

The legacy of deer overabundance: long-term delays in herbaceous understory recovery

Thomas H. Pendergast IV, Shane M. Hanlon, Zachary M. Long, Alejandro A. Royo, and Walter P. Carson

Abstract: Decades of white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) overpopulation have dramatically homogenized forests across much of the eastern United States, creating depauperate forest understory communities. The rate at which these communities recover once deer browsing has been reduced remains an open question. We evaluate overbrowsing legacy effects by examining how forest herbaceous layers respond in terms of biodiversity, density, and community composition over 11 years using exclosures and control plots within a mature beech–maple forest. Although little recovery occurred in the first 5 years, total density and preferred browse density rebounded substantially during the final years of the study. Although community composition began to diverge between exclosure and control plots after 5 years, diversity failed to recover even after 11 years of excluding browsers. Our findings show that vulnerable species can increase after excluding browsers but only if those species were initially present. Biodiversity recovery may be extremely slow because preferred browse species have been nearly extirpated from many forests and thus are unable to recruit into refugia. We empirically demonstrate the extent of the ghost of herbivory past or legacy effect of browsing, i.e., the substantial time delay between herbivore abatement and community response after decades of high deer densities.

Key words: white-tailed deer, *Odocoileus virginianus*, herbivory, understory, forest recovery.

Résumé : Des décennies de surpopulation du cerf de Virginie (*Odocoileus virginianus* (Zimmermann, 1780)) ont radicalement homogénéisé les forêts dans la majeure partie de l'est des États-Unis, créant des communautés végétales de sous-bois appauvries. On ignore à quelle vitesse ces communautés se rétablissent une fois réduit le broutement du cerf. Nous avons évalué les effets d'un héritage de broutement excessif en examinant la réponse des strates forestières herbacées en regard de la biodiversité, de la densité et de la composition végétale sur une période de 11 ans, au moyen d'exclus et de places-échantillons témoins dans une érablière à hêtre mature. Nous avons observé très peu de signes de rétablissement durant les 5 premières années, mais la densité totale de végétation et la densité des espèces préférées du cerf se sont substantiellement accrues au cours des six années suivantes. Bien que la composition des communautés végétales des exclos et des places-échantillons témoins ait commencé à différer après 5 ans, la diversité n'était pas rétablie même après 11 ans d'exclusion des brouteurs. Nos résultats montrent que la densité des espèces vulnérables peut augmenter après l'exclusion des brouteurs seulement si elles étaient préétablies. Le rétablissement de la biodiversité peut s'avérer extrêmement lent parce que les espèces préférées des brouteurs ont été presque éliminées de plusieurs forêts et qu'il n'y a plus de refuges pour soutenir le recrutement. Nous démontrons empiriquement l'importance du spectre d'un passé d'herbivorisme ou de l'effet d'un héritage de broutement qui s'expriment par un long délai entre la diminution des herbivores et la réponse des communautés végétales après des décennies de fortes densités de cerfs. [Traduit par la Rédaction]

Mots-clés : cerf de Virginie, *Odocoileus virginianus*, herbivorisme, sous-bois, rétablissement de la forêt.

Introduction

In many areas of the United States, the population density of white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) has dramatically increased over the past century to levels that are significantly greater than presettlement estimates (Horsley et al. 2003; McCabe and McCabe 1997; Porter et al. 1994). Deer display browse preferences among forest plant species, largely based on plant chemical defenses and nutrient content (Augustine and McNaughton 1998; Berteaux et al. 1998; Dostaler et al. 2011; Whitney 1984). Prolonged and selective overbrowsing by deer has strong impacts on population- and community-level processes, including reducing recruitment, diminishing sizes, and shifting

communities towards dominance by a small subset species that are browse tolerant, browse resistant, or both (Coté et al. 2004; Goetsch et al. 2011; Horsley et al. 2003; Rooney and Waller 2003; Waller 2014). In addition, in some cases, decades of overbrowsing can cause dramatic increases in browse-tolerant species that can spread to form dense and recalcitrant understory layers (Royo and Carson 2006; Young and Peffer 2010). These recalcitrant layers are often inimical to the recovery of vulnerable species even when browsing intensity is reduced or eliminated entirely (Royo and Carson 2006, 2008). Consequently, under heavy browsing pressure, tolerant or resistant species will spread whereas palatable or preferred species will become uncommon and sparsely distributed

Received 14 July 2015. Accepted 10 November 2015.

T.H. Pendergast* IV, S.M. Hanlon, and W.P. Carson. Department of Biological Sciences, University of Pittsburgh, A234 Langley Hall, 4249 Fifth Avenue, Pittsburgh, PA 15260, USA.

Z.M. Long. Department of Biology and Marine Biology, University of North Carolina Wilmington, Friday Hall 2015, 601 South College Road, Wilmington, NC 28403, USA.

A.A. Royo. USDA Forest Service, Northern Research Station, Forestry Sciences Lab, P.O. Box 267, Irvine, PA 16329, USA.

Corresponding author: Thomas H. Pendergast IV (email: thpiv@uga.edu).

*Present address: Department of Crop and Soil Sciences, University of Georgia, 3111 Plant Sciences Building, Athens, GA 30602, USA.

across the landscape (for reviews, see Carson et al. (2014) and Waller (2014)).

Forest herbaceous species are especially sensitive to overbrowsing by deer because they cannot reach a size refuge from browsers as trees can. Therefore, they are often subjected to repeated bouts of browsing throughout their lifespans, which can severely reduce plant fecundity (Russell et al. 2001). Furthermore, strong herbivore pressures can severely limit sexual reproduction of perennial herbs by clipping flowers, fruit, or early reproductive tissue. For example, Comisky et al. (2005) found that reproductive individuals of several species of wildflowers were two orders of magnitude more abundant at sites on large boulders that served as refugia from deer versus adjacent sites at the soil surface. If herbivore browsing levels remain consistently high, reproduction will be limited or nonexistent, and populations of perennial herbs are predicted to dwindle over time (McGraw and Furedi 2005). Although patterns of low-diversity wildflower populations and diminished reproduction are well documented, it remains an open question if plant communities can rebound from chronic overbrowsing if herbivore populations are reduced or eliminated. Long lag times in recovery are especially likely for many of these now low-density herbs due to short dispersal distances and slow rates of growth and reproduction, as well as low genetic diversity, Allee effects, and increased susceptibility to stochasticity (particularly physical disturbances, e.g., Chips et al. (2014)). Moreover, their former habitats may now be occupied by a dense and recalcitrant layer of browse-tolerant species.

Overall, the legacy of deer overabundance or ghost of herbivory past (Banta et al. 2005) is likely to either delay biodiversity recovery for decades or prevent any recovery at all because browsing may have created an alternative stable state (Banta et al. 2005; Carson et al. 2014; Frerker et al. 2014; Royo et al. 2010b; Stromayer and Warren 1997; Tanentzap et al. 2009). In fact, to date, the few studies of sufficient duration to evaluate the length of legacy effects strongly suggest that recovery will take decades, particularly for herbs and shrubs (Royo et al. 2010b; Tanentzap et al. 2009). Here, we ask to what degree does excluding deer via exclosures lead to understory recovery within a mature beech–maple forest over 11 years, in terms of plant density, species richness, species diversity, and plant species composition. We predict that long-term deer exclosures will act as refugia for preferred browse wildflower species, increasing the frequency of browse-susceptible understory species and overall diversity over time, relative to areas that experience continual deer browse. However, we predict considerable lag times before communities can recover from decades of intense herbivory.

