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Restoring forest herb communities through landscape-level deer herd reductions: Is recovery limited by legacy effects?

Alejandro A. Royo[a,*], Susan L. Stout[a,1], David S. deCalesta[a,1], Timothy G. Pierson[b,2]

[a] USDA Forest Service, Northern Research Station, Forestry Sciences Lab, P.O. Box 267, Irvine, PA 16329-0267, United States
[b] Penn State Cooperative Extension, P.O. Box 1504 17129 Rt., 6 Smethport, PA 16749-0504, United States

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ABSTRACT

White-tailed deer (*Odocoileus virginianus*) overbrowsing has altered plant species diversity throughout deciduous forest understories in eastern North America. Here we report on a landscape-level (306 km^2) project in Pennsylvania, USA that tracked the herbaceous community response to deer herd reductions. From 2001 to 2007, we estimated deer densities, browse impact on woody seedlings, and censused the herbaceous flora in permanent plots throughout the area. We assessed herb layer species richness, abundance, and dominance and measured three known phytoindicators of deer impact: *Trillium* spp., *Maianthemum canadense,* and *Medeola virginiana*. We predicted that browse-sensitive taxa would increase in abundance, size, and flowering as would overall species diversity following deer culls and browse impact that declined by an order of magnitude by 2007. Following intensified deer harvests, we observed a limited recovery of the herbaceous community. *Trillium* spp. abundance, height, and flowering; *M. canadense* cover; and *M. virginiana* height all increased following herd reductions. Similarly, forb and shrub cover increased by 130% and 300%, respectively. Nevertheless, species diversity (i.e., richness and dominance) did not vary. Our work demonstrates that reducing deer densities can provide rapid morphological and population-level benefits to palatable species without a concomitant recovery in diversity. We suggest that decreasing deer populations alone may not promote plant diversity in overbrowsed, depauperate forests without additional restoration strategies to mitigate a browse-legacy layer dominated by browse-resistant species.

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1. Introduction

High densities of native and exotic deer populations have caused extensive changes in understory plant communities throughout forested regions worldwide (Fuller and Gill, 2001; Vázquez, 2002; Husheer et al., 2003; Côte et al., 2004). The impacts of overbrowsing have been documented in a number of studies including both deer exclosure and enclosure experiments (Horsley et al., 2003; Webster et al., 2005; Tremblay et al., 2006), comparisons of plant communities across areas of varying ungulate density (Balgooyen and Waller, 1995; Augustine and Frelich, 1998; Gill and Morgan, 2010), and contrasts between historic and contemporary surveys (Potvin et al., 2003; Rooney et al., 2004; Taverna et al., 2005; Tanentzap et al., 2009). When evaluated in its entirety, the evidence compellingly demonstrates that long-term overbrowsing decreases plant size, growth, survival, and fecundity; shifts understory plant relative abundances; alters species diversity, and facilitates exotic plant invasions (Russell et al., 2001; Rooney and Waller, 2003; Côte et al., 2004; Eschtruth and Battles, 2009).

Although the negative impacts of long-term overbrowsing are substantially documented, few studies rigorously examine how understory plant communities respond once deer populations are reduced to levels representative of historic conditions. Deer exclosure experiments provide a vital tool to assess how plant species respond in the *absence* of browsing; however, this condition is not representative of natural browsing regimes. This approach may also provide limited inference regarding community-level responses to region-wide deer herd reductions given the small size, low replication, and potentially subjective (non-random) placement of exclosures relative to the high spatial and temporal variability exhibited by herbaceous communities. Large scale deer enclosure studies offer a powerful alternative to examine relationships between vegetation dynamics and known deer densities gradients (Horsley et al., 2003; Tremblay et al., 2006). Nevertheless, enclosure sizes (10–40 ha) are much smaller than the average white-tailed deer foraging area (64–235 ha) and thereby restrict the ability of enclosure experiments to mimic the dynamics that

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* Corresponding author. Tel.: +1 814 563 1040; fax: +1 814 563 1048.
E-mail address: aroyo@fs.fed.us (A.A. Royo).

[1] Tel.: +1 814 563 1040; fax: +1 814 563 1048.

[2] Tel.: +1 814 887 5613.

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occur as deer forage across a landscape with heterogeneity in plant composition and abundance (Tierson et al., 1985; Campbell et al., 2004; Schmitz, 2005).

Vegetation dynamics in response to deer herd reductions may be masked by the long-term effects of overbrowsing since contemporary plant communities often represent the cumulative effects of decades of herbivory (Russell et al., 2001). This ‘ghost of herbivory past’ (Banta et al., 2005) manifests itself in plant communities characterized by the low abundance and even local extirpation of browse-sensitive species and the high dominance of browse-tolerant species (Frelich and Lorimer, 1985; Rooney and Dress, 1997; Waller and Alverson, 1997; Coomes et al., 2003). In such depauperate conditions, plant community recovery from overbrowsing may be limited or even impossible due to the rarity of browse-sensitive plants, propagule limitation, short dispersal distances, and altered competitive neighborhoods (Russell et al., 2001; Royo and Carson, 2006). Clearly, a variety of factors may directly or indirectly influence vegetation responses to fluctuating deer browsing levels. Consequently, long-term experiments across broad spatial scales that incorporate heterogeneity in site-specific features are required to examine understory plant persistence and recovery in response to deer reductions across the landscape (Côte et al., 2004; Gordon et al., 2004).

In this study, we examine understory plant species responses to lowered white-tailed deer (*Odocoileus virginianus*) densities following nearly eight decades of overabundance in northwestern Pennsylvania, USA. We tested the hypothesis that reducing deer densities across the landscape will decrease overall browse impact and result in a recovery of the understory plant community. Specifically, we predicted that following deer herd reductions: (i) browse impact will decrease, (ii) species richness and diversity will increase, (iii) the abundance of browse-sensitive plant taxa will increase, and (iv) flowering, height, cover, and density of recognized browse indicator species of deer browsing will increase. By examining these impacts at a broad-scale, spanning sites with different aspects, topographic positions, canopy densities, and ownership, we hope to better understand how declines in deer impacts lead to forest understory plant recovery across a landscape.

