



REVIEW

# Differential and interacting impacts of invasive plants and white-tailed deer in eastern U.S. forests

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**Abstract** Forests in eastern North America are experiencing high densities of white-tailed deer (*Odocoileus virginianus*) and encroachment by invasive plants, both of which threaten native biodiversity. We review the literature on deer and invasive plant impacts focusing on studies that simultaneously evaluate the consequences of both. Deer have more frequent and more consistently negative effects than invasive plants. Widespread deer impacts now threaten many native plant species through much of their

range. In contrast, invasive plant effects currently remain more localized and/or of smaller extent within forests. Deer impacts are also cumulative, hitting preferred plant species especially hard as they decline in density. This generates difficult-to-reverse legacy effects. Invasive plant effects, in contrast, tend to be more diffuse and may be more readily reversed. High deer populations also shift physical and chemical conditions in soils promoting “invasion cascades” involving non-native earthworms and certain introduced plants. Removing invasive plants without reducing deer populations can increase deer impacts on native species. Management should be integrated to

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address both deer and invasive plants. To safeguard and restore native biota when resources are limited, however, it may be most effective for managers to first reduce deer populations before investing in efforts to reduce invasive populations (except when invasions are at an early stage). We should rethink and reform traditional approaches to managing deer so that we can better integrate land vegetation with wildlife management to achieve broad public objectives. Interacting effects of high ungulate populations and invasive plants deserve further study to determine whether similar recommendations apply to other regions.

**Keywords** Exotic plant species · Holistic management · *Odocoileus virginianus* · Restoration management

### Abbreviations

D Significant effect of deer

IP Significant effect of invasive plants

### Introduction

Forests in many parts of the world are affected by high populations of native ungulates (Gill and Beardall 2001; Côté et al. 2004; Ramirez et al. 2018). In many areas of North America, densities of white-tailed deer (*Odocoileus virginianus*) are much higher than during pre-European settlement (Rooney 2001) with well-documented effects on tree regeneration and understory plant composition and diversity (Rooney 2001; Russell et al. 2001; Bressette et al. 2012; Waller 2014; Habeck and Schultz 2015; Bradshaw and Waller 2016; Averill et al. 2018; McWilliams et al. 2018), animal populations (Allombert et al. 2005; Bressette et al. 2012; Lessard et al. 2012), ecosystem processes (Bressette et al. 2012; Mahon and Crist 2019), and

human disease vectors (Paddock and Yabsley 2007; Kilpatrick et al. 2014; Telford 2017; Ostfeld et al. 2018). Many forests are also being invaded by non-native plants (Liebhold et al. 2017; Riitters et al. 2018), with multiple negative effects on native plants (Jauni and Ramula 2015; Waller et al. 2016; Bialic-Murphy et al. 2019), animals (Litt et al. 2014), ecosystem functions (Vilà et al. 2011; Pyšek et al. 2012), and human disease vectors (Allan et al. 2010).

Although most acknowledge that we should work to reduce negative effects of both deer and invasive plants (Webster et al. 2006; McShea 2012), land managers usually lack authority or resources to adequately address both threats in a coordinated way. In order to evaluate the relative effectiveness of managing deer vs. invasive plants to achieve beneficial outcomes, we review the literature on how deer, invasive plants, and their interactions affect native biodiversity and ecosystems. We begin by conducting a comprehensive ‘vote-counting’ review of those studies that have simultaneously evaluated impacts of both white-tailed deer and invasive plants. We complement this with a qualitative review of additional studies focused on one of these stressors to illuminate important mechanisms. We restrict our attention to field studies of deer and non-native plants in forests of eastern North America. Nevertheless, our findings are relevant to broader geographic regions and to those supporting other ungulate species.

### Comprehensive review of studies of deer and invasive plant impacts

#### Methods

On 5 March 2020 we searched Web of Science using the search terms: Topic = (*Odocoileus virginianus* OR white-tailed\_deer) AND Topic = (invasi \* OR non-native OR exotic OR introduced). This generated 541 references. We then inspected titles to identify papers involving experimental investigations of the effects of deer and one or more invasive plant species (i.e., naturalized plant species that reproduce and spread over a large area). This resulted in 29 references. We then consulted abstracts of these to confirm each study’s objectives. This resulted in 23 references. Our own knowledge of the recent literature

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added 2 final references (Dornbush and Hahn 2013; Mahon and Crist 2019).

We read these papers to ascertain each study's design and the invasive plant species investigated. We then scored the effects of deer and invasive plants identified on several response variables (Table 1, Supplemental Table 1). In cases where two or more publications resulted from the same field study, we tallied the most recent report for each response. We examined statistical tests in the original papers to score how often deer or invasive plant effects were significant for each response variable. We also scored whether the deer X invasive plant interaction was significant and the nature of that interactive response. In particular, we ranked response variables by their values across all four combinations of deer being present or absent and invasive plants being present or absent using pair-wise contrasts from the publication (where available) or our own inspection of their figures.

