Browse by White-tailed Deer Decreases Cover and Growth of the Invasive Shrub, Lonicera maackii

JESSICA R. PEEBLES-SPENCER¹, CHRISTINA M. HAFFEY, AND DAVID L. GORCHOV² Department of Biology, Miami University, 700 East High Street, Oxford, Ohio 45056

ABSTRACT.—While arthropod herbivory on invasive plant species is generally low, herbivory by generalist mammals is often high. We tested whether exclusion of white-tailed deer, *Odocoileus virginianus*, increased the cover and growth of *Lonicera maackii*, an invasive shrub, in forested natural areas in Ohio, U.S.A. We found leaf frequency of *L. maackii* in two height ranges, 0.5–1 m and 1–1.5 m, was significantly greater where deer had been excluded for 4 y. Furthermore, the basal area growth of these shrubs over 5 y tended to be higher, and the final basal area of small shrubs was significantly higher, in exclosures. These findings, along with direct evidence of deer browse from the literature, indicate deer browse on this invasive shrub is sufficient to affect its architecture and growth, and potentially mitigate its negative effect on native plants.

INTRODUCTION

Herbivory on many invasive nonnative plant species is low (Cappuccino and Carpenter, 2005), consistent with the Enemy Release Hypothesis (ERH; Keane and Crawley, 2002; Colautti *et al.*, 2004). However, native herbivores often do consume nonnative plants (Morrison and Hay, 2011), suppressing invasion, consistent with the biotic resistance hypothesis (BRH, Elton, 1958). While novel chemical defenses likely account for the minimal herbivores are expected to tolerate these novel toxins by consuming a wide variety of plants with diverse toxins (Verhoeven *et al.*, 2009). This strategy is hypothesized to explain the finding that native generalist vertebrates commonly suppress nonnative plant species (Parker *et al.*, 2006a, b; Ricciardi and Ward, 2006). However, Parker *et al.*'s (2006a) review included no studies from temperate deciduous forest; therefore, the effects of native herbivores on invasive plants in these forests are as of yet poorly understood.

Generalist mammalian herbivores now occur at densities greater than historical levels with negative impacts on native plant communities (Côté *et al.*, 2004). Of particular concern in many areas of North America plants is white-tailed deer, *Odocoileus virginianus* Zimmerman, hereafter deer. Deer are notorious generalists, consuming several hundred different species of algae, fungi, herbs, shrubs, and trees (Atwood,1941). Deer densities in many parts of the United States are well above historical levels (McCabe and McCabe, 1997; McShea, 2012), causing negative impacts on tree regeneration (Horsley *et al.*, 2003, Côté *et al.*, 2004). At even moderate densities, deer greatly alter structure and composition of forests (Rooney, 2009; Bradshaw and Waller, 2016; Russell *et al.*, 2017). At densities as low as 3–10 deer/km², deer negatively impact preferred browse species (McShea, 2012).

Because many natural areas in North America are impacted by both abundant deer and invasive plants, attention is focused on how these drivers interact to impact native plant communities. Some invasive plant species increase where deer are abundant, apparently due to reduced competition from native plants that deer prefer to browse (Knight *et al.*, 2009;

¹ Current address: Department of Biology, Ball State University, Muncie, IN 47306

² Corresponding author: e-mail: GorchoDL@miamioh.edu

Eschtruth and Battles, 2009). However, a recent experiment showed deer preferences for invasive species varied widely, with some preferred over most native species and others avoided (Averill *et al.*, 2016).

