

# MAX GARFINKLE

NATURAL RESOURCE OFFICER PHILIPSTOWN, NY  
238 Main Street  
Cold Spring, NY 10516  
(845) 265-3929

## Wetland Permit Application

### MEMO TO APPLICANT

1. Use this form to apply for a Wetlands Permit as required by the Freshwater Wetlands and Watercourses Law of the Town of Philipstown, Chapter 93 of the code of the Town of Philipstown.
2. Fee: The application fee varies according to the nature of the activity. The fee schedule is attached. The full fee is required at the time you file the application.
3. Number of Copies: You must submit (9) copies and one PDF of the application form and all supporting documents. These (9) copies are in addition to any copies you must submit to any other agency to which you are making a separate application for the same activity. (Example: Application to the Planning Board for subdivision or site plan approval) application to the Zoning Board of Appeals for a variance or Special Use Permit.)
4. Supporting Documentation: See the application form for a list.
5. Return the (9) copies and (1) PDF of the application, supporting documentation, and the full fee by check made out to Town of Philipstown and dropped off at the Building Department. Applications should be submitted no later than 4pm on the last Tuesday of every month.
6. The Wetlands Inspector will review the application for completeness and make a site visit. After the site visit, he will refer your application to the Conservation Board, which will place your application on the agenda of its next meeting. After they have had a chance to also inspect the property. You will be notified of the time and place of that meeting. Your attendance is not required, but can be helpful.
7. If the CB also finds that you have provided enough information to allow a decision, it will determine whether or not to recommend granting a permit.
8. If you are applying for a Wetlands permit in conjunction with an application to the Planning Board, Zoning Board of Appeals or Town Board, you will be notified by that board of any difference in procedure.

### LIST OF REGULATED ACTIVITIES (~ 93-5, Code of the Town of Philipstown)

The law regulates most activities within 100 feet of a wetland or watercourse including but not limited to those listed below.

- A. Dredging or excavation; grading and removal of soil, mud, sand, gravel, silt, earth material and other aggregate, either directly or indirectly.
- B. Dumping or deposition of soil, stones, sand, gravel, mud, rubbish, material, matter or fill of any kind, either directly or indirectly.
- C. Construction or installation of any structure or facility, including, but not limited to, roads, buildings, driveways, parking facilities, swimming pools, tennis courts, bridges, pipes or conduits; installation of sewage disposal systems or sewer outcall, drilling of wells, placing of other obstructions, or driving of pilings.
- D. Alteration or diversion of any flow of watercourse or wetland. This includes, but is not limited to, docks, dams, pilings and bridges.
- E. Use of chemicals, dyes, fertilizers, animal waste, herbicides, pesticides, deicing materials or similar materials.
- F. Influent of high thermal content capable of causing harmful ecological effects unless water is properly treated in recycling, including, but not limited to, groundwater heat pumps for other than one-family dwellings.
- G. Clear-cutting or other vegetation removal affecting surface water runoff.
- H. Establishment of trails for such purposes as, but not limited to, walking, skiing, horseback riding, bicycling, motorcycling, snowmobiling and off-road vehicle travel.
- I. Installation of service lines, cable conduits or utilities.

- E. Use of chemicals, dyes, fertilizers, animal waste, herbicides, pesticides, deicing materials or similar materials.
- F. Influent of high thermal content capable of causing harmful ecological effects unless water is properly treated in recycling, including, but not limited to, groundwater heat pumps for other than one-family dwellings.
- G. Clear-cutting or other vegetation removal affecting surface water runoff.
- H. Establishment of trails for such purposes as, but not limited to, walking, skiing, horseback riding, bicycling, motorcycling, snowmobiling and off-road vehicle travel.
- I. Installation of service lines, cable conduits or utilities.
- J. Introduction of any form of pollution, by means including, but not limited to, the installation of a septic system, running of a sewer or storm water outfall, or discharge of sewage treatment or other solid waste into or so as to drain into a controlled area.
- K. Installation of drainage or water supply pipes or wells.
- L. Installation of dry wells, retention basins, filters, open swales or pond

#### WETLANDS PERMIT FEE SCHEDULE

- M. Wetland and watercourse determination by the Wetlands Inspector, regarding whether activity will be in a controlled area and describing permit application requirements: \$180.00
- N. Dwelling unit and accessory buildings and structures (including well and septic system if constructed contemporaneously with dwelling unit), or other structures (for example, stream crossing), in or containing a controlled area or portion thereof on a residential lot: \$500.00. Plus either a \$500.00 or \$1,000.00 escrow fee that may be refundable.
- O. Dredging or removal of soil, mud, sand, gravel, silt, or earth material and other aggregate from a controlled area, or dumping or deposition of any material in a controlled area when such activity is not associated with any of the other activities specified in this schedule and is not an activity of minor significance: \$500.00 Plus either a \$500.00 or \$1,000.00 escrow fee which may be refundable.
- P. Residential subdivision: \$500.00 for each lot in which a regulated activity is proposed in a controlled area. Plus 1,000.00 escrow fee which may be refundable.
- Q. Road, pipeline or in-ground utility: \$1,000.00 for the first 500 linear feet or fraction thereof in a controlled area, and \$1.50 for every linear foot over 500 feet in a controlled area. Plus 1,000.00 escrow fee, which may be refundable.
- R. Regulated activities not covered in Subsection B, C and D of this fee schedule: \$375.00 for the first affected acre of controlled area or fraction thereof, plus \$260.00 for each additional affected acre of controlled area or fraction thereof. Plus a 1,000.00 escrow fee, which may be refundable.
- S. Activities of minor significance, as defined in Section 93-7 of the Wetlands Law: \$125.00. Above fees are waived pursuant to Section 93-7.

TOWN OF PHILIPSTOWN  
PUTNAM COUNTY, NEW YORK

238 Main Street  
Cold Spring, NY, 10516  
(845) 265-5202

**APPLICATION FOR WETLANDS PERMIT**

**Note to Applicant:**

Submit the completed application to the appropriate permitting authority. The application for Wetlands Permit should be submitted simultaneously with any related application (e.g., subdivision approval, site plan approval, Special Use Permit, etc.), being made to the permitting authority.

(Office Use Only)

Application # \_\_\_\_\_ Permitting Authority \_\_\_\_\_  
Received by: \_\_\_\_\_  
Date \_\_\_\_\_ Conservation Board \_\_\_\_\_  
Fee \_\_\_\_\_ Wetlands Inspector \_\_\_\_\_

Pursuant to Chapter 93 of the Code of the Town of Philipstown, entitled "Freshwater Wetlands and Watercourse Law of the Town of Philipstown" (Wetlands Law), the undersigned hereby applies for a Wetlands Permit to conduct a regulated activity in a controlled area.

1. **Owner:** Name: 711 La Shinju LLC

Address: 11 La Shinju, Cold Spring, NY 10516

Telephone: 626-840-2589

If Corporation, give names of officers:

\_\_\_\_\_  
\_\_\_\_\_

Mailing Address: (same as above)

**2. Name of Agent**

*(Applicant must be owner of the land. The Application may be managed an authorized agent of such person.)*

Mailing Address: One Nature LLC 178 Main Street, Beacon, NY 12508

Telephone: Blair Patterson 214-636-7017

**3. Location of Proposed Activity:**

Approximately 5000 linear feet inside property boundary

Tax Map #: 38.-2-50.51; 38.-2-50.51

Acreage of Controlled Area Affected: 20 acres

Square footage of soil disturbed by the entire project: 85 square feet in regulated zone

**4. Type of Activity: (See list of regulated activities)**

Installation of a standard black, 8' deer fence.

**5. Other permit(s) required and agency or agencies responsible for granting such permits such as but not limited to P.C.B.O.H, N.Y.D.E.C, Army Core of Engineers, EPA, DOT, Building Dept. Planning Board, and Z.B.A.**

None

**6. Each copy of this application shall be accompanied by:**

- a. A detailed description of the proposed activity and a comparison of the activity to the criteria for approval specified in §93-8 of the Wetlands Law. (See below)
- b. A completed short form environmental assessment form (*included in the application folder*)
- c. A map prepared by a licensed surveyor, landscape architect or engineer showing:
  - 1. The controlled area(s) wetland buffer zone 100 feet from the edge of any wetlands, lakes, ponds or streams on the site;
  - 2. Any wetland or watercourse therein and the location thereof;
  - 3. The location, extent, and nature of the proposed activity.
- D. The names of claimants of water rights in the wetland or watercourse of whom the applicant has record notice and the names and addresses of all owners of record of properties abutting and directly across from the proposed activity as shown on the latest tax record.

(Note: Any map, plat or plan showing the above information that is required to be submitted for any other permit or approval in connection with the regulated activity, and that is acceptable to the Permitting Authority, may be used.)

Date: 2-16-22

Signature of Applicant:



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## Check List for a Complete Wetlands Permit Application

\*\*\*\*All supporting materials must be submitted to the Conservation Board/Wetland Inspector two weeks prior to the scheduled meeting date to allow to distribution to members before the meeting.

Ten (10) sets of all material as follows:

Application Form

Environmental Assessment Form (short form), unless other agencies have requested the long form in which case that should be presented.

A plan of your site drawn by a design professional, such as an engineer, architect or land surveyor. All plans must show: wetlands delineation boundaries, 100' buffer zones from wetlands and watercourses, location of access route for construction activities, the location of any well or sewage or wastewater disposal system and, in most cases, the topography of the site. Site plans must include all proposed work within the 100 'foot buffer zone and be full sized for easy reading by CB members

Copies of correspondence from all other agencies including, but not limited to; DEC, DOT, EPA, PCBOH, ACOE or other Town of Philipstown agencies; Town Board, Planning Board, ZBA, Building Dept.

A written outline of the proposed activity, along with a construction scenario that should include specific items such as the estimated quantities of material excavated or the amount of fill required and the total square footage of soil to be disturbed.

Names and addresses of all owners of record of properties abutting and directly across from the proposed activity as shown on the latest tax record as well as the names of claimants of water rights in the wetland or watercourse of whom the applicant has record notice.

A detailed description of the proposed activity and a comparison of the activity to the criteria for approval specified in §93-8 of the Wetlands Law.

**§ 93-8. Criteria for approval. [Amended 11-1-2001 by L.L. No. 4-2001]**

A. The following are criteria applicable to the approval of permits for Proposed regulated activities in controlled areas:

- (1) The activity will not have a substantial adverse effect upon the natural function and benefits of a wetland or watercourse as set forth in § 93-2B;
- (2) The activity will not substantially change the natural channel of a watercourse or substantially inhibit the dynamics of a watercourse system;
- (3) The activity will not result in the degrading or pollution of waters.
- (4) The activity will not increase the potential for flooding.
- (5) Sufficient provision has been made for control of pollution, erosion, Siltation and sedimentation during and after conduct of the activity;
- (6) No practicable alternative location is available on the subject parcel.
- (7) No additional technical improvements or safeguards can reasonably be added to the plan or activity which would minimize the impact on a controlled area; or
- (8) The activity will alleviate or remove a hazard to the public health or safety.

B. In evaluating the criteria and the determination required in § 93-8A above, the Council and the permitting authority shall utilize the objective methodology for determining the functions of a wetland set out in the publication entitled "A Rapid Procedure for Assessing Wetland Functional Capacity," dated May 1998, by Magee and Hollands, a copy of which is on file in the office of the Town Clerk of the Town of Philipstown. [Amended 7-14-2005 by L.L. No. 2-2005]

# Short Environmental Assessment Form

## Part 1 - Project Information

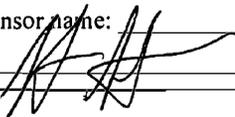
### Instructions for Completing

**Part 1 - Project Information.** The applicant or project sponsor is responsible for the completion of Part 1. Responses become part of the application for approval or funding, are subject to public review, and may be subject to further verification. Complete Part 1 based on information currently available. If additional research or investigation would be needed to fully respond to any item, please answer as thoroughly as possible based on current information.

Complete all items in Part 1. You may also provide any additional information which you believe will be needed by or useful to the lead agency; attach additional pages as necessary to supplement any item.

