

## LONG-TERM DEER EXCLUSION HAS COMPLEX EFFECTS ON A SUBURBAN FOREST UNDERSTORY

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**ABSTRACT.** Herbivory by deer is one of the leading biotic disturbances on forest understories (i.e., herbs, small shrubs, and small tree seedlings). A large body of research has reported declines in height, abundance, and reproductive capacity of forbs and woody plants coupled with increases in abundance of graminoids, ferns, and exotic species due to deer herbivory. Less clear is the extent to which (and the direction in which) deer alter herbaceous layer diversity, where much of the plant diversity in a forest occurs. We examined the effect of 15 y of deer exclusion on the understory of a suburban hardwood forest in Connecticut exposed to decades of intensive herbivory by white-tailed deer (*Odocoileus virginianus*). We compared species richness (at subplot and plot scale), individual species and life form group abundance (% cover), and community composition between grazed and enclosure plots, as well as between mesic and wet soil blocks. Forb cover was more than twice as abundant in enclosure as in grazed plots, whereas sedge (*Carex* spp.) cover was 28 times more abundant, and exotic species cover generally higher in grazed than in enclosure plots. Native and exotic species richness were both higher in grazed than enclosure plots at the subplot scale, and native herbaceous richness was higher in grazed plots at both spatial scales. In contrast, native shrub richness increased with deer exclusion at the plot scale. Our results suggest that deer exclusion had contrasting effects on species richness, depending on plant life form, but that overall richness of both exotic and native plants declined with deer exclusion. In addition, site heterogeneity remained an important driver of vegetation dynamics even in the midst of high deer densities.

**Key Words:** exotic species, herbaceous layer, herbivory, species richness, white-tailed deer

It is well established that intensive herbivory by *Odocoileus virginianus* Zimmerman (white-tailed deer) and other cervids has powerful effects on forest understory layers (herbs, small shrubs, and small tree

seedlings; Côté et al. 2004; Waller 2014). Browsing-induced declines in height, cover, and reproductive capacity of forbs and woody plants, coupled with increases in cover of graminoids, ferns and exotic species, have been reported by many authors (Côté et al. 2004; Eschtruth and Battles 2009; Frerker et al. 2014; Nuttle et al. 2014; Rooney 2009). Less clear is the extent to which, and the direction in which, deer alter species diversity (i.e., species richness and diversity indices) in the understory layer where much of the plant diversity in forests occur (Gilliam 2007). This uncertainty is due in part to the varied results that have been reported. Studies from regions with long histories of high deer densities reported declines in herb species richness or other species diversity measures from herbivory (Goetsch et al. 2011; Putman et al. 1989; Rooney and Waller 2003; Webster et al. 2005). Other authors reported increased herb diversity or species richness with cervid herbivory (Hegland et al. 2013; Perrin et al. 2011; Roberts and Gilliam 2014; Royo et al. 2010). Still others reported no significant effect by deer on richness or diversity (Kraft et al. 2004; Rooney 2009; Webb et al. 1956).

The direction in which cervids drive species diversity appears in some cases to be determined by animal density and forest disturbance. In one study, low to moderate deer densities (5–8 deer km<sup>-2</sup>) interacting with forest disturbance (treefall gaps and ground fire) resulted in greater herbaceous plant diversity (Royo et al. 2010), whereas studies in areas with high deer densities ( $\geq 10$ –15 deer km<sup>-2</sup>) in intact forests found declines in richness and diversity (Goetsch et al. 2011). However, in a study of closed and semi-open woodlands exposed to very high deer densities (18–82 km<sup>-2</sup>) in Ireland, herb diversity generally increased with browsing (Perrin et al. 2011). Other studies suggest that the direction in which herbivory alters species diversity depends on plant life form and height (Hegland et al. 2013). Ungulates may reduce the species richness of relatively tall woody plants (i.e., shrubs and tree saplings), but increase the richness of small herbs and small tree seedlings by reducing competition, creating spatial heterogeneity by trampling, depositing excreta, and dispersing seeds (Hegland et al. 2013; Hester et al. 2006; Kuijper et al. 2010). Soil nutrients also appear to be an important determinant of herbivore effects on species richness: plant diversity tends to increase with herbivory on relatively rich soils and to decline in sites with relatively poor soils (Hester et al. 2006). Although deer are known to facilitate the invasion of certain exotic species and increase overall exotic plant cover (Eschtruth and Battles 2009; Frerker et al. 2014), the extent to which deer impact exotic plant diversity either directly or indirectly (e.g., by reducing native diversity)

is not well documented. In short, the direction in which deer drive plant diversity in a particular forest is likely to be highly context dependent.

Here we examine the effects of 15 y of *Odocoileus virginianus* exclusion on herbaceous layer composition and species richness in a suburban forest in southwestern, CT, USA. Severe browse lines on the lower limbs of trees and shrubs have been noted for several decades in this landscape, suggesting strong effects by deer on the understory flora. We asked the following questions: has long-term deer exclusion (1) altered the floristic composition and structure of the herbaceous layer of this forest in a manner consistent with the literature? (e.g., reduced forb and shrub cover and increased graminoid and exotic species cover; Frerker et al. 2014; Waller 2014); (2) decreased (Goetsch et al. 2011) or increased (Perrin et al. 2011) the richness of native and exotic species? and (3) influenced the species richness of different plant life forms in different ways (Hegland et al. 2013)?

