderploeg and Scavia 1979). For each site we used the proportion of the number of twigs browsed to calculate r_i values (using twigs browsed of species i divided by total twigs browsed), p_i as the number of twigs of species i divided by the total number of twigs at the site, and n as the number of woody species in the data set for the site.

Once the electivities were calculated, species were sorted into more-preferred species (MPS) or less-preferred species (LPS) categories based on their electivity relative to *L. maackii* (Table 2; Supplementary Table A.2).

Land Cover Proportions

We quantified land cover at each site to explore whether access to alternative browse had any relationship with *L. maackii* electivity or proportion browsed. Though herbivores may select browse at finer scale (e.g., within a forest patch), large herbivores may be responding to coarser scales of vegetation due to landscape configuration (Royo et al. 2017; Weisberg et al. 2006). These differing spatial patterns might provide alternative sources of graze or browse within the home range (Hurley et al. 2012). Herbivores may focus foraging within a preferred, highly productive habitat (e.g., cornfield), resulting in diminished pressure on an adjacent forest understory (Takimoto et al. 2009). Hurley et al. (2012) found that sites with more interspersed perennial habitats (shrublands, wetlands, and early successional habitat) within a deer's home range had higher herb cover in the forest understory, indicating per capita rates of deer herbivory were lower where these perennial habitats provide additional browse. Similarly, Royo et al. (2017) found that across stands in the same stage of forest management, the impacts of deer on plant cover and richness were less negative in landscapes with greater percent of "forage-producing habitat" (recently managed forest, agriculture, and herbaceous habitats).

To approximate the influence of land cover composition within deer home ranges, we quantified landscapes in ArcMap using 30-m resolution land cover basemaps that used decision-tree classification of 2011 satellite data to distinguish 16 land cover types (Homer et al. 2015; U.S. Geological Survey 2014). This information was restricted to a 1-km radius buffer (3.14 km²) centered on the browse transects (Figure 2) to approximate the area within the home range of an individual doe that foraged in the area covered by the transects, based on literature estimates of home range size (Hewitt 2011; Nixon et al. 1991; Tierson et al. 1985; Vercauteren and Hygnstrom 1998; Walter et al. 2009; Webb et al. 2007).

The 16 categories from the land cover map were grouped into five broader categories: pasture/row crop, perennial (herb cover and shrubland/scrubland), open water, forest, and developed areas. The total area of each category was then found by the *calculate geometry* function in ArcMap. The total areas were converted to proportions of total land area, not including open water (Supplementary Table A.3). These proportions were then used as predictors in analyses of *L. maackii* electivity and browse proportions.

Data Analysis

Two response variables, the proportion of *L. maackii* twigs browsed and electivity of *L. maackii*, were regressed on each predictor variable: density of LPS twigs, density of MPS twigs, density of *L. maackii* twigs, stand basal area, and percentage of