<b>Part 1 - Project and Sponsor Information</b>							
Name of Action or Project: <b>Deer Exclusion Fence for 11 La Shinju</b>							
Project Location (describe, and attach a location map): <b>11 La Shinju, Cold Spring, NY 10516. Edited survey attached to application</b>							
Brief Description of Proposed Action: <b>Installation of an 8' standard black deer fence around approximately 20 acres.</b>							
Name of Applicant or Sponsor: <b>One Nature LLC</b>		Telephone: <b>214-636-7017</b>					
		E-Mail: <b>blair@onenaturellc.com</b>					
Address: <b>178 Main Street</b>							
City/PO: <b>Beacon</b>		State: <b>NY</b>	Zip Code: <b>12508</b>				
1. Does the proposed action only involve the legislative adoption of a plan, local law, ordinance, administrative rule, or regulation? If Yes, attach a narrative description of the intent of the proposed action and the environmental resources that may be affected in the municipality and proceed to Part 2. If no, continue to question 2.			<table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <th style="width: 50%; text-align: center;">NO</th> <th style="width: 50%; text-align: center;">YES</th> </tr> <tr> <td style="text-align: center;"><input checked="" type="checkbox"/></td> <td style="text-align: center;"><input type="checkbox"/></td> </tr> </table>	NO	YES	<input checked="" type="checkbox"/>	<input type="checkbox"/>
NO	YES						
<input checked="" type="checkbox"/>	<input type="checkbox"/>						
2. Does the proposed action require a permit, approval or funding from any other governmental Agency? If Yes, list agency(s) name and permit or approval:			<table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <th style="width: 50%; text-align: center;">NO</th> <th style="width: 50%; text-align: center;">YES</th> </tr> <tr> <td style="text-align: center;"><input checked="" type="checkbox"/></td> <td style="text-align: center;"><input type="checkbox"/></td> </tr> </table>	NO	YES	<input checked="" type="checkbox"/>	<input type="checkbox"/>
NO	YES						
<input checked="" type="checkbox"/>	<input type="checkbox"/>						
3.a. Total acreage of the site of the proposed action?		<b>27</b> acres					
b. Total acreage to be physically disturbed?		<b>.002</b> acres					
c. Total acreage (project site and any contiguous properties) owned or controlled by the applicant or project sponsor?		<b>27</b> acres					
4. Check all land uses that occur on, adjoining and near the proposed action.							
<input type="checkbox"/> Urban <input type="checkbox"/> Rural (non-agriculture) <input type="checkbox"/> Industrial <input type="checkbox"/> Commercial <input checked="" type="checkbox"/> Residential (suburban)							
<input checked="" type="checkbox"/> Forest <input type="checkbox"/> Agriculture <input type="checkbox"/> Aquatic <input type="checkbox"/> Other (specify): _____							
<input type="checkbox"/> Parkland							



<p>18. Does the proposed action include construction or other activities that result in the impoundment of water or other liquids (e.g. retention pond, waste lagoon, dam)?          If Yes, explain purpose and size: _____          _____          _____</p>	<p>NO</p> <p><input checked="" type="checkbox"/></p>	<p>YES</p> <p><input type="checkbox"/></p>
<p>19. Has the site of the proposed action or an adjoining property been the location of an active or closed solid waste management facility?          If Yes, describe: _____          _____          _____</p>	<p>NO</p> <p><input checked="" type="checkbox"/></p>	<p>YES</p> <p><input type="checkbox"/></p>
<p>20. Has the site of the proposed action or an adjoining property been the subject of remediation (ongoing or completed) for hazardous waste?          If Yes, describe: _____          _____          _____</p>	<p>NO</p> <p><input checked="" type="checkbox"/></p>	<p>YES</p> <p><input type="checkbox"/></p>
<p><b>I AFFIRM THAT THE INFORMATION PROVIDED ABOVE IS TRUE AND ACCURATE TO THE BEST OF MY KNOWLEDGE</b></p> <p>Applicant/sponsor name: <u>                    steve savitsky, Manager                    </u>      Date: <u>                    2-16-22                    </u></p> <p>Signature: <u>                                        </u></p>		

**PRINT FORM**



**ATTN: Max Garfinkle**

Natural Resources Review Officer  
Town of Phillipstown  
238 Main Street  
Cold Spring, NY 10516

February 10, 2022

Dear Max,

I am writing in regards to the 27-acre property at 11 La Shinju, Cold Spring, NY.

As you and I discussed by phone, we request permission to install a standard black deer exclusion fence around a portion of the property to exclude the majority of the property's deer population. This installation will allow for the forest to regenerate from its own seed without excessive disturbance, and permit future conservation initiatives on the property.

While deer fencing in the upland areas does not require a permit, we are requesting permission to continue our fence line across wetland areas and their surrounding 100' buffer.

Attached to this letter, you will find the following documents: photographs of the proposed fence material and how it is installed; a survey of the property with the approximate proposed fence line overlaid in red by us; and a summary page of two articles studying the benefits of deer exclusion fences with PDFs of the articles attached.

Please let me know if you need any further information.

Sincerely,

Blair Patterson  
Principal, One Nature LLC  
845-440-1677  
[blair@onenaturellc.com](mailto:blair@onenaturellc.com)

Cc: Terry Dresbach (property owner), Bryan Quinn (One Nature)

## **CONSTRUCTION PROJECT NARRATIVE FOR 11 La Shinju**

**Project Description:** The purpose of this project is to install an eight foot tall, standard black deer exclusion fence around a portion of the property to exclude the majority of the property's deer population. This installation will allow for the forest to regenerate from its own seed without excessive disturbance, and permit future conservation initiatives on the property.

**Proposed project timeline:** Deer fence will be constructed as soon as possible.

**Estimated wetland disturbance:** Deer fence posts will be placed, on average, every 15 feet. An estimated 170 fence posts will need to be installed within the 100' wetland buffer. Fence post installation requires little to no digging, therefore disturbance will be isolated to fence post sleeve placement. Posts are approximately 2" wide. The fence itself will be an 8', standard black deer fence with a nylon wire across the top. In areas where fencing crosses streams with active water flow, shorter panels will be installed 1' off the ground. In high flow situations or heavy storms, shorter panels will detach more easily and allow for simple repairs.

**Proposed maintenance:** The fence line will be monitored and repaired regularly, both through the placement of trail cameras at 5 different key locations, as well as monthly maintenance walks to assess and repair any damage.

### **Project goals:**

- To minimize the deer population within the exclusion area
- To minimize the occurrence of invasive species throughout the property
- To promote forest regeneration by minimizing deer browse and excessive disturbance to young seedlings
- To prepare for future conservation efforts on the property



## Deer exclusion case study summaries

### Long-Term Effects of White-Tailed Deer Exclusion on the Invasion of Exotic Plants: A Case Study in a Mid-Atlantic Temperate Forest

Shen X, Bourg NA, McShea WJ, Turner BL (2016) Long-Term Effects of White-Tailed Deer Exclusion on the Invasion of Exotic Plants: A Case Study in a Mid-Atlantic Temperate Forest. PLOS ONE 11(3): e0151825. <https://doi.org/10.1371/journal.pone.0151825>

In this study, scientists studied the effects of deer exclusion fencing on the presence of invasive species. The study took place on a 25.6 hectare mature temperate forest in Virginia. A 4 hectare enclosure that had been maintained since 1991 was compared with a 4 hectare reference site on the same plot. The fence was constructed of woven American wire, topped with six strands of high tensile wire. The exotic species that were studied were *Berberis thunbergii* (Japanese barberry), *Rubus phoenicolasius* (wineberry), *Rosa multiflora* (multiflora rose), and *Microstegium vimineum* (Japanese stiltgrass). *B. thunbergii* was found to be the most abundant, occurring 1.8 times more in the reference plot than in the fenced area. The presence of *B. thunbergii*, *R. phoenicolasius*, and *M. vimineum* were all found to be significantly lower in the enclosure. This paper provides evidence that reducing deer populations by a deer exclusion fence could limit the abundance of invasive species, and further aid in boosting native plant diversity.

### Evaluating the impacts of white-tailed deer (*Odocoileus virginianus*) browsing on vegetation in fenced and unfenced timber harvests

Parker, Larkin, J. T., Heggenstaller, D., Duchamp, J., Tyree, M. C., Rushing, C. S., Just Domoto, E., & Larkin, J. L. (2020). Evaluating the impacts of white-tailed deer (*Odocoileus virginianus*) browsing on vegetation in fenced and unfenced timber harvests. *Forest Ecology and Management*, 473, 118326–. <https://doi.org/10.1016/j.foreco.2020.118326>

This study tested the short-term impact of fenced and unfenced plots on timber harvests in Pennsylvania. Excess browsing by white tailed deer is found to be a cause of forest regeneration failure. Managers will use deer exclusion fencing until the stems of the woody species have become established and grow beyond the reach of deer. The study sites consisted of 10 pairs of fenced and unfenced timber plots within State Game Land (SGL). These forests were dominated by oak, dry-oak mixed hardwood, and red maple forest types. The fences were 2m tall woven-wire fencing. From this experiment, the authors found that tree species within the exclusion fence were taller. The results suggest that browsing by deer in the initial years may reduce seedling height, structure, and composition of vegetation. This could alter future overstory composition. The study provides evidence that deer exclusion fencing should be considered during the initial years to avoid the detrimental effects caused by deer browsing.



## Evaluating the impacts of white-tailed deer (*Odocoileus virginianus*) browsing on vegetation in fenced and unfenced timber harvests



Halie A. Parker<sup>a,\*</sup>, Jeffery T. Larkin<sup>a</sup>, Dan Heggenstaller<sup>b</sup>, Joseph Duchamp<sup>a</sup>, Michael C. Tyree<sup>a</sup>, Clark S. Rushing<sup>c</sup>, Emily Just Domoto<sup>d</sup>, Jeffery L. Larkin<sup>a,e</sup>

<sup>a</sup> Department of Biology, Indiana University of Pennsylvania, 1011 South Drive, Indiana, PA 15701, United States

<sup>b</sup> Pennsylvania Game Commission, Harrisburg, PA 17110, United States

<sup>c</sup> Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT 84322, United States

<sup>d</sup> Department of Conservation and Natural Resources, Harrisburg, PA 17110, United States

<sup>e</sup> American Bird Conservancy, The Plains, VA 20198, United States

### ARTICLE INFO

#### Keywords:

White-tailed deer  
Ungulates  
Browsing  
Herbivory  
Forest regeneration

### ABSTRACT

Ensuring the recruitment of desired tree species is a primary goal when considering successful regeneration of timber harvests. Deer populations that are overabundant relative to forage availability within their local landscapes pose a considerable challenge to successful forest regeneration. We evaluated the short-term (< 10 years) impact of white-tailed deer browsing on woody structure and composition in northcentral Pennsylvania. Specifically, we compared woody plant species density, height, and cover within 10 pairs of fenced and unfenced regenerating timber harvests. Percent of browsed stems was higher in unfenced harvests for red maple (*Acer rubrum*), oaks (*Quercus* spp.), *Rubus* spp., sassafras (*Sassafras albidum*), and witch hazel (*Hamamelis virginiana*). Stem density did not differ between fenced and unfenced harvests for any species except *Rubus* spp., which was greater in the former. However, height of serviceberry (*Amalanchier* spp.), sassafras, northern red oak (*Quercus rubra*), *Rubus* spp., and red maple was taller in fenced harvests. Both vertical and horizontal vegetation density were greater in fenced harvests, suggesting a more structurally complex understory in fenced harvests. *Rubus* spp. and tall (> 1.5 m) sapling cover were greater in fenced harvests, while unfenced harvests had greater forb, fern, and blueberry/huckleberry (*Vaccinium* spp./*Gaylussacia* spp.) cover. Our results suggest that browsing by deer in the years initially (< 10 years) following timber harvest may not immediately impact woody species density, but can considerably reduce seedling height, overall horizontal and vertical structure, and composition of vegetation strata. Reduced sapling height and greater prevalence of blueberry/huckleberry, forbs, and ferns in unfenced harvests threaten the successful recruitment of desired species into the future overstory. Our results from large, operational-scale timber harvests combined with those from previous small-scale studies stress the potential value of deer exclusion fencing to achieve successful forest regeneration. Future research should examine the timing of fence removal to achieve forest regeneration success, while also providing deer access to available foraging opportunities during the later portion of stand initiation.

### 1. Introduction

Direct and indirect modifications of ecosystems by ungulates has been well-documented worldwide (i.e., Bernes et al., 2018; Côté et al., 2004; Hobbs, 1996) and can result in both positive and negative effects (Hobbs, 1996; Rooney, 2001). Negative effects on plant communities are often most apparent when ungulates are overabundant or inhabit areas that lack adequate forage resources (Allombert et al., 2005; Berger et al., 2001; Miller et al., 2009). The consequences of these negative effects can be profound including the extirpation of sensitive

species (Augustine and Frelich, 1998) and trophic cascades that can influence the distribution of entire plant communities (Ripple et al., 2001; Baker et al., 2005).

Over the past several decades browsing by white-tailed deer (*Odocoileus virginianus*) has negatively impacted deciduous forests of eastern North America (McShea and Rappole, 2000; McWilliams et al., 2018). A subcontinental analysis of the United States revealed 59% of forest land throughout the Midwest and Northeast exhibited evidence of moderate or high deer impacts (McWilliams et al., 2018). The Mid-Atlantic region maintained the highest proportion (79%) of forest land

\* Corresponding author.

E-mail address: [gvzy@iup.edu](mailto:gvzy@iup.edu) (H.A. Parker).

<https://doi.org/10.1016/j.foreco.2020.118326>

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with moderate or high deer impacts (McWilliams et al., 2018). Chronic browsing by white-tailed deer can negatively affect forest ecosystems by altering plant community structure and species composition (Nuttall et al., 2013; Russell et al., 2001; Tilghman, 1989). Specifically, excessive browsing by white-tailed deer can reduce plant growth, recruitment, density, and fitness (Horsley et al., 2003; Rooney and Waller, 2003). In turn, deer-driven changes in vegetation structure and composition can influence the microclimate of the forest floor (i.e. soil moisture, humidity, temperature and light), the vertical complexity of the stand, forb cover, and nutrient cycling (Rooney and Waller, 2003; Rossell et al., 2005). Indeed, abundance of white-tailed deer was found to be just as influential as stand and site attributes (e.g. aboveground biomass, relative density, and stand age) on the development of forest understories (Russell et al., 2017).

Excessive browsing by white-tailed deer is often implicated as a cause of forest regeneration failure following timber harvest and other disturbances (Apsley and McCarthy, 2004; Marquis and Brenneman, 1981; Sage et al., 2003). A study in Pennsylvania attributed 50% of forest regeneration failures to overbrowsing by deer (Witmer and deCalesta, 1991). Regeneration of tree species desired for timber production and wildlife habitat can be substantially reduced by white-tailed deer browsing (Rooney and Waller, 2003; Rossell et al., 2005), thus lowering ecological value and future economic potential of forestlands (Marquis, 1974, 1981). Excessive deer browsing can require substantial economic investment to regenerate areas negatively impacted by deer (i.e., \$100–5800+/ha; Witmer and deCalesta, 1991; VerCauteren et al., 2006).