2. Methods

2.1. Study area

The study was conducted within the unglaciated Allegheny High Plateau region of northwestern Pennsylvania in the Kinzua Quality Deer Cooperative (KQDC) adaptive management demonstration area. The KQDC encompasses 306 km^2 of forested land managed by both private and public entities (Allegheny National Forest, Bradford Watershed, Forestry Investment Associates, Collins Pine, and RAM Forest Products) with an average elevation 613 m (range: 494–689 m). Forests within the area are typically 80–100 years-old, second growth Allegheny hardwood stands with canopies dominated by black cherry (*Prunus serotina*) and red maple (*Acer rubrum*; nomenclature follows USDA NRCS (2010)) and have a average basal area of 32.5 m^2/ha (range: 18.6–48.8 m^2/ha). The area has a humid temperate climate; annual precipitation averages 1077 mm, summer temperatures average 18.6 °C, and growing seasons last 100–130 days (Whitney, 1990). Soils are strongly acid, derived from relatively infertile sandstones and shales. Additionally, soils in the area have relatively low levels of exchangeable cations due to the dominant kaolinite material, a condition further exacerbated by acid precipitation, particularly on upper slope positions (Bailey et al., 2004).

White-tailed deer populations in the region have persisted at high densities following their near extirpation and subsequent reintroduction in 1905 (Frye, 2006). Deer populations rapidly exceeded historical population densities (*c.* 3–4 deer/km^2; McCabe and McCabe, 1997) by the 1930’s (McCain, 1939) and averaged densities of 16–23 deer/km^2 throughout much of the 20th century (McCain, 1939; Horsley et al., 2003). Over time, overbrowsing profoundly changed understory vegetation leading to the decline of palatable tree, shrub, and forb species and the concomitant increase of unpalatable tree, fern, and graminoid species (Hough, 1965; Whitney, 1984; Rooney and Dress, 1997). For detailed information on the composition and abundance of the vascular vegetation, see Anacker and Kirschbaum (2006).

We superimposed a grid of 2.6 km^2 blocks (1.609 km × 1.609 km) across the KQDC and selected 21 blocks at random for data collection (Fig. 1). Block size was chosen to encompass the average home range of deer in mixed hardwood stands in the northeastern USA and represents the minimum area necessary for estimating deer density (Tierson et al., 1985; Campbell et al., 2004). Within each block we nested seven 35.4×35.4 m (1250 m^2) vegetation monitoring plots within forest stands beginning in 2001. One plot was centered within the overall 2.6 km^2 block and the six others radiated out 400 m from the center point at 60° intervals beginning with a randomly chosen azimuth. At each corner of all plots we established a 2 m radius (12.54 m^2) woody vegetation monitoring subplot and a nested 1 m radius (3.14 m^2) herbaceous layer monitoring subplot. In 2007, we were only able to sample five randomly selected plots within each of 15 randomly selected blocks plus an additional plot in another block ($n = 76$ out of 147 possible plots) and that subset forms the basis of this study. For detailed a description of the vegetation monitoring network, see Kirschbaum and Anacker (2005).

2.2. Deer management

Our primary tool in reducing deer populations throughout the KQDC was participation in the Pennsylvania Game Commission, deer management assistance program (DMAP). This program allows forest landowners to obtain and distribute additional antlerless licenses to interested hunters in order to increase deer harvest rates on their properties. Thus, in addition to the 28,000–44,000 deer licenses issued for the larger region that encompasses the

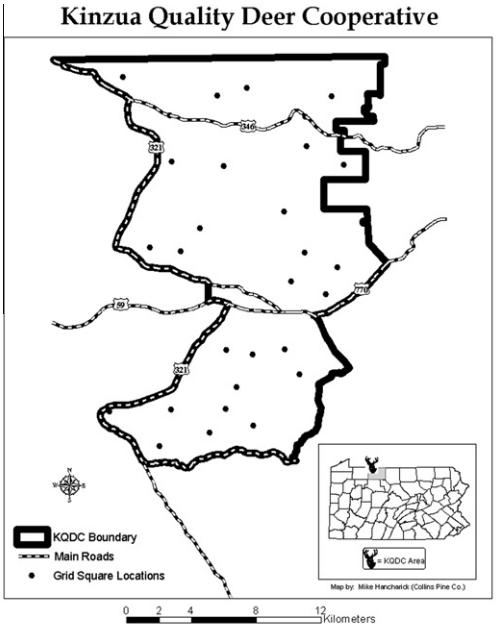

Fig. 1. The Kinzua quality deer cooperative (KQDC) area in Pennsylvania, USA.

KQDC, we issued an additional 6750 antlerless tags, specific to the KQDC, from 2003 to 2006. Of these, a total of 1387 tags were returned reporting a successful harvest.

2.3. Data collection

2.3.1. Deer densities

Within each sampling block, we estimated deer densities yearly from pellet group counts, beginning in 2002. Data were collected along five, 1.6 km transects spanning the block in April – early May of each year. Within each transect, deer pellet group counts were obtained on 52, 4.67 m^2 plots spaced 30.5 m apart. We estimated deer density per transect as follows:

$$\text{Deer density} = \sum \#\text{ of pellet groups/pellet deposition rate} \times \text{days} \times \text{area}$$

where pellet deposition rate = 25/day/deer (Sawyer et al., 1990), days is the length of time since leaf-off (approx. October 25th–November 10th), and area represents the total area sampled (km^2). Because deer numbers decline (mortality from hunting season, winter starvation/exposure) during the period of pellet group deposition (December–May), estimates derived from pellet group counts represent the average number of deer over-winter and therefore, the number of adult deer surviving into the spring and summer foraging season (see KQDC, 2008 for more details). We recognize that pellet survey methods are critiqued as imprecise measures of actual densities due to variability in fecal persistence and deposition rates across individuals, habitats, and years; however, these indices do provide a comparative index of abundance, particularly when shifts in population densities are large (Smart et al., 2004).

2.3.2. Understory vegetation and indicator species

In the summers of 2001, 2003, and 2007 we censused the percent cover of all herb layer species (non-arborescent species $\leqslant$1 m in height) within the 1 m radius subplots beginning in mid-May – August. In 2003 and 2007 we conducted a search across the entire 1250 m^2 plot to record the presence of any additional species. We collected detailed morphological and demographic data on three liliaceous herb species reported to be sensitive to deer browse (reviewed by Kirschbaum and Anacker (2005)): *Trillium* spp. (includes *T. erectum, T. undulatum,* and *T. grandiflorum*), Canada mayflower (*Maianthemum canadense*) as well as another liliaceous species, Indian cucumber-root (*Medeola virginiana*), considered a potential indicator in Pennsylvania (Diefenbach and Fritsky, 2007). For *Trillium* spp., we recorded the proportion of stems in three distinct demographic stages (one-leafed individual, three-leaf non-reproductive, three-leaf reproductive; Knight, 2004) and height in all three census periods as well as total stem density in 2003 and 2007. For *M. canadense*, we recorded longest leaf length (cm) and reproductive status (Yes/No) in all census periods. We recorded stem densities, heights, and reproductive status (Yes/No) of *M. virginiana* along a 2 × 50 m belt transect running through the plot from north to south in 2003 and 2007.