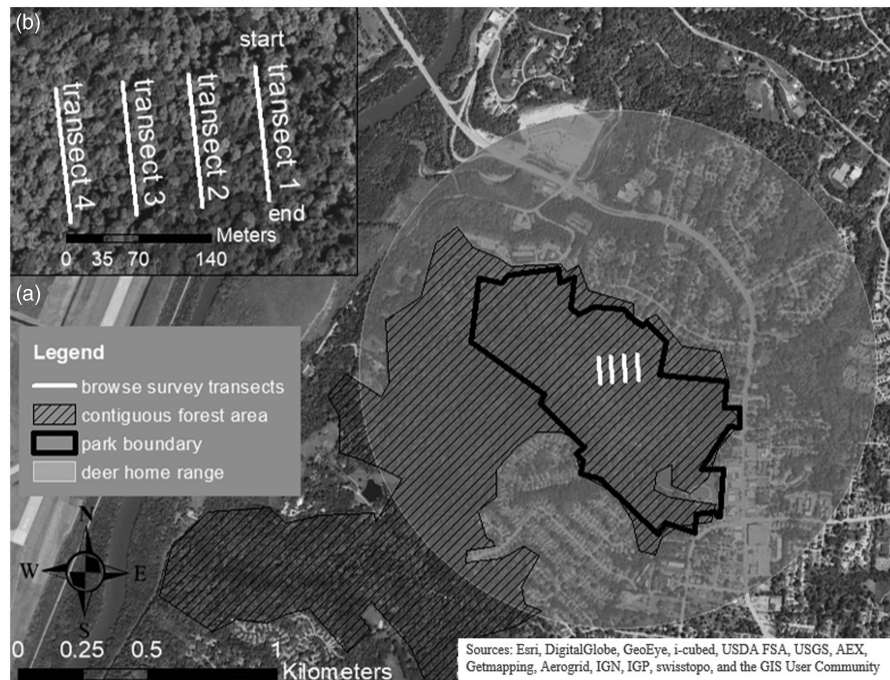


Figure 2. One of the eight study sites, Stanbery Park, with (A) overview of site layout, including contiguous forest area, park boundaries, browse survey transects, and 1-km radius centered on those transects to approximate the size of a deer home range; and (B) close-up of browse survey transects (100 m each).

each land cover type in the buffer (Table 3). Analysis of residuals of these regressions revealed that one of these predictors, density of *L. maackii* twigs, did not meet normality assumptions. We therefore log transformed this predictor (logLONM) and used this value instead in subsequent analyses. For each response variable, we selected the three predictors with the highest adjusted R^2 (LPS, MPS, and logLONMA twig densities) and included these in a multiple regression. Because logLONMA was correlated with each of the other two predictors, we supplemented the regression with “relative importance analysis” (Grömping 2007; Tonidandel and LeBreton 2011), which quantifies the contribution of each predictor to the explanatory capacity of a model for all combinations of predictors. We used the unweighted average (lmg) of these contributions as the measure of relative importance (contribution of each predictor to R^2); these were obtained with the *calc.relimp* function in the ‘relaimpo’ package in R (Grömping 2006).

For each of the three native species that were present at most sites, we regressed the proportion of twigs browsed on *L. maackii* density to find whether abundance of *L. maackii* had any impact on browse of other species.

Spring Browse Study

Analyses of these data revealed substantial deer browse on *L. maackii*, so we did an additional study to quantify how much of this occurs in early spring. This was done in an old-growth stand at Hueston Woods State Nature Preserve (HWSNP), where the canopy is dominated by *A. saccharum* and *F. grandifolia*, stand basal area is $35.1 \text{ m}^2 \text{ ha}^{-1}$ (Runkle 2013), and the understory has low density of *L. maackii*. We quantified density of new-growth *L. maackii* twigs 0.3 to 1.7 m and the number of these browsed along four parallel 100 by 2 m transects, and density and number browsed of new-growth twigs of other shrub and tree species in ten 2 by 2 m quadrats spaced at 10-m intervals on the same

transects. Sampling was done May 21–24, 2018, when species with the latest leaf expansion (e.g., pawpaw [*Asimina triloba* (L.) Dunal]) were still expanding, but about 5 wk after the midpoint of *L. maackii* leaf expansion.

Results and Discussion

Composition of the Browse Layer

Among the eight sites there was some variation in the woody species composition in the browse layer and in the twig densities of these species (Supplementary Table A.1). *Lonicera maackii*, *A. saccharum*, and white ash (*Fraxinus americana* L.) were present at all sites, with *L. maackii* accounting for the majority of twigs in the browse layer at all sites but two (MWW, WW). Other species present in most sites included *P. serotina*, American elm (*Ulmus americana* L.), and common hackberry (*Celtis occidentalis* L.). *Quercus* spp., typically favored by deer (Averill et al. 2016), were sparse in the browse layer at all sites.

Proportion of Twigs Browsed

The total twig density at each site ranged from 11 twigs m^{-2} at MWW to 54 twigs m^{-2} at DW (Table 1). The percentage of total twigs that were *L. maackii* varied among sites from 7% ($<1 \text{ twig m}^{-2}$) at MWW to 86% at DW (47 twigs m^{-2}) (Table 1).

