Recovery of the Herb Layer in a Southern Appalachian Forest Following Chronic Herbivory by Deer (*Odocoileus virginianus*)

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ABSTRACT The high abundance of ungulates in temperate zone forests is affecting biodiversity and ecosystem functions worldwide. A randomized, replicated experiment excluded white-tailed deer, *Odocoileus virginianus*, from six 10×10 m fenced plots for 10 years; six unfenced plots were maintained as controls. The effects of chronic herbivory were assayed by comparisons using the mean responses of ground-level vegetation in nine subplots within each of the 12 plots. Deer had a small effect on species richness but a strong effect on species prevalence, cover, and biomass, with repeatable differences in the responses of taxa to the treatments. Graminoids were favored in control plots, many other monocots and several dicots were favored in fenced plots, and parasitic plants and chemically defended herbs showed few detectable responses to fencing. The height of the vegetation represented by the shrub *Vaccinium erythrocarpum* and the herb *Medeola virginiana* was significantly taller in fenced than in control plots. This experiment demonstrated that many forest herbs, especially those in the Liliaceae sensu lato, tolerate repeated browsing without flowering, probably for decades. When released from browsing, the time required for these species to sequester sufficient resources to flower and successfully develop seeds varied from 1 to 10 years among species. Managers of forest ecosystems must consider the impacts of game management on biodiversity.

Key words: Deer, ground layer, herbivory, herb layer, ungulate.

INTRODUCTION The herb layer vegetation, also called the ground layer, is a critical link between forest dynamics, wildlife habitat, and conservation management. All canopy trees must pass through their seedling and juvenile stages in the herb layer, which is also the most diverse stratum in forests (Gilliam and Roberts 2003, Gilliam 2014). Important game species such as white-tailed deer (*Odocoileus virginianus*), black bear (*Ursus americanus*), turkey (*Meleagris gallopavo*), and ruffed grouse (*Bonasa umbellus*) feed and seek cover at or near the ground layer. Diversity of arthropods, reptiles, amphibians, small mammals, and many birds

depends on a structurally complex and species-rich herb layer. Currently herb assemblages in north temperate forests worldwide are being threatened by high abundance of ungulates (McShea et al. 1997, Russell et al. 2001, Côté et al. 2004, Speed et al. 2014). Peek and Stahl (1997, cited by Rooney and Waller 2003) reported over 150 species of vascular plant were extirpated from Sharon Woods Metro Park, Columbus OH, by a deer population allowed to exceed 100 animals per square kilometer.

Studies in many ecosystems indicate that selective feeding by ungulates (a) suppresses regeneration of woody species (George and Bazzaz 2014), (b) reduces the height and abundance of preferred or browse-tolerant herbs (Balgooyen and Waller 1995), (c) increases the abundance of unpalatable herbs (Wiegmann and

Waller 2006), (d) may favor invasive species (Wiegmann and Waller 2006), (e) may have cascading effects on other trophic levels above and below ground (Ostfeld et al. 1996), (f) may impact ecosystem nutrient cycling (Côté et al. 2004), and (g) may give ungulates the role of "ecosystem engineers" or "keystone species" that switch communities into alternative stable states (McShea and Rappole 1992). The white-tailed deer is generally accepted as a keystone species (sensu Paine 1995, Power et al. 1996) in the eastern deciduous forest of North America (McShea and Rappole 1992, Waller and Alverson 1997). Our study experimentally tests the hypotheses that deer in the southern Appalachians act as drivers of the structure of the vegetation in the herb layer, and that the exclusion of deer allows growth and reproduction of palatable herbs, regeneration of woody species, and suppresses graminoids.

Russell et al. (2001), reviewing the geographical distribution of studies of the effect of white-tailed deer ("deer" hereafter) on nonwoody vegetation in North America, found a strong bias toward studies of northern hardwood and mixed conifer forests in the Upper Midwest. This bias has continued since this review (Rooney 2001, Rooney et al. 2004, Wiegmann and Waller 2006, Rooney 2009, Begley-Miller et al. 2014, Roberts and Gilliam 2014, Waller 2014). The Allegheny Plateau of Pennsylvania is another area of extensive research (Hough 1965; Stromayer and Warren 1997; Horsley et al. 2003; Royo et al. 2010a, 2010b; Goetsch et al. 2011; Kain et al. 2011; Carson et al. 2014). Effects of deer on vegetation have been studied in the southern Appalachians at Cade's Cove in Great Smoky Mountain National Park, Tennessee (Webster et al. 2005a, 2005b; Griggs et al. 2006; Thiemann et al. 2009; Kuebbing et al. 2013) and in the central Appalachians at the Smithsonian Conservation Biology Institute in the Blue Ridge Mountains of Virginia adjacent to Shenandoah National Park (McShea and Rappole 1992, 1997). Our study in the Allegheny Mountains of the Ridge and Valley Province is between these two Appalachian sites.

Russell et al. (2001) also bemoaned the lack of rigorous studies demonstrating the perceived strong effects of deer on nonwoody individuals, populations, and communities. Many studies since their review have focused on the effects of white-tailed deer on ground layer herbs (e.g.,

Amatangelo et al. 2014), including genetic studies of natural selection by deer on herbs (Stinchcombe 2002; Knight 2003, 2007; Knight et al. 2009; Prendeville et al. 2015) and population dynamics of particular species, such as *Trillium*, a highly preferred perennial herb (Jenkins et al. 2007; Knight 2003, 2007; Gonzales et al. 2008; Koh et al. 2010). Herbs like *Trillium* spp. (Knight et al. 2009), *Aralia nudicaulis* (Edwards 1985), *Clintonia borealis* (Balgooyen and Waller 1995), *Lilium superbum* (Fletcher et al. 2001), *Medeola virginiana* (Tilghmann 1989), and geophytic orchids (Alverson et al. 1988, Goetsch et al. 2011) have been suggested for use as indicator species of the impact of deer. Deer may benefit these species by dispersing their seeds (Vellend et al. 2003), but may reduce their occurrence, height, flowering frequency, and other characteristics. The fitness trade-off between the effects of deer on a species' seed dispersal parameters and fecundity has not been explicitly studied to our knowledge. Heckel et al. (2010) found that deer also negatively impacted unpalatable species, such as *Arisaema triphyllum*, perhaps by compacting soil or reducing depth of leaf litter, contrary to the positive effect that would be expected from reducing competition with palatable herbs.