2.3.3. Additional site factors

We surveyed deer browsing damage on woody seedlings ($\leqslant$1.5 m) by species within the 2 m radius subplots. For each species we estimated the proportion of browsed growing tips using four browse categories: 0 = no browse, 1 = 1–33%, 2 = 34–66%, and 3 = 67–100%. Additionally, we inventoried overstory tree composition and sizes (diameter at breast height, d.b.h.) in all plots and calculated overstory relative density (Stout and Nyland, 1986). Relative density is an estimate of overstory crowding that integrates both tree size and species identity and serves as a surrogate for light availability (Stout and Nyland, 1986; Comeau and Heineman, 2003). Ownership of the plots was coded as 0 or 1 for public and private ownerships, respectively. Finally, we obtained the elevation (m) and aspect of each plot. Aspect values were converted to a linear scale using the formula $S = \text{Sin}(X - 90^\circ)$, where X is the actual azimuth. This transformation results in values ranging from -1 to 1, where northerly aspects are negative and southerly aspects are positive (Huebner et al., 1995).

2.4. Analyses

We estimated over-winter deer density for each block by averaging the density estimates obtained from the five pellet group transects within a block. For each plot, we calculated a local deer browse index based on browsing observed on the seven most abundant woody species (*Acer pensylvanicum*, *A. rubrum*, *A. saccharum*, *Betula* spp., *Fagus grandifolia*, *Fraxinus americana*, and *P. serotina*). Browse index was calculated only for individuals $\geqslant$0.3 m tall as deer preferentially browse seedlings and saplings in larger size classes (Horsley and Marquis, 1983); thus, including the large number of unbrowsed, small seedlings would greatly lower browsing estimates. We calculated overall richness (i.e., total species inventory including subplot sampling and additional search), species density (species/m^2), and the Berger–Parker dominance index ($d = N_{max}/N$, where N = the total number of individuals and N_{max} = the number of individuals in most abundant species; Magurran 2004) for each plot at each census period. This value ranges from 0–1 with larger numbers representing increasing dominance. Additionally, we calculated average percent cover in each census for each of four species groups: ferns and fern allies (e.g., *Lycopodium* spp.), graminoids, forbs, and shrubs. Finally, we obtained average abundance, size, and reproductive status estimates of the three herbaceous indicator species in each census period.

Our primary interest was to examine changes in response variables over time, and more specifically, whether these metrics differed following deer herd reductions. Thus, we used repeated measures general linear mixed modeling in PROC GLIMMIX (SAS/STAT, 2005) with plot(block) or transect(block) as random factors with year as the fixed effect. We controlled for potentially confounding effects of site differences by including our measured site-specific factors of aspect, elevation, overstory relative density, and ownership (public versus private) as covariates. We also included the two-way interaction between year and ownership as monitoring of hunting pressure has found harvest rates differ between ownerships, with higher pressure on public lands. The analyses used the restricted maximum likelihood (REML) estimation method and denominator degrees of freedom were calculated using the Kenward–Rogers adjustment (Littell et al., 2002). For analyses on species counts, we modeled the data using a negative binomial distribution a log-link function which performs well for overdispersed count data. For analyses on vegetation abundance, we modeled the data using a gamma distribution with a log-link function (Bolker, 2008). When significant differences were detected in the overall test, comparisons among means were obtained using Tukey-adjusted post hoc tests. We estimated the degree of association between each significant continuous variable and the response variable using the R^2_β statistic developed for mixed models (Edwards et al., 2008). This statistic is the direct extension of the univariate R^2 statistic to linear mixed models and allows comparison of fixed effects on repeated outcomes while retaining the covariance structure. Finally, we analyzed woody species browse impact using logistic regression with PROC LOGISTIC (SAS/STAT, 2005). For *F. americana* and *P. serotina*, maximum likelihood estimation was not feasible due to quasi-complete separation (i.e., in the year × browse category table, all individuals in 2007 are unbrowsed); thus we employed penalized maximum likelihood methods (see Heinze and Schemper, 2002).

3. Results

3.1. Deer densities and browse impacts

Estimated over-winter deer densities declined significantly over time, but only following the implementation of aggressive deer management strategies in the KQDC area beginning in fall 2003 (year: $F_{5,395} = 44.67$; $P < 0.0001$; Fig. 2). Deer populations averaged approximately 10.4 deer/km^2 in the period of 2002–2004 and declined to approximately 4.9 deer/km^2 from 2005–2007. As deer densities dropped, browsing on woody species declined by an order of magnitude ($F_{2,186} = 117.86$: $P < 0.0001$; $R^2 = 0.56$; Fig. 2). The degree of this reduction varied among species (year × species: Wald Chi-square = 21.73, $P = 0.005$; Fig. 3). Over time, browsing signifi-

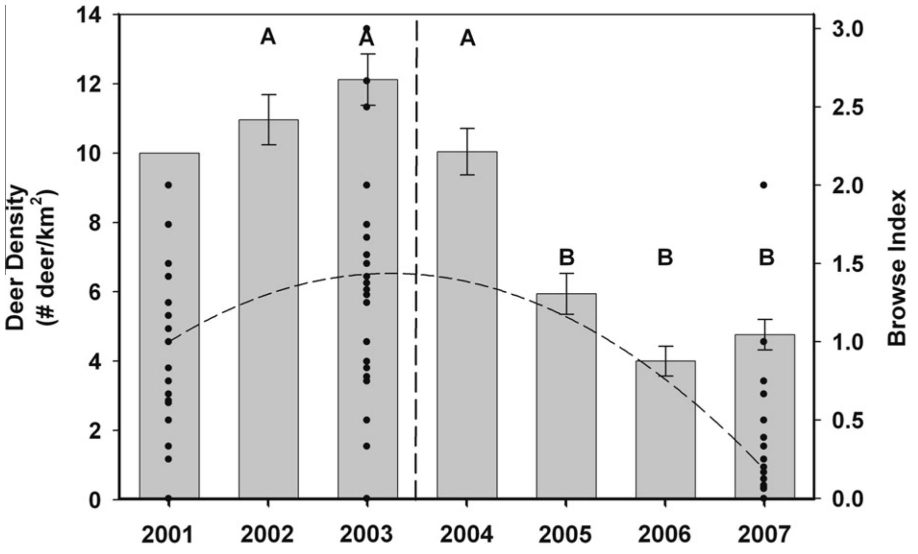

Fig. 2. Mean deer densities (# deer/km^2) across the KQDC from 2001–2007 and browse impact (●) for 2001, 2003, and 2007. Curved line represents the relationship between browse impact and year (browse = 0.99 + 0.39* year − 0.09* year^2; df = 2, 186; $R^2 = 0.56$). Vertical dashed line represents the initiation of the intensified deer harvests. Bars represent ±1 SE. 2001 deer density data from Kirschbaum and Anacker (2005).