The proportion of *L. maackii* twigs that were browsed (from early through mid-growing season) ranged from 4% to 66% among the eight sites (Table 4). This browse proportion was positively related to the density of LPS twigs among the sites (regression $P=0.005$; Figure 3A) and negatively related to the log-transformed density of *L. maackii* twigs (logLONMA) ($P=0.0007$, Figure 3C) (Table 3). There was a trend of a negative association between the proportion of *L. maackii* twigs browsed and MPS twig density, but this was not significant ($P=0.10$; Figure 3B). The other predictors, including the proportions of

Table 2. List of more- and less-preferred species.^a

More-preferred species		Less-preferred species	
<i>Acer saccharum</i> Marshall	Sugar maple	<i>Acer negundo</i> L.	Boxelder
<i>Aesculus flava</i> Aiton	Yellow buckeye	<i>Aesculus glabra</i> Willd.	Ohio buckeye
<i>Celtis occidentalis</i> L.	Common hackberry	<i>Asimina triloba</i> (L.) Dunal	Pawpaw
<i>Euonymus alatus</i> (Thunb.) Siebold	Burning bush	<i>Carya cordiformis</i> (Wangenh.) K. Koch	Bitternut hickory
<i>Fraxinus americana</i> L.	White ash	<i>Elaeagnus umbellata</i> Thunb.	Autumn olive
<i>Fraxinus quadrangulata</i> Michx.	Blue ash	<i>Euonymus fortunei</i> (Turcz.) Hand.-Maz.	Wintercreeper
<i>Ligustrum vulgare</i> L.	European privet	<i>Fagus grandifolia</i> Ehrh.	American beech
<i>Liriodendron tulipifera</i> L.	Tuliptree	<i>Lindera benzoin</i> (L.) Blume	Spicebush
<i>Lonicera japonica</i> Thunb.	Japanese honeysuckle	<i>Parthenocissus quinquefolia</i> (L.) Planch.	Virginia creeper
<i>Quercus muehlenbergii</i> Engelm.	Chinquapin oak	<i>Prunus serotina</i> Ehrh.	Black cherry
<i>Robinia pseudoacacia</i> L.	Black locust	<i>Quercus bicolor</i> Willd.	Swamp white oak
<i>Rosa multiflora</i> Thunb.	Multiflora rose	<i>Toxicodendron radicans</i> (L.) Kuntze	Poison ivy
<i>Rubus</i> spp.	Blackberry		
<i>Smilax</i> spp.	Greenbrier		
<i>Ulmus americana</i> L.	American elm		
<i>Ulmus rubra</i> Muhl.	Slippery elm		
<i>Viburnum dentatum</i> L.	Southern arrowwood		
<i>Vitis</i> spp.	Grape		

^aSpecies were sorted based on their electivities compared with *L. maackii* electivity (Supplementary Table A.2).

different land covers within a 1-km buffer, overstory tree density, and stand basal area, had no relationship with the proportion of *L. maackii* twigs browsed (P -values > 0.05; Table 3).

The three best univariate predictors of the proportion of *L. maackii* twigs browsed (LPS twig density, log LONMA twig density, and MPS twig density) were included in our multiple regression (multiple $R^2 = 0.92$; adj. $R^2 = 0.87$). In relative importance analysis, two variables accounted for most of the R^2 : logLONMA (42%) and LPS (40%) (Table 3). Only 18% was explained by MPS.

Our analysis of residuals of the univariate regressions revealed that one site (MWW) was influential. Repeating the multiple regression without this site reduced its explanatory power (multiple $R^2 = 0.65$; adj. $R^2 = 0.30$). However, there was no change direction of the relationships (signs of the coefficients) or the

relative importance of the predictors (logLONMA [55%], LPS [36%], MPS [10%]).