## Results

The 25 publications reflect 16 unique study plots (or networks of plots across multiple sites) in eastern/midwestern U.S. forests (Supplemental Table 1). Of these 16, 13 experimentally manipulated both deer (via exclusion) or invasive plants (12 removals, 1 addition). One study manipulated deer and compared plots with contrasting plant composition (invasive plants common or nearly absent), one compared sites before and 7 years after deer culling (with contrasting plant composition), and one compared plots scored for deer browse impact and non-native plant richness (Supplemental Table 1). Most studies manipulated only one invasive plant species (always the most prevalent at the site), and these were largely limited to one annual grass (*Microstegium vimineum*, 4 studies), a biennial forb (*Alliaria petiolata*, 3), and a shrub (*Lonicera maackii*, 4). Of the 13 experiments that manipulated both deer and invasive plants, 10 used split-plot designs (seven where deer plots were split into invasive plant plots, three where invasive plant plots were split into deer plots). The other three were fully crossed. Of the 25 publications, 14 (56%) reported data after 1–4 years of manipulation while ten (40%) reported findings after 5–12 years (Fischelli and Miller 2018 had no time frame).

## Woody Plant Responses

These studies investigated a variety of responses, but most involved understory woody and herbaceous plants (Table 1a). Eleven studies reported summary responses (cover, density, richness, growth) of understory woody plants and/or responses of individual woody species, for a total of 40 response variables. Deer had negative effects on 14 of these variables (Fig. 2a) and a positive effect on just one (density of tree seedlings < 30 cm in Connecticut, Table 1a). Invasive plants had negative effects in ten cases and positive effects in two (density of tree seedlings in Maryland and of *Acer saccharum* seedlings in Indiana). For seven of these variables, the only significant effect was deer, with no invasive plant effect or interaction (Figs. 1a, 2a). In contrast, only two responses were affected only by invasive plants (diameter growth of *Quercus rubra* seedlings and density of *Prunus serotina* seedlings in Indiana) (Figs. 1b, 2a). Both deer and invasive plants affected seven response variables, with five of these showing only negative effects (Figs. 1c, 2a). Only eight of the 40 response variables showed significant deer X invasive plant interactions (see further discussion below).

## Herbaceous plant responses

Fourteen studies reported richness, cover, or biomass of native herbaceous plants or all native understory plants, or responses of individual functional groups or herb species, for a total of 60 response variables (Table 1b). Of these, 26 were affected by deer (17 negatively, 9 positively) while 20 were affected by invasive plants (13 negatively, 7 positively) (Fig. 2a). Nine response variables were affected by both deer and invasive plants with the most frequent ( $n = 3$ ) being a positive effect of deer with a negative effect of invasive plants and no interaction (growth of *Carex blanda* and *Geranium maculatum* in Wisconsin, graminoid cover in Connecticut). Nine of the 60 response variables showed significant deer X invasive plant interactions (see below).

## Animal, soil, and ecosystem function responses

Two studies found that deer increased the density of invasive non-native earthworms (Mahon and Crist

**Table 1** Summary of investigations of white-tailed deer and invasive plant impacts on (A) native woody plants, (B) native herbaceous plants or all plants, and (C) animal, soil, and ecosystem responses

Invasive Plant	Reference	Response	Deer	Invasive	D × IP
(A) Native understory woody plant richness, cover, abundance, survival <sup>4</sup>					
<i>Microstegium vimineum</i>					
17		Cover	ns	ns	*
20		Tree seedling density	—	+	ns
1		Survival of naturally regenerating seedlings	—	—	ns
		RGR of cover of naturally regenerating seedlings	ns	ns	ns
		RGR of height of naturally regenerating seedlings	—	—	ns
11		<i>Acer</i> and <i>Quercus</i> survival	—	—	ns
		<i>Acer</i> and <i>Quercus</i> biomass	ns	—	*
<i>Alliaria petiolata</i>					
21		<i>Quercus</i> growth	ns	ns	*
		<i>Quercus</i> survival	ns	ns	ns
<i>Lonicera maackii</i>					
13		Survival of <i>Acer</i> seedlings	—	ns	ns
10,19		Richness, abundance	—	ns	ns
		Cover	ns	ns	*#
18		Density, richness, diversity of natural regenerated seedlings; <i>Castanea</i> diameter RGR	ns	ns	ns
		Survival of <i>Castanea</i> and <i>Quercus</i>	—	—	ns
		<i>Castanea</i> height RGR	—	ns	*
		<i>Quercus</i> height RGR	—	ns	ns
		<i>Quercus</i> diameter RGR; <i>Prunus</i> density	ns	—	ns
		<i>Acer</i> density	ns	+	ns
		<i>Ulmus</i> density	ns	ns	*
		density of each of 5 other taxa in natural regeneration	ns	ns	ns
All woody <sup>1</sup>					
22		Cover	ns	ns	ns
24		shrub volume	ns	ns	ns
		density of seedlings < 30 cm	+	—	ns
		density of seedlings 30–90 cm	—	ns	ns
		density of seedlings > 90 cm	ns	ns	*#
All					
2 <sup>2</sup>		richness; abundance	ns	ns	ns
		large woody seedling richness; abundance	—	ns	ns
		<i>Quercus</i> regeneration	ns	ns	*# <sup>5</sup>
		<i>Acer</i> regeneration	ns	ns	ns
B. All or herbaceous native richness or cover					
<i>Microstegium vimineum</i>					
17		cover of herbaceous species	ns	ns	ns
1		cover of all plants	ns	ns	ns
11		biomass of herbaceous species	ns	—	ns
<i>Alliaria petiolata</i>					
21		Survival of <i>Aster</i> ; <i>Carex</i> ; <i>Geranium</i>	ns	ns	ns