To reduce deer impacts on forest regeneration public and private land, managers often use deer exclusion fencing until stems of desired woody species have become established and grow beyond the reach of deer ( $\leq 1.8$  m) (Frerker et al., 2013; Gustafson, 2011; NRCS, 2017). Besides legal hunting, fencing is often cited as the best means for controlling deer damage (Behrend et al., 1970; Smith and Cogan, 1984). Moreover, due to declining numbers of hunters across much of the eastern U.S. (Winkler and Warnke, 2013) and hesitation by many hunters to harvest antlerless deer in Pennsylvania (Diefenbach et al., 1997), it is becoming more difficult for hunting to effectively reduce deer density in some landscapes (Brown et al., 2000), further necessitating the use of other management alternatives such as exclusion fencing. Typically, woven-wire fences are erected around timber harvests as long-term barriers (i.e., 6–12 years) to prevent deer from accessing valuable or vulnerable areas (Smith and Cogan, 1984; VerCauteren et al., 2006). Although installation of fencing is expensive (\$10–15/m) (VerCauteren et al., 2006, Pennsylvania DCNR, 2013), it is often warranted as chronic and wide-spread browsing can significantly impact herbaceous and woody species composition and have long-lasting effects (Augustine and Frelich, 1998; Kain et al., 2011; Nuttall et al., 2011). As such, the use of deer exclusion fencing is something forest managers must carefully consider when planning regeneration timber harvests. Given the interplay between the high economic cost associated with installing deer exclusion fencing and the high ecological costs when chronic deer browsing is not prevented, continued research that empirically evaluates the ecological outcomes of fencing is warranted. This research is especially important given the increased use of deer exclusion fencing as a conservation practice on private forests enrolled in cost-share programs such as Working Lands for Wildlife and Regional Conservation Partnership program (NRCS, 2017) and public lands. For example, the Pennsylvania Department of Conservation and Natural Resources (DCNR) maintained deer exclusion fencing across 16,187 ha between 1995 and 2013 (Pennsylvania DCNR 2013).

While previous studies provided insight into the influence of deer exclusion fencing on vegetation, the small size of study plots or lack of replication may limit transferability of their findings to larger scales such as operational timber harvests. Insight from studies that use paired fenced and unfenced operational-scale timber harvests that are adjacent

to each other are needed to isolate deer effects on vegetation from other potentially confounding factors (i.e., differences in topographic or soil conditions; Lesser et al., 2019; Begley-Miller et al., 2019). We compared the effect of white-tailed deer browsing between paired fenced and unfenced regenerating timber harvests in deciduous forests of central Pennsylvania. Specifically, we compared browsing intensity, vegetation density, stem height, and composition of vegetation strata between fenced and unfenced overstory-removal timber harvests. To our knowledge, no study has examined both browsing intensity and vegetation structure data simultaneously to quantify the direct effects of deer browsing on vegetation characteristics. Additionally, we are unaware of previous studies comparing the effects of browsing on vegetation inside and outside deer enclosures using multiple operational timber harvests. Our study builds upon existing literature and provides empirical evidence to help inform forest managers regarding the impact of deer browsing on regenerating timber harvests and the implications for the use of deer exclusion fencing.

## 2. Methods

### 2.1. Study sites

We used ten pairs of fenced and unfenced regenerating overstory removal harvests in Centre County in northcentral Pennsylvania (Table 1). All timber harvests were on State Game Lands (SGL) managed by the Pennsylvania Game Commission (PGC): SGL 033 (7,100 ha), SGL 060 (3,540 ha), and SGL 100 (8,400 ha). All three of these SGLs are dominated by forest (88–94%), comprised of mostly dry-oak heath, dry-oak mixed hardwood, and red maple cover types. The local landscapes (2.5 km<sup>2</sup>) surrounding our study sites were comprised of 8–35% forage producing cover types (i.e., forests < 10 years old, agriculture/herbaceous areas) (PGC, unpublished data). Each pair of fenced and unfenced sites were harvested at the same time by the same operators between 2009 and 2012. Immediately following harvest, fenced portions of the timber harvests were enclosed using 2-m tall woven-wire fencing specifically intended to exclude deer. Unfenced portions of the harvests were directly adjacent to the fenced portions and were completely accessible to deer. Thus, these treatments function as a randomized block design where each pair of control (unfenced) and treatment (fenced) harvests had the same local landscape characteristics. Fences were not constructed explicitly for the purpose of our study. However, fenced portions were selected based on economies of scale with the intention to maximize the area of each harvested that was fenced given limited funding. Residual species composition and residual basal area (m<sup>2</sup>/ha) for fenced ( $2.1 \pm 0.58$ ; mean  $\pm$  SE) and unfenced ( $3.3 \pm 0.66$ ) harvests were similar post-harvest. Fenced timber harvests ranged in size from 3.4 to 57.9 ha ( $18.8 \pm 5.9$  ha) and unfenced harvests ranged from 6.5 to 50 ha ( $20.2 \pm 4.9$  ha). Temporary damage to fencing occasionally resulted in deer entering some of our fenced harvests, however we are confident such instances were uncommon, involved few individuals, and were limited in duration. Fencing was removed at two study sites (Aikley Hollow and Firetower North) in 2018, less than one year prior to our study. These fences were removed after foresters determined the woody regeneration had achieved heights beyond the reach of deer. We included both pairs in our study because the fencing had only recently been removed and had been in place for the first 9–10 years of stand initiation, and thus would still reveal potential differences in vegetation due to deer browsing. Additionally, one fenced/unfenced pair (322 Salvage) was treated with a prescribed fire in spring 2016. This pair was also included in our study as the prescribed fire treatment was consistent for the fenced and unfenced portions of the harvest. Estimated deer densities for our study area between 2009 and 2015 was 9.2–14.1 deer/km<sup>2</sup> (Rushing et al., 2020). In addition to white-tailed deer, SGL 100 was also home to a small population of free-ranging elk (*Cervus elaphus*).

**Table 1**

Site descriptions for ten paired fenced and unfenced overstory removal timber harvests in northcentral Pennsylvania. Vegetation communities were sampled in each site in 2019. Note: RBA = residual basal area. Sites with more than one plot show average  $\pm$  SE for elevation and RBA.

Site	Harvest Name	Size (ha)	Year Cut	Elevation (m)	RBA (m <sup>2</sup> /ha)
SGL100	Aikley Hollow Fenced <sup>a</sup>	13.3	2010	531 $\pm$ 3.4	3.4 $\pm$ 0.6
	Aikley Hollow Unfenced	24.6		530 $\pm$ 5.0	4.2 $\pm$ 0.7
SGL60	Firetower N Unfenced	8.0	2009	689 $\pm$ 0.5	7.7 $\pm$ 4.9
	Firetower N Fenced <sup>a</sup>	4.0		700	0.0
	Firetower 1 Unfenced	15.9	2009	735 $\pm$ 2.1	2.5 $\pm$ 1.5
	Firetower 1 Fenced	3.4		740	0.0
	Firetower 2 Unfenced	6.5	2009	735	1.1
	Firetower 2 Fenced	8.1		732 $\pm$ 2.0	3.4 $\pm$ 2.9
	Firetower 3 Fenced	29.5	2009	713 $\pm$ 5.0	0.3 $\pm$ 0.3
	Firetower 3 Unfenced	23.1		678 $\pm$ 2.7	3.4 $\pm$ 1.8
	Firetower 4 Unfenced	6.7	2009	733	1.7
	Firetower 4 Fenced	4.7		762	2.3
SGL33	Hawk Run Unfenced	44.5	2012	596 $\pm$ 3.6	5.6 $\pm$ 1.5
	Hawk Run Fenced	57.9		620 $\pm$ 3.1	5.0 $\pm$ 1.6
	Red Horse Unfenced	13.4	2009	688	1.7
	Red Horse Fenced	7.8		692	4.0
	322 Salvage Unfenced <sup>b</sup>	50.0	2012	649 $\pm$ 6.8	2.3 $\pm$ 1.0
	322 Salvage Fenced <sup>b</sup>	42.2		608 $\pm$ 5.2	0.7 $\pm$ 0.1
	Crow's Nest Fenced	16.7	2012	576 $\pm$ 7.5	1.7 $\pm$ 1.1
	Crow's Nest Unfenced	9.5		595	2.3

<sup>a</sup> Exclosure fencing removed in 2018.

<sup>b</sup> Prescribed fire treatment.

## 2.2. Data collection

We evaluated browse intensity from 19 March – 2 April 2019, along four parallel transects that ran the length of each timber harvest. Transects consisted of a series of regularly spaced survey plots that were generated within ArcGIS version 10.6 (ESRI, Redlands, California, USA). Transects were spaced equally apart within each harvest and spacing ranged between 32 and 187 m depending on harvest size. The starting location of the first transect was selected using a random number generator to choose a number between 0 m and the maximum distance between transects that would allow for the placement of four transects per harvest. The number of 1 m radius circular plots varied for each harvest depending on harvest area. We established 20 plots for the first 4 ha and added one plot for each additional ha. For example, if a harvest was 17 ha we established 33 browse survey plots: 20 plots for the first 4 ha and 13 plots per additional 13 ha. Harvests that were less than 4 ha were sampled at 20 plots, similar to recommendations provided in the sampling protocol for Silviculture of Allegheny Hardwoods (SILVAH; Brose et al., 2008). Sampling plots were spaced equally along the transects with spacing between plots ranging from 44 to 127 m depending on harvest size and shape.

For each 1 m radius plot, we counted, identified, and recorded browse category (unbrowsed or browsed) of all woody stems (saplings and shrubs) and *Rubus* spp. We lumped some species into genera if they were difficult to identify to species without leaves such as oaks (*Quercus* spp.), *Rubus* spp., birch (*Betula* spp.), and serviceberry (*Amelanchier* spp.). A stem was counted if it was between 10 cm and 2 m in height. Woody stems > 2 m in height were not counted unless they had twigs below 2 m that were accessible to deer ( $\leq 1.8$  m). We categorized a stem as browsed if any portion of the plant exhibited damage to the primary or lateral branches likely caused by deer herbivory. In order to maximize our number of stems sampled, if a 1 m radius plot fell within an area that lacked woody regeneration, we recorded that the plot needed to be moved to a new random location. New plot locations were determined by spinning a compass and sampling the closest patch of regeneration in that direction. For each woody species observed, proportions (0–1) were calculated by dividing the number of browsed stems by the total number of stems recorded at each plot and then averaged across plots within either fenced or unfenced areas of each site.

We sampled growing season vegetation characteristics (Appendix A)

within each timber harvest from 14 June – 22 June 2019. We sampled vegetation at 28 and 27 randomly placed points in fenced and unfenced harvests, respectively. At each sampling point, we established three rectangular 5 m<sup>2</sup> plots (5 m  $\times$  1 m). The edge of each 5 m<sup>2</sup> plot was randomly located between 0 and 30 m along three 35 m long transects that radiated from point center along 0°, 120°, and 240° azimuths. Within each 5 m<sup>2</sup> plot, we recorded the species name and measured the height (m) of each woody stem. We also assessed horizontal and vertical vegetation density. We quantified horizontal vegetation density using a 2 m tall vegetation profile board that consisted of twenty 20  $\times$  20 cm squares (Nudds, 1977). One technician held the profile board 5 m from the plot center at the 0°, 120°, and 240° directions, while another observer viewed the profile board from point center at a height of 1 m and recorded the number of squares that were > 50% obstructed by vegetation. This process was repeated at the end of one of the 35 m transects that was randomly chosen. We quantified vertical vegetation density using a densiometer at four locations per point, once at point center and at the end of each 35 m transect (Lemmon, 1956). We recorded the number of squares that were > 50% obstructed by vegetation.

We used an ocular tube (i.e. Geographic Resource Solutions (GRS) densiometer) to estimate percent cover of various vegetation strata: canopy, sapling > 1.5 m, sapling < 1.5 m, shrub > 1.5 m, shrub < 1.5 m, *Rubus* spp., forb, fern, grass/sedge, leaf litter, bare ground, and *Vaccinium* spp./*Gaylussacia* spp. We recorded ocular tube readings at 10 locations per point: once at point center, once at 5 m along each 35 m transect, once at a random location between 0 and 35 m along each 35 m transect, and at the end of each of 35 m transect. We calculated an average percent cover for each strata type by summing the total number of presences and dividing that value by 10 (the maximum number of times a given strata could have been recorded). Lastly, we used a 10-factor wedge prism to estimate basal area at point center and at the end of each 35 m transect.

## 2.3. Analyses

We analyzed all data using program R via RStudio (R Core Team, 2019; RStudio Team, 2019). For each measurement, we averaged plot-level values across sample locations for the fenced and unfenced sections of each site. We used a principle components analysis to examine potential differences in the percent cover of each vegetation stratum

between fenced and unfenced harvests (Kabacoff, 2010; Oksanen et al., 2019). We also ran a series of paired t-tests comparing measurements of vegetation: horizontal vegetation density, vertical vegetation density, and species-specific measures for proportion of stems browsed (hereafter, browse intensity), average shrub/sapling stem height, and shrub/sapling stem density. The species/genus groups differed for browse intensity due to our ability to identify the plants during winter versus summer sampling and difference in sampling protocol. For browse intensity, we only compared species/genus groups with  $\geq 30$  stems total observations across all sites in both fenced and unfenced harvests. These included birch spp., black cherry (*Prunus serotina*), mountain laurel (*Kalmia latifolia*), oak spp., red maple (*Acer rubrum*), *Rubus* spp., sassafras (*Sassafras albidum*), serviceberry spp., and witch hazel (*Hamamelis virginiana*). For average height (m) and stem density (stems/5 m<sup>2</sup>), we included species with  $\geq 50$  stems in both treatment groups for all sites combined. These included: chestnut oak (*Quercus montana*), northern red oak (*Quercus rubra*), red maple, *Rubus* spp., sassafras, serviceberry, and witch hazel. For each test, we adjusted p-values based on the Holm-Bonferroni criteria to account for multiple testing among species (Holm, 1979).

### 3. Results

The first principal component (PC1) accounted for 41.6% of the variation in vegetation characteristics between fenced and unfenced harvests and was best at distinguishing between fenced and unfenced areas (Fig. 1). Fenced areas had greater amounts of *Rubus* spp. and  $> 1.5$  m saplings, while unfenced areas had greater cover of blueberry/huckleberry, forbs, and fern (Fig. 1; Table 2).