We investigated whether deer herbivory on an invasive nonnative shrub is sufficient to reduce its growth and cover and potentially mitigate its effect on native plants. *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), Amur honeysuckle, is a large shrub native to east Asia (Luken and Thieret, 1995) and one of several bush honeysuckles invasive in the eastern United States. The current distribution of *L. maackii* spans the eastern half of the United States, where this species is considered invasive and regulated in eight states (EDDMapS, 2015). Impacts of *L. maackii* on native species, communities, and ecosystems has been reviewed by McNeish and McEwan (2016). The success of *L. maackii* in North America has been attributed to its phenotypic plasticity (Luken *et al.*, 1995; 1997), extended leaf phenology (McEwan *et al.*, 2009; Wilfong *et al.*, 2009), and escape from specialist herbivores (Lieurance and Cipollini, 2012).

Herbivory by arthropods on *L. maackii* in its introduced range is very low (Lieurance and Cipollini, 2012; 2013), but herbivory by deer has only recently been reported, although the vine, *L. japonica*, has long been planted as deer forage (Stransky,1984). Guiden *et al.* (2015) reported $62 \pm 14\%$ of fruiting *L. maackii* branches in forest edge habitat near our southwest Ohio study area showed evidence of deer browse (severed branch or twig with shredded bark and no teeth marks during a 3 mo period from mid-fall to mid-winter (Swift and Gross, 2008). In our study area (deciduous forest in the Miami University Natural Areas), 26% of first-year twigs of *L. maackii* between the heights of 0.3 and 2.1 m incurred deer browse damage over a 12 mo period (Martinod and Gorchov, 2017). Browsing was greatest in early spring and late summer and consisted primarily of leaf tissue (Martinod and Gorchov, 2017). A similar invasive congeneric shrub, *L. morrowii* A. Gray, was highly preferred by deer in multiple choice preference trials (Averill *et al.*, 2016). DNA of introduced *Lonicera* spp. was recovered from fecal pellets of all 12 free-ranging deer in Virginia analyzed by Erickson *et al.*, (2017).

Methods

Field methods.— This study utilized deer exclosures and paired deer access plots in five sites in the Miami University Natural Areas, Butler County, Ohio $(39^{\circ}29'-39^{\circ}31'N, 84^{\circ}42'-84^{\circ}43'W)$. Sites were separated by ≥ 1 km and chosen to have (1) a similar, moderate level of invasion by *L. maackii* (stem basal area (BA) 0.58–1.57 m²/ha), (2) closed-canopy deciduous forest, and (3) level topography. Deer densities in this area range from 11.2 ± 0.6 (Mean ± sE) deer per km² in the summer to 15.4 ± 4.4 deer per km² in the winter (Barrett, 2014). Within each site, two 20 × 20 m plots that were very similar were selected and randomly assigned to deer exclosure and deer access treatments. Three meter tall fencing was placed around the deer exclosure plots in summer 2010. Each plot was divided into two 10 × 20 m "half-plots" that were randomly assigned to have all *L. maackii* removed or left intact ("*L. maackii* present"). Removal was done in fall 2010 by clipping all *L. maackii* stems ≥ 1 mm diameter and treating stumps with Tordon RTU. A few treated shrubs resprouted in 2011; these new stems were cut and treated with Tordon RTU.

The BA of *L. maackii* in each half-plot was determined in Oct. 2010 before stems were cut and again in May–June 2015, by measuring the diameter of each *L. maackii* stem ≥ 1 mm, using these to calculate each shrub's BA, and summing for all shrubs in the half-plot. For each *L. maackii*-present half-plot we calculated BA growth as BA₂₀₁₅–BA₂₀₁₀.

We distinguished three classes of *L. maackii* shrubs in the 2015 census; those that were too tall to be impacted much by deer herbivory, those that had much of their leaf mass within the range accessible to deer (0.3–2.1 m; Frelich and Lorimer, 1985), and young plants that recruited into the plots after the experiment was set up. Shrubs with basal diameter of the largest stem \geq 30 mm were classified as 'large,' based on a sample at College Woods in which 10 of 13 of such shrubs had the vast majority of their leaves above 2.1 m, whereas all seven shrubs with largest stem 20–30 mm had most of their leaves < 2.1 m. 'Recruits' were identified as shrubs with the largest stem of basal diameter \leq 2 mm based on annual ring counts and diameters in a nearby woodlot. Shrubs intermediate between these two size classes (largest stem 3–29 mm in diameter) were classified as 'small.'