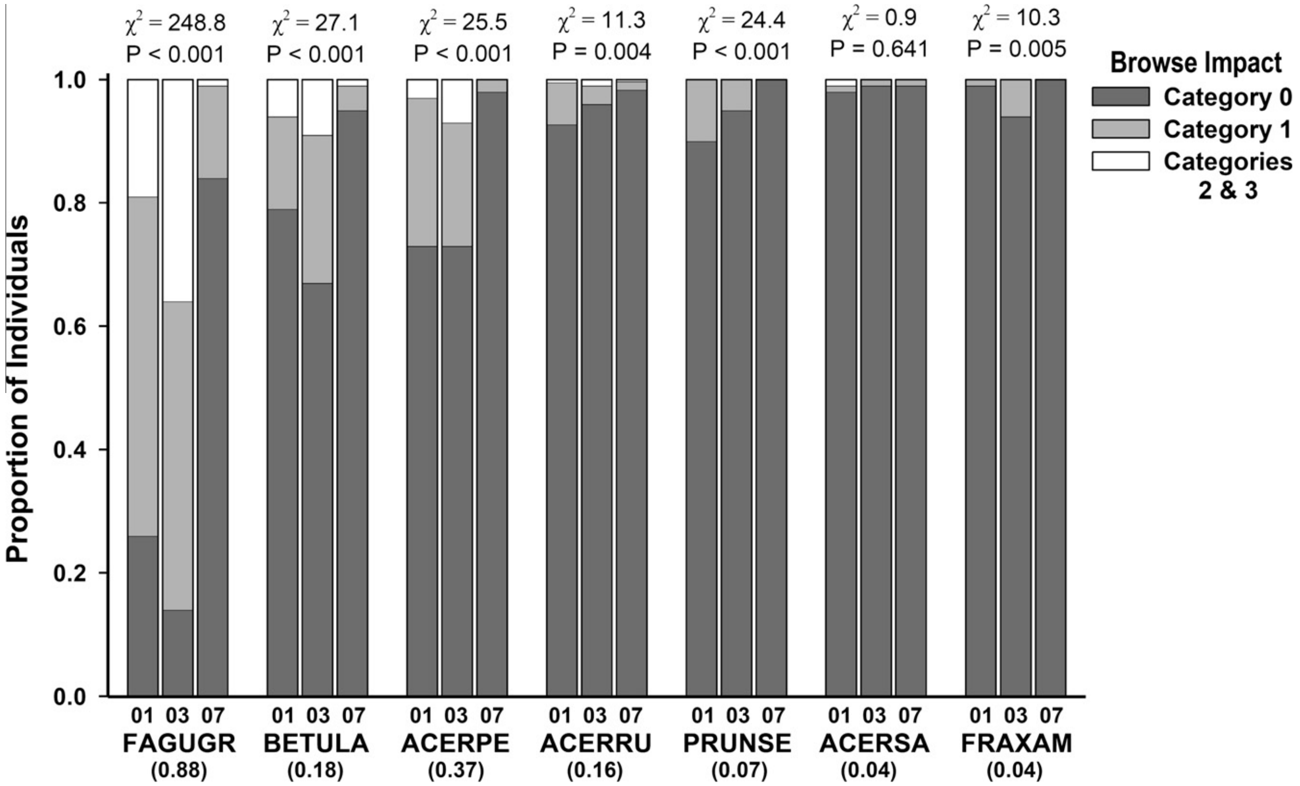

Fig. 3. Browse impact by species for individuals ⩾0.3 m in 2001, 2003, and 2007 (labels 01, 03, and 07, respectively). Browse categories are as follows: 0 = no browse, 1 = 1–33%, 2 = 34–66%, and 3 = 67–100%. Browse category 3 was combined with category 2 due to low frequency of occurrence. Wald Chi-square and penalized log-likelihood from individual logistic regression analyses are presented. ACERPE = *Acer pensylvanicum*, ACERRU = *Acer rubrum*, ACERSA = *Acer saccharum*, BETULA = *Betula* spp., FAGUR = *Fagus grandifolia*, FRAXAM = *Fraxinus americana*, and PRUNSE = *Prunus serotina*. Values in parentheses denote species abundance in 2007 (proportion of plots in which species was sampled).

cantly decreased for *A. pensylvanicum*, *A. rubrum*, *Betula* spp., *F. grandifolia*, *F. americana*, and *P. serotina*. *Acer saccharum* individuals experienced very low browsing across all censuses (Fig. 3). Our browse index was often negatively associated with our response variables, particularly with browse-sensitive taxa (Table 1). Nevertheless, as browse index covaried with our repeated factor of year, including browse as a covariate in the analyses would violate the assumption of independence among factors (Underwood, 1997) and was thereby excluded in all subsequent analyses.

3.2. Understory vegetation community

The understory vegetation layer across the entire KQDC area contains approximately 305 vascular plant species (Anacker and Kirschbaum, 2006). Over time, overall species richness, remained stable on public lands (33 species in 2003 and 2007), but significantly declined from 35 (±1.8) to 30 (±1.8) species per plot on private ownerships (significant year × ownership interaction; Table 2). Species density (species/m^2) remained similar across all three census periods (Table 2). Plots located on southern aspects and at lower elevations had greater overall species richness (Table 2). Similarly, species density increased at lower elevations (Table 2). Across the KQDC, plots were highly uneven (Berger–Parker dominance values ~0.60) and this metric was unaffected by time or any environmental gradient (Table 2). Approximately 75% of the plant species had very low abundance (<1% relative cover) and as many as 34% of the species were sampled in only one plot (Appendix A).

Table 1
Multivariate association between response variables and a browse index calculated as the proportion of growing tips browsed on woody stems $\geqslant$0.3 m tall as estimated by general linear mixed models. Values in bold are significant at $\alpha \leqslant 0.05$. The R^2_β statistic measures the strength of positive (↑) and negative (↓) relationships between browsing and the response variable.