Studies of ungulates' effects on forest herbs have employed various approaches reviewed by Waller (2014). The most rigorous experimental studies use fences to exclude all ungulates (e.g., Augustine et al. 1998, Horsley et al. 2003, Kraft et al. 2004, Webster et al. 2005a, Rooney 2009, Royo et al. 2010b, Goetsch et al. 2011, Holmes and Webster 2011, Kain et al. 2011, Begley-Miller et al. 2014), but these result in the extreme contrast between current overpopulation and the removal of deer. Exclosure studies have another important limitation (Rooney and Waller 2003), in that they cannot validly be used to contrast the conditions of deer present with deer absent, because vegetation within fences reflects the legacy of local deer densities. Exclosures do demonstrate, however, the process of recovery from the effects of deer, while they most certainly underestimate the local legacy of deer because species extirpated by deer will be missing from both enclosed and control plots.

We present results of a 10-yr experiment in which we excluded deer from replicated plots and studied the differential response of species in the herb layer to predict how forest commu-

nities would recover if deer densities were reduced. Our analyses first took a community approach using ordination to describe the effects of deer on the herb layer community. We then took a population approach to measure the impact of deer on selected species, including the time to resume reproduction after release from chronic herbivory. The density of deer on the study area is currently very high (Rearick et al. 2011) after recovering from local extinction in the last 75 yr (Knox, 1997). For 10 yr we maintained replicated plots randomly assigned as either an unfenced control group or to a treatment group in which we fenced plots to exclude deer but no other likely herbivores in the area.

METHODS

Study Site

This study took place in a second-growth hardwood stand on a gentle 5° northwest-facing slope at 1160 m elevation at Mountain Lake Biological Station (MLBS) atop Salt Pond Mountain, Giles County, Virginia, USA (37°22′22″N, –80°31′6″W). The acidic and low-nutrient soils at Mountain Lake Biological Station are sandy loam colluvium derived from Tuscarora, Juniata, and Rosehill sandstones (Swecker et al. 1985). Precipitation is weakly seasonal with the driest months being October and April. Snow cover is highly variable from late November into April. The mean total rainfall in the growing season, April through October, is 746 mm; fog is frequent. January mean daily minimum and maximum temperatures are –8°C and 2.12°C, respectively, and July mean daily minimum and maximum temperatures are 13.28°C and 24.35°C, respectively, (MLBS weather records 1972–1998). High winds and occasional ice storms in the winter, and rare hurricanes in the fall can cause considerable damage by thinning the canopy or creating gaps by windthrow. The last known wildfire at the station occurred around 1929.

The study site is in a second-growth stand strongly dominated by *Quercus rubra* with lesser densities in the canopy of (in order of decreasing abundance) *Quercus alba, Acer rubrum, Betula lenta, Carya glabra, Carya tomentosa, Amelanchier arborea, Robinia pseudo-acacia, Magnolia acuminata, Quercus montana,* and *Acer saccharum.* The shrub layer is co-dominated by *Acer pensylvanicum, Acer rubrum,* and *Castanea dentata,* with less common *Rhododendron calendulaceum, Vaccinium corymbosum, Hamamelis virginiana,* and *Crataegus* sp. also present. The station adjoins the Mountain Lake Wilderness Area of Jefferson National Forest and two large private tracts with low levels of hunting. Large areas of the ground layer are closed stands of the ferns *Dennstaedia punctilobula* or *Parathelypteris noveboracensis* and other areas are lawns of the sedge *Carex pensylvanica*, vegetation associated with high densities of deer (de la Cretaz and Kelty 1999, 2002; Royo and Carson 2006), and low diversity of herbs and tree seedlings (Powers and Nagel 2009). The stand used in this study has sparse patches of *C. pensylvanica* and *Parathelypteris noveboracensis*, which allows for a moderately rich cover of herbaceous species.

Experimental Design and Sampling

Twelve 10×10 m plots were chosen so that each included two or more *A. pensylvanicum* trees and clumps of *C. dentata* sprouts for another study. Half of the plots were randomly chosen to be fenced in the spring of 2006, with 2.25-m-tall plastic 4.5×5 cm mesh attached to metal posts. We chose a completely randomized design rather than pairing each fenced plot with a control plot because we considered the study area a reasonable homogeneous stand (Table 1) that was our statistical universe of inference. Paired plots would have been used if our study had included multiple sites to avoid confounding site differences with treatment differences. A 3×3 array of 3×3 m subplots were marked inside each plot with PVC stakes at their corners, with a 0.5 m buffer next to the fence on all edges of the plot. Fences were kept in good repair between late March and December. Any winter damage was repaired in March before the start of the growing season.