Electivities

Electivity of *L. maackii* ranged from -0.66 to $+0.57$ at the sites (Table 4) and was strongly positively correlated with the proportion of *L. maackii* twigs browsed ($r = 0.97$, $P < 0.0001$), suggesting they both measure the same underlying phenomenon of deer browse intensity on this invasive shrub. At seven of the sites, electivity values ranged from -0.66 to 0 , indicating a range from deer avoiding *L. maackii* to browsing in proportion to its abundance. Only at MWW was the electivity positive ($E_i = +0.57$), indicating *L. maackii* was preferred by deer.

Regressions revealed a positive linear relationship between *L. maackii* electivity values and the density of LPS twigs ($P = 0.001$; Figure 3D; Table 3). There was no trend between electivity and MPS twig density ($P = 0.29$; Figure 3E; Table 3). *Lonicera maackii* electivity had a negative relationship with logLONMA ($P = 0.004$, Figure 3F; Table 3). The other predictors, including land cover types and forest overstory parameters, had no relationship with electivity of *L. maackii* ($P > 0.05$; Table 3).

The multiple regression of *L. maackii* electivity on the same three predictors as for browse proportion (MPS, LPS, and logLONMA) resulted in a multiple $R^2 = 0.93$ and adjusted $R^2 = 0.87$. Relative importance analysis revealed that two variables accounted for most of the R^2 : LPS (47%) and logLONMA (43%) (Table 3). MPS explained only 10% of R^2 .

Evaluation of the Hypotheses

Our first hypothesis, that *L. maackii* is preferred by deer, was not supported, because the electivity of *L. maackii* was not positive at most sites. *Lonicera maackii* was “preferred” at MWW, but at the other seven sites, the values of *L. maackii* electivity were negative or close to 0 , indicating *L. maackii* was of low preference compared with the other woody species

Table 3. Adjusted R^2 values for univariate linear regressions of each of the two response variables, electivity (E_i) of *Lonicera maackii* and *L. maackii* twigs browsed/total *L. maackii* twigs (LMA browse) on single predictor variables among the eight sites, and unweighted average contribution (lmg) to R^2 of the three predictors used in multiple regression with relative importance analysis.^a

Predictor	Adjusted R^2		lmg	
	E_i	LMA browse	E_i	LMA browse
More-preferred twigs m^{-2}	0.05	0.28	0.10	0.18
Less-preferred twigs m^{-2}	0.83	0.71	0.47	0.40
\log_{10} (LMA twigs m^{-2})	0.75	0.83	0.43	0.42
Trees per hectare	-0.10	-0.08		
Stand basal area	-0.02	-0.14		
Forest	-0.07	0.00		
Perennial forage	-0.04	-0.09		
Pasture/row crop	-0.05	-0.09		
Perennial forage + pasture/row crop	-0.05	-0.08		
Urban	-0.16	-0.13		

^aThe last five predictor variables refer to the proportion of the land cover in the 1-km radius buffer. Bolded values indicate P -value < 0.05 in univariate regression.

Table 4. Electivity (E_i) values and proportion of twigs browsed (Prop. browsed) for *Lonicera maackii* and other common woody species at each of the study sites, and means and SDs for the eight values for each species.^a