Materials and methods

Site and deer densities

We conducted this experiment in Tryon-Weber Woods in Crawford County, northwestern Pennsylvania, USA (latitude, 41°36'N; longitude, 80°21'W).

This site is within a mesic temperate zone, with yearly rainfall averaging 103 cm and total snowfall averaging 165 cm (weather station, Linesville, Pennsylvania). This mature 10 ha beech–maple forest is at least 100 years old and is stewarded by the University of Pittsburgh's Pymatuning Laboratory of Ecology (see Long et al. (2007) for forest structure details). This forest is partially surrounded by younger secondary forest and exists within a landscape of forest fragments, old fields, and agriculture (Chips et al. 2014; Long et al. 2007). Although white-tailed deer were nearly extirpated in western Pennsylvania in the late 1800s, they were reintroduced and grew to large population densities by 1940 and density levels have remained high (Heckel et al. 2010; Smith 1989; Whitney 1984). Deer densities in Crawford County from 1996 to 1999 averaged ~14 deer·km⁻², but summer densities were likely much higher (e.g., 29 deer·km⁻², Wallingford 2000). In this region,

densities greater than 8 deer·km⁻² cause woody and herbaceous species declines (Horsley et al. 2003).

Herbivore exclusion and plant sampling

Within Tryon-Weber Woods, twelve paired plots, measuring 20 m × 20 m, were marked out in haphazard locations in March 1996 (see Chips et al. (2014) and Long et al. (2007)). Three meters separated paired plots, and treatment (herbivore exclosure or control) was assigned randomly between plot pairs. Exclosure plots had 2.4 m tall fences with 5 cm × 10 cm mesh constructed along their perimeter to exclude large herbivores. Within each plot, we established a 15 m × 15 m inner plot, which was subdivided into nine subplots, leaving a 2.5 m buffer around each inner plot. No major canopy gaps occurred across these plots for the duration of the study. In late May or early June of 1997, 1998, 1999, 2001, and 2007, we visually estimated the cover of each forb species using area templates of known size (e.g., 1%, 5%, etc.) in either six subplots (randomly selected) or all nine subplots within each large plot. Because visual cover estimates can vary among observers among years, we also quantified stem densities in 2001 and 2007. We used these data to calculate relative abundance (species cover:(total cover)⁻¹), plant density, species richness, Shannon's diversity index (as measured by cover and density), and community dissimilarity. We also grouped for analysis four species known to be preferred by deer, specifically *Maianthemum canadense* Desf., *Maianthemum racemosum* L., *Polygonatum pubescens* (Willd.) Pursh, and *Trillium grandiflorum* (Michx.) Salisb. (Comisky et al. 2005; Korschgen et al. 1980; Kraft et al. 2004; Mosbacher and Williams 2009). Finally, we also evaluated the impact of exclosures on *Podophyllum peltatum* L., a dominant understory species that is unpalatable and never browsed (Cassidy et al. 1982).

Statistical analyses

We evaluated whether excluding browsers would alter density, species richness, and diversity over time using Proc Mixed (SAS version 9.2, SAS Institute 2008) and performed repeated measures ANOVAs with autoregressive covariance structure. For 2001 and 2007 data, we also performed an ANOVA on total density. Analyses were conducted at the subplot level, with a random statement nesting subplot within plot. We used a Satterwaite unequal variance mixed model with a repeated statement (Proc Mixed) to test the effect of deer herbivory on preferred browse density over time (Ruxton 2006). We used identical methodology to test the effect of deer removal on the density of *P. peltatum*.

To test if exclosures created contrasting communities over time, we used a semi-metric Bray–Curtis dissimilarity index and nonparametric MANOVA, conducted in R (R Development Core Team 2011), using the vegan package and Adonis procedure (Oksanen et al. 2007). The Bray–Curtis method and nonparametric MANOVA allow for binary and zero-inflated data sets, as well as situations where rare species lead to violations of assumptions of normality required for parametric MANOVA (McArdle and Anderson 2001). The Bray–Curtis dissimilarity index (BC) is

$$(1) \quad BC = \frac{\sum_i |X_{ij} - X_{ik}|}{\sum_i (X_{ij} + X_{ik})}$$

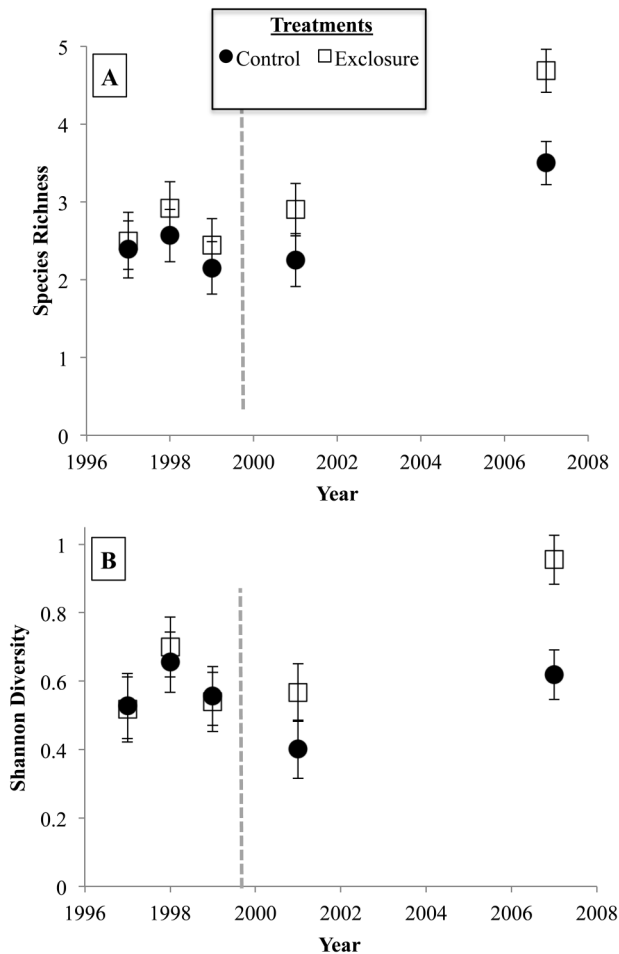
where X_{ij} is the abundance of the i th species in treatment j and X_{ik} is the abundance of the i th species in treatment k (Krebs 1989). Additionally, we repeated the analysis with the Horn and Jaccard dissimilarity indices to account for any abundance or sample size bias (Krebs 1989).