In late June or early July of 2006–2009, 2012, and 2014 the ground layer vegetation (<50 cm high) was sampled using a circle with an internal area of 1 m^2 in the center of each 3×3 m subplot. First, the percent cover of each species inside the circle was estimated by eye, and then the entire 9-m^2 subplot was searched for the occurrence of any species not recorded in the subsample. All vascular plants were identified to species. Taxonomy follows Weakley et al. (2012). Any uncertain individuals, usually juveniles, were photographed and followed through development until they could be identified. Unknowns were occasionally matched with

Table 1. Physical attributes of the study plots. Easting and northing are UTM coordinates (Zone 17) in meters. Slope is in degrees determined with an Abney level. Heat is a transformation of aspect to scale from 0 (northeast) to 1 (southwest; McCune and Grace 2002). Soil pH was determined from a 1:1 soil:water slurry. Skym and SkySD are the mean and standard deviation, respectively, of four spherical densitometer estimates of canopy openness (Lemmon 1956). CanPC1 and CanPC2 are the first two principal components of species composition of the canopy above the plots.

Plot	Treat	Easting	Northing	Slope	Heat	SoilpH	SkyM	SkySD	CanPC1	CanPC2
2	Control	542619	4136415	–	0.146	4.48	5.94	2.49	−1.1495	−2.4286
3	Control	542611	4136396	4.0	0.242	4.52	8.44	3.90	−1.2545	−0.6002
5	Control	542645	4136347	2.7	0.071	4.72	6.63	2.09	−0.4165	−0.8884
7	Control	542654	4136279	7.4	0.090	4.55	5.06	2.98	0.5396	0.3480
8	Control	542666	4136263	5.4	0.159	4.23	8.94	4.77	−1.4114	2.2520
12	Control	542664	4136328	4.3	0.439	4.39	4.13	1.71	2.0668	−0.1625
1	Fenced	542580	4136406	5.5	0.899	4.46	8.19	3.87	−1.7789	0.8249
4	Fenced	542651	4136385	5.7	0.047	4.76	5.94	2.84	0.4300	−1.5580
6	Fenced	542641	4136315	4.6	0.027	4.36	6.13	2.03	−1.4861	0.2752
9	Fenced	542697	4136265	7.5	0.000	4.41	10.06	3.51	0.9510	1.0840
10	Fenced	542690	4136283	3.7	0.095	4.49	5.69	2.44	0.4401	0.6436
11	Fenced	542683	4136279	4.0	0.000	4.55	5.13	0.96	3.0695	0.2099

plants outside the plots, which were transplanted to a protected place until they flowered and could be identified. Thus, the lowest levels of sampling included the 1-m^2 subsamples and the occurrence data within each of the nine 3×3 m subsamples per plot. The next level of sampling used means or sums of estimates from the nine subsamples within a plot to estimate values of variables for each plot; these variables were used as independent estimates of differences between the six replicates of the fenced and control treatments. The community data were approached from four angles: species occurrences (binary), species prevalence (0–9), species cover (%), and above-ground biomass (g).

In 2014, the canopy cover was estimated at the center of each plot using a spherical densitometer (Lemmon 1956). Other environmental variables included the plot's slope, aspect, soil pH (measured in a 1:1 by mass slurry with deionized water), and a principal component analysis of the species composition of canopy trees directly above each plot. The low variances of these measures of the habitat confirmed the homogeneity of the study site but rendered them uninformative covariates in our analyses. They are reported in Table 1, as they should prove useful in comparing the ecological context of this study to those of other studies.

Between August 12–16 of 2015 (yr 9 of the study), we clipped the vegetation at ground level in a 50×50 cm plot in the center of each of the 108 3×3 m subplots to determine above-ground biomass of all vascular plants <1.5 m tall. The clipped vegetation was dried at 60°C and then weighed to 0.001 g precision on a Mettler PR503 balance (Mettler-Toledo, Columbus, OH). *Conopholis americana* and *Monotropa uniflora*, two nonphotosynthetic parasites, were not collected. *Anemone quinquefolia* and *Viola hastata* were probably underrepresented in these biomass samples because they tend to die back in late summer, especially if they did not set seed. The height of the tallest individual in each subplot of *Medeola virginiana*, a typical shade-tolerant (Humbert et al. 2007), perennial herb (Bell 1974, Bierzychudek 1982, Cook 1988, Whigham and Chapa 1999) used previously as an indicator species of deer browsing (Tilghmann 1989, Royo et al. 2010a), and of *Vaccinium erythrocarpum*, a clonal shrub, were measured to represent the vertical extent of the vegetation. These two species were chosen because they occurred in all plots.

Occurrence, Species Diversity, and Prevalence

The effect of release from chronic herbivory by deer on the composition and structure of the herb layer were tested with three metrics of a species' importance in 2014: its occurrence, prevalence, and cover in the plot. The presence data for the 1-m^2 subsample and the search of the area in each 3×3 m subplots outside the subsample were combined to create the occurrence matrix. The resulting nine estimates of the species present in a 9×9 m plot were aggregated in a single species list for each of the 12 plots. These data were used to construct a Plot $\times$

Species binary occurrence matrix as input for tests of treatment effects. A difference in species richness between control and fenced plots was tested using the randomization methods of Cayuela et al. (2015). Prevalence was measured as the number of subplots per plot in which each species occurred. The second Plot × Species matrix had prevalence (integers 0–9) as its elements. These count data were considered to be Poisson-distributed and so were transformed to their square root before ordination. The average prevalence of all species was 1.70 in control samples and 1.97 in treatment samples. Given these low means, under the Poisson model the probabilities of observing a value ≤ 9 for prevalence in control and treatment samples are 0.9999 and 0.9995, respectively. This justifies the use of a Poisson model on counts confined to the interval 0–9.

Cover and Biomass

The percent cover of all vascular species, moss, dead wood, and rocks in the 1-m^2 subsamples in 2014 were estimated by eye into the following classes: 0.5%, 1%, 2.5%, 5%, 10%, 20%, 25%, 50%, 75%, and 90%. The nine subplot estimates were summed for each species in each plot. The transformation ln(sum + 1) was applied to account for their skewed distribution on the interval 0–900 for statistical tests. Biomasses of the nine subsamples for each species were also summed and log-transformed before analysis.