We collected browsing data at 320 and 349 1 m radius plots in fenced and unfenced harvests, respectively. We had to move 1.9% (6/320) of plots in fenced and 16.3% (57/349) of plots in unfenced harvests due to lack of woody regeneration. Based on paired t-tests, the proportion of browsed stems was higher in unfenced harvests for oak spp., red maple, *Rubus* spp., and sassafras when compared to fenced harvests (Table 3). *Rubus* spp. was the only species for which stem density (stems/5 m<sup>2</sup>) differed between unfenced and fenced harvests, with higher densities inside the later (Table 4; Fig. 2f).

Several species were taller in fenced harvests compared to unfenced harvests: red maple, northern red oak, sassafras, serviceberry, and *Rubus* spp. (Fig. 2a–g; Table 4). Chestnut oak and witch hazel heights did not differ between fenced and unfenced harvests (Fig. 2a and g). Many of the species in the unfenced harvest were not (on average) tall enough to outreach deer browsing height. Some species did not occur often, were present in only one or two paired harvests, and/or were assessed with multiple sampling techniques (e.g. both ocular tube and 5 m<sup>2</sup> plots) and thus were not considered for analysis (Appendix B).

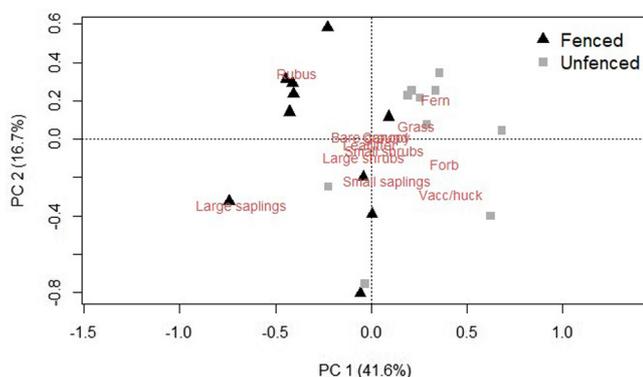


Fig. 1. Principal components analysis for 12 vegetation strata variables measured in fenced and unfenced timber harvests in central Pennsylvania. Vegetation strata variables represent a suite of measures taken using an ocular tube and represent relative amounts of each habitat component.

Table 2

Principal components analysis loadings for primary and secondary components with their percent of variation explained. Cover variables represent a suite of measures taken using an ocular tube and represent relative amounts of each habitat component within paired fenced and unfenced timber harvests.

Vegetation Strata	PC1 (41.6%)	PC2 (16.7%)
		Loadings
Canopy	0.08	0.005
Large saplings (> 1.5 m)	-0.68	-0.35
Small saplings (< 1.5 m)	0.08	-0.22
Large shrubs (> 1.5 m)	-0.04	-0.10
Small shrubs (< 1.5 m)	0.07	-0.06
<i>Rubus</i> spp.	-0.39	0.34
Forb	0.38	-0.13
Fern	0.34	0.21
Grass/sedges	0.24	0.07
Leaf litter	-0.002	-0.02
Bare ground	-0.007	0.004
Blueberry/Huckleberry	0.42	-0.29

Both horizontal ( $0.76 \pm 0.06$  in fenced vs.  $0.54 \pm 0.06$  in unfenced;  $p < 0.05$ ,  $t = 3.1$ ,  $df = 9$ ) and vertical ( $0.71 \pm 0.05$  in fenced vs.  $0.42 \pm 0.09$  in unfenced;  $p < 0.001$ ,  $t = 6.0$ ,  $df = 9$ ) vegetation density were greater in fenced harvests.

### 4. Discussion

Our study demonstrates the value of using deer exclusion fencing during the stand initiation phase following overstory removal timber harvests. More specifically, it provides strong empirical evidence that excessive deer browsing had a considerable impact on vegetation structure and habitat quality in regenerating stands and may alter future overstory species composition. These findings are particularly interesting given our study sites were large timber harvests and most were within local landscapes containing high amounts of available deer browse. Previous research suggested that deer browsing impact on regenerating timber harvests might be mitigated by satiating deer populations if local landscapes are comprised of approximately 14–20% forage producing habitats (Miller et al., 2009; Royo et al., 2017). Our study sites were within local landscapes (2.5 km<sup>2</sup>) comprised of 8–35% of forage producing habitats, yet still resulted in very noticeable browsing intensity and subsequent impacts on vegetation structure even at moderate local deer densities estimates (9.2–14.1 deer/km<sup>2</sup>). This observation suggests that deer densities within our study area were high enough that satiating deer by creating ample foraging opportunities throughout local landscapes was not possible (Beguin et al., 2009).

Deer browsing can drive biotic homogenization by increasing cover of non-preferred plants such as grasses, sedges, and ferns (Rooney, 2009). It was evident that excessive deer browsing was having this result within our unfenced harvests. Specifically, 16.3% of our browse intensity plots in unfenced harvests had to be moved due to lack of woody regeneration, whereas 1.9% of plots in fenced harvests required relocation. In most cases the original location of browse intensity plots that needed to be moved fell within dense patches of hay-scented fern (*Dennstaedia punctilobula*; Fig. 3). Moreover, our principal components analysis revealed that increased fern cover was a characteristic that most distinguished unfenced harvests from fenced harvests. Deer browsing favors unpalatable species like hay-scented fern, by allowing ferns to form expansive patches of dense foliage that outcompete regenerating tree and shrub seedlings for light (Horsley and Marquis, 1983; Hill, 1996; Horsley, 1993). Dense fern cover can further suppress tree establishment by increasing seed and seedling predation rates by small mammals (Royo and Carson, 2008).

Several studies have concluded deer preferentially browse some plant species more than others (i.e., Frerker et al., 2013; Pierson and

**Table 3**

Paired *t*-test results comparing the proportion of browsed stems by species between fenced and unfenced harvests. Browse surveys were conducted in March–April 2019 in northcentral Pennsylvania. Note: All *p*-values were Holm-adjusted.

Species Name	Number of stems		Percent of stems browsed		t-value	df	P – value
	Unfenced	Fenced	Unfenced	Fenced			
Oak ( <i>Quercus</i> spp.)	396	442	90%	16%	–11.7	8	< <b>0.001</b>
Red maple ( <i>Acer rubrum</i> )	1140	738	94%	22%	–11.4	9	< <b>0.001</b>
Sassafras ( <i>Sassafras albidum</i> )	144	478	80%	16%	–8.4	8	< <b>0.001</b>
<i>Rubus</i> spp.	450	1434	78%	6%	–8.8	7	< <b>0.001</b>
Witch hazel ( <i>Hamamelis virginiana</i> ) <sup>a</sup>	208	219	58%	7%	–4.0	5	0.05
Birch ( <i>Betula</i> spp.)	78	80	42%	4%	–2.3	3	0.4
Black cherry ( <i>Prunus serotina</i> )	34	93	47%	0%	–2.0	4	0.4
Serviceberry ( <i>Amelanchier</i> spp.)	58	76	81%	32%	–2.7	2	0.4
Mountain laurel ( <i>Kalmia latifolia</i> )	168	170	8%	1%	–2.8	2	0.4

<sup>a</sup> *p* < 0.05 before Holm-adjustment.

deCalesta, 2015; Rooney, 2009). Our browse intensity results suggest that deer selectively foraged on oak spp., red maple, sassafras, *Rubus* spp., and witch hazel, while birch, black cherry, serviceberry, and mountain laurel were not browsed regularly in our study area. Consistent with our study, oak spp. (Blossey et al., 2019; Long et al., 2007; McWilliams et al., 2018) and *Rubus* spp. (Marquis and Grisez, 1978; Miller et al., 2009; Rawinski, 2014) are reported as species preferred by deer. However, previous studies have reported mixed results regarding forage preferences for red maple (Abrams and Johnson, 2012; Bradshaw and Waller, 2016; Long et al., 2007), sassafras (Apsley and McCarthy, 2004; Rawinski, 2014), and witch hazel (Brose et al., 2008; Rawinski, 2014). In our study area it was quite evident that deer intensively browsed red maple and sassafras. Inconsistencies in findings regarding species-specific browse preference could stem from several factors, from relative abundance of each species on the landscape to growth form available (e.g. seedling or sprout). Our results show that under the browse pressure on these landscapes, many species previously reported as less preferred are still highly impacted by deer.

Differences in browsing intensity among species and between our fenced and unfenced harvests manifested in several ways, including greater horizontal and vertical vegetation density in fenced harvests. We expected that we would find species-specific differences in both stem density and height between fenced and unfenced harvests. While we did find strong differences in the average heights of several species between fenced and unfenced harvests, our prediction did not hold true for stem density. This pattern is similar to a study conducted in northern Virginia that reported no difference in seedling abundance or community composition inside and outside a deer enclosure but did find that height of seedlings was on average 2.25 times greater inside the fence (McGarvey et al., 2013). Only *Rubus* spp. stem density was greater in our fenced harvests. Many of the tree and shrub seedlings we sampled were likely present prior to the timber harvest as advanced regeneration, but *Rubus* spp. was most likely absent or scarce in the pre-

harvest stands due to its shade intolerance. A lack of established advanced seedlings coupled with its highly preferred status may explain the observed difference in *Rubus* spp. density between fenced and unfenced harvests. Indeed, previous research has reported that *Rubus* spp. often declines at sites accessible to deer and is replaced by grasses, sedges, and forbs (Horsley et al., 2003; Marquis and Grisez, 1978; Trumbull et al., 1989). Our analyses provide evidence that deer browsing likely drives the replacement of *Rubus* spp. as the dominant low-growing woody vegetation by ferns and blueberry/huckleberry in unfenced harvests, which may result in long-term challenges to tree regeneration (Horsley, 1993; Jäderlund et al., 1997). Moreover, *Rubus* spp. is known to be an important habitat component for many game and non-game species (Anders et al., 1998; Bellush et al., 2016; Stevens and Barry, 2002) and thus its reduced availability in unfenced harvests has implications for their relative value to wildlife.

We were not surprised to see differences in heights for red maple, sassafras, and *Rubus* spp. because our browse intensity surveys found that stems for all three species were browsed more in unfenced harvests than fenced harvests. Additionally, differences in sassafras stem density in fenced and unfenced harvests trended toward significance and might be considered biologically significant (Table 4). Our results for northern red oak and chestnut oak height are particularly interesting when considering patterns in browse intensity and vegetation heights. We found oak spp., in general, to be highly browsed in unfenced harvests, however, only northern red oak was taller in fenced harvests. Another study found a difference in the percent of chestnut oak (~3%) and northern red oak (~24%) stems browsed in unfenced plots (Apsley and McCarthy, 2004). Additionally, northern red oak seedlings protected from deer grew significantly taller than those that were unprotected (Blossey et al., 2017) and browsed red oak stems grew significantly slower and were less likely to transition into saplings than stems protected from deer (Blossey et al., 2019). When considered as a collective, the consequences of the variation in species-specific patterns for stem

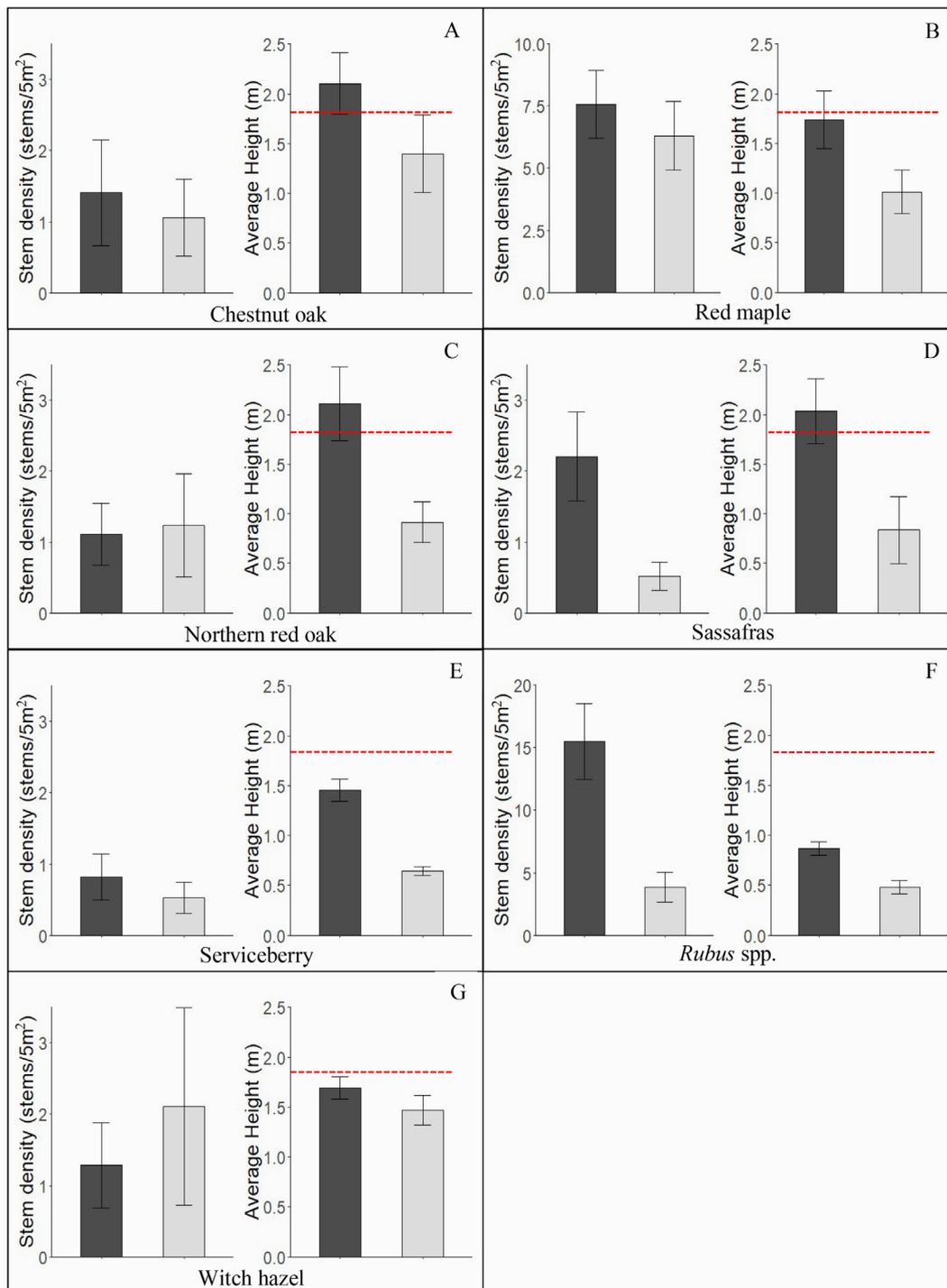
**Table 4**

Total number of stems, mean height (m), and stem density (stems/5 m<sup>2</sup>) for woody shrub and sapling species in fenced and unfenced harvests in northcentral Pennsylvania. Note: All *p*-values were Holm-adjusted.