#### MATERIALS AND METHODS

The study was conducted at Highstead, a 60-ha woodland preserve in Redding, southwestern Connecticut (41.327, -73.394; Figure 1). Deer densities in southwestern CT (SWCT) have been high since the mid to late 1980s, and for the past three decades SWCT has supported the highest deer densities in the state and among the highest densities in southern New England (Adams et al. 2009; Gregonis 2000; Kilpatrick 2009; SE Cooperative Wildlife Disease Study 2015). Estimates of 21–24 deer km<sup>-2</sup> were reported near Highstead between 2009 and 2013 (Kilpatrick 2013).

The study was located in an *Acer rubrum* L.–*Fraxinus americana* L. forest with the shrub and herb layer dominated by *Berberis thunbergii* DC., *Lindera benzoin* (L.) Blume, and various graminoid species including *Cinna arundinacea* L., *Leersia virginica* Willd. and *Carex* spp. L. Over the past 8–10 y, the exotic grass, *Microstegium vimineum* (Trin.) A. Camus, has rapidly invaded the woodland and become one of the dominant herbaceous species. Tree sapling recruitment above 30 cm in height was relatively sparse due to decades of herbivory, but very small tree seedlings below this height remained common, especially *F. americana*. The site is positioned below a prominent drumlin that rises 35–40 m in elevation approximately 300 m to the east and connects across a forested swamp to an expansive oak forest. The topography is gently sloping, and the fine sandy loam soils range from wet to mesic (poorly to moderately well drained) and are acidic (Faber 2008). This forest was cleared historically for pasture in the 18<sup>th</sup> and 19<sup>th</sup> centuries,

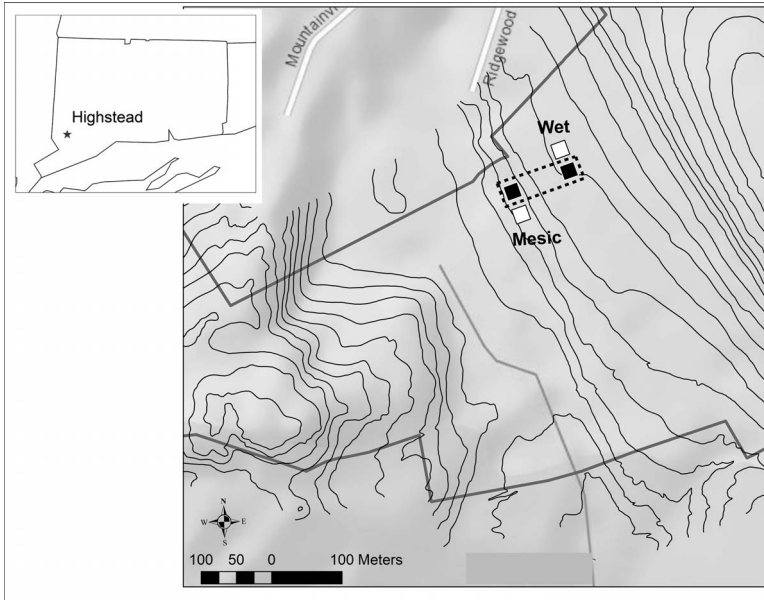


Figure 1. Study area showing location of Highstead in Connecticut (inset) and the topographical setting of the study plots and blocks. The two enclosure plots are black with a white border and enclosed in the dotted rectangle, and the two grazed plots are white with a black border.

and the land reverted back to forest in the early to mid-20<sup>th</sup> century. The combination of past land use history, moist soils, and proximity to the edge of an open field and residential development has resulted in a forest heavily invaded by exotic species (cf. DeGasperis and Motzkin 2007).

One large deer enclosure, 2.1 m high, 0.40 ha in size (120×35 m) was erected in 1998. The upslope halves of the enclosure and adjacent unfenced area were located on level ground with poorly drained soils and within relatively young forest (30–40 y old; hereafter “wet” block). The lower halves of the fence and control plot were positioned on gently sloping and moderately well drained soils and in relatively old forest (70–80 y old; hereafter “mesic block”). Soil pH was higher in the wet block (4.9–5.0) than the mesic block (4.6–4.8; Faison et al. unpubl. data). Because the enclosure was originally constructed for demonstration purposes, no baseline herbaceous or shrub layer data were gathered inside or outside the fence. However, given the same soil types, forest age, and overstory tree communities between enclosure

and grazed areas, we doubt there were important vegetative differences in the two treatment areas prior to construction of the fence. Because of the size of the enclosure and the discrete, undisturbed environments at opposite ends of the fence, we decided to use a replicated block design with deer exclusion as treatment and soil type as block to examine the vegetation in the fenced and unfenced area after 15 y of deer exclusion. We established two paired 20×20 m plots (enclosure and grazed) in the wet and mesic block, approximately 5–6 m from the fence edge, resulting in four total plots (Figure 1). Although replicates within the single large enclosure were technically not independent and therefore constituted “pseudoreplication” (cf. Hurlburt 1984), the plots in the two blocks were located 75–100 m apart and thus functioned more as independent replicates. Additionally, Oksanen (2001) argues that pseudo-replication should not be considered a problem in studies that are deductive rather than inductive. We took a deductive approach in this study by examining how general patterns of ungulate browsing documented in the literature applied specifically to our forest parcel. Other deer enclosure studies have also analyzed subsamples from single large enclosures (Goetsch et al. 2011; Kain et al. 2011; Knight et al. 2009).