**Table 1** continued

Invasive Plant	Reference	Response	Deer	Invasive	D × IP
		<i>Uvularia</i> survival	—	—	ns
		<i>Aster</i> growth	ns	ns	*#
		<i>Carex</i> growth; <i>Geranium</i> growth	+	—	ns
		<i>Uvularia</i> growth	—	+	ns
	3	large <i>Trillium</i> survival	+	ns	*
		small <i>Trillium</i> survival	+	ns	*
		<i>Trillium</i> growth	—	ns	ns
	8	richness of all plants; richness of planted spp.; flowering of <i>Elymus</i>	ns	ns	ns
		cover of all plants; cover of planted spp.; flowering of <i>Cryptotaenia</i> ; <i>Ageratina</i> ; <i>Scutellaria</i>	—	ns	ns
<i>Lonicera japonica</i>					
	12	RGR of <i>Trillium</i> leaf area	—	ns	ns
<i>Lonicera maackii</i>					
	4	richness of herbaceous species; abundance of summer perennials; <i>Carex</i> abundance	ns	ns	ns
		abundance of spring perennials; <i>Maianthemum</i> leaf number	—	—	*
		abundance of annuals	—	—	ns
		abundance of graminoids	+	ns	ns
		<i>Viola</i> abundance	—	ns	ns
		<i>Sanicula</i> abundance	ns	—	ns
	19	<i>Sanicula</i> flowering	—	ns	ns
	10	richness of all native plants, cover of annuals	+	ns	ns
		cover of graminoids	ns	—	ns
		cover of all native plants; ferns; summer perennials; moss; biennials	ns	ns	ns
		cover of spring perennials; vines	ns	ns	*#
All woody <sup>1</sup>					
	23	cover of tall perennials	ns	—	*
		cover of graminoids	+	—	ns
		cover of short perennials; annuals + biennials	ns	—	ns
<i>Alliaria</i> , <i>Microstegium</i> , <i>Berberis</i>					
	6	<i>Agrimonia</i> survival	ns	+ <sup>6</sup>	ns
	6	<i>Agrimonia</i> growth; <i>Aristolochia</i> survival; <i>Carex</i> survival	ns	+	ns
	6	<i>Agrimonia</i> reproduction	—	ns	ns
	6	<i>Aristolochia</i> growth	+ <sup>6</sup>	ns	ns
	7	<i>Aristolochia</i> recruitment	ns	+ <sup>7</sup>	ns
	6	<i>Carex</i> growth, <i>Carex</i> reproduction; <i>Trillium</i> growth	ns	ns	ns
	7	<i>Trillium</i> emergence	—	+ <sup>7</sup>	ns
	6, 7	<i>Trillium</i> survival	—	+ <sup>6</sup>	ns
All					
	2 <sup>2</sup>	richness of herbaceous species	ns	ns	*#
C. Animal, soil, and ecosystem function responses					
<i>Alliaria petiolata</i>					
	3	C:N ratio	ns	—	ns
		pH; P; NH <sub>4</sub> N	ns	ns	ns

**Table 1** continued

Invasive Plant	Reference	Response	Deer	Invasive	D × IP
<i>Lonicera maackii</i>					
5		litter arthropod abundance; Araneae abundance	–	ns	ns
		Acari abundance	ns	ns	*#
		litter depth; arthropod diversity; abundance of Coleoptera; Collembola; Hymenoptera	ns	ns	ns
15		ant abundance	ns	ns	*
		ant richness	–	+	ns
14		non-native earthworm density	+	ns	ns
		litter mass	–	ns	ns
		non-native earthworm biomass	ns	ns	*
16		litter decomposition	+	ns	ns
		litter N retention	ns	ns	*
10		bare ground	+	ns	ns
18		soil N	ns	ns	ns
25		pH; enzymes of C cycling	–	ns	ns
		soil moisture	ns	ns	*
All invasive plants					
9 <sup>3</sup>		non-native earthworm presence	+	n/a	

Only statistically significant ( $p < 0.05$ ) effects of deer and invasive plants are scored, – indicates negative effect of deer (positive effect of exclusion) or invasive plants (positive effect of removal), + positive effect of deer or invasive plants; otherwise effect is listed as not significant (ns). The D\*IP column indicates whether the deer (D) \* invasive plant (IP) interaction was significant. A # in this column indicates responses where neither main effect was significant, but the interaction reflected higher values for deer exclusion (D-) and invasive plant removal (IP-) than for the other three treatments. All of the studies experimentally manipulated both deer and invasive plants, except #9 compared sites with different levels of deer browse and IP richness, #20 compared a set of sites before vs after deer culling, and #6 and #7 involved experimental manipulation of deer (see Supplemental Table for more complete description of study designs and measured responses in each study). RGR = relative growth rate

<sup>1</sup>Mostly *Berberis thunbergii*

<sup>2</sup>*Microstegium*, *Alliaria*, *Lonicera japonica*, others

<sup>3</sup>Species not specified

<sup>4</sup>Responses in part A refer to all woody species in the understory except where specified