Response variables	Predictor	*F*-value	*P*	R^2_β	
Overall richness	Browse	$\boldsymbol{F_{1,139} = 9.49}$	**0.003**	**0.06**	(↑)
Species density	Browse	$F_{1,187} = 0.05$	0.815	0.00	
Berger–Parker	Browse	$F_{1,126} = 0.03$	0.853	0.00	
Fern cover	Browse	$F_{1,118.5} = 1.11$	0.295	0.01	
Graminoid cover	Browse	$F_{1,127.5} = 1.00$	0.319	0.01	
Forb cover	Browse	$\boldsymbol{F_{1,139.1} = 15.92}$	**<0.001**	**0.10**	(↓)
Shrub cover	Browse	$\boldsymbol{F_{1,.2} = 14.86}$	**<0.001**	**0.10**	(↓)
Trillium density	Browse	$\boldsymbol{F_{1,75.1} = 8.73}$	**<0.004**	**0.11**	(↓)
Trillium height	Browse	$\boldsymbol{F_{1,132} = 30.68}$	**<0.001**	**0.19**	(↓)
Trillium flowering	Browse	$\boldsymbol{F_{1,131} = 10.26}$	**0.002**	**0.07**	(↓)
Maianthemum cover	Browse	$\boldsymbol{F_{1,129} = 21.45}$	**<0.001**	**0.14**	(↓)
Maianthemum leaf length	Browse	$\boldsymbol{F_{1,52.1} = 10.86}$	**0.002**	**0.17**	(↓)
Medeola density	Browse	$\boldsymbol{F_{1,66.9} = 8.16}$	**0.006**	**0.11**	(↓)
Medeola height	Browse	$\boldsymbol{F_{1,46.2} = 18.70}$	**<0.001**	**0.29**	(↓)

Ferns and fern allies accounted for approximately three quarters of the total herbaceous cover across all three census periods (Appendix A). Average fern cover did not vary across census periods and was greatest at higher elevations and northern aspects (Table 2). Similarly, graminoid abundance did not vary across census periods, but did decline at higher elevations (Table 2). In contrast, forb abundance was equivalent in the years preceding deer herd reductions (2001 and 2003), and then significantly increased ~125% by 2007 (Table 2). Forb abundance did not vary across any environmental or ownership gradient (Table 2). Similarly, shrub cover was low (<0.1%) in both 2001 and 2003 and then significantly increased by an order of magnitude by 2007. Shrub cover was greater at lower elevations and in understories beneath more open canopies (Table 2).

3.3. Herbaceous indicator species

For all three species liliaceous indicator species, recognized morphological, reproductive, and population-level browse metrics improved over time (Table 3). More importantly, most of these metrics increased significantly only by 2007, following deer herd reductions (Table 2). By 2007, *Trillium* spp. were 60% more abundant, individuals were 46–56% taller, and the proportion of reproductive individuals more than doubled (Table 3). Similarly, *M. canadense* percent cover more than doubled by 2007 (Table 3). *M. canadense* leaf lengths increased over time, but lengths did not differ between 2003 and 2007 (Table 3). Finally, *M. virginiana* individuals were approximately 36% taller in 2007, relative to 2003 (Table 2). Although *M. virginiana* density increased by 32%, between 2003 and 2007, the analyses failed to detect this difference (Table 3). No analyses were possible on reproductive success for *M. virginiana* as the total number of reproductive individuals was low (<1%) irrespective of deer densities.

4. Discussion

4.1. Reducing deer densities allowed recovery of browse-sensitive plants

As predicted, reductions in deer densities within the KQDC area to levels approaching historic estimates (3–4 deer/km^2; McCabe

Table 2
Effects of predictor variables on diversity and abundance of the herbaceous layer in KQDC. For the main effect of year we include the untransformed means (±1 SE). Values in bold are significant at $\alpha \leqslant 0.05$. Significant differences among means are denoted by superscripts and ↑ or ↓ represent positive or negative relationships between continuous predictors and response variables.

Predictors	Stand richness (*S*)	Plot richness (# species/m^2)	Berger–Parker (*d*)	Fern cover (%)	Graminoid cover (%)	Forb cover (%)	Shrub cover (%)
Year	$\mathbf{F_{1,145} = 10.59}^{**}$	$F_{2,196} = 0.47$	$F_{2,127} = 0.89$	$F_{2,127.1} = 2.53$	$F_{2,129.1} = 1.43$	$\boldsymbol{F_{2,128.9} = 11.63}^{***}$	$\boldsymbol{F_{2,129.6} = 14.60}^{***}$
2001	–	7.5 (±0.48)	0.6 (±0.03)	20.4 (±2.44)	1.5 (±0.39)	2.6 (±0.50)^a	0.08 (±0.04)^a
2003	34.4 (±1.24)^a	8.0 (±0.42)	0.6 (±0.02)	23.4 (±2.12)	1.8 (±0.33)	2.4 (±0.27)^a	0.09 (±0.03)^a
2007	31.9 (±1.03)^b	7.4 (±0.36)	0.6 (±0.02)	23.4 (±2.03)	1.3 (±0.27)	5.7 (±1.25)^b	0.35 (±0.10)^b
Aspect	$\boldsymbol{F_{1,69.5} = 4.94}^{*}$	$F_{1,69.5} = 0.07$	$F_{1,71.3} = 0.04$	$\boldsymbol{F_{1,71.9} = 2.61}^{*}$	$F_{1,72.8} = 2.35$	$F_{1,72.7} = 3.21$	$\boldsymbol{F_{1,73.1} = 0.02}^{**}$
	$\boldsymbol{R^2_\beta = 0.07}$ **(↑)**			$\boldsymbol{R^2_\beta = 0.04}$ **(↓)**			$\boldsymbol{R^2_\beta = 0.08}$ **(↑)**
Elevation	$\boldsymbol{F_{1,69.1} = 10.37}^{**}$	$\boldsymbol{F_{1,65.4} = 5.43}^{*}$	$F_{1,.1} = 1.00$	$\boldsymbol{F_{1,70.5} = 5.59}^{*}$	$F_{1,70.2} = 3.68$	$F_{1,70.3} = 0.20$	$\boldsymbol{F_{1,70.2} = 16.18}^{***}$
	$\boldsymbol{R^2_\beta = 0.13}$ **(↓)**	$\boldsymbol{R^2_\beta = 0.08}$ **(↓)**		$\boldsymbol{R^2_\beta = 0.07}$ **(↑)**			$\boldsymbol{R^2_\beta = 0.19}$ **(↓)**
Relative density	$F_{1,70.8} = 0.44$	$F_{1,67.4} = 1.59$	$F_{1,69.4} = 0.31$	$F_{1,70.7} = 1.95$	$F_{1,70.6} = 0.00$	$F_{1,70.6} = 0.01$	$\boldsymbol{F_{1,70.6} = 11.67}^{**}$
							$\boldsymbol{R^2_\beta = 0.14}$ **(↓)**
Ownership	$F_{1,70.2} = 0.18$	$F_{1,71.3} = 2.07$	$F_{1,70.9} = 2.70$	$F_{1,71.7} = 1.00$	$F_{1,72.3} = 0.17$	$F_{1,72.3=}1.78$	$F_{1,72.5} = 0.99$
Year × Ownership	$\mathbf{F_{1,145} = 5.83}^{*}$	$F_{2,196} = 0.20$	$F_{2,127} = 0.28$	$F_{2,127} = 0.02$	$F_{2,129.1} = 0.37$	$F_{2,128.9} = 2.60$	$F_{2,129.6} = 2.01$

Asterisks (*) denote the following significance values.