To determine the effect of deer on the cover of *L. maackii* we sampled $18\ 20 \times 50$ cm (1000 cm²) subplots (every 2 m along two 20 m transects) in each of the 10 *L. maackii*-present halfplots. Between 16–22 July 2014, we recorded the presence/absence of *L. maackii* leaves in each of three height ranges, 0–0.5 m, 0.5–1 m, and 1–1.5 m in each subplot. From these we calculated the frequency of *L. maackii* in each height range in each half-plot.

Data analysis.—For L. maackii-present half plots,, we tested whether BA growth of all shrubs and BA₂₀₁₅ of small L. maackii differed between deer exclosure and access plots with linear mixed models using lmer in the lme4 package of R, with site as the random effect. For these same half-plots, we tested whether deer exclosure resulted in higher L. maackii foliage frequency at each of the height ranges using mixed model logistic regression using the glmer command in the lme4 package, with subplots as replicates, foliage presence/absence as the response, exclosure as the fixed effect, and site as the random effect. For all 20 half-plots we tested whether the number of recruits was affected by deer treatment, L. maackii treatment, or their interaction with a split-plot generalized linear mixed model fit by maximum likelihood (Laplace Approximation) using glmer. Because the response variable (recruits) was a count variable, a Poisson link function was used in this analysis. All analyses were completed using the lme4 package of R, version 3.3.0 (R Core Team 2016).

RESULTS

Lonicera maackii shrubs tended to grow more, based on change in total BA, in half-plots where deer had been excluded than where they had access (F = 4.99, df = 1, 4.001, P = 0.0892, Fig. 1). Considering only 'small' *L. maackii* shrubs, BA was about 50% greater where deer were excluded than where they had access (F = 11.648, df = 1, 4.00, P = 0.0270, Fig. 2).

Recruitment of new *L. maackii* shrubs was significantly affected by *L. maackii* treatment but not by deer treatment (Table 1, Fig. 3), more recruits were present in the half-plots where *L. maackii* shrubs had been removed in 2010. There was a marginally significant interaction term (Table 1), with the *Lonicera*-removed plots tending to show *lower* recruitment where deer were excluded compared to where they had access (Fig. 3).

In half-plots where *L. maackii* was left intact, the frequency of its leaf cover was significantly greater where deer were excluded than where they had access at two height ranges; 0.5-1 m and 1-1.5 m (P = 0.0019 and P = 0.0024, respectively, Fig. 4). Frequency of *L. maackii* leaf frequency in the 0–0.5 m height range did not differ between deer treatments (P = 0.368).

DISCUSSION

Our findings indicate deer browse on *L. maackii* is sufficient to affect its cover and growth. While deer browse does not kill *L. maackii* shrubs, the findings of our study indicate it is



FIG. 1.—Boxplot of *Lonicera maackii* basal area change between 2010 and 2015 in half-plots where *L. maackii* was present (not removed in 2010). N = five sites, each with one deer access (AC) and a deer exclosure (EX) plot. There was a trend (P = 0.09) for greater growth where deer were excluded

sufficient to impact its architecture, *i.e.*, the vertical distribution of foliage. Exclusion of deer resulted in greater cover of *L. maackii* leaves in two height ranges (0.5-1.0 m, 1.0-1.5 m) while not impacting cover below 0.5 m. In our study area, nearly all deer browse on *L. maackii* occurred on twigs 0.3-1.2 m above the ground, with less browse 1.2-1.7 m, and virtually none 1.7-2.1 m (Martinod, 2016).