Species	Total number of stems		Density (stems/5 m <sup>2</sup> ) mean ± SE				Height <sup>a</sup> (m) mean ± SE					
	Fenced	Unfenced	Fenced	Unfenced	t - value	P - value	df	Fenced	Unfenced	t - value	P - value	df
Chestnut oak ( <i>Quercus montana</i> )	135	113	1.4 ± 0.74	1.1 ± 0.54	0.6	1	9	2.1 ± 0.31	1.4 ± 0.39	1.8	0.35	3
Red maple ( <i>Acer rubrum</i> )	682	617	7.6 ± 1.4	6.3 ± 1.4	1.4	1	9	1.7 ± 0.29	1.0 ± 0.22	3.1	<b>0.05</b>	9
Northern red oak ( <i>Quercus rubra</i> )	86	76	1.1 ± 0.44	1.2 ± 0.73	–0.1	1	9	2.1 ± 0.37	0.91 ± 0.20	3.2	<b>0.05</b>	7
Sassafras ( <i>Sassafras albidum</i> )	187	60	2.2 ± 0.63	0.52 ± 0.2	3.1	<b>0.08<sup>b</sup></b>	9	2.0 ± 0.33	0.84 ± 0.34	3.8	<b>0.04</b>	6
Serviceberry ( <i>Amelanchier</i> spp.)	90	59	0.82 ± 0.32	0.53 ± 0.22	1.0	1	9	1.5 ± 0.11	0.65 ± 0.04	9.9	<b>0.02</b>	3
<i>Rubus</i> ( <i>Rubus</i> spp.)	1415	444	15.5 ± 3.0	3.9 ± 1.2	2.9	<b>0.02</b>	9	0.86 ± 0.07	0.48 ± 0.07	4.0	<b>0.02</b>	8
Witch hazel ( <i>Hamamelis virginiana</i> )	176	128	1.3 ± 0.6	2.1 ± 1.4	–0.6	1	9	1.7 ± 0.11	1.5 ± 0.15	1.0	0.28	3

<sup>a</sup> Variable was log-transformed prior to statistical analysis.

<sup>b</sup> Species *p*-value was significant prior to holm-adjustment.

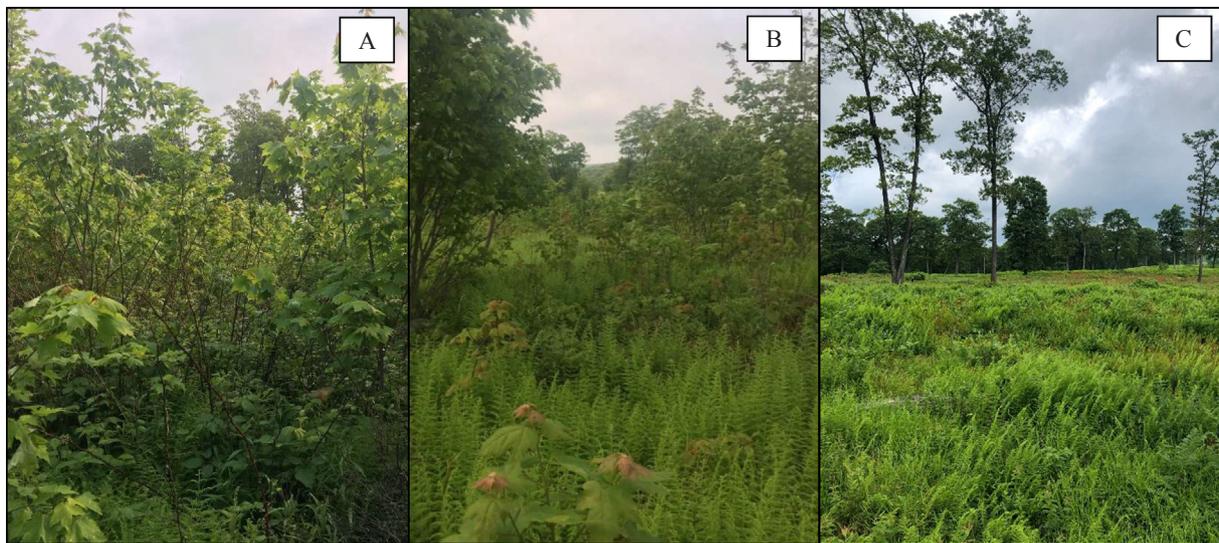


**Fig. 2.** Average  $\pm$  SEM stem density (stems/5 m<sup>2</sup>) and average height (m) a) Chestnut oak, b) Red maple, c) Northern red oak, d) Sassafras, e) Serviceberry, f) Rubus spp., g) Witch hazel in fenced and unfenced harvests. Dark grey bars represent fenced harvests, light grey bars represent unfenced harvests. The red dashed line represents typical height of browse line ( $\leq 1.8$  m). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

density and heights between our fenced and unfenced harvests may become more evident as these stands continue to regenerate (i.e., Nuttle et al., 2011).

Our timber harvests (ages 7–10 years post-harvest) were still in the stand initiation stage and while we observed differences in stem height it may not be until the stem exclusion stage (~12–15 years post-harvest) that species-specific differences in stem density are realized. The failure of stands to regenerate is influenced by limited availability of advanced tree-seedling regeneration (McWilliams et al., 1995) and/or

regenerated seedlings not advancing to taller height classes (Blossey et al., 2017; Marquis and Grisez, 1978; Tilghman, 1989). Shorter average heights in unfenced harvests suggests most species we monitored will not outgrow the reach of deer and will continue to be heavily browsed. Hence, fenced and unfenced portions of our study sites could exhibit species-specific differences in stem density as they transition from stand initiation to stem exclusion stages. High deer browsing intensity during the stand initiation stage can negatively impact diversity of canopy trees and will favor browse-tolerant species (Nuttle et al.,



**Fig. 3.** Photos from regenerating timber harvests (10 years post-harvest) in SGL 060, panel a); typical vegetation structure of fenced harvests, panel b) and c) vegetation structure of unfenced harvests ranging from low amounts of woody regeneration (b) to no woody regeneration (c).

2011). Thus, continued monitoring of sapling stem densities in our sites would be worthwhile to assess whether differences in species-specific stem densities between fences and unfenced harvests result after the stem exclusion phase.

**4.1. Conclusions**

Our study provides strong evidence that deer exclusion fencing should be considered to avoid the detrimental effects caused by deer during the stand initiation stage. Excessive browsing by deer has great potential to impart significant ecological and economic costs over the next rotation of these stands (i.e., 80–100 years) (Nuttle et al., 2014; Ward et al., 2004). In the short term, deer browsing in our unfenced harvests reduced vegetation cover (e.g. *Rubus* spp.), density, and height. These conditions not only effect future forest conditions, but also habitat quality for wildlife that depend on young seral stage forest. Deer exclusion fencing is and will continue to be particularly valuable for cost share programs that desire to restore degraded forest stands and improve wildlife habitat through regeneration harvests (i.e., McNeil et al., 2020). Failing to fence such areas could limit both forest health and wildlife habitat goals. Future research should examine the timing of fence removal to maximize forest regeneration success, while also providing deer access to available foraging opportunities during the later portion of stand initiation. Additionally, studies that use data from

paired fenced and unfenced harvests to model and compare long-term economic potential would be helpful for assessing the return on investment when installing deer exclusion fencing (i.e., Ward et al., 2004).

**Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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**Appendix A. Vegetation features measured in the ten paired fenced and unfenced harvests in northcentral, Pennsylvania.**

Vegetation feature	Area measured along/within	Description
Proportion of browsed stems (0–1)	1 m radius plots along transects	Proportion of woody stems browsed relative to all stems of that species recorded
Woody height (m)	3, 1 × 5 m <sup>2</sup> transects at each point	Woody height is represented by all woody species ≥ 0.1 m measured with a meter stick
Woody density (stems/5 m <sup>2</sup> )	3, 1 × 5 m <sup>2</sup> transects at each point	Woody density is represented by number of woody stems of each species counted per transect (5 m <sup>2</sup> )
Horizontal vegetation density	Along three 35 m transects at each point	Quantified using a vegetation profile board (Nudds 1977) that consists of 20, 20 × 20 cm squares. Density was measured by the proportion of squares ≥ 50% obstructed by vegetation
Vertical vegetation density	Along three 35 m transects at each point	Quantified using a densiometer (Lemmon 1956) that consists of 25 squares. Density was measured by the proportion of squares ≥ 50% obstructed by vegetation
Vegetation cover	Along three 35 m transects at each point	Quantified using a GRS densitometer (i.e. ocular tube). Averaged by the number of times a strata type was encountered by adding the number of presences (1) or absences (0) and dividing by the total number of times a strata type could have been detected (10) at each plot.
Basal area	35 m transects at each point	Quantified residual basal area (RBA) using a 10-factor wedge prism

Appendix B. . Occurrence of woody species observed in 5 m<sup>2</sup> vegetation plots within fenced (n = 84 plots) and unfenced (n = 81 plots) timber harvests. Occurrence was calculated by dividing the total number of plots a species was recorded on by the total number of plots for each harvest type. Species with > 10% difference in occurrence are bolded.

Common name	Scientific name	% Occurrence fenced harvest	% Occurrence unfenced harvest
American black currant	<i>Ribes americanum</i>	0.0%	1.2%
Appalachian gooseberry	<i>Ribes rotundifolium</i>	0.0%	1.2%
Bigtooth aspen	<i>Populus grandidentata</i>	6.0%	0.0%
Black birch	<i>Betula lenta</i>	3.6%	2.5%
Black cherry	<i>Prunus serotina</i>	21.4%	18.5%
<b>Black gum</b>	<b><i>Nyssa sylvatica</i></b>	<b>14.3%</b>	<b>0.0%</b>
Black oak	<i>Quercus velutina</i>	9.5%	12.3%
Chestnut oak	<i>Quercus montana</i>	26.2%	21.0%
Chokeberry	<i>Aronia</i> spp.	2.4%	1.2%
Cucumber tree	<i>Magnolia acuminata</i>	0.0%	1.2%
Devil's walkingstick	<i>Aralia spinosa</i>	20.2%	11.1%
Fire cherry	<i>Prunus pensylvanica</i>	6.0%	2.5%
Hawthorn	<i>Crataegus</i> spp.	4.8%	9.9%
Huckleberry	<i>Gaylussacia</i> spp.	16.7%	19.8%
Mountain laurel	<i>Kalmia latifolia</i>	11.9%	6.2%
Nannyberry	<i>Viburnum lentago</i>	1.2%	1.2%
Northern red oak	<i>Quercus rubra</i>	34.5%	27.2%
Pitch pine	<i>Pinus rigida</i>	1.2%	0.0%
Quaking aspen	<i>Populus tremuloides</i>	4.8%	0.0%
Red maple	<i>Acer rubrum</i>	81.0%	76.5%
<b>Brambles</b>	<b><i>Rubus</i> spp.</b>	<b>83.3%</b>	<b>53.1%</b>
<b>Sassafras</b>	<b><i>Sassafras albidum</i></b>	<b>52.4%</b>	<b>25.9%</b>
Scarlet oak	<i>Quercus coccinea</i>	3.6%	1.2%
Serviceberry	<i>Amelanchier</i> spp.	32.1%	29.6%
Staghorn sumac	<i>Rhus typhina</i>	1.2%	0.0%
Striped maple	<i>Acer pensylvanicum</i>	1.2%	1.2%
Sweet azalea	<i>Rhododendron arborescens</i>	8.3%	3.7%
Sweet fern	<i>Comptonia peregrina</i>	19.0%	18.5%
Blueberry	<i>Vaccinium</i> spp.	71.4%	72.8%
White oak	<i>Quercus alba</i>	22.6%	21.0%
Winterberry	<i>Ilex</i> spp.	2.4%	0.0%
Witch hazel	<i>Hamamelis virginiana</i>	34.5%	29.6%
Yellow birch	<i>Betula alleghaniensis</i>	2.4%	2.5%

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RESEARCH ARTICLE

# Long-Term Effects of White-Tailed Deer Exclusion on the Invasion of Exotic Plants: A Case Study in a Mid-Atlantic Temperate Forest

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## Abstract

Exotic plant invasions and chronic high levels of herbivory are two of the major biotic stressors impacting temperate forest ecosystems in eastern North America, and the two problems are often linked. We used a 4-ha deer enclosure maintained since 1991 to examine the influence of a generalist herbivore, white-tailed deer (*Odocoileus virginianus*), on the abundance of four exotic invasive (*Rosa multiflora*, *Berberis thunbergii*, *Rubus phoenicolasius* and *Microstegium vimineum*) and one native (*Cynoglossum virginianum*) plant species, within a 25.6-ha mature temperate forest dynamics plot in Virginia, USA. We identified significant predictors of the abundance of each focal species using generalized linear models incorporating 10 environmental and landscape variables. After controlling for those predictors, we applied our models to a 4-ha deer exclusion site and a 4-ha reference site, both embedded within the larger plot, to test the role of deer on the abundance of the focal species. Slope, edge effects and soil pH were the most frequent predictors of the abundance of the focal species on the larger plot. The abundance of *C. virginianum*, known to be deer-dispersed, was significantly lower in the enclosure. Similar patterns were detected for *B. thunbergii*, *R. phoenicolasius* and *M. vimineum*, whereas *R. multiflora* was more abundant within the enclosure. Our results indicate that chronic high deer density facilitates increased abundances of several exotic invasive plant species, with the notable exception of *R. multiflora*. We infer that the invasion of many exotic plant species that are browse-tolerant to white-tailed deer could be limited by reducing deer populations.

data collection and analysis, decision to publish, or preparation of the manuscript.