<sup>5</sup>Only where invasives were initially low

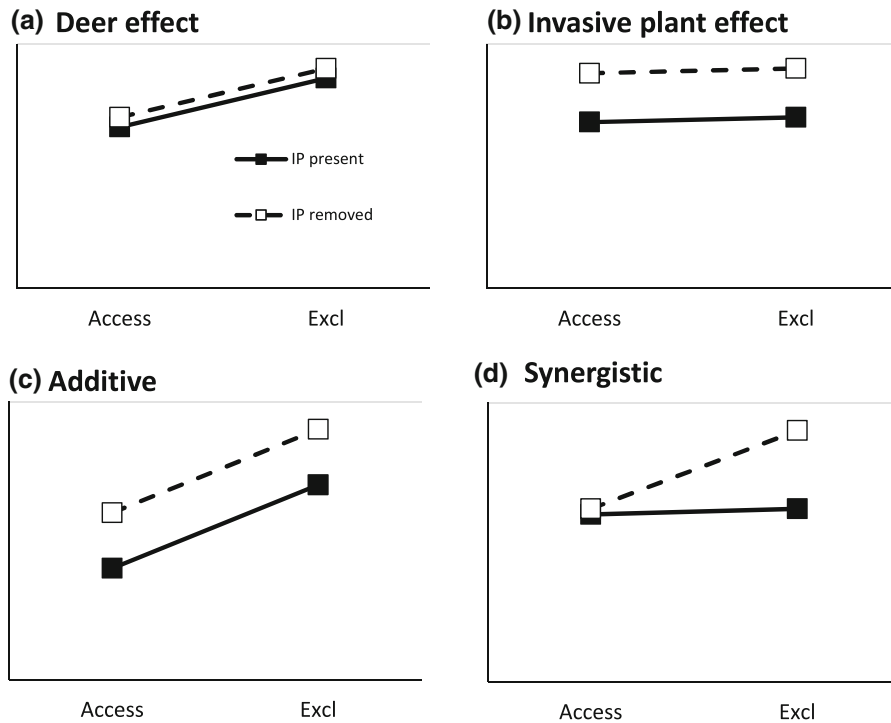
<sup>6</sup>When slugs were present; effect was negative where slugs were excluded

<sup>7</sup>Only in *Microstegium* sites

2019; Fisichelli and Miller 2018). Mahon and Crist (2019) also studied effects of an invasive plant where there was no significant main effect but a significant interaction (Table 1c). Two studies investigating effects on native animals evaluated nine response variables (included with ‘animal, soil, and ecosystem responses’ in Fig. 2). Deer had negative effects in three cases (with one of these, richness of ants in Ohio,

showing positive invasive effects, but no interaction). Two cases showed significant deer X invasive plant interactions.

Seven studies investigated soil and/or ecosystem processes (Table 1c). Of 13 response variables, five were affected only by deer. All these responses were either negative (3) or involved increases in variables (bare ground and litter decomposition) generally



**Fig. 1** Interaction plots illustrating stylized, common patterns of a response variable (such as those in Table 1) in deer (D) access (open) plot and deer exclosures with invasive plants (IP) present or removed. In **a**, there is a negative effect of deer, but no significant IP effect or D\*IP interaction. In **b**, there is a negative effect of invasive plants, but no significant deer effect or D\*IP interaction. In **c** both main effects are negative, but there is no significant interaction. When the D\*IP interaction is

significant, there are many different patterns based on the direction of main effects and sign of the interaction, but the most common pattern found in this review is shown in **d**: the main effects are not significant but the interaction reflects a synergy between D exclosure and IP removal, such that the response variable has its highest value in plots without deer and invasives and similar values in the other three treatment combinations

considered to be undesirable as they facilitate invasive plant establishment (e.g., Bartuszevige et al. 2007; Oswalt and Oswalt 2007; Nuzzo et al. 2009; Kuhman et al. 2013) (Fig. 2a). In contrast, invasive plants depressed just one of 13 response variables (soil C:N in Pennsylvania). Two showed no main effect but significant deer X invasive plant interactions.