We compared differences in cover between 2006 and 2014 within plots between fenced and control plots to assay the dynamics of the vegetation on a decadal time scale. We had far more confidence in species identifications in 2014 than in the earliest years because our ability to identify juvenile and nonflowering plants of difficult taxa had improved. Not all 2006 records could be identified retrospectively using photographs and field notes, so all species were sorted into 11 groups: juvenile trees, deciduous dicots, evergreen dicots, Liliaceae sensu latro (=Colchicaceae, Liliaceae, Melanthiaceae, Ruscaceae, and Trilliaceae), Orchidaceae, sedges and rushes, grasses, ferns, shrubs, vines, and parasites (see Table 2 for assignment of species to these functional groups). These groups are intended to reflect differences in growth form, stature, and palatability that might affect their use by deer. Rooney and Waller (2003) advocate the use of such groups in preference to focusing on "winner" and "loser"

species that are "inefficient and lacks predictive power."

The engine for analysis was nonmetric multidimensional scaling (NMS) ordination as implemented in PC-Ord (McCune and Grace 2002, Peck 2010). The default options (e.g., Sorenson distance) were used except final runs used the "slow and accurate" option for NMS numerical solutions. Sorenson ("city block") distances were used rather than Euclidean distance because they reflect the stepwise addition or subtraction of species from an assemblage in the S-dimensional space where S is the number of species (McCune and Grace 2002).

Nonparametric MANOVA was used to test treatment differences by the method of Anderson (2001) as implemented in PC-Ord (McCune and Grace 2002). The GLM Procedure in SAS Version 12.3 (SAS Institute 2012) was used for analysis of total biomass and height of *M. virginiana* and *V. erythrocarpum*. The general linear model (GLM) tested for differences between fenced and control plots for each of the two species using the plot means of height and biomass.

RESULTS

Species Richness and Prevalence

Across all 12 plots, 87 species were observed in 2014; 63 species were observed on the control plots and 72 on the fenced plots (Table 2), with a Jaccard index (a coefficient of similarity on the interval 0–1) of 0.5517. The test for differences between species richness of samples recently introduced by Cayuela et al. (2015) failed to reject the null hypothesis that the two sets of samples were drawn from a common pool of species ($z_{ecol} = 36.65$, p > 0.18). Differences in species composition are addressed by the analysis of the binary occurrence matrix. The NMS ordination of the binary Plot × Species occurrence matrix required a three-dimensional solution. Permutation-based nonparametric MANOVA calculated with the method of Anderson (2001) indicated a significant difference ($F_{1,10} = 2.34$; p = 0.03) in the occurrence of species in fenced and controlled plots, although the treatments accounted for only 18.3% of the total variation among the 12 plots. The differences in the species compositions of fenced and control plots reflect, for example, the herbs *Coreopsis major* and *Gillenia trifoliata* and seedlings of *Sorbus americana* that occurred in

Table 2. Species encountered on the plots, their assignment to a group, and the number of plots in which they occurred (0 to 6) in the control and fenced treatment groups. Nomenclature follows Weakley et al. (2012).

Species	Group	Control	Fenced
Acer pensylvanicum L.	Tree	6	6
Acer rubrum L.	Tree	6	6
Agrostis perennans (Walter) Tuck.	Grass	1	0
Amelanchier arborea (Michx. F.) Fernald	Tree	6	6
Amianthium muscitoxicum (Walter) A. Gray	Decid. monocot	4	4
Anemone quinquefolia L.	Deciduous dicot	6	6
Athyrium asplenioides (Michx) A. A. Eaton	Fern	0	1
Betula lenta L.	Tree	0	1
Carex appalachica J. Webber & P. W. Ball	Sedge	1	0
Carex digitalis Willd.	Sedge	3	2
Carex flexuosa Muhl. ex Willd.	Sedge	2	0
Carex pensylvanica Lam.	Sedge	6	6
Carex swanii (Fernald) Mack.	Sedge	2	0
Carya tomentosa (Lam. ex Poir.) Nut.	Tree	0	1
Castanea dentata (Marshall) Borkh.	Tree	5	6
Chimaphila maculata (L.) Pursh	Evergreen	0	1
Clintonia borealis (Aiton) Raf.	Decid. monocot	0	1
Clintonia umbellulata (Michx) Morang	Decid. monocot	2	5
Conopholis americana (L) Wallr.	Parasite	6	6
Coreopsis major Walter	Deciduous dicot	0	5
Crataegus sp.	Tree	0	1
Danthonia compressa Austin ex Peck	Grass	2	0
Dichanthelium clandestinum (L.) Gould	Grass	6	5
Dioscorea villosa L.	Vine	6	6
Festuca subverticillata (Pers.) Alexeev	Grass	2	1
Galax urceolata (Poir.) Brumitt	Evergreen	5	6
Gaultheria procumbens L.	Evergreen	3	3
Gaylussacia baccata (Wangenh.) K. Koch	Shrub	0	1
Gentiana austromontana Pringle & Sharp	Deciduous dicot	5	3
Gillenia trifoliata (L.) Moench	Deciduous dicot	0	5
Goodyera pubescens (Willd.) R. Brown	Orchid	4	2
Hamamelis virginiana L.	Shrub	1	1
Ilex montana Torr. &A. Gray ex A. Gray	Shrub	5	6
Isotria verticillata (Muhl ex Willd.) Raf.	Orchid	0	3
Lapsana communis L.	Deciduous dicot	1	0
Ligusticum canadense (L.) Britton	Deciduous dicot	1	1
Lilium canadense L.	Liliales	1	1
Lilium superbum L.	Liliales	4	6
Luzula bulbosa (Wood) Smyth & Smyth	Sedge	1	0
Lysimachia quadrifolia L.	Deciduous dicot	2	1
Magnolia acuminata L.	Tree	0	3
Maianthemum canadense Desf.	Liliales	1	0
Maianthemum racemosum (L.) Link	Liliales	5	6
Medeola virginiana L.	Liliales	6	6
Menziesia pilosa (Michx. ex Lam.) Juss. ex Pers.	Shrub	0	3
Monotropa uniflora L.	Parasite	3	2
Nabalus altissimus (L.) Hook.	Deciduous dicot	5	5
Nabalus trifoliolatus Cass.	Deciduous dicot	0	1
Nyssa sylvatica Marshall	Tree	0	1
Oclemena acuminata (Michx.) Greene	Deciduous dicot	4	2
Parathelypteris noveboracensis (L.) Ching	Fern	2	5
Pinus strobus L.	Tree	1	0
*Platanthera orbiculata (*Pursh) Lind.	Orchid	0	1
Poa sp.	Grass	0	1
Polygonatum biflorum (Walter) Elliott	Liliales	4	4
Polystichum acrostichoides (Michx.) Schott	Fern	0	1
Potentilla simplex Michx.	Deciduous dicot	3	2
Prosartes lanuginosa (Michx.) D. Don	Liliales	2	2
Prunus serotina Ehrh.	Tree	2	6