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## Introduction

Long-term study of the temperate forest ecosystem in the Mid-Atlantic region of eastern North America has revealed a large decline of biodiversity and decrease in abundance of native plant species [1–3]. Among the several driving mechanisms, chronic high herbivore abundance and exotic plant invasion are two stressors causing the increase of homogeneity of local plant communities, especially the forest understory species component [2,4]. The density of white-tailed deer (*Odocoileus virginianus* Zimmermann, henceforth deer) has dramatically increased throughout the region since European settlement, and has chronically exceeded historical levels in many forests [5]. Deer consume a large amount of plant biomass (i.e., leaves, buds, flowers and fruits) and directly reduce the growth, reproduction and survival of herbaceous and woody plant species. By foraging selectively, deer can change the relative abundance and thus alter competitive relationships of plant species [6]. Chronic high deer density reduces understory plant cover and diversity, impedes the regeneration of seedlings and saplings, alters nutrient and carbon cycling, and eventually may redirect succession of canopy tree species [7,8]. Sustained heavy browsing also exerts cascading effects on invertebrates, birds, and other mammals by altering resource availability at other trophic levels [9]. Many studies have demonstrated that deer may act as a keystone species, strongly affecting the structure and functioning of the temperate forests of eastern North America [5].

Mid-Atlantic temperate forests have suffered from the invasion of exotic plant species for over 100 years [10]. Several herbaceous and woody exotic species have established in many of these forests, such as garlic mustard (*Alliaria petiolata*), Japanese stiltgrass (*Microstegium vimineum*), multiflora rose (*Rosa multiflora*), wineberry (*Rubus phoenicolasius*), Japanese honeysuckle (*Lonicera japonica*) and Japanese barberry (*Berberis thunbergii*). These exotic species were naturalized in the early 20<sup>th</sup> century and expanded out from areas adjacent to human development into intact forest. They compete for resources with native plants and indirectly suppress the growth of native plants by changing soil chemistry, microbial community dynamics, nutrient cycling and biotic interactions [11,12], resulting in profound effects on the composition and function of native plant communities.

Recent experimental studies show that these dual stressors, deer and exotic invasive plants, may be linked, as invasive plants decrease in abundance when deer are excluded from forest communities or maintained at low densities [13–15]. Previous studies have found deer may facilitate the dispersal and colonization of exotic invasive plants by epizoochory (seeds transported externally by animals) and endozoochory (seed dispersal via ingestion) [16,17]. They may also facilitate invasion, through either competitive release following selective consumption of native species [14,18] or soil and litter disturbance resulting from foraging and bedding [19]. Exotic plants that are unpalatable and/or browse-tolerant, a common characteristic of many invasive plants, may have a competitive advantage over browsed native plants [20]. Facilitation of exotic plant invasion by extensive deer browsing has been observed by both short-term (e.g., 3-year deer exclusion by Eschtruth and Battles 2009 [13] and 6-year deer exclusion by Kalisz et al. 2014 [14]) and long-term experimental studies (e.g., 13-year deer exclusion by Kuebbing et al. 2013 [21]; 18-year deer exclusion by Abrams and Johnson 2012 [22]).

Here, we report a case of a long-term deer exclusion experiment to examine the impact of white-tailed deer browsing on the abundance of four exotic invasive plant species (three woody: *R. multiflora*, *B. thunbergii*, *R. phoenicolasius*; one herbaceous: *M. vimineum*), all widely found throughout the Mid-Atlantic region, at a large (25.6 ha) forest plot located in Virginia, USA. We investigated the abundance of these exotic invasive species and the environmental characteristics under which they occurred. After controlling for potential confounding factors, we compared the abundance of these species in a 4-ha fenced deer exclusion area established in

1991, and a paired 4-ha reference site, both found within the larger plot. Our study has value in being long-term due to the slow process by which deer impact native plant communities [3]. In addition, exotic species invasion processes progress at slower rates in closed-canopy forests where the light levels are consistently low and the lag-time to invade the forests is generally long [23,24], so short-term resistance to invasive species may not accurately assess their impact. We also used a common native herbaceous species, wild comfrey (*Cynoglossum virginianum*), that is known to be deer-dispersed and unpalatable to deer [25], as a comparison species. While the lack of replication limited the scope of inference of our study, our enclosure and reference sites are larger than most enclosures, and we could take advantage of highly detailed environmental data from a large forest plot and a long-term deer exclusion experiment.

## Materials and Methods

### Study site

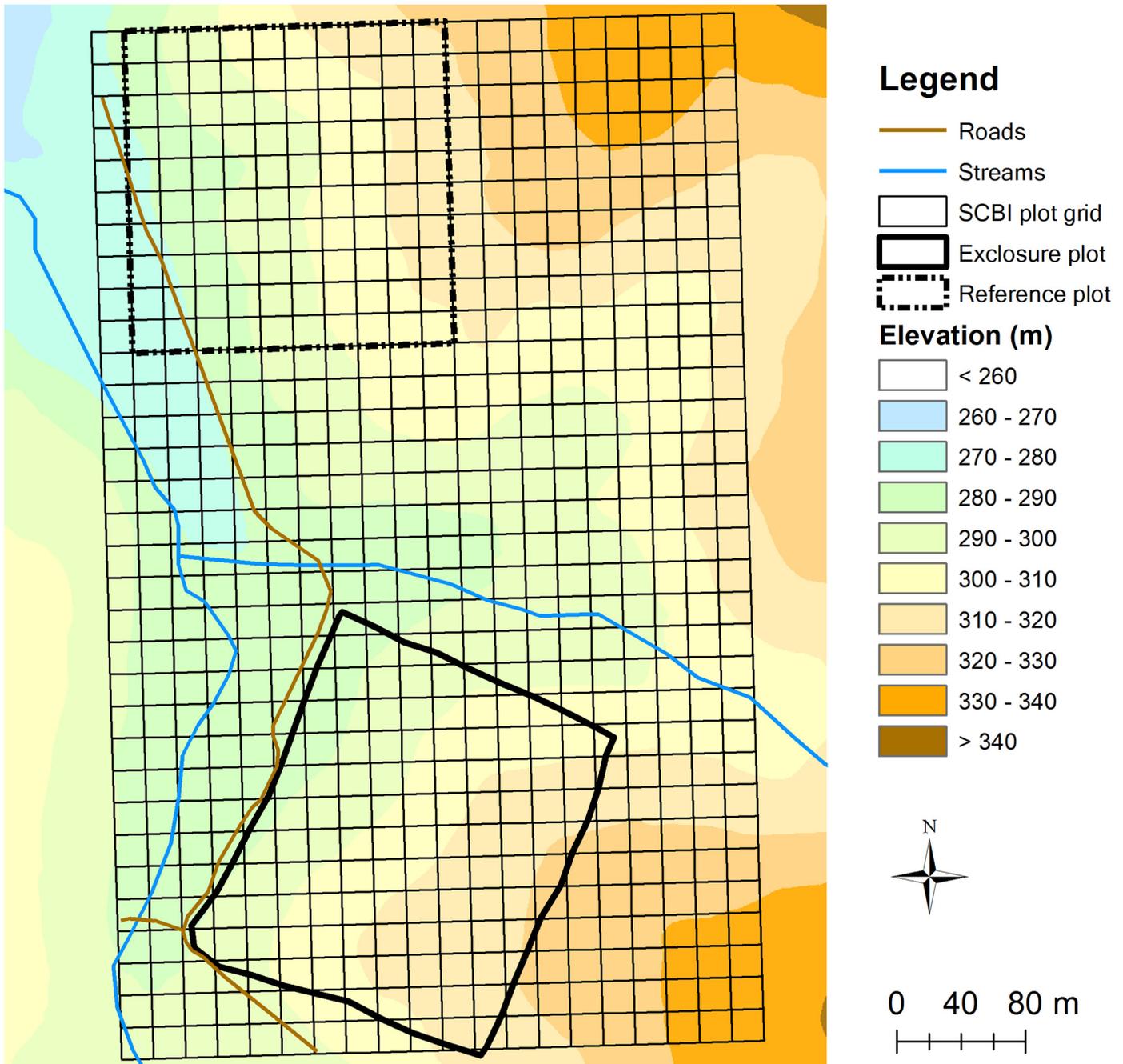
This study was conducted at the 25.6-ha SCBI large forest dynamics plot (38°53' N, 78°9' W) located at the Smithsonian Conservation Biology Institute (SCBI), approximately 5 km south of Front Royal, VA, USA (see Bourg et al. 2013 [26] for details). Mean elevation of the SCBI plot is 302 m (range 273–338 m). The 2011 mean annual temperature was  $12.7 \pm 0.66^\circ\text{C}$  and the mean annual precipitation was  $96.2 \pm 15.8$  cm based on climate data obtained from a nearby weather station (Carr, University of Virginia, 2011 unpublished data). The dominant soil series in the plot are Myserville and Montalto, which are stony, steep, and well-drained. The vegetation of the SCBI plot represents a typical mature secondary mixed deciduous forest in the mid-Atlantic region of eastern North America, with overstory tree ages ranging from 84 to 124 years [8]. Landform variation across the plot supports upland and bottomland forests. Its woody vegetation was censused in 2008, using standardized methods [27], with all free-standing stems  $\geq 1$  cm DBH (Diameter at Breast Height) identified, measured, tagged and mapped. Dominant canopy trees include tulip poplar (*Liriodendron tulipifera*), white, red and black oak (*Quercus alba*, *Q. rubra*, and *Q. velutina*), white ash (*Fraxinus americana*), pignut and mockernut hickory (*Carya glabra* and *C. tomentosa*), and black gum (*Nyssa sylvatica*). Prominent understory components include spicebush (*Lindera benzoin*), paw-paw (*Asimina triloba*), American hornbeam (*Carpinus caroliniana*), and eastern redbud (*Cercis canadensis*).

The SCBI plot was gridded into 640 20 m x 20 m quadrats using iron rebar posts (Fig 1). Within the plot there is embedded a 4-ha (200 m x 200 m, containing 92 20 m x 20 m quadrats completely within the enclosure) fenced site that has excluded deer since 1991. This enclosure is constructed of woven American wire, topped with six strands of high tensile fence wire for a total height of 2.4 m, and supported by 2.4 m wooden posts at regular intervals. A 4-ha reference site (containing 100 20 m x 20 m quadrats) was identified in the SCBI plot as a comparison area for the deer enclosure. The location of the reference plot was determined by choosing an equal-sized area to the deer enclosure with similar topographic attributes (i.e., slope and aspect) and overstory composition (i.e., basal area by species), achieved by performing a cluster analysis of the ten dominant canopy tree species in each quadrat (see McGarvey et al. 2013 [8] for details).

White-tailed deer have been the only large herbivore present within the forest for at least the past century. Deer density in the SCBI forest has been consistently estimated at 30–40 deer / km<sup>2</sup> over the past thirty years [26].

### Data collection

We conducted surveys to record the number of individuals of our study species within each quadrat, with the exception of the exotic invasive grass *M. vimineum*, where we visually estimated % cover in the quadrat. All four exotic invasive species colonized this forest after the



**Fig 1. Map of the 25.6-ha (400 m x 640 m) SCBI forest plot as divided into 20 m x 20 m quadrats.** The locations of the enclosure and reference plots are indicated.

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construction of the deer enclosure in 1991 and were not detected in initial plant surveys of the area [9]. Surveys were conducted during the summer months for three species (i.e., *R. multiflora*, *B. thunbergii*, and *R. phoenicolasius*) in 2009, one species (*M. vimineum*) in 2010 and one species (*C. virginianum*) in 2011. During each survey, 3–4 surveyors systematically searched each quadrat across the entire SCBI plot. For *B. thunbergii*, *R. multiflora* and *R. phoenicolasius*, which can be multi-stemmed shrubs, we considered all stems emanating from a distinct

**Table 1. The abundance measures (as per quadrat) of the five study species and the variables included in the generalized linear models.**

	Min	Max	Mean	SD
<b>SPECIES ABUNDANCE</b>				
<i>Woody (No. of individuals)</i>				
Exotic invasive				
<i>Rosa multiflora</i>	0	33	1.01	2.96
<i>Berberis thunbergii</i>	0	138	6.44	11.79
<i>Rubus phoenicolasius</i>	0	125	6.33	12.96
<i>Herbaceous</i>				
Native				
<i>Cynoglossum virginianum (No. of individuals)</i>	0	116	10.99	18.73
Exotic invasive				
<i>Microstegium vimineum (categorical %) cover</i>	0	4	1.76	1.2
<b>PREDICTOR VARIABLES</b>				
<b>EDGE</b>				
Distance to forest edge (m)	21	523	282.89	115.5
<b>ASPECT</b>				
Transformed aspect	-1	1	-0.009	0.72
<b>SLOPE</b>				
Slope (°)	1.9	21.4	10.34	3.81
<b>TCI</b>				
Topographic Convergence Index	0	280.8	34.45	30.35
<b>WRICH</b>				
Woody species richness	3	19	10.07	2.81
<b>WSTEM</b>				
No. of woody stems	7	582	60.37	71.22
<b>CANOPY</b>				
Canopy openness (%)	3.69	20.8	9.07	2.16
<b>pH</b>				
pH	3.96	6.11	5.09	0.47
<b>N</b>				
Nitrogen (NH <sub>4</sub> <sup>-</sup> and NO <sub>3</sub> <sup>-</sup> , mg/kg)	2.13	9.09	4.30	1.17
<b>P</b>				
Phosphorus (mg/kg)	10.31	35.05	20.10	5.82

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rooting point as an individual. For *M. vimineum*, we estimated its % cover in five categories: 0 = absent, 1 = 0–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%.