Results

Species richness

Across the six surveys over an 11 year period, we identified 54 species of herbaceous vines and forbs. In the final census in

Fig. 1. Species richness and Shannon's diversity indices of herbaceous understory species in fenced (exclosure) and unfenced (control) plots established in 1996 and monitored from 1997 through 2007. The vertical, gray dashed line indicates when antlerless deer harvest was increased. (A) Species richness at the 5 m × 5 m subplot level. Species richness increased if the plots were protected from deer (i.e., exclosure plots; $p = 0.0421$) and over time ($p < 0.0001$). (B) Shannon's diversity indices did not differ in the first 5 years, but exclosure plots showed only a trend of increased diversity by 2007 ($p = 0.0615$) and increased over time ($p = 0.0233$). Relevant statistics presented in Table 1.



2007, we found a total of 38 plant species, 24 in control plots and 32 in fenced plots. Excluding deer caused a modest (<2 species) but significant increase ($p = 0.042$) in mean species richness by 2007, but species richness did not increase relative to control plots until after 2001, i.e., at least 7 years after the fences were built (Fig. 1A; Table 1). Species richness also increased over time both inside the exclosures and in control plots (Fig. 1A; Table 1).

Shannon's diversity index

Excluding browsers did not cause a significant increase in Shannon's diversity index (Fig. 1B; Table 1), but it did increase over time when using both cover and stem densities as abundance metrics ($p = 0.0233$ and $p < 0.0001$, respectively; Fig. 1B; Table 1). It is important to point out that there was no significant exclosure × time interaction; therefore, even after 11 years, there was no significant increase in Shannon's diversity index inside the exclosures (Fig. 1B; Table 1).

Table 1. Response of species richness, herbaceous cover, and Shannon's diversity index (1997, 1998, 1999, 2001, and 2007), as well as total wildflower density, preferred browse density, and *Podophyllum peltatum* density (2001 and 2007), to deer exclosures, analyzed using a repeated measures ANOVA in SAS Proc Mixed.

| Source of variation | F | DF (N, D) | P value |
|---|-------|-----------|-------------------|
| Species richness | | | |
| Exclosure | 4.24 | 1, 106 | 0.0421 |
| Year | 13.52 | 4, 266 | <0.0001 |
| Exclosure × year | 1.04 | 4, 266 | 0.3868 |
| Shannon's diversity index (by cover) | | | |
| Exclosure | 3.59 | 1, 86.5 | 0.0615 |
| Year | 5.29 | 1, 109 | <0.0233 |
| Exclosure × year | 0.42 | 1, 109 | 0.5177 |
| Shannon's diversity index (by density) | | | |
| Exclosure | 2.08 | 1, 106 | 0.1518 |
| Year | 7.5 | 4, 266 | <0.0001 |
| Exclosure × year | 1.75 | 4, 266 | 0.1389 |
| Total density | | | |
| Exclosure | 12.19 | 1, 176 | 0.0006 |
| Year | 39.16 | 1, 176 | <0.0001 |
| Exclosure × year | 8.72 | 1, 176 | 0.0036 |
| Preferred browse density | | | |
| Exclosure | 9.7 | 1, 108 | 0.0024 |
| Year | 30.46 | 1, 143 | <0.0001 |
| Exclosure × year | 9.43 | 1, 108 | 0.0027 |
| <i>Podophyllum peltatum</i> density | | | |
| Exclosure | 4.87 | 1, 127 | 0.0291 |
| Year | 14.74 | 1, 154 | 0.0002 |
| Exclosure × year | 3.15 | 1, 127 | 0.0784 |

Note: Boldface P values indicate significance. DF, degrees of freedom.

Plant cover and density

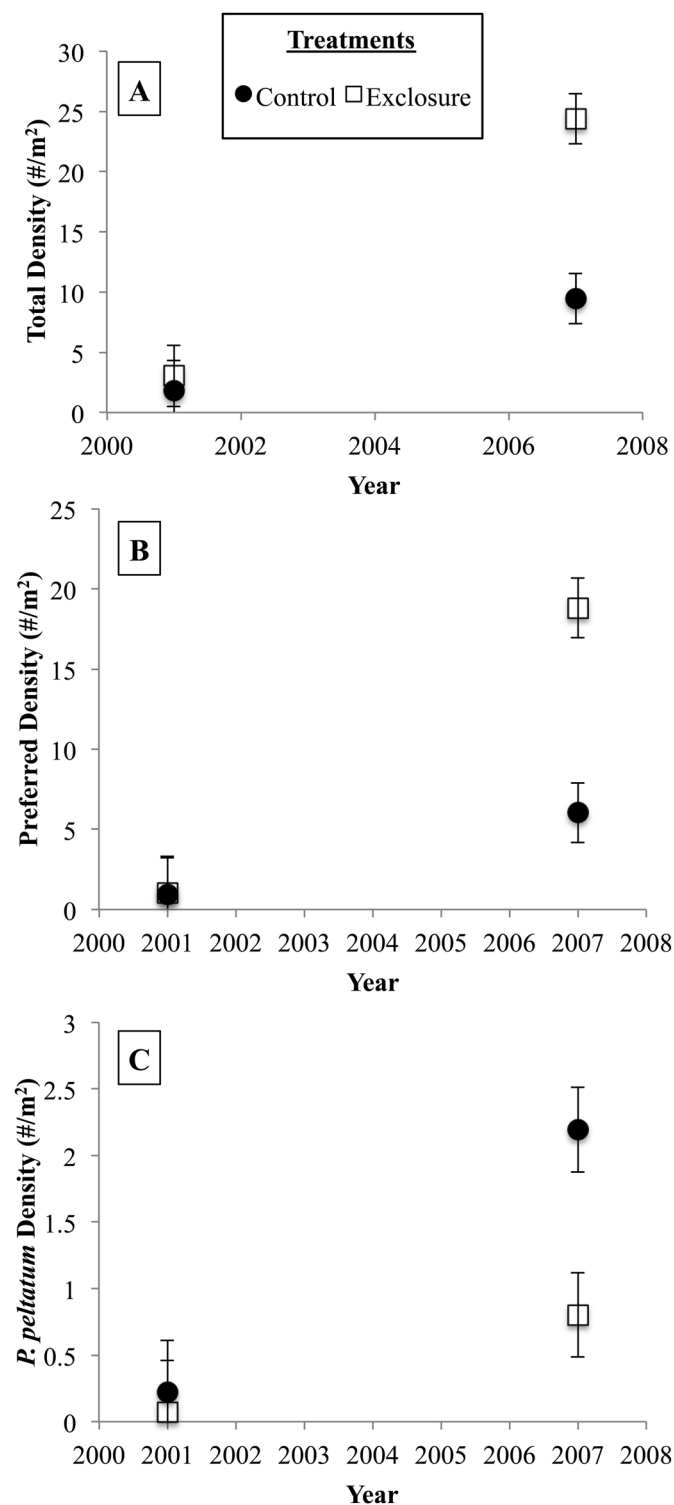
Because absolute cover data exhibited substantial year-to-year variability, we used our cover data only to look at patterns of relative abundance and community composition using dissimilarity indices (see below). Cover estimates likely varied because of observer bias among years or timing of sampling relative to the onset of warming during each spring among years.