In 2013, we established 13 1-m<sup>2</sup> subplots along five successive parallel transect lines within each of the larger 20×20 m treatment plots (Figure 1; cf. Frerker et al. 2014). Three subplots were positioned on the two outer and middle rows, and two subplots in the second and fourth rows. Subplots were 6 m apart within the same row and 4.5 m apart between rows. At each 1×1 m subplot, all vascular plants in the herbaceous layer were recorded by the first author and a botanical expert in the region (William Moorhead, consulting botanist, Litchfield, CT, pers. comm.). We defined “herbaceous layer” as all plants <2 m in height (Carson et al. 2014; Oliver and Larson 1996). Abundance, assessed as percent aerial cover, was estimated for each species and for each plant group (i.e., woody plants, graminoids, and forbs) in one of 7 cover classes (1=<1%, 2=1–5%, 3=6–15%, 4=16–25%, 5=26–50; 6=51–75%, 7=76–100%). Cover of individual species often overlapped with other species and, therefore, total percent cover could and often did exceed 100% in each subplot. In addition, we performed a 15-min. “meander” survey throughout the entire 400 m<sup>2</sup> area of each plot and recorded the presence (but not the percent cover) of all woody and herbaceous plant species that did not occur in the subplots (Goetsch et al. 2011; Huebner et al. 2007). Using habitat descriptions from species information pages on New England Wild Flower Society’s (2016) Go Botany website, we assigned each taxon to one of two habitat

categories: (1) *forest* (not listed as occurring in human disturbed areas or meadows and fields) or (2) *generalist* (listed as occurring in human disturbed areas or meadows and fields). Nomenclature follows Haines (2011).

We used linear mixed effects models (package lme4, R Statistical software) with ungulate treatment as a fixed effect and block as a random effect to examine the response of species richness, composition, and abundance to deer herbivory. Before analysis, we converted cover classes to percent cover midpoints (e.g., cover class 1=0.5%, cover class 2=3%, cover class 3=10.5% etc.) and then calculated the mean percent cover for species and species group across the 13 1-m<sup>2</sup> subplots in each plot as a measure of abundance. We examined species richness at two scales in each plot: subplot (mean number of species per 13 1-m<sup>2</sup> quadrat, which did not include species identified in the meander survey) and plot (number of species 400 m<sup>-2</sup>, which included all species found in the subplots and the meander survey). Although these measurements are technically species density (Gotelli and Colwell 2001), we hereafter refer to species density as “species richness.”

For response variables of abundance and species richness, we examined the residuals for normal and log normal models and selected the model that fit the data best. For tests of treatment effects on abundance and species richness, we simulated the posterior distribution 10,000 times to calculate 95% confidence intervals and approximate p-values for the fixed effects (Bagchi et al. 2011; Rapp et al. 2013). To test for significant differences in community composition between treatments we used adonis (package vegan), the analysis of variance of distance measures, grouped by block (1000 permutations; Bray in Oksanen et al. 2015). Mean percent cover abundance for each species that occurred in the subplots was entered into the multivariate test, and rare species that occurred in only 1 of the 4 treatment plots were removed prior to analysis (McCune, Grace, and Urban 2002). Data were analyzed using R statistical software, Vienna, Austria. Alpha was set = 0.05.

## RESULTS

Across the four plots in two blocks, 112 native vascular plant taxa were recorded, of which 104 were identified to species, 7 to genus, and 1 to family. Eighty-four taxa were native, 27 exotic, and one unknown. Growth forms included 6 fern species, 37 forbs, 28 graminoids, 15 trees, 20 shrubs, and 6 lianas (Tables 1, 2). Fifty-four taxa were common to both treatments; 27 were found only in the enclosure plots, and 31 taxa

Table 1. Mean abundance of common plant species and growth form groups in the herbaceous layer (<2m in height) by treatment in 2013. Only species that occurred in the 13, 1×1 m subplots of at least 2 of the 4 treatment plots are included. Standard errors are in parentheses; \*p≤0.05.