For each quadrat we collected or derived 10 variables for further analysis as predictors that could potentially determine the abundance and distribution of the study species (Table 1). We estimated distance from quadrat center to forest edge, as well as the aspect, slope and landform using a 10-m Digital Elevation Model (DEM, MassGIS website). We standardized the aspect of each quadrat, calculated as “-1 x cos (45—aspect)” [28] (range -1 to 1). For landform we used a Topographic Convergence Index (TCI) [29], which is calculated as:

$$TCI = \ln(\alpha/\tan\beta)$$

where  $\alpha$  is the upslope contributing area (the number of grid cells that might contribute water drainage to the point) and  $\beta$  is the local slope angle. TCI is positively related to water availability owing to drainage from upslope areas. Topography Toolbox 9.3 [30] embedded in ArcGIS

9.3 (ESRI, Redlands, CA, USA) was used to compute the TCI of each 10-m pixel and average TCI within each quadrat.

SCBI plot tree census data were used to calculate woody species richness and number of woody stems ( $\geq 1$  cm DBH) as plant community attributes of each quadrat. Biophysical factors measured included canopy openness, soil characteristics, and nutrients (i.e., pH, nitrogen, and phosphorus).

An index of canopy openness in each quadrat was derived from hemispherical photographs [31] taken at 1.5 m above the ground using a Nikon FC-E8 Fish-Eye lens converter mounted on a Nikon E995 camera body. We took one horizontally leveled photograph at the center of each quadrat, either in early morning or late afternoon to avoid direct solar radiation. Photographs were interpreted using the image analysis software Gap Light Analyzer (GLA, version 2.0) [31] to obtain the percentage of open sky for each quadrat. Posthoc examination resulted in excluding those photographs taken under direct solar radiation and we obtained values for 412 quadrats.

Soil characteristics and nutrient values concentrations in the mineral topsoil (at 0–10 cm depth) were obtained at 300 points systematically located in the SCBI plot in 2010. Two hundred of the sampled locations were arrayed throughout the plot by using a regular grid of points at 33 m intervals. Each alternate grid point was paired with an additional sampling point at 2, 8, or 20 m away at a random compass bearing from the grid point to capture the variation in soil properties at finer scales. At each sample point, we collected the topsoil from approximately five cores (2.5 cm diameter). Nitrogen was extracted from fresh soil immediately following collection in 2.0 M KCl and determined as  $\text{NH}_4^+$  and  $\text{NO}_3^-$  by automated colorimetry on a Lachat Quikchem 8500 (Hach Ltd, Loveland, CO). Moisture was calculated by drying at 105°C. Soil pH was determined in a 1:2 soil-to-deionized water ratio using a glass electrode. Readily-extractable P, a measure of plant-available phosphate, was extracted from air-dried soil in Bray-1 solution, with detection by automated molybdate colorimetry. All soil variables were extrapolated for each 10 x 10 m grids in the plot by kriging the known values [32], and we used the averaged value of 4 10 x 10 m grids within each quadrat.

## Data analysis

We fitted generalized linear models (GLMs) to determine the most informative factors explaining the variation in abundance of our study species across the study plot. Poisson regression models were applied for *Microstegium vimineum* and negative binomial regression models were used for the other four species because their abundances exhibited over-dispersion. We used a two-step procedure when examining the effect of deer on the distribution of the study species. First, we fitted a GLM for each species with the data from the larger plot quadrats ( $n = 426$ ) excluding quadrats found inside the enclosure ( $n = 92$ ) and reference ( $n = 100$ ) plots. After identifying significant predictor variables for the larger plot, we then constructed a second GLM for each species using the values of the relevant significant variables from the enclosure and reference plots and the additional covariate of presence/absence of deer (referred to as “FENCED” in our models). The reason we used this two-step procedure was to take advantage of the large dataset of the forest plot and identify the significant variables affecting the abundance of the species using a suite of quadrats over the broadest area possible. As the sample sizes within the enclosure (FENCED) and reference plots were relatively small ( $n = 192$ ), the first step narrowed the suite of potential variables and ensured only those species-specific variables be entered into the second models. For each species-specific model we verified that the range of values for all predictor variables used in the second GLM were within the range encountered during the first phase of modeling. Twenty-two quadrats that were split by the enclosure fence (i.e., only partially inside the enclosure) were not included in either of the two models.

As the quadrats were arrayed within a grid, we investigated spatial autocorrelation of species abundance by calculating Moran's  $I$  [33] using the `ape` package within the R statistical analysis program (R Development Team, 2008). The abundance of all species in the quadrats were spatially auto-correlated ( $p < 0.05$ ) both within the 426 unfenced quadrats and the 192 fenced and reference quadrats, respectively, except for the abundance of *B. thunbergii* within the fenced and reference quadrats ( $p = 0.63$  for fenced quadrats and  $0.66$  for reference quadrats). Thus, we added an autocovariate term ( $AUTOCOV_i$ ), a distance-weighted function of neighboring response variables [34] in all the GLMs to account for spatial correlation among neighboring quadrats, except for the second model of *B. thunbergii*.  $AUTOCOV_i$  is calculated as:

$$AUTOCOV_i = \frac{\sum_{j=1} \frac{y_j}{d_{ij}}}{\sum_{j=1} \frac{1}{d_{ij}}}$$

where  $y_j$  is the response value of  $y$  at quadrat  $j$  among quadrat  $i$ 's neighbors, in our case, eight surrounding quadrats were the neighbors of the centered quadrat;  $d_{ij}$  is the distance between the center of quadrat  $j$  and quadrat  $i$ .

We did not take interspecific relationships of the invasive species into account in the modeling process as Spearman's correlation tests showed that the abundances of invasive species were not highly correlated with each other among quadrats ( $p > 0.05$ , not correlated among fenced quadrats;  $r < 0.32$  among unfenced quadrats. [S1 Table](#)).

All the GLMs were constructed in the R software, and negative binomial regression models were constructed utilizing the `MASS` package. During the first phase of model selection, we examined the performance of each site covariate individually and retained the 6–8 variables whose model had the lowest Akaike Information Criterion value (AIC; [35]) in order to restrict the set of candidate models. We then ran models with all possible combinations of the retained site covariates and selected the best models according to AIC value. All models whose  $\Delta AIC \leq 2$  were considered as equivalent best models [36]. A final GLM with selected variables with most occurrences from the likely models was run to identify the effects of species-specific variables for both steps. We conducted Chi-squared test using residual deviance to evaluate the goodness of fit of each model. We reported the final models from the two-step procedure for each species and a significance level of 0.05 was used for all statistical tests.

## Results

Among the three exotic invasive woody species, *B. thunbergii* was most abundant (4,120 individuals) and was found in 491 (77%) quadrats across the SCBI plot, including 46 (50%) in fenced and 90 (90%) in reference quadrats. *R. phoenicolasius* (4,052 individuals) was found in 367 (57%) quadrats, with 13 (14%) in fenced and 78 (78%) in reference quadrats. *R. multiflora* (646 individuals) was found in 188 (29%) quadrats, including 27 (29%) in fenced and 18 (18%) in reference quadrats. The exotic invasive herbaceous *M. vimineum* was widespread in 551 (85%) quadrats (44 (48%) in fenced and 98 (98%) in reference quadrats) at an average categorical cover value of 1.8, while the native *C. virginianum* was recorded as 1,642 individuals in 299 (47%) quadrats (1 (1%) in fenced and 85 (85%) in reference quadrats) ([Table 1](#)).

## Species-specific relationships with deer abundance

The abundance of the native species *C. virginianum* across the larger plots was best predicted by EDGE, SLOPE, TCI, pH and  $AUTOCOV$  ([Table 2](#)). More *C. virginianum* individuals were found in quadrats further away from the forest edge, in drier places, and on the slopes than in

**Table 2. Parameter estimates, standard errors and p-values (\*\*\*) <0.001, \*\* <0.01, \* <0.05, <0.1) for final generalized linear models estimating the effects of site covariates on the abundance of native *Cynoglossum virginianum* in the SCBI forest plot.**

<i>Cynoglossum virginianum</i> (CYVI)				
	Estimate( $\beta$ )	SE	p	Exp.( $\beta$ )
<i>Step 1: within unfenced, non-reference area</i>				
EDGE	0.006	0.0008	***	1.006
SLOPE	0.064	0.022	**	1.066
WRICH				
WSTEM				
TCI	-0.009	0.003	**	0.991
pH	-0.392	0.169	*	0.676
N				
CANOPY				
Autocov	0.059	0.005	***	1.061
Model fit: res.deviance = 357.1588, df = 340, p = 0.25				
<i>Step 2: within deer-free (fenced) and reference areas</i>				
EDGE	0.012	0.003	***	1.012
SLOPE	0.128	0.044	**	1.137
N				
Autocov	0.049	0.011	***	1.05
FENCED	-5.519	1.023	***	0.004
Model fit: res.deviance = 126.286, df = 185, p = 0.99				

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flatter areas. Higher soil pH was correlated with decreased abundance of *C. virginianum*. When we examined the matched quadrats inside and outside the deer enclosure, EDGE, SLOPE and AUTOCOV were retained in the second negative binomial regression model, and deer presence/absence (FENCED) was an influential factor determining its abundance. *C. virginianum* plants were found 250 times more often in the reference quadrats than in the deer-free quadrats.

The most predictive factors for *R. multiflora* in the larger plot were EDGE, SLOPE, and AUTOCOV (Table 3A). Soil pH and N were in the final negative binomial regression model but their effects were not significant. The quadrats with higher *R. multiflora* abundance were found near the forest edge and in flatter areas. For the comparison of enclosure and reference quadrats, the abundance of *R. multiflora* was predicted by presence/absence of deer (FENCED) and N. The number of *R. multiflora* in the deer-free quadrats was 3.8 times that of the reference quadrats.

The significant variables retained in the *B. thunbergii* model for the larger plot were EDGE, SLOPE, pH and AUTOCOV (Table 3A), among which EDGE and SLOPE had negative effects and pH had positive effects on the abundance of *B. thunbergii*. For the comparison of enclosure and reference quadrats, only deer presence/absence (FENCED) was a significant predictor. The number of *B. thunbergii* within the reference was 1.8 times that of the deer-free quadrats.

The predictive factors in the *R. phoenicolasius* model for the larger plot were pH, N, CANOPY and AUOTCOV (Table 3B). Soil pH and N were positively associated with the abundance of *R. phoenicolasius*, while a negative relationship was found between canopy openness and *R. phoenicolasius* abundance. For the comparison of enclosure and reference quadrats, N and AUTOCOV were retained in the model, and deer presence/absence (FENCED) was identified

**Table 3. Parameter estimates, standard errors and p-values (\*\*\*) <0.001, \*\* <0.01, \* <0.05, . <0.1) for final generalized linear models estimating the effects of site covariates on the abundance of four exotic invasive species in the SCBI forest plot.**

<b>A.</b>								
	<i>Rosa multiflora</i> (ROMU)				<i>Berberis thunbergii</i> (BETH)			
	Estimate( $\beta$ )	SE	p	Exp.( $\beta$ )	Estimate( $\beta$ )	SE	p	Exp.( $\beta$ )
<i>Step 1: within unfenced, non-reference area</i>								
EDGE	-0.003	0.0009	***	0.997	-0.001	0.0005	*	0.999
SLOPE	-0.09	0.026	***	0.914	-0.033	0.013	*	0.968
WRICH					0.029	0.02		1.029
WSTEM								
TCI								
pH	0.432	0.224	.	1.54	0.385	0.114	***	1.47
N	0.152	0.103		1.164				
CANOPY	0.077	0.022	***	1.08	0.021	0.011	.	1.021
Autocov	0.167	0.043	***	1.182	0.073	0.006	***	1.076
Model fit: ROMU: res.deviance = 311.9267, df = 419, p = 0.99; BETH: res.deviance = 484.699, df = 419, p = 0.02								
<i>Step 2: within deer-free (fenced) and reference areas</i>								
EDGE								
SLOPE								
N	0.359	0.138	**	1.432				
Autocov								
FENCED	1.343	0.373	***	3.831	-0.592	0.164	***	0.553
Model fit: ROMU: res.deviance = 117.6605, df = 189, p = 0.99; BETH: res.deviance = 214.9352, df = 190, p = 0.10								
<b>B.</b>								
	<i>Rubus phoenicolasius</i> (RUPH)				<i>Microstegium vimineum</i> (MIVI)			
	Estimate( $\beta$ )	SE	p	Exp.( $\beta$ )	Estimate( $\beta$ )	SE	p	Exp.( $\beta$ )
<i>Step 1: within unfenced, non-reference area</i>								
EDGE								
SLOPE					-0.022	0.009	*	0.978
WRICH								
WSTEM					-0.001	0.0006	.	0.999
TCI								
pH	0.453	0.161	**	4.348				
N	0.253	0.078	**	1				
CANOPY	-0.033	0.016	*	2.777				
Autocov	0.085	0.007	***	2.932	0.474	0.042	***	1.606
Model fit: RUPH: res.deviance = 449.5587, df = 421, p = 0.16; MIVI: res.deviance = 194.6704, df = 422, p = 1								
<i>Step 2: within deer-free (fenced) and reference areas</i>								
EDGE								
SLOPE								
N	0.28	0.091	**	1.323				
Autocov	0.139	0.035	***	1.149	0.465	0.124	***	1.592
FENCED	-1.565	0.283	***	0.209	-0.675	0.257	**	0.509
Model fit: RUPH: res.deviance = 170.5647, df = 188, p = 0.81; MIVI: res.deviance = 100.5712, df = 189, p = 1								

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as important. The number of *R. phoenicolasius* in the reference plot was 4.8 times that of the deer-free plot.