Five years after the exclosures were built, the exclusion of browsers had not caused an increase in total plant density or in the density of preferred species (Figs. 2A and 2B; Table 1). However, during the next 6 years, excluding browsers caused substantial increases in plant density, and nearly all of this (83%) was accounted for by an increase in the density of preferred species (Figs. 2A and 2B; Table 1). It is important to note that total density and, in particular, preferred density also increased significantly over time in control plots but increased most dramatically inside exclosures (exclosure × time interaction for preferred species; Figs. 2A and 2B; Table 1). *Podophyllum peltatum*, a species that deer never consume, was 2.5 times more dense in control plots ($p = 0.0291$; Fig. 2C; Table 1).

Plant community composition

Excluding browsers caused community composition to diverge for all three community dissimilarity indices but only beginning in 2001, i.e., 5 years after erecting the fences (Fig. 3; Table 2). This was largely caused by the dominance of *P. peltatum* in the control plots and the increase of preferred species such as *Mitchella repens* L. inside the exclosures (Fig. 3). *Mitchella repens* was by far the most abundant species (by cover) inside the exclosures by 2007.

Fig. 2. Subplot stem densities of all herbaceous understory species and preferred browse species in fenced (exclosure) and unfenced (control) plots established in 1996, monitored from 2001 through 2007. (A) Stem density was not only significantly higher in the exclosure treatment in 2007 ($p = 0.006$), but also increased over time ($p < 0.0001$). (B) Preferred browse density increased with deer exclosure and over time but increased most dramatically in exclosure plots (fence \times year interaction; $p = 0.0027$). (C) The herbivore-resistant *Podophyllum peltatum* density increased over time ($p = 0.0002$) but ore substantially in control plots ($p = 0.0291$). Relevant statistics presented in [Table 1](#).



Discussion

Within large parts of the eastern deciduous forest biome, decades of overbrowsing has created depauperate herbaceous communities dominated by browse-tolerant or browse-resistant species (Frerker et al. 2014; Nuttle et al. 2013; Rooney and Dress 1997). In some cases, some of these browse-tolerant or browse-resistant species can spread to form dense and recalcitrant understory layers that are inimical to biodiversity recovery (Royo and Carson 2006). What is far less clear is the amount of time required for herbaceous understory communities to recover their lost diversity. Here, we demonstrate that excluding deer for 11 years did not lead to a significant recovery of biodiversity in terms of species richness or species diversity (Fig. 1; Table 2). Although species richness did increase significantly inside the exclosures, this increase was modest. We did, however, see a four-fold increase in the combined density of four preferred species, which were present in the understory at the start of the experiment (Fig. 2B). Our results demonstrate that preferred species, if they are present, will increase following the exclusion of deer; however, even these preferred species showed no increase in density during the first 5 years of deer exclusion. Overall, substantial diversity recovery will likely take much longer than the 11 year duration of this experiment, especially under low light regimes of mature forest (Anderson et al. 1969). Our data, coupled with a few other studies (Royo et al. 2010b; Tanentzap et al. 2011; Tanentzap et al. 2009), suggest that even if deer are reduced to zero (i.e., excluded) or to near zero levels, lag times in biodiversity recovery will last at least a decade and will likely last much longer. One bright spot is that species composition inside the fences began to diverge from control plots after 5 years (Table 2), suggesting that some recovery had begun.

We were only able to classify 4 species of over 50 species as being preferred by deer (c.f. Vankat and Snyder 1991). This is not surprising as deer have been overabundant in the region for well over 50 years (Horsley et al. 2003), and depauperate understories are common throughout the eastern deciduous forest (reviewed by Waller (2014) and, in particular, in Pennsylvania (Carson et al. 2014). Thus, it was no surprise that *P. peltatum*, which is defended by potent lignans and glycosides (Cassidy et al. 1982), was the dominant understory species in control plots (Fig. 3), and it increased in total density during the study (Fig. 2C). It is now well known that overbrowsing can lead to an increase in the abundance of resistant or tolerant species and, in some cases, the formation of dense recalcitrant understory layers that are inimical to biodiversity recovery (Carson et al. 2014; Royo and Carson 2006; Waller 2014; Young and Pepper 2010). Indeed, Carson et al. (2014) demonstrated that even a stand replacement disturbance or canopy gaps will cause few changes in understory diversity or abundance, because these disturbances occur over a depauperate understory created by nearly a century of overbrowsing. In contrast, when deer are closer to historical levels, they can promote herbaceous diversity following disturbance by acting as keystone species via reducing the abundance of fast-growing woody pioneers (Royo et al. 2010a).

One curious feature of our results is that plant species richness, diversity, and density increased over time after 2000 in the control plots, as well as inside the exclosures (Figs. 1 and 2). Understory populations can certainly fluctuate with climate, pathogen outbreaks, and non-ungulate herbivory (and their interactions, McDowell et al. (2011)), and control plots also had low tree seedling densities that continued to decline over time (0.24 and 0.04 stems·m⁻² in 1996 and 2005, respectively; Long et al. 2007), thus lack of competition may have aided herbaceous response. However, seedling densities in enclosed plots increased but plateaued at ~0.4 stems·m⁻² by 1999 (Long et al. 2007), a level that clearly did not significantly hinder population growth of herbaceous species (Fig. 2). The substantial herbaceous increase in control

Fig. 3. Relative abundance (by total cover) of herbaceous species in control and exclosure plots from 1997 to 2007. We have identified, by genus, the 10 most abundant species in the 2007 control plots in the legend; all other abundance data can be found in [Appendix A, Table A1](#). These two wildflower communities are significantly disparate (Bray–Curtis dissimilarity index, $p = 0.001$). Figure is provided in colour online.