Site	<i>L. maackii</i>		<i>P. serotina</i>		<i>A. saccharum</i>		<i>U. americana</i>		<i>C. occidentalis</i>		<i>F. americana</i>	
	E_i	Prop. browsed ^b	E_i	Prop. browsed	E_i	Prop. browsed	E_i	Prop. browsed	E_i	Prop. browsed	E_i	Prop. browsed
Davidson Woods	-0.53	0.05 (0.03)	-0.23	0.11	-0.02	0.17	0.53	0.58	NA	NA	0.04	0.14
Hueston Woods	-0.15	0.18 (0.07)	-0.23	0.15	0.14	0.33	0.34	0.50	0.34	0.50	-1	0.27
Miami Whitewater East	-0.06	0.27 (0.08)	-0.45	0.12	-0.02	0.30	0.37	0.67	0.16	0.43	-0.13	0.23
Miami Whitewater West	0.57	0.66 (0.10)	0.5	0.55	-0.6	0.05	0.53	0.59	0.23	0.29	-0.68	0.06
Mt Airy	-0.63	0.07 (0.06)	NA	NA	0.19	0.46	0.29	0.57	0.32	0.60	-0.51	0.06
Stanbery Park	-0.66	0.04 (0.01)	-1	0.00	-0.09	0.15	-1	0.00	0.59	0.71	-0.15	0.32
Taylorville Metropark	-0.52	0.09 (0.02)	NA	NA	-0.27	0.17	0.26	0.50	-0.08	0.25	-0.34	0.15
Winton Woods	0.00	0.20 (0.16)	-0.37	0.09	-0.18	0.14	0.45	0.52	0.03	0.21	0.27	0.00
Mean	-0.25	0.20	-0.30	0.17	-0.11	0.22	0.22	0.49	0.23	0.43	-0.31	0.15
SD	0.42	0.20	0.48	0.19	0.25	0.13	0.50	0.21	0.22	0.19	0.41	0.11

^aNA, not applicable, species not sampled in plots.

^bFor the proportion of *L. maackii* browsed, the SD (based on values from four transects) for each site is in parentheses.

present at the same site. While some invasive species are low-preference foods for deer, no consistent preference pattern emerged from cafeteria experiments involving several native and invasive species (Averill et al. 2016). While *L. maackii* was not included in those experiments, closely related *L. morrowii* was highly preferred (positive electivity).

The second hypothesis, that *L. maackii* is not preferred compared with other woody species but consumed where preferred browse is depleted, generated our prediction of a negative relationship between the other response variable, *L. maackii* electivity, and the density of twigs of more-preferred species (MPS), but we found no such relationship. However, both electivity and the proportion of *L. maackii* twigs browsed were greatest at the site that had the lowest MPS (MWW). This suggests there may be some threshold level of availability of preferred foods, and only below that threshold do deer shift to *L. maackii*. Support for this idea comes from our finding that MWW was an influential point in univariate regressions of proportion of *L. maackii* browsed, and when it was removed from analysis, the relative importance of MPS was even lower.

Our third hypothesis, that *L. maackii* serves as an important browse in early spring, led us to predict low *L. maackii* browse proportions at sites that had high *L. maackii* twig densities. Consistent with this prediction, there was a negative relationship between *L. maackii* browse proportion and log-transformed *L. maackii* twig density, and the latter variable had the highest relative importance in explaining variation in *L. maackii* browse among the sites. The finding that log transformation improved the linearity of this relationship reflects the fact that the *L. maackii* browse proportion declined from low to moderate *L. maackii* density, but remained low across moderate to high density. (The very high browse percentage at the site with the lowest *L. maackii* density [MWW] is a manifestation of this same pattern.) This pattern suggests that this inverse density-dependent effect on browse intensity on *L. maackii* is greatest at lower *L. maackii* densities. However, even when MWW was excluded from analysis, logLONMA remained the most important predictor of the percent *L. maackii* browsed, and the relative importance of this predictor was a bit greater. An alternative explanation, that *L. maackii* browse proportion is related to overall browse scarcity, is not supported: there was no

relationship between *L. maackii* browse proportion and total twig density among sites (adj. $R^2 = 0.08$).

We argue that the special food source that *L. maackii* provides is a function of its ELP (Fridley 2012; Smith 2013), specifically, leaf expansion earlier in the spring than native woody plants (McEwan et al. 2009). Smith (2103) argued that leafy twigs of many invasive plants provide more nutrition to deer than leafless twigs of native plants in early spring. Indeed, leafy *L. maackii* twigs cut to match nearby deer bites in May, before leaf out of native plants, had 2.07% nitrogen (12.9% crude protein), much greater than literature values for leafless twigs of native trees (Martinod and Gorchoy 2017). Many other invasive woody species expand leaves earlier in the spring than most native plants in deciduous forests of eastern North America and may provide a comparable resource (Smith 2013), although on average non-native woody species do not expand leaves earlier than natives (Fridley 2012). In early spring, ELP shrubs in forest understory (e.g., *L. maackii* at our sites) are strikingly visible to humans, and we suggest to deer as well, enabling deer to find these shrubs when they are sparse.