[*] $P < 0.05$.

[**] $P < 0.01$.

[***] $P < 0.001$.

Table 3

Effects of predictor variables on indicator species responses in KQDC. For the main effect of year we include the untransformed means (±1 SE). Values in bold are significant at $\alpha \leqslant 0.05$. Significant differences among means are denoted by superscripts.

Predictors	*Trillium* spp.			*M. canadense*		*M. virginiana*	
	Density (N/1 250 m^2)	Height (cm)	Flowering (%/100)	Percent cover (%)	Leaf length (cm)	Density (N/100 m^2)	Height (cm)
Year	**$F_{1,73.9}$ = 14.60*****	**$F_{2,107}$ = 35.51*****	**$F_{2,108}$ = 8.48*****	**$F_{2,148}$ = 21.59*****	**$F_{2,58.8}$ = 11.31*****	$F_{1,73=}0.37$	**$F_{1,46.6}$ = 18.27*****
2001	–	10.2 (±0.86)^a	0.09 (±0.05)^a	0.20 (±0.04)^a	3.7 (±0.10)^a	–	–
2003	48.2 (±10.63)^a	12.1 (±0.50)^a	0.08 (±0.02)^a	0.28 (±0.05)^a	4.1 (±0.12)^b	50.3 (±12.25)	7.3 (±0.28)^a
2007	77.4 (±15.06)^b	17.7 (±0.59)^b	0.21 (±0.03)^b	0.63 (±0.15)^b	4.6 (±0.11)^b	66.4 (±18.33)	9.9 (±0.46)^b
Aspect	$F_{1,71.1} = 2.57$	$F_{1,62.5} = 1.36$	$F_{1,59.4} = 0.28$	$F_{1,71} = 1.51$	$F_{1,36.1} = 0.32$	$F_{1,71.1} = 3.25$	$F_{1,43.2} = 0.03$
Elevation	$F_{1,71.1} = 1.43$	$F_{1,69.5} = 2.24$	$F_{1,68.2} = 2.63$	$F_{1,71} = 0.97$	$F_{1,31.7} = 1.32$	$F_{1,71.1} = 0.38$	$F_{1,49.7} = 2.65$
Relative density	$F_{1,71} = 0.00$	$F_{1,70.6} = 1.28$	$F_{1,67.5} = 0.01$	$F_{1,71} = 1.15$	$F_{1,37.2} = 1.48$	$F_{1,71.1} = 1.71$	$F_{1,48.1} = 0.73$
Ownership	$F_{1,71.1} = 1.59$	$F_{1,66.9} = 1.52$	$F_{1,64.9} = 0.24$	$F_{1,71} = 0.13$	$F_{1,34.1} = 2.97$	$F_{1,71.1} = 0.14$	$F_{1,45.5} = 0.49$
Year × ownership	$F_{1,73.9} = 3.85$	$F_{2,107} = 0.36$	$F_{2,109} = 0.10$	$F_{2,148} = 0.67$	$F_{2,58.7} = 0.09$	$F_{1,73} = 0.47$	$F_{1,46.6} = 0.42$

Asterisks (*) denote the following significance values.
$^*P < 0.05$.
$^{**}P < 0.01$.
*** $P < 0.001$.

and McCabe, 1997) were associated with a reduction in browse impact by an order of magnitude. Concomitant with these reductions in browsing, the abundance of browse-sensitive herb layer taxa increased. The shrub (predominantly *Rubus* spp.) and forb layers contain many highly palatable, browse-sensitive species that form a large portion of white-tailed deer spring and summer forage (Healy, 1971; Skinner and Telfer, 1974; Stockton et al., 2005). In sharp contrast, the generally unpalatable and browse-tolerant ferns and graminoids (Horsley et al., 2003) did not manifest any marked changes in abundance following the culling of the deer herd. The increase in relative abundance of forb and shrub taxa coinciding with deer herd reductions parallels results from nearby sites that document higher abundance of these taxa historically, prior to the increase in deer herds (Rooney and Dress, 1997) or on contemporary browse refugia (Banta et al., 2005). The release of understory plant species from intense landscape-level browsing is further supported by the recovery in multiple liliaceous indicator species metrics *only after* deer herd reductions. The height of *Trillium* spp. and *M. virginiana*, the abundance of *Trillium* spp. and *M. canadense*, as well as the proportion of reproductive individuals of *Trillium* spp., were consistently greater only following the culling of the deer herd. There was a non-significant tendency for greater *M. virginiana* densities in 2007, relative to 2003; however, the small sample sizes (species present in only 59% of sample plots) likely generated low power for this test.

Given the consistent benefit of deer herd reductions on browse-sensitive herbaceous species in dozens of plots that varied among ownerships, canopy density, aspect, and topographic position across a 306 km^2 study area, we suggest that deer are a dominant force structuring vegetation across the landscape. Our localized browse impact estimates were often negatively, albeit weakly (low R^2_β), correlated with response variables (Table 1). Other studies have similarly found these fine-scale browse indices are generally poor (low R^2) or non-significant predictors of understory plant species abundance (Rooney et al., 2000; Barnett and Stohlgren, 2001; Kirschbaum and Anacker, 2005). This disconnect between the imprecise plant community response to localized browse impact versus the distinct response observed between years with high and low deer pressure may be reconciled by the fact that browse indices represent localized ‘snapshots’ of herbivory when in reality, ungulate foraging impacts are often accrued over much wider temporal and spatial scales (e.g., Barnett and Stohlgren, 2001). Furthermore, browse impact is a function, not only of deer densities, but also forage composition, relative abundance, and structure at both the local (Palmer and Truscott, 2003) and landscape scale (deCalesta and Stout, 1997). Thus, low browse damage may reflect low deer densities and/or dominance by unpalatable seedlings.

Among the other site-specific factors, only aspect and elevation exerted any consistent effect on response variables (Table 2). Gradients in topographic features have long been known to influence understory plant species diversity (e.g., Whittaker, 1956; Glenn-Lewin, 1977). Such vegetation shifts across topographic gradients are often linked to changes in resource availability (e.g., light, moisture, nutrients; Hutchinson et al., 1999; Small and McCarthy, 2002). We found species richness, and graminoid and shrub cover decreased and fern abundance increased at higher elevations. Despite the fairly low relief found across our sites (maximum elevation difference: 195 m), Williams and others (1999) found similar patterns in richness, graminoid cover and fern cover and attributed these, in part, to flooding potential within the region. Additionally, the availability of key elements (e.g., Ca and Mg) can differ by as much as an order of magnitude across these gradients and can strongly influence herbaceous species diversity in the region (Horsley et al., 2008). We also found richness increased and fern cover decreased on southern aspects. Huebner et al. (1995) hypothesized that increased environmental stress levels caused by higher temperatures and atmospheric moisture demands on southern aspects may mediate competitive outcomes. Thus, the opposing relationships for fern cover and richness for both aspect and elevation suggest that abiotic limitations on fern dominance may indirectly benefit overall plant diversity.