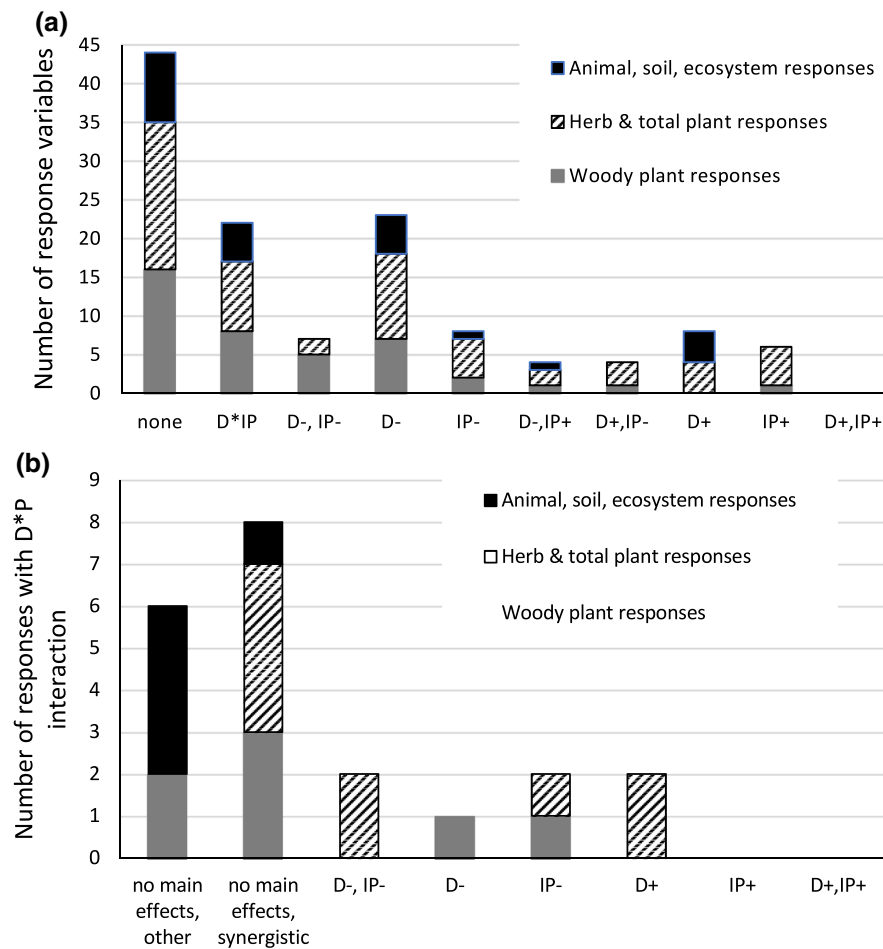
### Interactions

We were surprised to find just 21 of the 125 response variables (17%) showing significant deer X invasive plant interactions (Fig. 2a). Of these, the most frequent pattern showed no main effect of deer or invasive plants, but removing both deer and invasive plants generated higher responses than the other 3 treatment combinations ( $n = 8$  indicated by # in the last column of Table 1, Figs. 1d, 2b). This synergistic effect of removing both deer and invasive plants (or

sub-additive effect of adding both deer and invasive plants) occurred both among woody plants (3 of the 8 response variables showing interactions) and among herbaceous plants (4 of 9). The other 14 responses showing significant interactions were diverse with no more than two showing the same combination of main effects and interactions (Fig. 2b).

### Conclusions from literature review

Only a limited number of studies to date have experimentally investigated the separate and combined effects of deer and invasive plants in eastern North American forests. Most of these are limited to just three invasive species, revealing a need for studies investigating other species (e.g., genera with commonly introduced forest species: *Euonymus*, *Elaeagnus*, *Ligustrum*, and *Rosa* species). Our ‘vote-counting’ analysis reveals that deleterious impacts of



**Fig. 2** The number of response variables in the literature review showing main effects of deer (D− : negative effect, D+ : positive effect), invasive plants (IP− , IP+), and interactions of these main effects. **a** separates all response variables based on main effects; ‘none’ indicates responses with no significant main effects or interaction, D\*P indicates responses where the deer \* invasive plant interaction was significant, these include responses with and without significant D and/or IP effects; these are examined in **b**. **b** For only those response variables with a

significant interaction of deer (D) and invasive plant (IP) effects, response variables are stratified by significance of main effects. Responses with no significant effect main effects were separated into ‘synergistic,’ where the response was greatest for the treatment with deer excluded and invasive plants removed (D− , IP−) (Fig. 1d) with the other three treatment combinations similar, and ‘other,’ comprised of all other patterns of responses

deer on native plant species and environmental conditions are more prevalent than impacts of non-native plants that are considered invasive. These negative deer effects exist for all three sets of responses that we considered, on woody plants, herbaceous plants, and animal/soil/ecosystem functions. Deer and invasive plant effects interacted less frequently (17% of response variables) than we expected. Among the interactions that did occur, the most frequent pattern was a synergistic effect wherein removing both deer and invasive plants had greater

positive effects than expected from removing either alone. To more confidently reach a more generalizable set of conclusions a broader base of studies is needed; when those are available a quantitative meta-analysis of deer and invasive plant impacts would be compelling.





**Fig. 3** Deer exclosure located in Cades Cove, Great Smoky Mountains National Park, TN, USA. Coverage of invasive Japanese stiltgrass (*Microstegium vimineum*) has declined dramatically within exclosures over time, but remains a near

monodominant green carpet outside of the fences. Note the abrupt decline in this carpet at the fence line where it meets the dense growth of woody plants within the exclosure. Photo credit: Christopher Webster

### Insights from a broader literature review on deer and/or invasive plant impacts

#### Deer effects are more prevalent than invasive plant effects

Because relatively few studies simultaneously investigated impacts of deer and invasive plants, we also considered the far larger literature on their separate effects. The smaller subset of studies reviewed above detected more and larger impacts from deer than invasive plants on both woody and herbaceous plants and on animal/soil/ecosystem responses. We know that deer are now abundant enough to represent a widespread stressor across most eastern forests. Virtually no forests in Northeastern or Midwestern North America, outside of major cities, remain deer-free. Although deer clearly vary in abundance over areas that differ in local site productivity, climate, agricultural use, or other factors, abundant deer and their impacts now reach even remote and relatively undisturbed habitats. This realization has led many to investigate the almost universally negative impacts that deer have on woody plants including shrubs and the tree seedlings and saplings necessary for forest

regeneration (e.g., Habeck and Schultz 2015; Bradshaw and Waller 2016; Fig. 3). Interestingly, in the studies reviewed above, deer almost always depress the growth and/or survival of woody plants, yet deer enhanced the growth/survival of herbaceous species in about a third of significant responses (9 vs. 17 of 60 response variables). These differences by growth habit probably reflect both the selectivity of deer herbivory and the capacity for deer browsing on saplings and shrubs to enhance light conditions in the herb layer (Heberling et al. 2017). Deer consistently suppress some herb functional groups and species, as with members of the lily family in general, or *Trillium* spp. (Anderson 1994; Nuzzo et al. 2017). In contrast, deer appear to enhance the growth of many grasses and sedges (Wiegmann and Waller 2006; Rooney 2009). Deer impacts (both consumptive and non-consumptive) on non-woody plant demography are documented, but may be greatly underestimated (Knight et al. 2009a; McGraw and Furedi 2005; Heckel et al. 2010; Dávalos et al. 2014; Bialic-Murphy et al. 2019, 2020). Non-consumptive effects of high deer populations result from changes in soil properties (e.g., soil compaction by trampling, local enrichment by excretion—Heckel et al. 2010) or changes in plant

community dynamics via positive feedbacks with other agents of change, including facilitation of negative soil feedback mechanisms (Kardol et al. 2014) or non-native earthworms (Dávalos et al. 2015; Cope and Burns 2019). Furthermore, evidence from the substantial literature on the direct effects of high deer populations suggest they are true ecosystem engineers, contributing to a cascade of negative trophic and abiotic consequences.