Evidence that this finding of inverse density-dependent browse on *L. maackii* was due to early spring foraging comes from our follow-up study of early spring browse at HWSNP. The proportion of *L. maackii* twigs browsed at HWSNP was 0.19 (Table 5), comparable to the mean of the other eight study sites (0.20; Table 1), consistent with our argument that deer browse on this invasive occurs mostly in early spring. The proportion of new twigs browsed was higher for *L. maackii* than for other woody species (Table 5).

Other ELP invasives might be expected to experience similar patterns of inverse density-dependent deer browse in early spring, warranting further research. Use of ELP invaders by deer and other generalist herbivores during periods of scarcity of native foods would be expected to elevate herbivore populations, and under a range of conditions negatively impact native plants via apparent competition (Martinod and Gorchoy 2017; Smith and Hall 2016).

Our finding that both *L. maackii* percent browsed and electivity were positively related to LPS was not anticipated. This pattern is consistent with “neighbor contrast susceptibility,” wherein a palatable plant is attacked more by an herbivore if it is

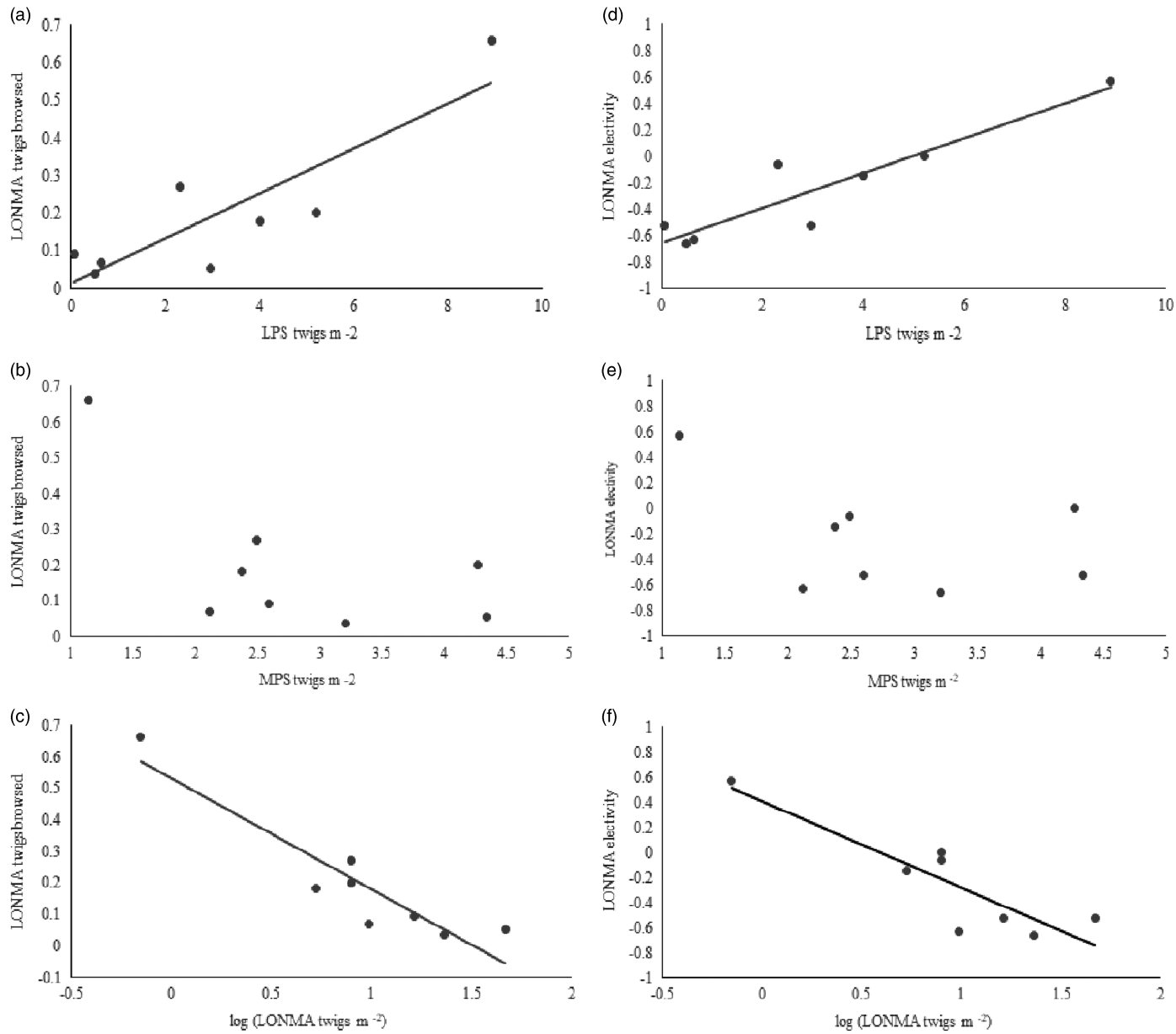


Figure 3. Scatter plots of (A–C) *Lonicera maackii* (LONMA) proportion browsed and (D–F) *L. maackii* electivity at each of the eight sites vs. twig densities with fitted linear regression lines where significant. Independent variables are (A, D) less-preferred species (LPS), (B, E) more-preferred species (MPS), and (C, F) *L. maackii* (\log_{10} transformed). Equations for significant regressions are (A) $Y = 0.060x + 0.012$, $R^2 = 0.75$; (C) $Y = -0.352x + 0.530$, $R^2 = 0.85$; (D) $Y = 0.131x + 0.645$, $R^2 = 0.85$; and (F) $Y = -0.693x + 0.411$, $R^2 = 0.78$.