Species	Native	Exclosure	Grazed	Generalist Species
WOODY PLANTS		36.1 (2.6)	32.3 (0.02)	–
TOTAL				
TREES TOTAL		5.6 (2.9)	2.1 (1.4)	–
<i>Acer rubrum</i> L.	N	0	0.10 (0.02)	yes
<i>Fraxinus americana</i> L.	N	2.73 (0.27)	1.94 (1.4)	no
<i>Liriodendron tulipifera</i> L.	N	0.79 (0.79)	0.02 (0.02)	yes
<i>Prunus serotina</i> Ehrh.	N	1.44 (1.2)	0	yes
SHRUBS AND LIANAS TOTAL		30.5 (2.7)	30.2 (0.06)	–
<i>Berberis thunbergii</i> DC.	E	6.4 (0.73)	20.8 (4.2)*	yes
<i>Celastrus orbiculatus</i> Lam.	E	8.2 (3.88)	2.1 (0.5)	yes
<i>Euonymus alatus</i> (Thunb.) Siebold	E	4.5 (2.1)	0.42 (0.38)	yes
<i>Ilex verticillata</i> (L.) Gray	N	0.25 (0.02)	0.06 (0.06)	no
<i>Lindera benzoin</i> (L.) Blume	N	8.1 (7.9)	4.0 (3.96)	no
<i>Parthenocissus</i> <i>quinquefolia</i> (L.) Planch.	N	0.56 (0.29)	1.36 (1.3)	yes
<i>Rosa multiflora</i> Murray	E	0.13 (0.10)	0.37 (0.14)	yes
<i>Rubus flagellaris</i> Hook.	N	0.64 (0.64)	0.52 (0.29)	yes
<i>Rubus phoenicolasius</i> Maxim.	E	0.56 (0.25)	0.12 (0.12)	yes
<i>Toxicodendron radicans</i> (L.) Kuntze	N	0.56 (0.52)	0.11 (0.04)	yes
<i>Vitis ×novae-angliae</i> Fernald	N	0.12 (0.12)	0.17 (0.10)	yes
GRAMINOIDS TOTAL		3.0 (2.97)	24.3 (17.3)	–
Carex TOTAL		0.6 (0.54)	16.8 (10.7)*	–
<i>Carex gracillima</i> Steud. & Hochst.	N	0	1.1 (0.67)	yes
<i>Carex intumescens</i> Rudge	N	0	0.42 (0.38)	no
<i>Carex laxiculmis</i> Schwein.	N	0	0.77 (0.27)	no
<i>Carex radiata</i> Small	N	0.54 (0.54)	12.8 (11.7)	no
<i>Carex swanii</i> Mack.	N	0.02 (0.01)	0.69 (0.12)	no
<i>Cinna arundinacea</i> L.	N	1.2 (1.2)	2.1 (1.62)	no

Table 1. Continued.

Species	Native	Exclosure	Grazed	Generalist Species
<i>Dactylis glomerata</i> L.	E	0.12 (0.12)	0.02 (0.02)	yes
<i>Glyceria striata</i> (Lam.) Hitchc.	N	0.14 (0.14)	0.40 (0.40)	yes
<i>Leersia virginica</i> Willd.	N	0.40 (0.40)	0.12 (0.12)	yes
<i>Microstegium vimineum</i> (Trin.) A. Camus	E	0	3.94 (3.9)	yes
FORBS TOTAL		11.0 (1.42)	5.1 (0.39)*	—
<i>Arisaema triphyllum</i> Schott	N	0.63	0.50 (0.46)	no
<i>Circaea canadensis</i> (L.) Hill	N	2.1 (2.1)	0.12 (0.12)	no
<i>Eurybia divaricata</i> (L.) Nesom	N	3.1 (3.0)	0.6 (0.1)	no
<i>Galium triflorum</i> Michx.	N	0	0.15 (0.08)	no
<i>Geum</i> sp. L.	N	0	0.13 (0.10)	yes
<i>Impatiens capensis</i> Meerb.	N	1.8 (1.8)	0.14 (0.14)	yes
<i>Maianthemum canadense</i> Desf.	N	0.52 (0.52)	0.65 (0.04)	yes
<i>Mitchella repens</i> L.	N	0	0.13 (0.10)	no
<i>Oxalis stricta</i> L.	N	0.08 (0)	0.06 (0.06)	yes
<i>Persicaria longiseta</i> (Bruijn) Moldenke	E	0.06 (0.06)	0.11 (0.08)	yes
<i>Persicaria sagittata</i> (L.) H. Gross	N	0.06 (0.06)	0.93 (0.93)	yes
<i>Ranunculus recurvatus</i> Poir.	N	0.02 (0.02)	0.04 (0.02)	no
<i>Symplocarpus foetidus</i> (L.) Salisb. ex Nutt.	N	1.64	0.23	no
<i>Trillium erectum</i> L.	N	0.27 (0.27)	0.02 (0.02)	no
<i>Viola sororia</i> Willd.	N	0.02 (0.02)	0.68 (0.67)	yes
FERNS TOTAL	—	6.3 (6.3)	0.52 (0.52)	—
<i>Polystichum acrostichoides</i> (Michx.) Schott	N	2.25 (2.25)	0.5 (0.52)	no
EXOTIC TOTAL	—	21.4 (6.9)	28.7 (8.8)	—
NATIVE TOTAL	—	35.1 (6.25)	33.4 (8.35)	—

were found only in the grazed plots. Overall, species composition did not differ significantly by treatment (adonis:  $F=1.412$ ;  $R^2=0.41$ ;  $p=0.5$ ). Still, important differences emerged in the understory between treatments after 15 y. Forb cover was more than twice as high in



Table 2. Relatively uncommon plant taxa (<2m in height) that occurred in ≤2 of the 4 treatment plots (including meander surveys). \*Denotes species detected in meander survey but not in subplots.