Table 2. Continued

Species	Group	Control	Fenced
Pteridium aquilinum (L.) Kuhn	Fern	0	1
Quercus alba L.	Tree	6	4
Quercus rubra L.	Tree	6	6
Quercus velutina Lam.	Tree	2	3
Rhododendron calendulaceum (Michx.) Torr.	Shrub	5	6
Robinia pseudoacacia L.	Tree	2	0
Rubus hispidus L.	Deciduous dicot	1	0
Rubus sp. (blackberry)	Deciduous dicot	0	1
Smilax glauca Walter	Vine	0	1
Smilax herbacea L.	Vine	5	6
Solidago curtisii Torr. & A. Gray	Deciduous dicot	1	6
Sorbus americana Marshall	Tree	0	5
Stellaria pubera Michx.	Deciduous dicot	2	2
Taraxacum officinale G. H. Webber ex Wigg.	Deciduous dicot	0	1
Trientalis borealis Raf.	Deciduous dicot	1	0
Uvularia perfoliata L.	Liliales	6	4
Uvularia puberula Michx.	Liliales	3	3
Vaccinium angustifolium Aiton	Shrub	5	5
Vaccinium corymbosum L.	Shrub	4	4
Vaccinium erythrocarpum Michx.	Shrub	6	6
Vaccinium pallidum Aiton	Shrub	6	6
Vaccinium simulatum Small	Shrub	0	1
Vaccinium stamineum L.	Shrub	0	2
Viburnum cassinoides L.	Shrub	1	0
Viola blanda Willd.	Deciduous dicot	1	0
Viola hastata Michx.	Deciduous dicot	6	6
Viola palmata L.	Deciduous dicot	0	1
Viola rotundifolia Michx.	Deciduous dicot	2	1
Zizia trifoliata (Michx.) Fernald	Deciduous dicot	1	3

no control plots but were all were found in five of the six fenced plots.

Prevalence is a measure of commonness of a species within plots in which they occur. The NMS ordination of the prevalence of species in the Plot × Species matrix recommended a two–dimensional solution (Figure 1). Permutation-based nonparametric MANOVA indicated a strongly significant ($F_{1,10} = 2.99$; p = 0.0020) effect of fencing on the mean number of subplots per plot in which species occurred (prevalence). The treatments accounted for 24.2% of the total variation among the 12 plots. The species with the greatest difference in prevalence in the herb layer of fenced compared with control plots were juveniles of the woody species *C. dentata, Prunus serotina, Q. rubra, R. calendulaceum,* and *Ilex montana,* and the herbaceous vine *Smilax herbacea.* Differences in prevalence of the herbs *Maianthemum racemosum* and *Gillenia trifoliata* were slightly less. The species with lesser prevalence in fenced plots compared with control plots were *Dichanthelium clandestinum, Viola hastata, A. pensylvanicum, Conopholis americana,* and *Viola rotundifolia*

(Table 2). These results demonstrate both positive and negative effects of deer on the commonness of species. These results are largely repeated in the analysis of cover.

Cover

Cover is a measure of the spatial extent of a species within a subplot. The NMS ordination of cover expressed as ln(sum of subplot percent covers + 1) recommended a two-dimensional solution that clearly separated the fenced from the control plots (Figure 2). Permutation-based nonparametric MANOVA indicated a strongly significant ($F_{1,10} = 8.17$; p = 0.0026) effect of fencing that accounted for 54.45% of the total variation across all 12 plots. Among the species that occurred in both fenced and control plots, those that increased cover the most in the fenced plots compared with control plots were shrubs and juvenile trees below 50cm high, specifically *Vaccinium erythrocarpum, A. rubrum, Q. rubra, C. dentata, R. calendulaceum, Gaultheria procumbens, Q. alba, Vaccinium stamineum,* and *Gaylussacia baccata,* as well as the fern *P. noveboracensis* and herbs *Dioscoria*
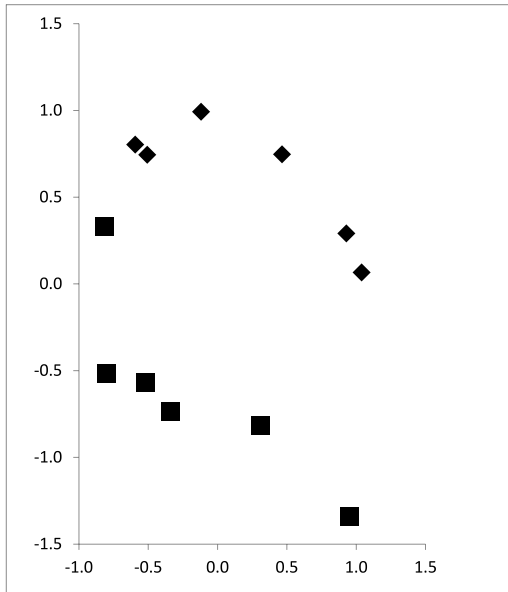
Figure 1. NMS Ordination of Prevalence (PC-Ord; McCune and Mefford 2011). Each point represents a plot sampled in 2014. The control plots are represented by squares; the fenced plots are represented by diamonds.