In contrast, despite the continuing growth and spread of invasive plant populations, these still mostly occur locally in patches within forests. Shaded forests may also be intrinsically less prone to invasion than more open habitats, given that invasive plants often rely on rapid growth and resource acquisition to invade habitats and displace native species. However, this assumption is not always true, as many invasive plants are shade tolerant, presenting especially difficult management challenges (Martin et al. 2009). Although plant invasions in eastern forests correlate with declines in native plants, both phenomena likely reflect responses to disturbances of various kinds (Hobbs and Huenneke 1992; Eschtruth and Battles 2009, 2014; Hoven et al. 2017). This conclusion would make plant invaders more ‘passengers’ than drivers of ecological change (MacDougall and Turkington 2005). Even as passengers, invasive plants do compete directly with native plants in eastern forests via both resource competition (e.g., Orrock et al. 2015 and citations in Gioria and Osborne 2014) and allelopathy (e.g., Warren et al. 2017). They also compete indirectly, e.g., by disrupting plant-microbial symbioses (e.g., Hale et al. 2016) or by increasing herbivory on palatable native species (e.g., via neighbor contrast susceptibility (Alm Bergvahl et al. 2006) or apparent competition (Martinod and Gorchov 2017)).

Legacy effects of deer are difficult to reverse while those of invasive plants are less well known

Legacy effects of high deer densities on canopy trees and herb layers persist for decades or longer even if deer decline in density, with effects percolating through entire food webs (Wardle and Bardgett 2004). Tanentzap et al. (2012) identified reasons for this slow recovery including the slow growth of forest plants and the depletion of seed sources. These processes can allow alternate vegetation types to

form, such as the ‘recalcitrant layer’ of hay-scented fern (*Dennstaedtia punctilobula*) in Pennsylvania forests (Royo and Carson 2006). Most stands in northern hardwood forests are older than 40 years (Shifley et al. 2014), meaning the canopy trees established before deer populations increased dramatically (McCabe and McCabe 1997). Today’s regenerating tree seedlings, and saplings establishing in gaps following tree falls or harvest openings must run a gauntlet of hungry deer. Deer often repeatedly harvest seedlings of maple (*Acer*), birch (*Betula*), oak (*Quercus*), or other trees, and consume acorns and other tree seeds, reducing forest tree recruitment and diversity. We know from field studies and large-scale field experiments that eastern hemlock, northern white cedar, yellow birch, and other slow-growing trees are particularly vulnerable to repeated deer browsing (Côté et al. 2004; Alverson et al. 2019). One study maintained four large (12.9–25.8 ha) fenced plots for 10 years to assess the impacts of varying deer densities in Pennsylvania after clearcutting (Nuttall et al. 2011). Greater deer density resulted in lower tree diversity in these regenerating forests. Areas with high deer densities were increasingly dominated by black cherry (*Prunus serotina*), lacked pin cherry (*Prunus pensylvanica*), and had five times higher fern cover, but lower angiosperm species richness. Structural influences of deer on woody diversity extended through the entire food web and persisted long after the experiment was terminated, leading to lower insect diversity, caterpillar abundance, and bird diversity and abundance (Nuttall et al. 2011). These impacts seem likely to persist until future harvest or natural tree mortality reset successional trajectories.

Deer also have lasting effects on forest herbs. In the Apostle Islands in Lake Superior, densities of *Clintonia borealis*, a species sensitive to deer herbivory, declined in response to estimated deer densities from 30 to 40 years ago even more strongly than to deer densities from recent years (Balgooen and Waller 1995). Excluding deer for five years at a site in Pennsylvania allowed the herb community to recover relative to control plots, yet total herb density and especially the density of species preferred by deer recovered far more slowly, or not at all if chronically browsed to near extirpation (Pendegast et al. 2016). Similarly, in a six-year study in northern Pennsylvania where deer abundance was reduced via hunting, browse-sensitive herbaceous species increased in

height and abundance, but species richness and dominance were unchanged (Royo et al. 2010). Eight years of excluding deer from sites in Great Smoky National Park allowed some species to recover, but only those able to persist during decades of high deer density (Webster et al. 2005). In contrast, after deer were reduced 90% at the Fermi Lab in Illinois, it took only a few years for species richness, cover, height, and the flowering of palatable prairie trillium (*Trillium recurvatum*) to increase (Nuzzo et al. 2017). This quicker recovery may reflect higher light levels in this more open environment or the fact that deer had only recently increased to high levels, allowing managers to respond quickly to avoid a persistent legacy effect. In contrast, deer legacy effects on plant community composition also persisted at West Point, New York over the entire six-year study period, with little changes in plant community composition or abundance inside fenced areas, although individuals of certain plant species responded with increased growth and subsequent reproduction (Nuzzo et al. 2017). Furthermore, the persistent effect of high deer populations led to > 90% declines in many orchids in Maryland (Knapp and Wiegand 2014) and to dramatic abundance declines in forest macrolepidoptera specialized on understory species in New Jersey (Schweitzer et al. 2014).