Species	Native	Treatment	Block	Generalist Species
<b>TREES</b>				
<i>Acer palmatum*</i> Thunb.	E	exclosure	wet	yes
<i>Acer platanoides</i> L.	E	exclosure	wet	yes
<i>Acer saccharum</i> Marshall	N	exclosure	mesic	no
<i>Betula</i> sp.	N			
<i>Carya cordiformis*</i> (Wangenh.) K. Koch	N	grazed	mesic	no
<i>Fagus grandifolia</i> Ehrh.	N	grazed	wet	no
<i>Pinus strobus*</i> L.	N	exclosure	wet	yes
<i>Prunus avium</i> (L.) L.	E	exclosure	wet	yes
<i>Quercus rubra</i> L.	N	grazed/exclosure	wet	no
<i>Tsuga canadensis</i> (L.) Carrière	N	grazed	mesic	no
<i>Ulmus americana*</i> L.	N	exclosure	wet	yes
<b>SHRUBS AND LIANAS</b>				
<i>Benthامidia japonica*</i> (Siebold & Zucc.) H. Hara	E	exclosure	mesic	yes
<i>Eleagnus umbellata*</i> Thunb.	E	exclosure	wet	yes
<i>Euonymus fortunei</i> (Turcz.) Hand.-Mazz	E	exclosure	wet	yes
<i>Lonicera morrowii*</i> Gray	E	exclosure	wet	yes
<i>Lonicera japonica*</i> Thunb.	E	grazed	wet	yes
<i>Rubus allegheniensis*</i> Porter	N	exclosure	mesic	yes
<i>Rubus hispidus*</i> L.	N	grazed/exclosure	mesic	yes
<i>Rubus occidentalis</i> L.	N	grazed	wet	yes
<i>Sambucus nigra*</i> L.	N	exclosure	wet	yes
<i>Swida rugosa*</i> (Lam.) Rydb.	N	exclosure	wet	no
<i>Swida racemosa*</i> (Lam.) Moldenke	N	exclosure	wet	yes
<i>Viburnum dentatum*</i> L.	N	grazed/exclosure	wet/mesic	yes
<i>Viburnum lentago*</i> L.	N	exclosure	wet/mesic	yes
<b>GRAMINOIDS</b>				
<i>Anthoxanthum</i> <i>odoratum</i> L.	E	grazed	wet	yes

Table 2. Continued.

Species	Native	Treatment	Block	Generalist Species
<i>Carex blanda</i> Dewey	N	grazed	mesic	no
<i>Carex digitalis</i> Willd.	N	grazed	mesic	no
<i>Carex laevivaginata</i> (Kük.) Mack.	N	grazed	wet	yes
<i>Carex leptoneuria</i> * (Fernald) Fernald	N	grazed/exclosure	wet/mesic	no
<i>Carex normalis</i> Mack.	N	grazed	mesic	yes
<i>Carex rosea</i> * Schkuhr ex Willd.	N	grazed	mesic	no
<i>Carex scoparia</i> Schkuhr ex Willd.	N	grazed	wet	yes
<i>Carex</i> sp.	N	grazed	wet	?
<i>Carex stipata</i> Muhl. ex Willd.	N	grazed/exclosure	wet	yes
<i>Carex vulpinoidea</i> * Michx.	N	grazed	wet	yes
<i>Danthonia compressa</i> Austin ex Peck	N	grazed/exclosure	wet	yes
<i>Holcus lanatus</i> * L.	E	grazed	wet	yes
<i>Luzula multiflora</i> (Ehrh.) Lej.	N	exclosure	wet	yes
<i>Phalaris arundinacea</i> * L.	N	grazed	wet	yes
<i>Poa alsodes</i> Gray	N	grazed	wet	yes
<i>Poa nemoralis</i> L.	E	exclosure	wet	yes
<i>Poa trivialis</i> * L.	E	grazed	wet	yes
<i>Sphenopholis intermedia</i> (Rydb.) Rydb.	N	grazed	wet	no
FORBS				
<i>Alliaria petiolata</i> (M. Bieb.) Cavara & Grande	E	exclosure	wet/mesic	yes
<i>Cardamine impatiens</i> * L.	E	grazed	wet	yes
<i>Epilobium</i> sp.*	N	grazed	wet	?
<i>Erythronium americanum</i> Ker-Gawl.	N	exclosure	mesic	no
<i>Galium</i> sp. (4 leaves)	N	exclosure	mesic	?
<i>Lapsana communis</i> * L.	E	exclosure	wet	yes
<i>Nabalus</i> sp.*	N	grazed/exclosure	mesic	?
<i>Persicaria virginiana</i> * (L.) Gaertn.	N	grazed/exclosure	wet	no

Table 2. Continued.

Species	Native	Treatment	Block	Generalist Species
<i>Polygonatum pubescens*</i> (Willd.) Pursh	N	grazed	mesic	no
<i>Potentilla simplex*</i> Michx.	N	grazed/exclosure	wet	yes
<i>Ranunculus acris</i> L.	E	exclosure	wet	yes
<i>Ranunculus abortivus</i> L.	N	grazed	wet	no
<i>Smilax herbacea</i> L.	N	grazed	wet	yes
<i>Solidago caesia</i> L.	N	exclosure	wet	no
<i>Solidago patula*</i> Muhl. ex Willd.	N	grazed	wet	no
<i>Solidago rugosa</i> P. Mill.	N	grazed	wet	yes
<i>Symphotrichum lanceolatum</i> (Willd.) Nesom	N	grazed/exclosure	wet	yes
<i>Symphotrichum puniceum</i> (L.) A. & D. Löve	N	grazed/exclosure	wet	yes
<i>Sisyrinchium</i> sp.*	N	grazed/exclosure	wet	yes
<i>Veronica officinalis*</i> L.	E	grazed/exclosure	wet/mesic	yes
<i>Viola affinis*</i> Le Conte	N	exclosure	mesic	yes
FERNS				
<i>Athyrium angustum</i> C. Presl*	N	exclosure	mesic	no
<i>Dennstaedtia punctilobula*</i> (Michx.) T. Moore	N	grazed	mesic	yes
<i>Deparia acrostichoides</i> (Sw.) M. Kato	N	exclosure	mesic	no
<i>Onoclea sensibilis*</i> L.	N	grazed	wet/mesic	yes
<i>Parathelypteris noveboracensis</i> (L.) Ching	N	exclosure	mesic	no