We recognize that the strength of our inference is limited by the lack of a control site where deer remained overabundant. The establishment of such an area was not only impractical due to our landscape-level approach, but also economically untenable to most large landowners throughout northwest Pennsylvania. These landowners relied heavily on the increased doe allocations afforded by DMAP to control deer numbers and thereby ensure adequate tree regeneration following overstory harvests in lieu of the much costlier alternative of erecting deer exclosures around harvested areas (Marquis and Grisez, 1978). Despite these limitations, the plant community and phytoindicators responded as predicted. The fact that overall abundances of browse-sensitive species and phytoindicators remained consistent between 2001 and 2003, during a period when deer numbers were high ($\sim$10–12 deer/km^2), and increased only by 2007, supports our assumption that reduced deer browsing, and not stochastic events, was the major factor underlying the responses. The most marked changes in growing season (May–August) moisture availability, as measured by the Palmer drought severity index (PDSI), occurred between 2001 and 2003 (mean PDSI: −2.05, 1.76, and 2.04 in 2001, 2003, and 2007, respectively; National Climatic Data Center, 2009). These values indicate moderate drought conditions existed in 2001, whereas slightly to moderately wet conditions existed in 2003 and 2007 (Palmer, 1965). Alternatively, native and exotic canopy defoliators may indirectly alter understory plant dynamics by increasing resource availability at the forest floor (e.g., Eschtruth et al., 2006); however, we found no evidence of any major defoliation events during the study period (PA DCNR, 2010). Therefore, although alternative mechanisms may influence herbaceous dynamics, we believe decreased browse pressure following deer herd reductions is the most parsimonious explanation for the observed response.

4.2. Extending the value of deer impact phytoindicators

Several authors have advocated the use of palatable, browse-sensitive herbaceous species as useful phytoindicators of deer browsing impacts (reviewed by Kirschbaum and Anacker (2005)). Collectively, these studies find that a variety of morphological (e.g., height, leaf length) and population-level characteristics (abundance, stable-age distributions) are negatively impacted by higher deer impacts. Our results on three of these taxa, *M. canadense*, *M. virginiana*, and *Trillium* spp. are consistent with prior work demonstrating increases in morphological and population-level metrics following release from overbrowsing (Balgooyen and Waller, 1995; Rooney, 1997; Augustine and Frelich, 1998; Webster et al., 2005). Prior to deer herd reductions, *Trillium* spp. heights and the percentage of reproductive individuals within the KQDC area fell below levels indicative of healthy populations (12–14 cm height and 21–34% flowering; Anderson, 1994). After the deer populations were cut by half, *Trillium* spp. populations met both criteria. Similarly, as reported by others (Rooney, 1997; Diefenbach and Fritsky, 2007), *M. virginiana* height and *M. canadense* cover both increased following deer herd reductions. Nevertheless, we caution that gauging deer impact solely from a few palatable herbaceous phytoindicators may prove unreliable as overbrowsing may have driven many of these species to low abundance or local extirpation (Appendix A).

Augustine and Calesta (2003) evaluated the utility of herbaceous browse indicators and hypothesized that ideal phytoindicators would consist of palatable, long-lived, shade tolerant species. Similarly, Kirschbaum and Anacker (2005) argued the best indicators should persist at relatively high abundances across the landscape over a wide range of deer impacts. Throughout the entire KQDC area, only *F. grandifolia* meets all these criteria. We found this highly shade-tolerant woody species was by far the most abundant seedling in our study despite consistently experiencing the highest browse impact (Fig. 3). Although classified as a moderately preferred browse species (Horsley et al., 2003), *F. grandifolia* is heavily browsed, likely as a function of its high abundance (i.e., functional response; Holling, 1959) yet remains dominant throughout forest understories due to its high resprouting ability and vegetative connections to mature, 'parent' trees (Nyland et al., 2006). Given these characteristics, we suggest *F. grandifolia* functions as an ideal indicator of deer impact, both locally as well as regionally due to its widespread occurrence throughout northeastern US hardwood forest understories (Nyland et al., 2006; Royo and Carson, 2006).

The sensitivity of phytoindicator responses may vary depending on the specific parameters being measured. Morphological characteristics may respond almost instantaneously to changes in deer abundance as browsing results in the direct removal of plant tissue. Population-level characteristics may shift over a longer-term as species released from intense browsing are allowed to mature, reproduce, and expand (Knight, 2004; McGraw and Furedi, 2005). Finally, changes to community-level metrics (e.g., species richness, dominance, diversity) may occur only after significant time lags (see Section 4.3) as the direct and indirect effects of moderate browsing lead to greater species establishment and co-existence. Given the dynamic nature of the various phytoindicator metrics, we concur with other researchers who advocate the use of multiple measures in order to robustly assess changes in browse impacts (Williams et al., 2000; Webster et al., 2001; Rooney and Waller, 2003; Côte et al., 2004; Latham et al., 2005). Furthermore, we recommend researchers and managers expand their definition of suitable browsing indicators to include *any* plant species that is selected by herbivores yet is tolerant enough to remain abundant across the landscape.

4.3. Legacy layers may limit recovery

Despite observing increases in both morphological and population-level characteristics of palatable plant species, we observed no increases in overall richness or diversity following deer herd reductions. Our vegetation surveys reveal a depauperate understory herbaceous community that is highly dominated by the browse-tolerant ferns, including the native invasive *Dennstaedtia punctilobula* (de la Cretaz and Kelty, 1999), and woody saplings (e.g., *F. grandifolia*; Fig. 3). Once these browse-resistant species overtake a site they become highly resistant to displacement and strongly suppress plant recruitment through both direct and indirect mechanisms (reviewed by Royo and Carson, 2006). The degree of control over plant recruitment may be so complete that some have characterized the novel understory community as a nearly irreversible 'alternative stable state' (Stromayer and Warren, 1997). We suggest that the ubiquity of this legacy layer coupled with the rarity and limited dispersal distances of many understory plants, particularly ant-dispersed species (Gómez and Espadaler, 1998), may slow or even impede landscape-level recovery of plant diversity (Tanentzap et al., 2009). In order to sustain and promote plant diversity, targeted measures including control of the legacy layer via chemical or mechanical means (Engelman and Nyland, 2006) and transplanting desired species into forest stands (e.g., Honnay et al., 1999; Foster and Wetzel, 2005) may be necessary to aid the restoration process in addition to maintaining lowered deer herds.