In contrast to the long-term impacts of high deer density, reducing invasive plant abundance may allow rapid recovery of at least some native plant species, if the invasion was recent and especially if the invader is short-lived or adapted to disturbance. Although native plants often grow back rapidly after hand-pulling or spraying of invasive plants, the natives rarely fully recover (Kettenring and Adams 2011). In addition, eradicating non-native plant species is usually impossible except for small local populations (Rejmánek and Pitcain 2002; Quirion et al. 2018). In many cases, other invasive plants replace the targeted invasive species (Seastedt et al. 2008; Kuebbing and Nuñez 2015). These results suggest that invasive plants benefit from various ongoing types of ecological change, such as in land-use change, ungulate herbivory, non-native earthworm invasions, and modified soil microbial communities (Kardol et al. 2007, 2014; van der Putten et al. 2013; Meisner et al. 2014).

Removing invasive plants (such as common buckthorn, *Rhamnus cathartica*, or garlic mustard, *Alliaria petiolata*) can reduce the abundance of non-native

earthworms (Heneghan et al. 2007; Stinson et al. 2018) and their negative impacts on native plants and litter food webs (Maerz et al. 2009; Nuzzo et al. 2009; Dávalos et al. 2015a). However, in some cases, introduced plants may act as protection for certain native plant species. Just as native shrubs can provide shelter from ungulate browsing in Europe (e.g., Harmer et al. 2010) and North America (e.g., Borgmann et al. 1999; Champagne, et al. 2018), Amur honeysuckle (*Lonicera maackii*) shrubs increased survival and leaf number of sugar maple (*Acer saccharum*) seedlings, although not those of white oak (*Quercus alba*) or shagbark hickory (*Carya ovata*) (Peebles-Spencer and Gorchov 2017). Removing these invasive shrubs while deer populations remain high could increase browse pressure on sensitive native species.

The abundance and persistence of introduced plant species may decline slowly after their initial increase in eastern forests (Warren et al. 2019), as evidenced by monitoring and demographic studies of garlic mustard (Blossey et al. 2020). The mechanisms behind such declines are not yet well understood. Increasing biotic resistance as species accumulate natural enemies, evolutionary responses of resident native species, and/or negative soil feedback due to changes in microbial communities may all be involved (Lankau et al. 2009; Diez et al. 2010; Callaway et al. 2013; Blossey et al. 2020). The ultimate goal of managing invasive plant species is to protect and recover populations of native species. Whether other invasive plant species exhibit similar declines needs more research effort. Deer population control, along with halting early plant invasions, should be prioritized.

Invasions of some plant species are a consequence of high deer populations

Non-native species such as garlic mustard, Japanese barberry (*Berberis thunbergii*), and Japanese stiltgrass (*Microstegium vimineum*) often thrive in the presence of high deer populations (Eschtruth and Battles 2009; Knight et al. 2009a, b). Reducing deer density can reduce the abundance of all three of these major plant invaders (Fig. 3) plus other invasive plants including hairy bittercress (*Cardamine hirsuta*), common chickweed (*Stellaria media*), and wineberry (*Rubus phoenicolasius*) (Webster et al. 2005; Abrams and Johnson 2012; Dávalos et al. 2015b; Shen et al. 2016; Bourg



et al. 2017). One demographic study of garlic mustard suggests this species would go locally extinct in the absence of deer (Kalisz et al. 2014). These findings are buttressed by a meta-analysis of 23 deer enclosure experiments that demonstrated how consistently deer reduce native plant abundance, species richness, and diversity, while increasing the proportion of plant richness and abundance comprised of non-native species, and the cover of three invasives: garlic mustard, Japanese stiltgrass, and perilla (*Perilla frutescens*) (Averill et al. 2018).

How deer increase the abundance of introduced species is not yet clear, but may include consumptive as well as indirect effects. Deer avoid garlic mustard, stiltgrass, and barberry in preference trials, but readily consume Oriental bittersweet (*Celastrus orbiculatus*), European privet (*Ligustrum vulgare*), and Morrow's honeysuckle (*Lonicera morrowii*) (Averill et al. 2016). We also find the conundrum that while some invasive shrubs are widespread and abundant in areas with many deer, excluding deer by fencing can increase abundance of species palatable to deer including multiflora rose (*Rosa multiflora*), Amur and Japanese honeysuckle (*Lonicera japonica*), burning bush (*Euonymus alatus*), and Indian strawberry (*Duchesnea indica*) (Ward et al. 2013; Shen et al. 2016; Averill et al. 2018; Peebles-Spencer et al. 2018; Haffey and Gorchov 2019). These findings highlight the importance of isolating factors that may facilitate initial establishment of palatable invasive species from those that determine abundance and spread after establishment. For example, deer not only reduce native plant diversity and cover but also amplify invasive earthworm populations (Dávalos et al. 2015c; Mahon and Crist 2019). This increase in earthworms can alter litter and soil characteristics in ways that facilitate plant invasions (Nuzzo et al. 2009; Kardol et al. 2014). Deer thus play a central role in determining not only forest regeneration but also forest biodiversity and invasion dynamics (Dávalos et al. 2015a, b; Fisichelli and Miller 2018).