villosa, Medeola virginiana, Anemone quinque-folia, Maianthemum racemosum, Smilax her-bacea, and *Amianthium muscitoxicum.* The species that had reduced cover in fenced compared with control plots were *C. pensylva-nica, Viola hastata, Dichanthelium clandesti-num,* and *Vaccinium pallidum.* As in the analysis of prevalence, excluding deer had both positive and negative effects on different spe-cies, but increased the total cover and biomass.

Cover of herbaceous dicots increased slightly on control plots between 2006 and 2014; all other groups decreased in cover (Figure 3). Over the course of the experiment, shrubs (*Vaccinium spp.*) experienced a much greater increase in cover on fenced than on control plots; sedges (primarily *C. pensylvanica*) showed a larger loss in cover on fenced plots compared with control plots.

Biomass and Height
The fenced plots on average produced 4.8 times the biomass of control plots; this difference was significant (ANOVA, $F_{1,10} = 7.27$; p = 0.02). When biomass was partitioned between woody and herbaceous species, the difference between fenced and control plots remained significant
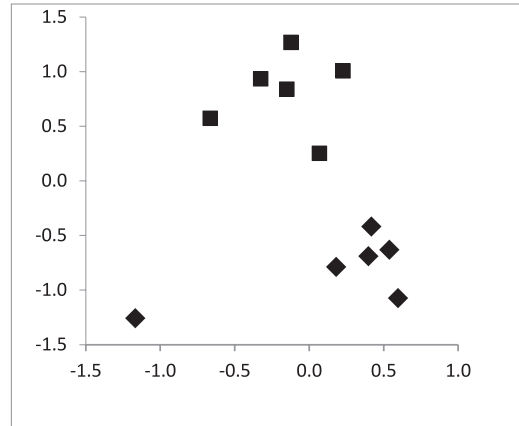

Figure 2. NMS Ordination of Cover (PC-Ord; McCune and Mefford 2011). Each point represents a plot sampled in 2014. The control plots are represented by squares; the fenced plots are represented by diamonds.

(MANOVA, Wilks' $\lambda = 0.1134$; $F_{2,9} = 35.17$; p < 0.0001). A further partitioning between trees (<50 cm high), shrubs, graminoids, other mono-cots, and dicots was also significant (MANOVA, Wilks' $\lambda = 0.0352$; $F_{5,6} = 32.04$; p = 0.0003), with graminoids producing more biomass in control plots and all other groups producing more biomass in fenced plots (Figure 4). The maxi-mum heights of *Vaccinium erythrocarpum* and *Medeola virginiana* were significantly higher in fenced than in control plots (Figure 5; *Vacci-nium* $F_{1,10} = 158.99$, p < 0.0001; *Medeola* $F_{1,10} = 31.97$, p < 0.0002). These results demonstrate that deer are controlling the biomass and height of individuals as well as the species composition in the herb layer.

DISCUSSION
The Community and Population Ecology of Recovery from Chronic Herbivory
Rooney and Dress (1997) estimated that 80.4% of herbaceous and shrubby species were eliminat-ed in 66 yr of browsing by white-tailed deer in a virgin hemlock-beech stand in Pennsylvania. Our results suggest such dramatic effects take decades to manifest themselves. Recovery from the currently historic high densities of deer (Knox 1997) on our study site resulted not in increased species richness but by reorganization of the occurrences and local abundances of species. We have only weak observational evidence that deer have caused local extinctions,
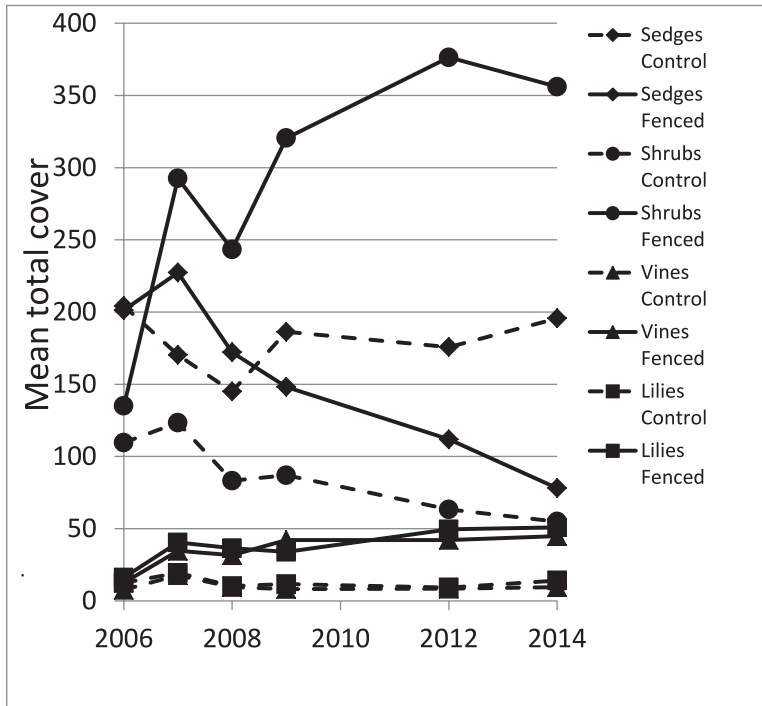
Figure 3. Changes between 2006 and 2014 in the percent cover summed over the nine subsamples and averaged over the six replicates for fenced and control plots. Functional groups have different symbols; fenced plots have solid lines and control plots have dashed lines. Only the groups that showed strong differences between fenced and control plots are illustrated. See Table 2 for species composition of the groups.