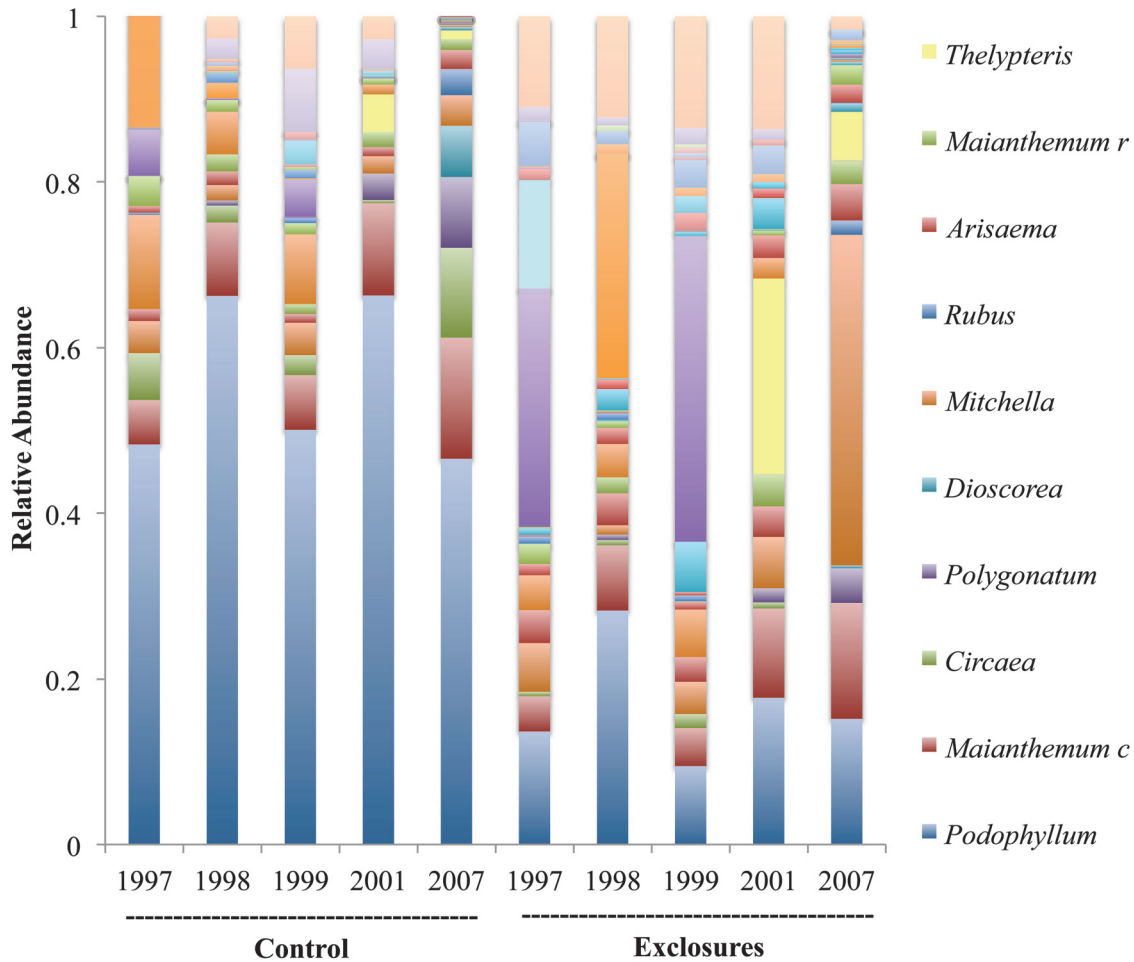


Table 2. Bray–Curtis, Jaccard, and Horn indices of community dissimilarity.

| Year | Bray–Curtis | | Jaccard | | Horn | |
|------|-------------|---------------|---------|---------------|---------|---------------|
| | F model | P value | F model | P value | F model | P value |
| 1997 | 1.5976 | 0.1268 | 1.4106 | 0.0899 | 1.3872 | 0.2368 |
| 1998 | 1.5551 | 0.1179 | 1.5017 | 0.9191 | 1.9215 | 0.1349 |
| 1999 | 1.5576 | 0.1044 | 1.4640 | 0.0869 | 1.3921 | 0.2198 |
| 2001 | 3.1071 | 0.0090 | 2.2542 | 0.0070 | 3.7531 | 0.0042 |
| 2007 | 2.5795 | 0.0040 | 2.0240 | 0.0010 | 2.5723 | 0.0350 |

Note: Boldface P values indicate that fenced and unfenced herbaceous communities are significantly different.

plots coincided with a state-wide initiative by the Pennsylvania Game Commission designed to bring deer more into balance with their habitat (Frye 2006). This initiative increased antlerless harvests statewide by 55% and total deer harvests by 31% relative to rates in the 1990s (see Appendix A, Fig. A1, compiled from www.pgc.state.pa.us). This may provide a possible explanation for the observed increases in richness and density outside of the exclosures after 2000. Unfortunately, this conservation-oriented deer management program quickly floundered (Carson et al. 2014; Frye 2006), and deer densities again began to rise in the latter part of the decade (Rosenberry et al. 2011). We should note, however, that Tryon-Weber Woods and other forests in the region remain depauperate (Carson et al. 2014; Waller 2014) relative to forests without chronic deer overpopulation. For example, Vankat and

Snyder (1991) found two to three times the number of herbaceous species in similar glacial moraine mature beech-maple forests in Ohio, where deer densities were consistently less than 1 deer·km⁻² for decades (ODNR 1996). This was true even though our vegetation surveys cover ~13 times the area sampled by Vankat and Snyder (1991).

The next step in understanding legacy effects is to further quantify the severity of these effects in regions both within the eastern deciduous forest biome and biomes elsewhere (e.g., Wright et al. 2012). Perhaps, however, it is more important to parse out the myriad of potential causes that underlie long lag times in biodiversity and community recovery. Understorey species face sparse distributions, slow growth rates, low fecundity, limited dispersal, and Allee effects (Bierzychudek 1982; Handel et al. 1981; Matlack 1994). However, there may be an array of additional hurdles, including dense recalcitrant understorey layers, low light levels, disruption of mutualisms (e.g., arthropod seed dispersers, pollinators, and mycorrhizal fungi), invasive plant species (e.g., garlic mustard), and exotic earthworms. Many of these factors may be operating simultaneously. Though speculative, all of these factors together may be creating the perfect storm of events that contribute to the development of alternative stable states that may create fundamentally different and depauperate forest herbaceous communities across broad regions (Stromayer and Warren 1997). These communities are already forming for woody species throughout the east (e.g., Nuttle et al. 2013) and in other temperate forests around the world (Askins 2014; Wright et al. 2012).

Conclusions

The chronic high deer densities throughout many regions of the eastern United States have critical implications for the current and future understory diversity. Our results strongly support forest management techniques that decrease deer populations to promote viable understory communities. Additionally, we must expect time lags on the scale of decades before herbaceous populations can recover following a decrease in top-down pressure. Although refugia may provide local seed sources to reestablish palatable species following herbivory abatement, alternative successional pathways may result in lower diversity recalcitrant understories, with herbivore sensitive species functionally extirpated.

Acknowledgements

Jill T. Anderson, Aileen Wertz, Chad Kirschbaum, Kelly A. Kumm, David M. Krayesky, Amy Long, Andrea Quesada, Todd Ristau, Garland Waleko, and many others helped maintain the enclosures and collect data. We thank J. Anderson for helpful comments and statistical advice. The Pennsylvania Academy of Science, Sigma Xi, and the Pymatuning Laboratory of Ecology provided financial support.