While the largest shrubs in these forests have most of their twigs above the height where deer browse, most twigs of smaller shrubs are accessible to deer, and the loss of photosynthetic tissue could be sufficient to reduce carbon gain and subsequently growth. This hypothesis is supported by our finding that the basal area of small shrubs was significantly greater where deer were excluded. This difference is not due to differential survival but rather to some combination of growth of existing stems and recruitment of new stems on existing shrubs, because the number of individual shrubs (excluding recruits) did not differ between deer access and deer exclusion plots (linear mixed model F = 0.12, df = 1,



FIG. 2.—Mean (+SE) basal area of small *L. maackii* shrubs (diameter of largest stem 3–29 mm) in 2015 in half-plots where *L. maackii* was present (not removed in 2010) and deer had access (AC) or were excluded (EX)

3.9997, P = 0.7475). These 'small' shrubs accounted for the majority (59–95%) of the total *L.* maackii BA in eight of the 10 half-plots. The other two half-plots, in which most *L. maackii* BA was comprised of large shrubs, were both at College Woods. This was the only one of the five sites where total BA growth from 2010 to 2015 was not greater in the exclosure, strengthening our inference that deer suppress growth of small, but not large, *L. maackii* shrubs.

Interestingly, recruitment of new *L. maackii* shrubs was not greater where deer were excluded. Recruitment of *L. maackii* from 2011 to 2015 was significantly enhanced by removal of established *L. maackii* shrubs in 2010, presumably due to the lack of intraspecific competition. However, where *L. maackii* was removed, new recruitment of this invasive actually tended to be greater where deer were present. This could be due to greater seed

TABLE 1.—Table of fixed effects of a split-plot generalized linear mixed model of the number of *L.* maackii recruits (shrubs with largest stem $\leq 2 \text{ mm}$ diam.) in half-plots in 2015, fit by maximum likelihood (Laplace Approximation) using glmer in R. Deer treatment (exclusion v access) and *Lonicera* treatment (removed in 2010 v present) were fixed effects and site (N = 5) was a random effect

	Estimate	Std. error	Z value	$Pr(\geq[z])$
(Intercept)	3.1134	0.2864	10.870	< 0.0001
Deer Exclusion	-0.2055	0.2256	-0.911	0.3624
Lonicera removal	0.6828	0.1013	6.742	< 0.0001
Deer *Lonicera	-0.2741	0.1621	-1.691	0.0909



FIG. 3.—Interaction plot showing the mean number of *L. maackii* recruits (shrubs with largest stem ≤ 2 mm) in 2015 in half-plots where deer had access (AC) or were excluded (EX) and *Lonicera maackii* was present or had been removed in 2010

dispersal, as deer disperse viable *L. maackii* seeds (Guiden *et al.*, 2015), or reduced competition on *L. maackii* seedlings where other plants in the understory are browsed by deer. We suggest deer browse has minimal effect on the number of *L. maackii* recruits because seedlings are initially below the typical browse height range (0.3–2.1 m; Frelich and Lorimer, 1985) and later not killed when the tops are browsed.

The substantial deer browse on *L. maackii* in the study area is likely attributable to the low frequencies of more preferred woody species, such as *Quercus* and *Acer* spp., in heights accessible to deer (Martinod and Gorchov, 2017). In addition the early leaf expansion of this invasive (McEwan *et al.*, 2009) provides deer with leafy forage in early spring when protein needs of deer are high and other native woody plants are leafless (Smith, 2013). Leafy spring twigs of *L. maackii* contain 12.9% crude protein (Martinod and Gorchov, 2017), about double that of leafless twigs of native woody species that co- occur in this study area.