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Appendix A

Relative abundance (% cover) and frequency of occurrence (proportion of plots) of herbaceous species sampled in 2001, 2003, and 2007 within the cover subplots. List is restricted to species that occurred on >1 plot. Taxonomic nomenclature follows USDA NCRS (2008).

Latin name	Species group	2001		2003		2007	
		Cover	Frequency	Cover	Frequency	Cover	Frequency
Dennstaedtia punctilobula (Michx.) T. Moore	Fern & fern allies	28.2	0.64	23.8	0.62	18.8	0.58
Dryopteris carthusiana (Vill.)	Fern & fern allies	0.1	0.04				
Dryopteris intermedia (Muhl. Ex Willd.) Gray	Fern & fern allies	31.2	0.91	38.9	0.92	32.5	0.83
Huperzia lucidula (Michx.) Trevisan	Fern & fern allies			1.9	0.17	2.3	0.17
Lycopodium L.	Fern & fern allies	2.7	0.23			1.2	0.06
Lycopodium annotinum L.	Fern & fern allies	0.8	0.11	0.3	0.09	0.6	0.09
Lycopodium dendroideum Michx.	Fern & fern allies					1.4	0.11
Lycopodium obscurum L.	Fern & fern allies	3.5	0.36	3.1	0.38	5.1	0.26
Lycopodium tristachyum Pursh	Fern & fern allies			0.5	0.09	0.1	0.06
Onoclea sensibilis L.	Fern & fern allies	0.1	0.02	0.1	0.06	0	0.02
Osmunda cinnamomea L.	Fern & fern allies	0.1	0.02	0	0.02	0	0.02
Polystichum acrostichoides (Michx.) Schott.	Fern & fern allies	1.2	0.08	0.5	0.06	0.7	0.06
Thelypteris noveboracensis (L.) Nieuwl.	Fern & fern allies	8.7	0.26	9	0.38	10	0.36
Arisaema triphyllum (L.) Schott	Forb	0.8	0.23	0.4	0.21	0.4	0.19
Aster L.	Forb	0.2	0.04	0.1	0.02	0.1	0.02
Circaea lutetiana L.	Forb	0	0.02	0.1	0.06		
Coptis trifolia (L.) Salisb.	Forb	0.3	0.08	0.3	0.08	0.3	0.09
Erythronium americanum Ker-Gawl.	Forb	0.7	0.04	1.3	0.08	2.9	0.08
Eurybia divaricata (L.) Nesom	Forb			0	0.02	0	0.02
Galium L.	Forb	0	0.04	0.1	0.04	0.3	0.04
Impatiens L.	Forb			0	0.02	0.1	0.04
Laportea canadensis (L.) Weddell	Forb	0.9	0.04	0.8	0.04	1.7	0.06
Maianthemum canadense Desf.	Forb	1.8	0.42	1.4	0.42	2.7	0.40
Maianthemum racemosum (L.) Link	Forb	0.1	0.04	0.2	0.06		
Medeola virginiana L.	Forb	1.2	0.30	1.7	0.26	1.4	0.32
Mitchella repens L.	Forb	0.6	0.23	0.7	0.19	0.6	0.13
Osmorhiza claytonii (Michx.) C.B. Clarke	Forb	0	0.02	0	0.02	0.1	0.04
Oxalis montana Raf.	Forb	1.8	0.34	1.5	0.34	0.7	0.17
Oxalis stricta L.	Forb	0	0.02	0	0.02		
Pilea pumila (L.) Gray	Forb	0.1	0.02	0	0.02		
Podophyllum peltatum L.	Forb	0.4	0.02			0.2	0.02
Polygonatum pubescens (Willd.)Pursh	Forb			0.1	0.02	0	0.02
Polygonum caespitosum Blume	Forb	0	0.02	0	0.02		
Prenanthes trifoliolata (Cass.) Fern	Forb	0.1	0.02	0	0.02	0.1	0.04
Streptopus lanceolatus (Ait.)	Forb	0.1	0.02	0.1	0.02	0.2	0.04
Tiarella cordifolia L.	Forb	0.1	0.04	0.1	0.02		
Trientalis borealis Raf.	Forb	1.4	0.25	0.4	0.26	0.4	0.26
Trillium L.	Forb			0.2	0.06	0	0.04
Trillium erectum L.	Forb	0	0.04	0.1	0.06	0.1	0.08
Trillium undulatum Willd.	Forb	0.3	0.13	0.2	0.09	0.3	0.11
Uvularia L.	Forb					0.1	0.06
Uvularia sessilifolia L.	Forb	0.6	0.17	0.5	0.17	0.5	0.17
Veronica chamaedrys L.	Forb			0	0.02	0.3	0.02
Veronica officinalis L.	Forb	0.1	0.02	0	0.02		
Viola L.	Forb			0	0.02	3.9	0.30
Viola blanda Willd.	Forb	1.2	0.42	0.9	0.36	1.1	0.13
Viola canadensis L.	Forb			0.2	0.02	0	0.02
Viola macloskeyi Lloyd	Forb	0.7	0.15	1.3	0.28	0.3	0.09
Viola pubescens Ait.	Forb			0.1	0.04		
Viola rotundifolia Michx.	Forb					0.9	0.23
Viola sororia Willd.	Forb	0.1	0.04	0	0.04	0	0.02
Brachyelytrum erectum (Schreb. ex Spreng.)	Graminoids	3.2	0.38	2.8	0.40	2	0.32
Carex L.	Graminoids	2.4	0.45	2	0.53	2.1	0.36
Carex platyphylla Carey	Graminoids	0.2	0.04				
Cinna latifolia (Trev. ex Goepp.) Griseb.	Graminoids	0.9	0.17	1.4	0.11	0.2	0.11
Danthonia compressa Austin ex Peck	Graminoids	0.4	0.09	0.2	0.09	0.1	0.02
Elymus hystrix L.	Graminoids	0.1	0.04			0.4	0.02
Festuca subverticillata (Pers.)Alexeev	Graminoids			0.1	0.04		
Poa L.	Graminoids	0.2	0.06	0.1	0.06		

Appendix A (*continued*)

Latin name	Species group	2001		2003		2007	
		Cover	Frequency	Cover	Frequency	Cover	Frequency
Poa alsodes Gray	Graminoids	1.3	0.09	1.2	0.15	0	0.02
Unidentified Grass	Graminoids			0	0.02	0.1	0.08
Crataegus L.	Shrub			0	0.02	0.1	0.02
Rubus L.	Shrub	1.1	0.11	1.3	0.13	2.5	0.15

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