The significant variables retained in the *M. vimineum* model for the larger plot were SLOPE and AUOTCOV (Table 3B). There were higher levels of % coverage for quadrats in flatter

areas. The comparison of enclosure and reference quadrats resulted in a final model with just deer enclosure (FENCED) as explanatory. The average categorical cover of *M. vimineum* in the reference was about 2 times that of the deer-free quadrats.

## Discussion

### Important predictors of species abundance

Our species-specific models for the entire 25.6-ha plot identified landscape and soil parameters related to the abundance of the species. Among the variables examined, slope, distance to forest edge and soil pH was the most frequent predictors of the abundance of the focal species on the larger plot. The deviance goodness-of-fit test indicated that all the GLMs fitted the data well, except for the first step model of *B. thunbergii* where the environmental and landscape variables had weak effects on its abundance. The autocovariate term, AUTOCOV, was retained in most models and was a highly significant predictor of the abundance of the study species, indicating a strong spatial correlation of their abundance among neighboring quadrats.

Slope was an important predictor of the abundance of four of our study species (*C. virginianum*, *R. multiflora*, *B. thunbergii* and *M. vimineum*). Indeed, it was identified as the only important predictor of *M. vimineum* abundance. SLOPE was correlated with TCI ( $r = -0.564$ ,  $p < 0.001$ ) and its effects on the abundance of the four species may reflect the influence of soil water level on the abundance of these species. TCI was not related to the abundance of any of our exotic invasive species (Table 3A and 3B), but correlation tests between TCI and their abundance did indicate a relationship for all but *R. phoenicolasius* (*R. multiflora*,  $r = 0.271$ ,  $p < 0.001$ ; *B. thunbergii*,  $r = 0.333$ ,  $p < 0.001$ ; *M. vimineum*,  $r = 0.214$ ,  $p < 0.001$ ; *C. virginianum*,  $r = -0.341$ ,  $p < 0.001$ ). *C. virginianum* is an upland species preferring dry soils, confirmed by the negative relationship between TCI and *C. virginianum* abundance (Table 2,  $\beta = -0.009$ ,  $p < 0.05$ ). The other three exotic invasive species (*R. multiflora*, *B. thunbergii* and *M. vimineum*) all preferred flatter areas, which in our plot were the riparian areas, a nutrient-rich habitat, and swales at the bottom of slopes. The higher abundance of these species in these areas was possibly attributable to the higher seed or fruit densities carried by water, which is especially true for *M. vimineum* [37], or a more optimal surface for their seed germination provided by richer soils and more moisture [38,39].

Distance to the forest edge was another important predictor of the abundances of three of our study species (*C. virginianum*, *R. multiflora* and *B. thunbergii*). Similar to slope, the direction of this predictor varied between the native *C. virginianum* (positively associated with its abundance) and the two exotic invasive species (negatively associated). Beyond being the possible entry point of invasion for exotic species, the edge is associated with increased anthropogenic disturbance and resource availability [40]. In our study site, soil nitrogen and water (as measured by TCI) levels decreased with distance into the forest (Spearman correlation,  $r = -0.339$ ,  $p < 0.001$ ;  $r = -0.158$ ,  $p < 0.001$  respectively). The presence of a stream along the western portion of the SCBI plot resulted in the quadrats in this area having both proximity to the forest edge and high soil moisture. Increased nitrogen, water and light along the forest edge would foster the invasion of *R. multiflora* and *B. thunbergii* and a positive edge effect has been described for both species [41,42]. For *C. virginianum*, a long-lived and shade-tolerant summer perennial [25], drier soils in the forest interior may lead to its higher abundance.

Soil pH was another frequent model variable and important predictor of the abundance of three of our study species (*C. virginianum*, *B. thunbergii*, and *R. phoenicolasius*). At our forest (pH = 3.96–6.11), lower pH soils were preferred by the native *C. virginianum*, while higher pH soils were preferred by the two exotic invasive species (*B. thunbergii* and *R. phoenicolasius*). Ehrenfeld et al (2001) demonstrated that the invasion of *B. thunbergii* can elevate soil pH via

nitrate uptake, and such changes may establish a positive feedback system that further enhances its invasion [11]. While we could find no studies relating pH to *R. phoenicolasius* abundance, it is well known in agricultural production that *Rubus* species prefer a soil pH range of 5.6–6.5 [43,44].

Other variables that were correlated with the abundance of our study species were extractable N and canopy openness. Nitrogen was the important predictor of *R. phoenicolasius* abundance, and as previous studies show, high N concentrations facilitated its invasion [45]. Higher canopy openness led to higher abundance of *R. multiflora*, but unexpectedly, canopy openness was negatively associated with the abundance of *R. phoenicolasius*. Gorchoff et al. (2011) found that *R. phoenicolasius* required large canopy gaps to establish in mature Mid-Atlantic deciduous forest, but established plants could survive canopy closure at light levels as low as 5% full sun [46]. Given that canopy openness of our forest was low across the plot ( $9.0\% \pm 2.1\%$ ), large canopy gaps required for establishment were largely lacking and *R. phoenicolasius* was more dispersed in the understory. Although light has long been recognized as an important plant resource in the temperate forest understory [47], it was not correlated with most of our study species.

## Deer as an important driver of exotic plant invasion

When we included the presence of deer as a covariate in our models for each species, regardless of the environmental variables added into the models, FENCED was a highly significant predictor of the abundance of all species and its effect was the strongest (stronger than the AUTO-COV term) for most of the species. The native plant *C. virginianum*, and the exotic plants *B. thunbergii*, *R. phoenicolasius* and *M. vimineum*, were more abundant where deer were present, whereas *R. multiflora* was less abundant in the presence of deer.

We included the native *C. virginianum* in this study because deer are seed-dispersal agents for this species [25]. Although most seeds of *C. virginianum* are found near the parental plant [25], occasional seed dispersal events by animals, such as white-tailed deer, are important for its long-distance dispersal [48]. We only detected one individual of *C. virginianum* in the enclosure and it was located directly next to the fence. *C. virginianum* is in the Boraginaceae, a family with pyrrolizidine alkaloids [49], which can protect plants to some degree from generalist herbivores [48] and *C. virginianum* is not a preferred forage plant of deer [50]. *C. virginianum* was present within the enclosure prior to fence erection [9]; its loss from the area indicates that, in addition to limited dispersal, the loss of deer removed any competitive advantage derived from its chemical defenses and deer-assisted dispersal.

White-tailed deer significantly affected the abundance of the four exotic invasive species. One exotic invasive species, *R. multiflora*, had a higher density within the enclosure than in the reference quadrats, indicating little or no role for deer in facilitating invasion. The distribution pattern of *R. multiflora* within the enclosure indicated its occurrence was stochastic. The fence was constructed prior to the colonization of this exotic species and there was no significant correlation between plant density and distance to the fence ( $r = -0.103$ ,  $p = 0.329$ ). *R. multiflora* is mainly dispersed by birds and Stiles (1982) [51] presents a strong association between the range expansions of *R. multiflora* and the northern mockingbird (*Mimus polyglottos*) in North America. Seeds of *R. multiflora* are also preferred food items for white-footed mice (*Peromyscus leucopus*) [52], a common species in our forest [53]. Studies at the same site found higher abundances of small mammals [53] and birds [9] in the enclosure relative to the reference site as understory vegetation advanced through successional processes after deer exclusion. Thus, it is possible that higher density of *R. multiflora* in the enclosure is attributable to the higher activities of its primary dispersal agents (i.e. birds and small mammals), which facilitated its dispersal and colonization by ingestion and defecation or caching in the enclosure.

For three exotic invasive species, the absence of deer was negatively correlated with their abundance, and for *B. thunbergii* and *R. phoenicolasius*, FENCED was the only predictor of their abundance within enclosure and reference quadrats. These results suggest that deer contributed more to predicting the abundance of exotic invasive plants in our forest than did abiotic factors (i.e., nitrogen, light, water and distance to the forest edge) at the local scale. The AUTOCOV term as a predictor of the abundance of these three species in the species-specific models indicated that they spread from the established sites, and the fence lines did slowdown their rate of spread into the deer enclosure. Our results concur with other studies [13,18] showing that deer acted as facilitators for the invasion of *B. thunbergii*, *R. phoenicolasius* and *M. vimineum*. They also agree with our subsequent observations in summer 2011, of the occurrence of wavyleaf basketgrass (*Oplismenus hirtellus* ssp. *undulatifolius*), a new exotic invasive species [54], in the reference plot and its absence within the enclosure (N.A. Bourg, unpublished data). If deer facilitated the expansion of three exotic invasive species, we hypothesize four potential causal mechanisms including endozoochory, changes to soil nutrients, selective browsing, and increased resistance to invasion of local communities.

Endozoochory by deer might facilitate the dispersal and establishment of the exotic invasive species in our forest as recent studies found viable seeds of *R. multiflora*, *R. phoenicolasius* and *M. vimineum* in deer fecal pellets [16,17]. Myers et al. (2004) identified 72 taxa germinated from deer feces collected in mixed deciduous forests in Ithaca, New York, including *R. multiflora* and *Rubus* spp. (frequency in pellet groups: 2% and 3% respectively) [16]. Williams et al. also recorded *R. multiflora*, *R. phoenicolasius* and *M. vimineum* (2%, 6% and 0.5% respectively) as among the 86 taxa germinated from deer pellets collected on a forested water authority property in southern Connecticut [17]. Deer also occasionally consume the fruits of *B. thunbergii* [55]. Deer may not be the major dispersal agent of our study species (e.g., *R. multiflora* and *B. thunbergii* mainly by birds and *M. vimineum* by surface water runoff), but considering the dense populations of white-tailed deer in our forest, the importance of deer ingestion in dispersing these species into forest interiors should be considered.

A comparison of soil nutrient levels between the enclosure and reference quadrats indicated higher nitrogen and phosphorus levels in the reference quadrats (Mann-Whitney U test,  $Z = -3.022$ ,  $p = 0.003$ ;  $Z = -11.153$ ,  $p < 0.001$  respectively). Several studies have found that white-tailed deer and other cervids (e.g., *Capreolus capreolus*) transfer nutrients from adjacent land types into forest patches [56, 57]. Deer may be the source of higher nitrogen and phosphorus levels in the reference quadrats, thereby increasing susceptibility of the native community in the reference area to invasion.

An indirect route by which deer could have facilitated invasion by the three exotic plants is via selective browsing. Sustained browsing pressure in forests of North America has shifted herbaceous and woody plant composition towards unpalatable and/or browse-resistant species (including invasive species) and led to low species abundance and diversity [58]. Selective herbivory of preferred native species over exotic species, compounded with other disturbances by deer (e.g., trampling [19]; soil compaction [59]), would release exotic invasive plants from intense competition with native species by increasing availability of resources such as open space, light, and soil nutrients. A study of woody species at our site [8] suggested 20-year deer browsing has remarkably suppressed seedling height growth and small sapling abundance in the reference quadrats with seedling height on average 2.25-times greater and sapling (1–5 cm DBH) stem counts 4.1-times greater inside the enclosure. Heckel et al. also documented larger plant sizes and higher population viability of five unpalatable herbaceous species (e.g., *Arisaema triphyllum*, *Actaea racemosa* and *Osmorhiza claytonii*) in the enclosure relative to paired deer access plots at our study site [59].

The deer enclosure was constructed prior to the colonization of the exotic species in our forest. As discussed above, the exclusion of deer since 1991 has increased the density and diversity of understory woody plants relative to the reference quadrats [8,9], and possibly increased the abundance and diversity of herbaceous species as well [59]. Higher native species diversity does confer greater community-level resistance to invasion, because species-rich communities more completely and efficiently use available resources [60, 61]. Kalisz et al. observed that excluding deer increased the growth rate of a native forb, *Trillium erectum*, leading to the restoration of the potent biotic resistance of the native community to the exotic invasive *Alliaria petiolata* [14]. The exclusion of deer prior to invasive arrival may have made the enclosure site more resistant to exotic plant invasion through the increased growth of the native plant community.

Although it is generally assumed that intact forests are highly resistant to plant invasions [24], our long-term large-scale deer exclusion experiment shows that exotic invasive plants were able to penetrate into the forest with the assistance of anthropogenic disturbance, even when the deer were excluded from the forest prior to their invasion. All exotic invasive species had established in the enclosure at the time of our survey. *R. multiflora*, *B. thunbergii*, and *R. phoenicolasius* were present in 29%, 50% and 14% of the fenced quadrats, respectively, in 2009 and *M. vimineum* was present in 48% of fenced quadrats in 2010. A resurvey of these species in the enclosure in 2014 found fast spread of *R. multiflora* and *B. thunbergii* (present in 63% and 89% fenced quadrats, respectively). The distribution of *R. phoenicolasius* remained stable (12%) and that of *M. vimineum* shrank (17%) as the drought in subsequent year reduced its coverage. The absence of these exotic invasive plants in our forest before the establishment of the deer enclosure and their colonization and fast spread in the enclosure 20 years later suggest that even when deer densities can be maintained at a relatively low level, it alone will not be enough to prevent exotic invasive plants from spreading into forest communities.

## Conclusions

Our study highlighted the important role of white-tailed deer in determining the distribution and abundance of several exotic invasive species. Although multiple factors, such as slope, edge effects, and soil pH, influenced the distribution and abundance of our study species, deer presence contributed more strongly to predicting their abundance at a local scale. It reflected the cumulative effects of sustained deer browsing and movement on the distribution of the study plants in our forest over the past 20 years. These interactions between deer and exotic species may accelerate the invasion of exotic species into similar forests in the Mid-Atlantic region of North America.

## Supporting Information

**S1 Table. Spearman's rank correlation coefficient of the abundance of invasive species in each quadrat within the SCBI forest plot.**

(DOCX)

**S2 Table. Abundance of the study species and environmental variables used in the generalized linear models.**

(XLSX)

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## Author Contributions

Conceived and designed the experiments: XS NAB WJM. Performed the experiments: XS NAB. Analyzed the data: XS NAB WJM. Contributed reagents/materials/analysis tools: BLT. Wrote the paper: XS NAB WJM BLT.

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