These findings on the impact of deer browse on *L. maackii* are consistent with Bowers' (1997) finding that deer exclosure resulted in higher prevalence of stems of the invasive shrub, *Lonicera tartarica* L., after 8 y of succession in an old field. The differences in *L. maackii* cover and BA reported here manifested after only 4 and 5 y of deer exclosure, respectively. That *L. maackii* has grown to be the dominant shrub in these stands and others in the Midwest may be a result of deer initially failing to recognize *L. maackii* as food source (Morrison and Hay, 2011). Deer now seem to have overcome that naivety, exploiting *L. maackii* for browse. While seedlings of this shrub appear little impacted by deer, when the shrubs grow a bit larger deer browse is sufficient to slow their growth, at least where deer are overabundant. But once shrubs reach sufficiently height, most of their leaves are out of reach, and growth likely unaffected. At this point browse is limited to the lower twigs, resulting in a 'browse line' of low cover in the understory.



FIG. 4.—Mean frequency of *Lonicera maackii* foliage at each height range in deer access and deer exclosure plots. Error bars are sE based on data from five plots. Asterisk indicates significant difference between treatments (P < 0.01)

Our findings have implications for understanding the combined effects of deer and invasive plants on native plants. Where deer reduce *L. maackii* cover, they would be expected to mitigate its shading of native plants, which suggests the negative effects of deer and this invasive plants would be antagonistic, *i.e.* the combined negative effect on natives would be less than expected from the individual negative effects. This statistical interaction has been found both for spring perennial herb abundance and *Maianthemum racemosum* L. leaf number in an experiment that combined deer exclosure and *L. maackii* removal (Christopher *et al.*, 2014). Similarly, Peebles-Spencer *et al.* (2017) found a marginally significant antagonistic interaction between *L. maackii* and deer on ground-layer plant species richness; the negative effect of *L. maackii* was greater where deer were excluded. At a larger scale, deer consumption of invasive shrubs might inflate the population density of this generalist herbivore, which in turn may suppress native plants, an example of apparent competition (Smith, 2013). The hypothesis *L. maackii* elevates deer populations in some locations is supported by the finding that this shrub comprises 14–47% of the annual deer

diet in the Miami University Natural Areas and provides high protein leafy twigs early in the spring when native woody plants were leafless (Martinod and Gorchov, 2017).

Acknowledgments.—We thank Miami University Natural Areas Committee for permission to carry out the field work and Miami University's Howard Hughes Scholar Program for financial support. We thank R. Spencer, M. Hassett, C. Brakers, J. Samu, and K. Martinod for assistance in the field and Tom Crist, Hank Stevens, Melany Fisk, Jim Hickey, and anonymous reviewers for valuable input on earlier drafts of this manuscript.