#### Research needs

Research investigating how deer and invasive plants affect community composition, successional dynamics, and food webs should embrace a more holistic, multiple stressor framework to avoid making erroneous conclusions. For example, building fences to

restrict deer access will not only reduce direct herbivory, but also deer excreta, trampling, and soil compaction, and alter dispersal of plant seeds (and possibly earthworm cocoons). Investigators should recognize the potential for associated changes in biota and processes to ensure that they do not make inappropriate recommendations to land managers. Large-scale, ecosystem-level studies involving researchers from a variety of backgrounds would be especially valuable. After further studies involving more taxa have been carried out, we should, as noted above, be able to conduct a more comprehensive and quantitative meta-analysis of deer and invasive plant interactions.

#### Conclusions and management recommendations

Although both invasive plants and abundant white-tailed deer often have negative effects on native biota and ecosystem function, we found that deer impacts are strong, pervasive, and usually more severe, long-lasting, and difficult to reverse than impacts of invasive plants. Additionally, deer promote invasions of non-native earthworms and some non-native plants while these invasive populations decline as deer densities are reduced. Removing established palatable invasive plants without first reducing deer density thus risks increasing browse pressure on native plants.

These findings suggest that reducing deer browse pressure should generally take precedence over reducing invasive plant populations. This recommendation (also voiced by Waller and Maas 2013) contrasts with the common practice of first controlling invasive plants, because forest and land managers lack authority to manage local deer populations (or may assume that invasive plants pose a greater threat to the habitats they oversee). We also note, however, that in areas with established populations of palatable invasive woody shrubs or vines, fencing or culling may be ineffective without simultaneously removing the invasive plant species. The legacy effects of deer make it important to include active restoration plans (e.g., reseeding and replanting) in cases where depauperate seed banks or a lack of nearby propagule sources inhibit natural regeneration. Such efforts may still fail if deer populations are not adequately reduced.

## Toward more effective modes of deer management and land stewardship

In this review, we sought to highlight the many, often complex, interactions that occur among high deer densities, invasive plants, and other stressors to native species and habitats. To address these interactions effectively, it will be necessary to adopt a more holistic approach to managing forests and landscapes as the integrated ecosystems they are. The evidence presented makes clear that this holistic approach will often require us to reduce deer populations. Although this point has been recognized for many years (e.g., Leopold et al. 1947; Alverson et al. 1988), our inability to adopt a broad ecological perspective resulting in integrated and effective approaches to steward habitats and species has resulted in understories depleted of native wildflowers (Waller 2014), accelerated invasions of non-native earthworms and plants (Blossey and Gorchov 2017), and led to the widespread failures of forest tree regeneration throughout central and eastern North America (McWilliams et al. 2018). We recognize management of deer is a complex issue with components that differ dramatically from the management of exotic plant species; widespread consensus exists that invasive exotic plants should be removed where possible, whereas deer are a native species with widespread support among some constituencies. However, to better meet our public trust responsibilities to protect natural resources and the long-term interests of both humans and wildlife, scientists must begin to work more closely with state and federal management agencies and elected officials to redesign and reform deer management (Hare and Blossey 2014).

Despite this clear management need and substantial increases in deer densities across most of our region over the past half-century, we see little evidence that wildlife managers have significantly modified and adapted their approaches to address the substantial impacts of high deer populations and some states continue outdated management actions to increase deer herd sizes. Management agencies continue to rely on recreational hunting as a management tool despite growing recognition that such efforts are rarely effective (DeNicola et al. 1997; DeNicola and Williams 2008; DeCalesta and Eckley 2019). Sterilization or birth control efforts are expensive and similarly show low promise for reducing impacts in free-

ranging deer herds (Merrill et al. 2006; Boulanger and Curtis 2016; Blossey et al. 2019). This failure to adapt deer management strategies continues to allow further substantial erosion of biodiversity (Côté et al. 2004; Wardle and Bardgett 2004; Nuttle et al. 2011; Knapp and Wiegand 2014). Dense deer herds also contribute to the recent rapid spread of chronic wasting disease (CWD) and other diseases of wildlife in the eastern and midwestern U.S. (e.g., heart and brain parasites—Escobar et al. 2020). Recent increases in Lyme disease, Ehrlichiosis and other tick-borne human diseases also appear to be related to high deer populations (Wiznia et al. 2013; Telford 2017). Reducing deer densities could thus simultaneously address concerns over ecosystem, wildlife, and human health.

The need to reduce deer densities has led to calls for further incentives to shoot females (e.g., “Earn-a-Buck” programs) and increase how many deer are taken. This extends even to regulated market hunting (Vercauteren et al. 2011; McShea 2012; Williams et al. 2013). At a minimum, a renewed effort is required to find creative and novel political solutions that incorporate decision-making processes that consider more than hunter interests and that take collective stewardship and responsibilities to the public seriously. Where feasible, expanding legal protection to predators of deer, such as wolves (*Canis lupus*) and mountain lions (*Felis concolor*) so they could recolonize more of their traditional ranges could shift deer behavior and reduce deer impacts (Crête 1999). If predators selectively prey on infected individuals, predators could also help to control the incidence of CWD and other wildlife diseases (Robbins 2020). Conserving biodiversity and protecting human and wildlife health should become high priorities when setting deer population targets. The future of our forests, the biodiversity within them, and our ability to mitigate climate change through carbon offsets from forest regeneration (Bastin et al. 2019), will require that we are willing and able to make difficult and controversial decisions. The status quo is unacceptable.

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