exclosure (11.0; SE=1.4) than in grazed plots (5.1; SE=0.39; Treatment=-0.06; 95% CI=-0.103 to -0.015; p=0.031; Figure 2); and forest forbs comprised 76% (SE=0.20) of forb cover in exclosure plots compared with only 40% (SE=0.19) of forb cover in grazed plots. Ferns had a 12-fold greater cover in exclosure than in grazed plots, and ferns only occurred in the mesic block. In contrast, *Carex* spp. had a 28-fold greater cover in grazed than exclosure plots (Treatment=3.78; 95% CI=1.2 to 6.48; p=0.023). Total graminoid cover also trended higher in

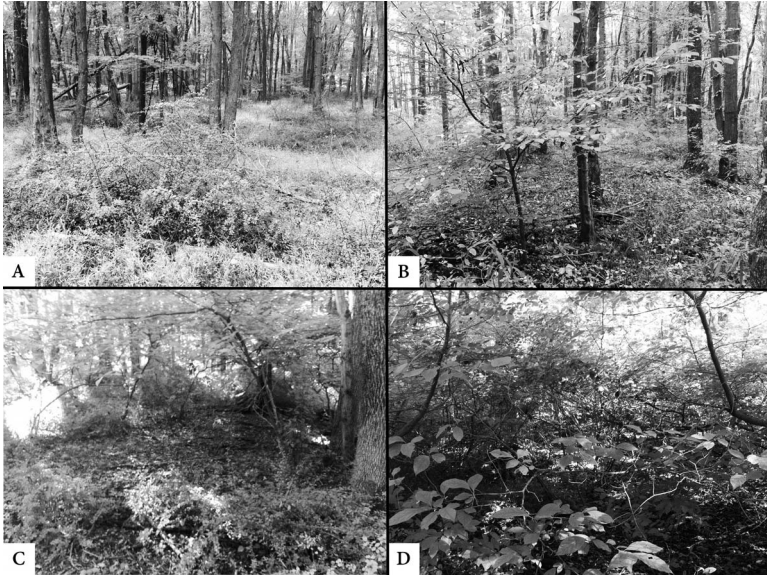


Figure 2. Photos of the four treatment plots in 2013. (A) wet block grazed plot dominated by graminoids [*Microstegium vimineum* and *Carex radiata*] and *Berberis thunbergii*; (B) wet block enclosure plot dominated by the forbs *Eurybia divaricata*, *Impatiens capensis*, and a mix of native and exotic shrubs; (C) mesic block grazed plot with sparse herb layer and *B. thunbergii*–*Lindera benzoin* shrub layer; and (D) mesic block enclosure plot dominated by dense *L. benzoin* shrub layer.

grazed plots by a factor of eight ( $p=0.12$ ) and in the wet block by a factor of seven ( $p=0.15$ ). Total woody plant cover (combined native and exotic) was similar between treatments and blocks (Table 1), but native woody cover ( $p=0.13$ ) was almost twice as high in enclosure compared to grazed plots and in mesic compared to wet plots ( $p=0.11$ ). Total native plant cover, however, was similar between the two treatments (Table 1).

Total exotic plant cover was marginally higher in grazed than enclosure plots ( $p=0.06$ ) and almost twice as high in the wet block (32.9%) compared to the mesic block (17.2%;  $p=0.02$ ). Over 70% of exotic species cover was comprised of *Berberis thunbergii*, which was approximately three times more abundant in grazed than fenced plots ( $p=0.04$ ; Figure 2). *Microstegium vimineum* was the second most

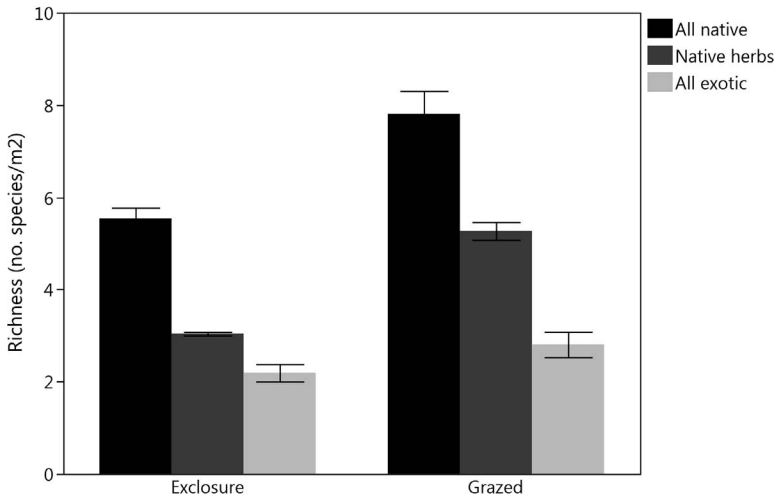


Figure 3. Effects of deer exclusion on native and exotic species richness <2 m in height at the subplot scale (mean # of species in 13 1-m<sup>2</sup> subplots in each plot). Bars represent mean  $\pm$ SE. All plant groups differed significantly at  $p \leq 0.05$ .

important exotic species in the grazed plots, comprising 14% of the exotic flora cover and was absent from the enclosure plots.