LITERATURE CITED

- ATWOOD, E. L. 1941. White-tailed deer foods of the United States. J. Wildlife Manage., 5:314-332.
- AVERILL, K.M., D.A. MORTENSEN, E.A. SMITHWICK, AND E. POST. 2016. Deer feeding selectivity for invasive plants. *Biol. Invasions*, 18:1247–1263.
- BARRETT, M. L. 2014. Comparison of estimated white-tailed deer *Odocoileus virginianus* population densities during two different seasons in the Miami University Natural Areas. Unpublished master's thesis, Miami University, Oxford (OH). 44 p.
- BOWERS, M.A. 1997. Influence of deer and other factors on an old-field plant community: an eight-year exclosure study, p. 310–326. *In*: W.J. McShea, T. B. Underwood, and J.H. Rappole, (eds.). The science of overabundance: Deer ecology and population management. Smithsonian Institution Press, Washington, DC.
- BRADSHAW, L. AND D. M. WALLER. 2016. Impacts of white-tailed deer on regional patterns of forest tree recruitment. *Forest Ecol. Manage.*, 375:1–11.
- CAPPUCCINO, N. AND D. CARPENTER. 2005. Invasive exotic plants suffer less herbivory than non-invasive exotic plants. *Biol. Lett.* 1:435–438.
- CHRISTOPHER, C., S. MATTER, AND G. CAMERON. 2014. Individual and interactive effects of Amur honeysuckle (*Lonicera maackii*) and white-tailed deer (*Odocoileus virginianus*) on herbs in a deciduous forest in the eastern United States. *Biol. Invasions*, 16:2247–2261.
- COLAUTTI, R.I., A. RICCIARDI, I.A. GRIGOROVICH, AND H.J. MACISAAC. 2004. Is invasion success explained by the enemy release hypothesis? *Ecol. Lett.*, 7:721–733.
- Côté, S.D., T.P. ROONEY, J.-P. TREMBLAY, C. DUSSAULT, AND D.M. WALLER. 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. S., 35:113–147.
- EDDMAPS. 2015. Amur honeysuckle (*Lonicera maackii*) EDDMapS State Distribution. Early Detection & Distribution Mapping System. The University of Georgia Center for Invasive Species and Ecosystem Health. http://www.eddmaps.org/distribution/usstate.cfm?sub=3040. Accessed June 1, 2015.
- ELTON, C. S. 1958. The ecology of invasions by animals and plants. Springer US, Boston, MA. 181 p.
- ERICKSON, D.L., E. REED, P. RAMACHANDRAN, N.A. BOURG, W. McSHEA, A. OTTESEN. 2017. Reconstructing an herbivore's diet using a novel rcbl DNA mini-barcode for plants. AoB PLANTS 9: plx015; doi:10. 1093/aobpla/plx015.
- ESCHTRUTH, A.K., AND J.J. BATTLES. 2009. Acceleration of exotic plant invasion in a forested ecosystem by a generalist herbivore. *Conserv. Biol.*, 23:388–399.
- FRELICH, L.E. AND C.G. LORIMER. 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. *Biol. Conserv.*, **34**:99–120.
- GUIDEN, P., D.L. GORCHOV, C. NIELSEN, AND E. SCHAUBER. 2015. Seed dispersal of an invasive shrub, Amur honeysuckle (*Lonicera maackii*), by white-tailed deer in a fragmented agricultural-forest matrix. *Plant Ecol.*, 216:939–950.
- HORSLEY, S.B., S.L. STOUT, AND D.S. DECALESTA. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecol. Appl.*, **13**:98–118.
- KEANE, R.M., AND M.J. CRAWLEY. 2002. Exotic plant invasions and the enemy release hypothesis. Trends Ecol. Evol., 17:164–170.
- KNIGHT, T.M., J.L. DUNN, L.A. SMITH, J. DAVIS, AND S. KALISZ. 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. *Nat. Areas J.*, 29:110–116.