but strong experimental evidence that chronic herbivory has altered relative abundances and has reduced the stature and reproduction of most components of the herb layer. A similar outcome was noted by Kraft et al. (2004) 5 yr after exclosures were constructed in Michigan, and by Webster et al. (2005a) 8 yr after fences were erected in Cades Cove, Tennessee. Our results suggest that the restoration of healthy population dynamics of forest herbs that have survived decades of browsing can take place on less than a decadal time scale as by the 10th year nearly all species of herbs in the fenced plots had some flowering individuals. For example, *Clintonia umbellulata*, *Ligusticum canadense*, and *Platanthera orbiculata* first bloomed in years 8, 9, and 10, respectively. Our experiment demonstrates that species can disappear from the floral display but when released from the effects of deer, suppressed plants are able to slowly increase sequestered resources below ground until they have sufficient reserves to reproduce. La Pointe et al. (2010) demonstrated

experimentally that species of Liliaceae (sensu latro) with large carbohydrate reserves and a low shoot to root ratio, such as *Trillium erectum*, can be very tolerant to herbivory. Our results agree with Kraft et al. (2004), who found in Michigan that reproduction of herbs was a more sensitive response to deer browsing than cover or species richness. Several of the species in their study, as in our study, (e.g., *Clintonia borealis* and *Maianthemum racemosum*) grew taller, flowered, and set seed on plots protected from deer.

Continued high densities of deer are predicted to cause local extinctions by two processes: (a) Repeated cropping of shoots can exhaust underground storage reserves, leading to death of individuals and eventually to local extinction of populations; and (b) suppression of flowering by preferentially cropping taller, flowering individuals can reduce or eliminate recruitment into the seed bank or juvenile stage of the population so that if mortality exceeds recruitment for a sufficient time, extinction is inevitable. A corol-
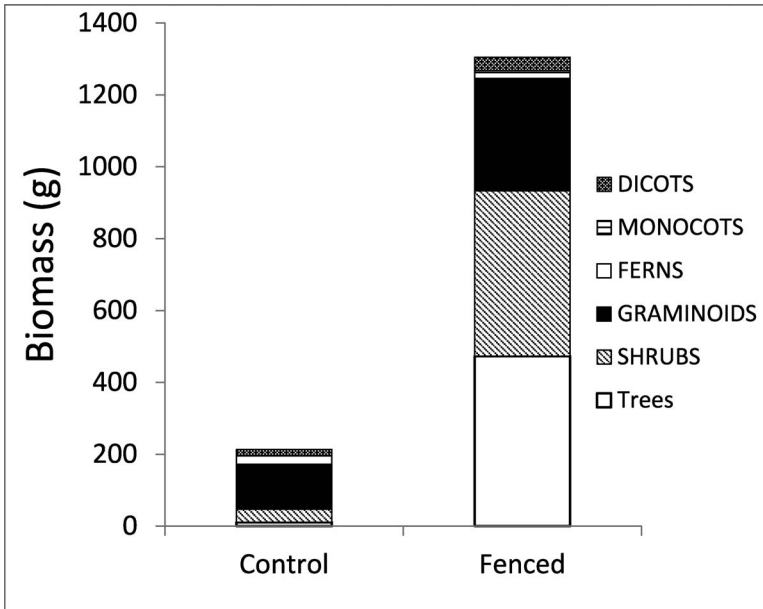
Figure 4. Mean biomass of functional groups of plants in control and fenced plots in August 2014. Means are the treatment means of the biomass (dry weight) summed over the nine subsamples from each plot.

lary of these processes is that the herb layer is dominated by perennials (Bierzychudek 1982, Whigham 2004, Jolls and Whigham 2014). *Lapsana communis*, a native of Europe, is the only annual and the only nonnative species encountered on our plots.

Documentation of local extinctions requires surveys spanning perhaps three to five decades. Two authors (HMW and RBW), who have spent every summer at MLBS for over 30 years (1984–2016), have observed a dramatic decline in flowering of the herbs *L. superbum, L. canadense, Gentiana austromontana, Aureolaria laevigata, A. pediculata,* and *A. virginica,* as well as declines of *R. calendulaceum, C. dentata,* and *V. corymbosum* in the shrub layer, although it is difficult to separate the impact of deer from confounding effects such as forest succession and climate change. Restoration of locally extinct species requires either a regional seed source or intentional reintroductions. We observed little evidence for recruitment of herbs
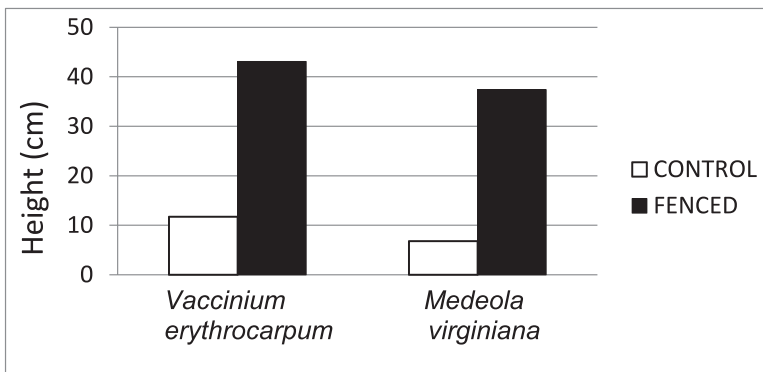

Figure 5. Mean height of the tallest stem of *Medeola virginiana*, a perennial herb, and *Vaccinium erythrocarpum*, a shrub. Means are from the nine subplots in the six replicate plots for the fenced and control treatment groups.

by seedling establishment in the fenced plots. Several trees (e.g., *Ilex montana*, *A. rubrum*, and *P. serotina*), however, had abundant seedlings in fenced plots near seed sources. Fenced plots developed dense populations of woody stems of *Vaccinium erythrocarpum* by vegetative spread with greatly enhanced flowering and fruit production.