**Effect on species richness at the subplot scale (1m<sup>2</sup>).** Total mean species richness was lower in enclosure plots (7.7 species; SE=0.43) than in grazed plots (10.8 species; SE=0.31; Treatment=0.33; 95% CI=0.06 to 0.59;  $p=0.031$ ). Both native species (Treatment=2.27; 95% CI=-0.11 to 4.52;  $p=0.053$ ) and exotic species richness (Treatment=0.615; 95% CI=0.22 to 1.01;  $p=0.020$ ) were significantly higher in grazed than enclosure plots (Figure 3). Exotic richness was also higher in the wet block than the mesic block ( $p=0.031$ ). Grazed plots had more than twice as many native herb species, on average, than did enclosure plots (Treatment=0.55; 95% CI=0.38 to 0.715;  $p=0.004$ ; Figure 3). Native forb richness trended higher in grazed than enclosure plots ( $p=0.094$ ), but the reverse was true with respect to richness of forest forbs ( $p>0.10$ ). Neither native woody nor native shrub richness differed between treatments ( $p>0.10$ ), but native shrub richness ( $p=0.039$ ) and native forb richness ( $p=0.034$ ) were higher in the mesic than in the wet block.

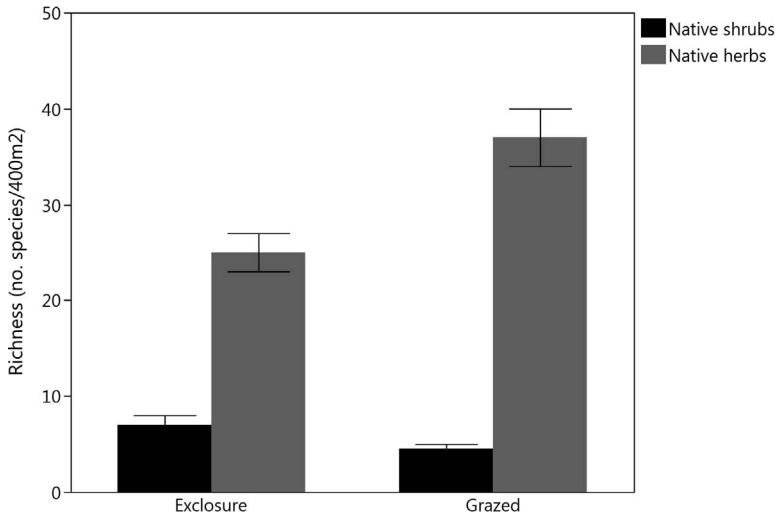


Figure 4. Contrasting effects of deer exclusion on species richness  $<2$  m in height at the plot scale ( $\# \text{species}/400 \text{m}^2$ ). Native herbaceous richness was higher in grazed plots, and native shrub richness was higher in exclosure plots. Bars represent mean  $\pm$  SE. Both groups differed significantly at  $p \leq 0.05$ .

**Effect on species richness at the plot scale (400 m<sup>2</sup>).** Total species richness trended higher in grazed (62 species; SE=4) than in exclosure plots (54.5 species; SE=9.5), but the difference was not significant ( $p=0.318$ ). Almost 10 more native species, on average, were sampled in grazed than in exclosure plots, a marginally significant difference ( $p=0.066$ ). Native herbaceous richness was significantly higher in grazed plots, with 12 more species, on average, than in exclosure plots (Treatment=12; 95% CI=7.54 to 16.58;  $p=0.007$ ; Figure 4). Number of forb species characteristic of undisturbed forests were also significantly higher in grazed plots (10 species; SE=0) than in exclosure plots (7.5 species; SE=0.5; Treatment=0.29; 95% CI=0 to 0.58;  $p=0.049$ ). In contrast, native shrub richness was lower in grazed plots, by almost 3 species, on average, compared to exclosure plots (Treatment= -0.25; 95% CI= -4.71 to -0.42;  $p=0.036$ ; Figure 4). Exotic species richness and native woody richness did not differ between treatments ( $p>0.10$ ). Native shrub richness (1.5 species more, on average;  $p=0.018$ ) and native herb richness (5 species more, on average;  $p=0.039$ ) were both higher in the wet block than the mesic block. All other richness variables did not differ between block ( $p>0.10$ ).

## DISCUSSION

Results from this long-term study suggest a suburban forest understory transformed by high deer densities (21–24 km<sup>-2</sup>), with relatively diverse communities of both native and exotic plants coexisting with intensive herbivory. To our knowledge, this exclosure experiment is the first in New England—and one of only a handful in the eastern deciduous forest—to examine the effects of deer on herbaceous understories over an at least 15-y time frame (Frerker et al. 2014; Goetsch et al. 2011; Rooney 2009; Webb et al. 1956). However, our study was restricted to a single exclosure site without pre-treatment observations (cf. Goetsch et al. 2011), limiting its extrapolative power. In addition, like most other exclosure studies, the fence was built in a landscape in which deer densities had been moderate to high for at least the previous 10 y. Therefore, it is possible that past herbivory could have limited the available species and propagules able to recover inside the exclosure plots (Banta et al. 2005; Waller 2014).