Table 5. Density of new-growth twigs and proportion of these browsed in early spring (before census in late May 2018) in Hueston Woods State Nature Preserve.^a

Species	Twig density twigs m ⁻²	Proportion browsed
<i>L. benzoin</i>	24.26 (10.42)	0.002 (0.002)
<i>F. grandifolia</i>	2.39 (1.67)	0.042 (0.032)
<i>A. triloba</i>	1.37 (0.88)	0.000 (0.000)
<i>L. maackii</i>	1.02 (0.37)	0.192 (0.091)
Other	1.09 (0.60)	0.126 (0.085)
Total	30.13 (12.84)	0.037 (0.015)

^aSDs, based on values from four transects, are in parentheses.

growing among unpalatable plants (Alm Bergvall et al. 2005). The importance of this phenomenon, as well as the converse (“associational defense” or “associational avoidance”; Milchunas and Noy-Meir 2002), wherein a plant suffers less herbivory in the neighborhood of unpalatable plants, likely depends on the scale of patchiness versus foraging decisions, and has been little studied for deer (but see Alm Bergvall et al. 2005).

Alternative Factors Influencing Browse on *Lonicera maackii*

One site (MWW) had a much lower density of *L. maackii* and a much higher proportion of this shrub’s twigs browsed than the other sites (Figure 3C). Although this site was not an outlier in the univariate regression, we did explore whether factors other than low *L. maackii* density might alternatively account for its high browse at this site. As noted earlier, the very low density of MPS twigs may have been below some threshold where deer shift to *L. maackii*. Another explanation, higher deer density, was ruled out, as MWW did not have higher density than several other sites, based on aerial surveys, harvest data (Table 1), or fecal pellet counts (Wright 2017).