The ground layer of the forest at MLBS is currently a patchwork of what may be alternative stable states. Areas dominated by dense stands of the sedge *C. pensylvanica* or of the ferns *D. punctilobula* or *P. noveboracensis* exist within a matrix of a more diverse community of juvenile trees, shrubs, and herbaceous perennials. The stands of *Carex* roughly fit the concept of a grazing lawn proposed by McNaughton (1984). "Fern parks" dominated by *D. punctilobula* also characterize over-browsed forests in Pennsylvania (Carson et al. 2014). This fern is a highly efficient competitor for nutrients and thus, it is difficult for native species to invade stands even after deer are excluded. This may explain suppression of *Q. rubra* seedlings (Lyon and Sharpe 2003) and likely other species (Horsley and Marquis 1983, Horsley 1993, Rooney and Dress 1997, George and Bazzaz 1999, Hill and Silander 2001, George and Bazzaz 2014) especially on acidic, low-nutrient soils, such as those on our study site. On the other hand, *P. noveboracensis*, a fern abundant on one of our plots spreads more slowly and tends to be on moister sites (Hill and Silander 2001) than *D. punctilobula*, although the two species frequently interdigitate in the southern Appalachians. In general, deer do not eat ferns, which are protected by triterpene hydrocarbons, cyanogenic glycosides, and phenols (reviewed by Rooney and Dress 1997); thus, overgrazing likely favors such species. The landscape dynamics of these alternative states would be an important study for predicting trends of forest composition and structure on decadal to centennial time scales. It may be necessary to perturb the stability of populations of sedges and ferns to allow herbaceous species to invade after ungulate densities are reduced.

Managing Forests to Sustain Diversity in the Herb Layer
The comparison of fenced and control plots can help set standards for assaying the effects of deer. Many authors have identified "indicator species" to more easily make such assays. Waller

(2014) reviews these efforts and advises assays that involve multiple species. Our study suggests that *M. virginiana*, *L. superbum*, *Dioscorea villosa*, *Clintonia umbellulata*, and *Maianthemum racemosum* would be excellent indicators in areas where they are common. For example, the proportion of individuals of *M. virginiana* with two tiers of leaves would be an accurate index of the reproductive status of the population, as flowering occurs only from the second tier. Waller (2014) stresses that indices of browsing must be related to densities of deer to allow a link between health of the herb layer and management of the deer herd. This stresses the importance of studying the herb layer in enclosures with a range of densities of deer.

Several other studies have predicted that recovery from browsing requires decades (Kraft et al. 2004, Webster et al. 2005a, Goetsch et al. 2011, Tanentzap et al. 2011, Carson et al. 2014). Jenkins et al. (2014), however, found significant recovery 20 yr after controlled hunting in Indiana state parks. Most studies, including ours, demonstrate that, with protection from herbivory, suppressed plants can grow to reproductive size and assure sustained diversity. The restoration of extinct species is trickier. First, managers must decide which species have likely become locally extinct. Then they must decide if regional seed sources and natural dispersal can operate or if direct reintroductions are advised. Ruhren and Handel (2003) reintroduced nine species of perennial herbs to a national park by planting seedlings inside and outside replicated exclosures. Five of the nine species flowered and fruited 4 yr after planting inside the exclosures, but none outside due to low survival and chronic herbivory. Such reintroductions may require disturbance of recalcitrant stands of sedges or ferns.

The elimination of deer, however, would not be desirable because the increased shrub layer of *Vaccinium* and juvenile trees would shade the ground layer and probably lead to further loss of herbaceous species. Moderate levels of woodland grazing has been promoted as a conservation measure in Europe (Watkinson et al. 2002, Boulanger et al. 2011, Hegland et al. 2013), but in North America deer are often viewed as only a threat to rare plants (McGraw and Furedi 2005, Jenkins et al. 2007, Knight et al. 2008, Dávelos et al. 2014, but see Royo et al. 2010a) for a counterexample.

Management should be based on randomized, replicated manipulations of deer densities in

enclosures large enough to allow reasonably normal ungulate behavior that can suggest mathematical descriptions of how properties of communities and species respond to increasing densities of ungulates (Hobbs et al. 1996, Horsley et al. 2003, Tremblay et al. 2006). Such experiments are costly but very powerful if run for a decade or more with proper controls, since they can account for confounding effects of succession and climate change on the ground layer. The policy challenge is to educate stakeholders about the studies required to determine an optimal deer density—one that would balance the demands for healthy deer (for the hunter), a forest that can regenerate (for the forester), tolerable risk of crop loss (for the farmer), and microhabitat diversity that fosters high α, β, and γ diversity (for the naturalist). The growing body of literature (e.g., Alverson et al. 1988, Ostfeld et al. 1996, Porter and Underwood 1999, Carson et al. 2014, Waller 2014) on mechanisms that determine the effects of deer on managed systems is providing the knowledge required to have informed, scientific discussion of this contentious task. Carson (2014) reviews the difficulty of convincing hunters that deer densities are too high for long-term forest health. We have found that our fenced plots provide an excellent demonstration for the public during open houses at the biological station. We strongly encourage nature centers, parks, and managed forests to construct fenced plots as a public demonstration of the need to manage deer herds.

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