Despite the inherent limitations of our study, several results on plant life form abundance corroborated broad-scale and well-documented deer–forest relationships. Exclusion of deer resulted in greater forb cover and much lower *Carex* spp. cover compared to areas grazed by deer (cf. Rooney 2009; Waller 2014). In addition, a disproportionately high cover of forest forbs occurred in exclosure, relative to grazed plots, suggesting a shift from a forb community dominated by generalist species to one dominated by forest species as a result of deer exclusion (cf. Rooney et al. 2004; Table 1). Deer exclusion also generally resulted in reduced exotic species cover ( $p=0.06$ ), most notably of the unpalatable and invasive *Berberis thunbergii* and *Microstegium vimineum*, relative to grazed plots (cf. Eschtruth and Battles 2009; Frerker et al. 2014). Still, some prominent invasive exotic species including *Euonymus alatus* and *Celastrus orbiculatus* appeared to benefit from protection from deer browsing (cf. Rossell et al. 2007; Table 1).

In contrast to life-form abundance, our results on deer species richness relationships were more complex than and less consistent with existing literature. Greater native species richness (subplot scale) and herb richness (subplot and plot scale) in the grazed plots corroborated results from a recent long-term study in European woodlands (Perrin et al. 2011), but contrasted with several North American studies reporting negative effects by deer on herb diversity in eastern deciduous forests (Goetsch et al. 2011; Rooney and Waller 2003; Webster et al. 2005). Our results could be explained, in part, by the moist and relatively productive soils on which the study occurred. In the absence of large

herbivores, productive soils typically support high plant biomass, resulting in reduced ground-level light and low species richness relative to grazed areas (Borer et al. 2014; Hester et al. 2006). Indeed, the super-dominant *Lindera benzoin* shrub layer in the mesic block exclosure plot (Figure 2d) coincided, by far, with the lowest species richness of the four plots.

Another possible driver of higher species richness in grazed plots was the diverse landscape context of the study area and the resulting large pool of species available to fill gaps created by grazing and trampling by deer (Hester et al. 2006; Olf and Ritchie 1998). Our plots were located 50–100 m from open fields, shrub thickets, and residential houses. The total species count (112 taxa) in the four plots was 4–5 times higher than those found in other long-term deer-exclosure studies in which species richness either declined, or remained unchanged with herbivory (Goetsch et al. 2011; Rooney 2009). Interestingly, despite much greater cover by forest-specialist forbs in exclosures, relative to grazed plots, richness of forest forbs remained higher in grazed areas at the plot scale.

The coincidence of lower cover of forest forbs and greater species richness of forest forbs in grazed areas seems counterintuitive, particularly in light of well-documented declines of browse-sensitive forest species such as *Polygonatum* spp., *Trillium* spp., and *Uvularia* spp. due to deer herbivory (Knight 2004; Waller 2014; Webster et al. 2005). However, significant reductions in plant biomass from browsing do not necessarily correspond with a decline in diversity; indeed, diversity and plant biomass can be inversely related if herbivory is evenly distributed across a plant community (Ritchie and Olf 1999). Thus, although browse-sensitive forest species such as *Eurybia divaricata* and *T. erectum* were greatly reduced in density by deer in our study area, these species persisted as small, scattered individuals in the grazed plots, alongside many other species of low stature and density.

Dynamics in the shrub layer were notably different from the herb layer. Greater native shrub richness occurred with deer exclusion at the plot scale, revealing contrasting effects by deer on the richness of different plant life forms (cf. Hegland et al. 2013). Browse-sensitive shrub species such as *Sambucus nigra* L., *Swida racemosa* (Lam.) Moldenke, *S. rugosa* (Lam.) Rydb., and *Viburnum lentago* L. were found only inside the exclosure plots. Declines in shrub richness due to deer have been documented in many studies in the eastern temperate forest (Banta et al. 2005; Goetsch et al. 2011; Royo et al. 2010).



The concurrently higher native and exotic species richness (subplot scale) in grazed plots corroborate recent studies showing little negative effect by exotic plants on native plant richness (Davis et al. 2015; Flinn et al. 2014). In fact, native and exotic plant richness may simultaneously increase in response to similar environmental gradients (Gilbert and Lechowicz 2005). Exotic and native species not only responded similarly to deer activity in our study area but also, in several cases, to the different soil and land use history conditions of the mesic and wet blocks. Greater exotic plant cover and richness and native herb and shrub richness in the wet block (plot scale) may be attributed to a younger, more recently disturbed forest or to higher pH and lower nitrate levels of the soils (Gilbert and Lechowicz 2005; Faison et al. unpubl. data).

Our results reveal that intensive deer herbivory influenced the richness and abundance of different plant life forms in contrasting ways, and that the outcome of deer activity on native and exotic vegetation was often strongly determined by spatial scale. In addition, site heterogeneity exerted a powerful and scale-dependent effect on vegetation patterns, even in the midst of intensive deer herbivory (cf. Hunter and Price 1992).

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