- LIEURANCE, D. AND D. CIPOLLINI. 2012. Damage levels from arthropod herbivores on *Lonicera maackii* suggest enemy release in its introduced range. *Biol. Invasions*, 14:863–873.
- LIEURANCE, D. AND D. CIPOLLINI. 2013. Exotic *Lonicera* species both escape and resist specialist and generalist herbivores in the introduced range in North America. *Biol. Invasions*, **15**:1713–1724.
- LUKEN, J.O., L.M. KUDDES, AND T.C. THOLEMEIER. 1997. Response of understory species to gap formation and soil disturbance in *Lonicera maackii* thickets. *Restor. Ecol.*, 5:229–235.
- LUKEN, J.O. AND J.W. THIERET. 1995. Amur honeysuckle (Lonicera maackii, Caprifoliaceae): its ascent, decline, and fall. Sida, 16:479–503.
- LUKEN, J.O., T.C. THOLEMEIER, L.M. KUDDES, AND B.A. KUNKEL. 1995. Performance, plasticity, and acclimation of the nonindigenous shrub *Lonicera maackii* (Caprifoliaceae) in contrasting light environments. *Can. J. Bot.*, **73**:1953–1961.
- MARTINOD, K.L. 2016. Importance of an invasive shrub, *Lonicera maackii*, in the diet of white-tailed deer: nutritional quality and browse rates. MS Thesis, Miami University, Oxford, Ohio, U.S.A.
- MARTINOD, K.L. AND D.L. GORCHOV. 2017. White-tailed deer browse on an invasive shrub with extended leaf phenology meets assumptions of an apparent competition hypothesis. AoB PLANTS 9: plx006.
- McCABE, T.R. AND R.E. McCABE. 1997. Recounting whitetails past, p. 11–26. In: W.J. McShea, T. B. Underwood, and J.H. Rappole, (eds.). The science of overabundance: Deer ecology and population management. Smithsonian Institution Press, Washington, DC.
- McEwan, R.W., M.K. BIRCHFIELD, A. SCHOERGENDORFER, AND M.A. ARTHUR. 2009. Leaf phenology and freeze tolerance of the invasive shrub Amur honeysuckle and potential native competitors. *J. Torrey Bot. Soc.*, 136:212–220.
- McShea, W.J. 2012. Ecology and management of white-tailed deer in a changing world. Ann. NY Acad. Sci., **1249**:45–56.
- MCNEISH, R. E., AND R. W. MCEWAN. 2016. A review of the invasion ecology of Amur Honeysuckle (Lonicera maackii, Caprifoliaceae) a case study of ecological impacts at multiple scales. J. Torrey Bot. Soc., 143:367–385.
- MORRISON, W.E. AND M.E. HAY. 2011. Herbivore preference for native vs. exotic plants: generalist herbivores from multiple continents prefer exotic plants that are evolutionarily naïve. PLoS ONE 6:e17227.
- PARKER, J.D., D.E. BURKEPILE, AND M.E. HAY. 2006a. Opposing effects of native and exotic herbivores on plant Invasions. *Science*, **311**:1459–1461.
- PARKER, J.D., D.E. BURKEPILE, AND M.E. HAV. 2006b. Response to comment on "opposing effects of native and exotic herbivores on plant invasions." *Science*, **313**:298–298.
- PEEBLES-SPENCER, J.R., D.L. GORCHOV, AND T.O. CRIST. 2017. Effects of an invasive shrub, *Lonicera maackii*, and a generalist herbivore, white-tailed deer, on forest floor plant community composition. *For. Ecol. Manage.* 402:204–212. http://dx.doi.org/10.1016/j.foreco.2017.05.053
- R CORE TEAM. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- RICCIARDI, A., AND J.M. WARD. 2006. Comment on "opposing effects of native and exotic herbivores on plant invasions." *Science*, **313**:298–298.
- ROONEY, T. 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. *Plant Ecol.*, **202**:103–111.
- RUSSELL, M.B., C.W. WOODALL, K.M. POTTER, B.F. WALTERS, G.M. DOMKE, AND C.M. OSWALT. 2017. Interactions between white-tailed deer density and the composition of forest understories in the northern United States. *For. Ecol. Manage.*, 384:26–33.
- SMITH, L. M. 2013. Extended leaf phenology in deciduous forest invaders: mechanisms of impact on native communities. J. Veg. Sci., 24:979–987.
- STRANSKY, J.J. 1984. Forage yield of Japanese honeysuckle after repeated burning or mowing. J. Range Manage., 37:237–238.
- SWIFT, C.E. AND M. K. GROSS. 2008. Preventing deer damage. Colorado State University extension. http:// www.ext.colostate.edu. Accessed March 9, 2017.

- VERHOEVEN, K.J.F., A. BIERE, J.A. HARVEY, AND W.H. VAN DER PUTTEN. 2009. Plant invaders and their novel natural enemies: who is naïve? *Ecol. Lett.*, 12:107–117.
- WILFONG, B.N., D.L. GORCHOV, AND M.C. HENRY. 2009. Detecting an invasive shrub in deciduous forest understories using remote sensing. *Weed Sci.*, 57:512–520.

SUBMITTED 4 MAY 2017

Accepted 14 September 2017

Copyright of American Midland Naturalist is the property of University of Notre Dame / American Midland Naturalist and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.