References

- Anderson, R.C., Loucks, O.L., and Swain, A.M. 1969. Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. *Ecology*, **50**(2): 255–263. doi:10.2307/1934853.
- Askins, R.A. 2014. Saving the world's deciduous forests: ecological perspectives from East Asia, North America, and Europe. Yale University Press.
- Augustine, D.J., and McNaughton, S.J. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *J. Wildl. Manage.* **62**(4): 1165–1183. doi:10.2307/3801981.
- Banta, J.A., Royo, A.A., Kirschbaum, C., and Carson, W.P. 2005. Plant communities growing on boulders in the Allegheny National Forest: evidence for boulders as refugia from deer and as a bioassay of overbrowsing. *Nat. Areas J.* **25**(2): 10–18.
- Berteaux, D., Crete, M., Huot, J., Maltais, J., and Ouellet, J. 1998. Food choice by white-tailed deer in relation to protein and energy content of the diet: a field experiment. *Oecologia*, **115**: 84–92. doi:10.1007/s004420050494.
- Bierzychudek, P. 1982. Life histories and demography of shade-tolerant temperate forest herbs: a review. *New Phytol.* **90**(4): 757–776. doi:10.1111/j.1469-8137.1982.tb03285.x.
- Carson, W.P., Royo, A.A., and Peterson, C.J. 2014. A pox on our land: a case study of chronic deer overbrowsing throughout the Allegheny National Forest region in Pennsylvania. In *The herbaceous layer in forests of eastern North America*. 2nd edition. Edited by F.S. Gilliam and M.R. Roberts. Oxford University Press, New York.
- Cassidy, D.E., Drewry, J., and Fanning, J.P. 1982. Podophyllum toxicity: a report of a fatal case and a review of the literature. *J. Toxicol.* **19**(1): 35–44. doi:10.3109/15563658208990364.
- Chips, M.J., Magliocca, M.R., Hasson, B., and Carson, W.P. 2014. Quantifying deer and turkey leaf litter disturbances in the eastern deciduous forest: have nontrophic effects of consumers been overlooked? *Can. J. For. Res.* **44**(9): 1128–1132. doi:10.1139/cjfr-2014-0045.
- Comisky, L., Royo, A.A., and Carson, W.P. 2005. Deer browsing creates rock refugia gardens on large boulders in the Allegheny National Forest, Pennsylvania. *Am. Midl. Nat.* **154**(1): 201–206. doi:10.1674/0003-0031(2005)154[0201:DBCRRJ]2.0.CO;2.
- Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., and Waller, D.M. 2004. Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Syst.* **35**: 113–147. doi:10.1146/annurev.ecolsys.35.021103.105725.
- Dostaler, S., Ouellet, J., Therrien, J., and Côté, S.D. 2011. Are feeding preferences of white-tailed deer related to plant constituents? *J. Wildl. Manage.* **75**(4): 913–918. doi:10.1002/jwmg.118.
- Frerker, K., Sabo, A., and Waller, D. 2014. Long-term regional shifts in plant community composition are largely explained by local deer impact experiments. *PLoS One*, **9**(12): e115843. doi:10.1371/journal.pone.0115843.
- Frye, R. 2006. Deer wars: science, tradition, and the battle over managing white-tails in Pennsylvania. Penn State University Press, University Park, Pennsylvania.
- Goetsch, C., Wigg, J., Royo, A.A., Ristau, T., and Carson, W.P. 2011. Chronic over browsing and biodiversity collapse in a forest understory in Pennsylvania: results from a 60 year-old deer exclusion plot. *J. Torrey Bot. Soc.* **138**(2): 220–224. doi:10.3159/TORREY-D-11-00013.1.
- Handel, S.N., Fisch, S.B., and Schatz, G.E. 1981. Ants disperse a majority of herbs in a mesic forest community in New York State. *Bull. Torrey Bot. Club*, **108**(4): 430–437. doi:10.2307/2484443.
- Heckel, C.D., Bourg, N.A., McShea, W.J., and Kalisz, S. 2010. Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. *Ecology*, **91**(2): 319–326. doi:10.1890/09-0628.1.
- Horsley, S.B., Stout, S.L., and DeCalesta, D.S. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecol. Appl.* **13**(1): 98–118. doi:10.1890/1051-0761(2003)013[0098:WTDIOT]2.0.CO;2.
- Korschgen, L.J., Porath, W.R., and Torgerson, O. 1980. Spring and summer foods of deer in the Missouri Ozarks. *J. Wildl. Manage.* **44**(1): 89–97. doi:10.2307/3808354.
- Kraft, L.S., Crow, T.R., Buckley, D.C., Nauertzd, E.A., and Zasadae, J.C. 2004. Effects of harvesting and deer browsing on attributes of understory plants in northern hardwood forests, Upper Michigan, U.S.A. *For. Ecol. Manage.* **199**: 219–230. doi:10.1016/j.foreco.2004.05.044.
- Krebs, C.J. 1989. *Ecological methodology*. Harper Collins, New York, New York, U.S.A.
- Long, Z.T., Pendergast, T.H., IV, and Carson, W.P. 2007. The impact of deer on relationships between tree growth and mortality in an old-growth beech-maple forest. *For. Ecol. Manage.* **252**: 230–238. doi:10.1016/j.foreco.2007.06.034.
- Matlack, G.R. 1994. Plant-species migration in a mixed history forest landscape in eastern North America. *Ecology*, **75**(5): 1491–1502. doi:10.2307/1937472.
- McArdle, B.H., and Anderson, M.J. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, **82**: 290–297. doi:10.1890/0012-9658(2001)082[0290:FMMTC]2.0.CO;2.
- McCabe, T.R., and McCabe, R.E. 1997. Recounting whitetails past. In *The science of overabundance: deer ecology and population management*. Edited by W.J. McShea, H.B. Underwood, and J.H. Rappole. Smithsonian Institution Press, Washington D.C., U.S.A. pp. 11–26.
- McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F., and Stitt, M. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends Ecol. Evol.* **26**(10): 523–532. doi:10.1016/j.tree.2011.06.003.
- McGraw, J.B., and Furedi, M.A. 2005. Deer browsing and population viability of a forest understory plant. *Science*, **307**(5711): 920–922. doi:10.1126/science.1107036.
- Mosbacher, E.V., and Williams, C.E. 2009. Browse preference and browsing intensity of white-tailed deer (*Odocoileus virginianus*) in Allegheny high plateau riparian forests, USA. *Wildl. Biol. Pract.* **5**: 11–21. doi:10.2461/wbp.2009.5.4.
- Nuttall, T., Royo, A.A., Adams, M.B., and Carson, W.P. 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. *Ecol. Monogr.* **83**(1): 3–17. doi:10.1890/11-2263.1.
- Ohio Department of Natural Resources (ODNR). 1996. Deer-season results. Division of Wildlife Publication 166. Waterloo Wildlife Experiment Station, New Marshfield, Ohio.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., and Stevens, M.H.H. 2007. vegan: community ecology akeage. In R package version 1.8-7.
- Porter, W.F., Coffey, M.A., and Hadidian, J. 1994. In search of a litmus test: wildlife management in the U.S. National Parks. *Wildl. Soc. Bull.* **22**: 301–306.
- R Development Core Team. 2011. R: a language and environment for statistical computing. Vienna, Austria. Available from <http://www.R-project.org>.
- Rooney, T.P., and Dress, W.J. 1997. Patterns of plant diversity in overbrowsed primary and mature secondary hemlock northern hardwood forest stands. *J. Torrey Bot. Soc.* **124**(1): 43–51. doi:10.2307/2996597.
- Rooney, T.P., and Waller, D.M. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *For. Ecol. Manage.* **181**(1–2): 165–176. doi:10.1016/S0378-1127(03)00130-0.
- Rosenberry, C.R., Flegle, J.T., and Wallingford, B.D. 2011. Monitoring deer populations in Pennsylvania. Bureau of Wildlife Management, Pennsylvania Game Commission.
- Royo, A.A., and Carson, W.P. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Can. J. For. Res.* **36**(6): 1345–1362. doi:10.1139/x06-025.
- Royo, A.A., and Carson, W.P. 2008. Direct and indirect effects of a dense understory on tree seedling recruitment in temperate forests: habitat-mediated predation versus competition. *Can. J. For. Res.* **38**(6): 1634–1645. doi:10.1139/X07-247.
- Royo, A.A., Collins, R., Adams, M.B., Kirschbaum, C., and Carson, W.P. 2010a. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. *Ecology*, **91**(1): 93–105. doi:10.1890/08-1680.1.
- Royo, A.A., Stout, S.L., deCalesta, D.S., and Pierson, T.G. 2010b. Restoring forest herb communities through landscape-level deer herd reductions: is recovery limited by legacy effects? *Biol. Conserv.* **143**(11): 2425–2434. doi:10.1016/j.biocon.2010.05.020.
- Russell, F.L., Zippin, D.B., and Fowler, N.L. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *Am. Midl. Nat.* **146**(1): 1–26. doi:10.1674/0003-0031(2001)146[0001:EOWTDO]2.0.CO;2.
- Ruxton, G.D. 2006. The unequal variance t-test is an underused alternative to