Alternatively, the high browse on *L. maackii* at MWW might be explained by the very low density/low availability of other (e.g., non-woody) foods. Our exploration into whether differences in land cover proportions, as surrogate measures of other foods (e.g., fields providing perennial herb forage), affected browse on *L. maackii* revealed no role for these predictors, although their importance has been documented in other studies (Hurley et al. 2012; Royo et al. 2017). However, we did not measure herbaceous plants within each forested site. Herbs comprise a large portion of deer diets during spring and summer (Crawford 1982; Halls and Crawford 1960; Kohn and Mooty 1971) and have reduced cover in deer access areas versus exclosures (Kalisz et al. 2014; Peebles-Spencer et al. 2017). Years of deer browse pressure could have reduced the abundance of spring ephemerals, such as *Trillium* spp., that are preferred by deer (Anderson 1994; Augustine and DeCalesta 2003; Augustine and Frelich 1998; Augustine and Jordan 1998; Rooney and Waller 2001), resulting in more intense browse on woody species with ELP.

Effect of *Lonicera maackii* on Browse of Other Woody Species

Based on counts of browsed twigs, *L. maackii* comprised the largest portion of overall browse (r_i) at each site, except MA, where it was the second largest (Supplementary Table A.1). Three other woody species were sufficiently abundant at most sites so

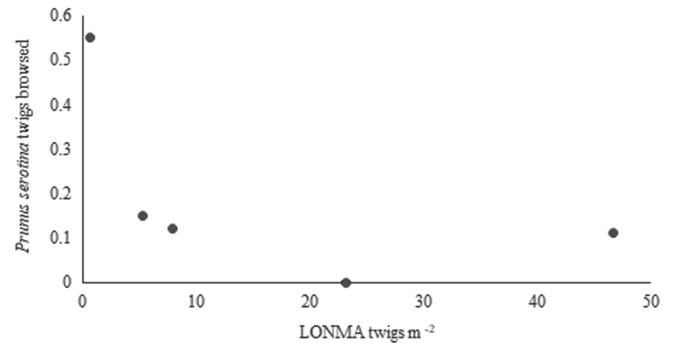



Figure 4. Scatter plot of proportion of *Prunus serotina* twigs browsed vs. *Lonicera maackii* (LONMA) twig density among the six sites where *P. serotina* was present.

that we could explore how the proportion of their twigs that were browsed related to *L. maackii* twig density. One of these species, *P. serotina*, was less preferred than *L. maackii*, and its browse percentage was negatively associated with *L. maackii* twig density (Figure 4). The other two species, *U. americana* and *A. saccharum*, were more preferred than *L. maackii* and showed no trend between proportion browsed and *L. maackii* density (Wright 2017). The negative relationship between *L. maackii* density and deer browse on *P. serotina* suggests that removal of *L. maackii* as a management practice could result in higher browse on species such as *P. serotina*. Under some circumstances, similar browse impacts may manifest on preferred species: *A. saccharum* seedlings experience less browse and show higher survival and growth when planted under rather than next to *L. maackii* shrubs (Peebles-Spencer and Gorchov 2017).

Conclusions

The findings of this study best support hypothesis 3, that *L. maackii* serves as an important food in early spring. We think that deer seek *L. maackii* in early spring, when its leaves have expanded but those of native woody species have not, but do not prefer it at other times of year. Thus, for a brief period, deer browse is likely focused on this invasive shrub, and where it is sparse, this herbivory can impact a majority of the twigs. At sites with abundant *L. maackii*, the abundance of leafy twigs greatly exceeds this early spring consumption by deer, manifesting in low proportional browse.

Our research also reveals a limitation of quantifying herbivore preference based on the proportion of each species eaten or electivity. These two measures were correlated in our study, both when comparing values for *L. maackii* across sites and when comparing the six most common species (Table 4) ($r=0.98$). However, either measure could be misleading in cases in which a species is preferred only during a particular season, or its density leads to an overabundance of food. To determine whether deer browse more heavily on *L. maackii* twigs versus other species during the early spring, future research should focus on measuring deer browse on these species during this season.

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Supplementary materials. To view supplementary material for this article, please visit <https://doi.org/10.1017/inp.2018.30>

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