- Student's *t*-test and the Mann-Whitney *U* test. *Behav. Ecol.* **17**(4): 688–690. doi:10.1093/beheco/ark016.
- SAS Institute Inc. 2008. SAS/STAT 9.2 user's guide. Introduction to analysis of variance procedures (book excerpt). Cary, North Carolina. Available from <https://support.sas.com/documentation/cdl/en/statugvariance/61753/PDF/default/statugvariance.pdf>.
- Smith, T.L. 1989. An overview of old-growth forest in Pennsylvania. *Nat. Areas J.* **9**(1): 40–44.
- Stromayer, K.A.K., and Warren, R.J. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildl. Soc. Bull.* **25**: 227–234.
- Tanentzap, A.J., Burrows, L.E., Lee, W.G., Nugent, G., Maxwell, J.M., and Coomes, D.A. 2009. Landscape-level vegetation recovery from herbivory: progress after four decades of invasive red deer control. *J. Appl. Ecol.* **46**(5): 1064–1072. doi:10.1111/j.1365-2664.2009.01683.x.
- Tanentzap, A.J., Bazely, D.R., Koh, S., Timciska, M., Haggith, E.G., Carleton, T.J., and Coomes, D.A. 2011. Seeing the forest for the deer: do reductions in deer disturbance lead to forest recovery? *Biol. Conserv.* **144**(1): 376–382. doi:10.1016/j.biocon.2010.09.015.
- Vankat, J.L., and Snyder, G.W. 1991. Floristics of a chronosequence corresponding to old field-deciduous forest succession in southwestern Ohio. I. Undisturbed vegetation. *Bull. Torrey Bot. Club.* **118**(4): 365–376. doi:10.2307/2997088.
- Waller, D. 2014. Effects of deer on forest herb layers. In *The herbaceous layer in forests of eastern North America*. 2nd edition. Edited by F.S. Gilliam and M.R. Roberts. Oxford University Press, New York, New York, U.S.A.
- Wallingford, B.D. 2000. Estimating county deer population sizes & growth rates. Bureau of Wildlife Management, Pennsylvania Game Commission.
- Whitney, G.G. 1984. Fifty years of change in arboreal vegetation of Heart's Content, an old-growth hemlock white-pine northern hardwood stand. *Ecology*, **65**(2): 403–408. doi:10.2307/1941403.
- Wright, D.M., Tanentzap, A.J., Flores, O., Husheer, S.W., Duncan, R.P., Wisser, S.K., and Coomes, D.A. 2012. Impacts of culling and exclusion of browsers on vegetation recovery across New Zealand forests. *Biol. Conserv.* **153**: 64–71. doi:10.1016/j.biocon.2012.04.033.
- Young, T.P., and Pepper, E. 2010. "Recalcitrant understory layers" revisited: arrested succession and the long life-spans of clonal mid-successional species. *Can. J. For. Res.* **40**(6): 1184–1188. doi:10.1139/X10-066.

Appendix A

Fig. A1. Between 2000 and 2004, Pennsylvania increased the number of antlerless deer tags, resulting in 55% increase in antlerless (largely doe) deer harvest. Deer densities decreased to approximately 14 deer·km⁻² in 2004 but increased to 20 deer·km⁻² by 2006 (Rosenberry et al. 2011). Deer harvest data obtained from the Pennsylvania Game Commission website (available from www.pgc.state.pa.us).

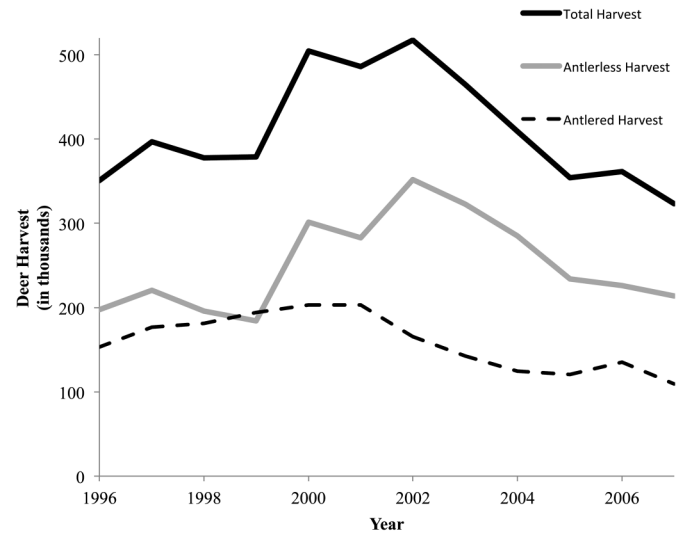


Table A1. Relative abundance, by cover, of all wildflower species sampled in 1997, 1998, 1999, 2001, and 2007. For brevity and possible identification issues, we have combined data for species in the *Actaea*, *Discorea*, *Galium*, and *Viola* genera.

| Species | Control | | | | | Exclosure | | | | |
|--|----------------------|---------|---------|---------|---------|----------------------|---------|---------|---------|----------------------|
| | 1997 | 1998 | 1999 | 2001 | 2007 | 1997 | 1998 | 1999 | 2001 | 2007 |
| <i>Actaea</i> spp. | 0 | 0 | 0 | 0 | 0 | 0.00818 | 0.02568 | 0.06085 | 0.03752 | 0.00489 |
| <i>Arisaema triphyllum</i> (L.) Schott | 0.01433 | 0.01646 | 0.01053 | 0.01095 | 0.02298 | 0.03983 | 0.03852 | 0.02993 | 0.03683 | 0.04385 |
| <i>Asarum canadense</i> L. | 0 | 0 | 0 | 0 | 0 | 1.6×10 ⁻⁵ | 0 | 0 | 0 | 0 |
| <i>Carex</i> spp. | 0.03647 | 0.0144 | 0.01353 | 0.0076 | 0.00133 | 0.02454 | 0.00803 | 0.001 | 0.00546 | 0.02362 |
| <i>Chimaphila maculata</i> (L.) Pursh | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.4×10 ⁻⁵ |
| <i>Circaea lutetiana</i> L. | 0.05666 | 0.02058 | 0.02406 | 0.00395 | 0.10851 | 0.00533 | 0.00642 | 0.01696 | 0.00728 | 0 |
| <i>Claytonia virginica</i> L. var. <i>virginica</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0.01124 | 0 | 0.01137 | 0 |
| <i>Comandra umbellata</i> (L.) Nutt. | 0 | 0 | 0 | 0 | 0 | 0.00164 | 0 | 0 | 0 | 0 |
| <i>Dennistaedia punctiloba</i> (Michx.) T. Moore | 0.056 | 0 | 0.04511 | 0 | 0 | 0.28788 | 0 | 0.36911 | 0 | 0 |
| <i>Dioscorea</i> spp. | 0 | 0 | 0 | 0 | 0.06182 | 0 | 0 | 0 | 0 | 0.00339 |
| <i>Disporum lanuginosum</i> (Michx.) G. Nicholson | 0 | 0 | 0 | 0.00152 | 0 | 0 | 0.00161 | 0.00499 | 0.00682 | 0.00263 |
| <i>Dryopteris carthusiana</i> (Vill.) H.P. Fuchs | 0 | 0.01852 | 0.0015 | 0 | 0 | 0 | 0.27127 | 0 | 0 | 0.00376 |
| <i>Epifagus americana</i> (L.) W. Bartram | 0.00132 | 0.01235 | 0.01053 | 0 | 0 | 0.00025 | 0 | 0.001 | 0 | 0 |
| <i>Fragaria virginia</i> Duchesne | 0.0013 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Galium</i> spp. | 0.114 | 0.05144 | 0.08421 | 0.01156 | 0.00252 | 0.04212 | 0.04013 | 0.05736 | 0.02478 | 0 |
| <i>Geranium maculata</i> L. | 0.00052 | 0.00206 | 0.00301 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Geum canadense</i> Jacq. | 0 | 0 | 0 | 0 | 0 | 0.13086 | 0 | 0 | 0 | 0 |
| <i>Glechoma hederaceae</i> L. | 0 | 0 | 0 | 0 | 0 | 6.5×10 ⁻⁵ | 0 | 0 | 0 | 0.00038 |
| <i>Impatiens pallida</i> Nutt. | 0 | 0 | 0 | 0 | 0.00015 | 0 | 0.00161 | 0 | 0.00136 | 0.00141 |
| <i>Ipomoea pandurata</i> (L.) G. Mey. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.00019 |
| <i>Lycopodium complanatum</i> L. | 0.00781 | 0 | 0 | 0 | 0.00148 | 0.01349 | 0.01926 | 0.00898 | 0.02729 | 0.02174 |
| <i>Maianthemum canadense</i> Desf. | 0.05356 | 0.08848 | 0.06617 | 0.11131 | 0.14617 | 0.04253 | 0.07865 | 0.04589 | 0.10778 | 0.13993 |
| <i>Maianthemum stellatum</i> (L.) Link | 0.03543 | 0.00206 | 0.00301 | 0 | 0 | 0.01358 | 0 | 0.02195 | 0 | 0 |
| <i>Mianthemum racemosum</i> L. | 0 | 0.02058 | 0.01203 | 0.01825 | 0.01357 | 0 | 0.01926 | 0 | 0.03865 | 0.02785 |
| <i>Mitchella repens</i> L. | 0.03875 | 0.01852 | 0.0391 | 0.02099 | 0.0371 | 0.05889 | 0.01124 | 0.03891 | 0.06207 | 0.39917 |
| <i>Monotropa uniflora</i> L. | 0 | 0 | 0 | 0 | 0.00119 | 0 | 0.00161 | 0 | 0 | 0.00376 |
| <i>Onoclea sensibilis</i> L. | 0 | 0 | 0 | 0 | 0.00133 | 0 | 0 | 0 | 0 | 0 |
| <i>Osmorhiza claytonii</i> (Michx.) C.B. Clarke | 0 | 0 | 0.00602 | 0 | 0.00059 | 0.00867 | 0.00803 | 0.00698 | 0.00068 | 0.0016 |
| <i>Parthenocissus quinquefolia</i> (L.) Planch. | 0 | 0 | 0 | 0.00061 | 0 | 0 | 0 | 0 | 0 | 0.00085 |
| <i>Phytolaca americana</i> L. | 0 | 0.66255 | 0 | 0 | 0 | 0.00123 | 0.2825 | 0 | 0 | 0 |
| <i>Poa</i> sp. | 0.0026 | 0 | 0 | 0 | 0.00237 | 0 | 0 | 0 | 0 | 0.00075 |
| <i>Podophyllum peltatum</i> L. | 0.4832 | 0.00412 | 0.50075 | 0.66302 | 0.46592 | 0.13658 | 0.01124 | 0.09477 | 0.17735 | 0.15188 |
| <i>Polygonatum biflorum</i> (Walter) Elliot | 0 | 0.00617 | 0.02857 | 0.00517 | 0 | 0 | 0.00642 | 0.02045 | 0.00159 | 0 |
| <i>Polygonatum pubescens</i> (Willd.) Pursh | 0 | 0 | 0 | 0.03193 | 0.08539 | 0 | 0 | 0 | 0.01705 | 0.04187 |
| <i>Polygonum</i> spp. | 0.00912 | 0 | 0 | 0 | 0 | 0.00147 | 0 | 0.00998 | 0 | 0.00395 |
| <i>Polygonum virginianum</i> L. | 0 | 0 | 0 | 0.00182 | 0 | 0 | 0 | 0 | 0.0091 | 0 |
| <i>Polystichum acrostichoides</i> (Michx.) Schott | 0 | 0 | 0 | 0 | 0.00119 | 0 | 0 | 0 | 0 | 0.00207 |
| <i>Potentilla simplex</i> Michx. | 0.0293 | 0.00412 | 0.0015 | 0.00091 | 0 | 0.05398 | 0.01605 | 0.03382 | 0.03456 | 0.01214 |
| <i>Pyrola elliptica</i> Nutt. | 0 | 0.00206 | 0.00902 | 0 | 0 | 0 | 0 | 0.00299 | 0.00682 | 0 |
| <i>Ranunculus</i> sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0.00161 | 0 | 0 | 0 |
| <i>Rubus</i> sp. | 0 | 0 | 0 | 0 | 0.03158 | 0 | 0 | 0 | 0 | 0.01731 |
| <i>Sanicula</i> sp. | 7.8×10 ⁻⁵ | 0 | 0 | 0 | 0 | 0.00164 | 0 | 0 | 0 | 0 |
| <i>Smilax</i> spp. | 0 | 0 | 0 | 0 | 0.0003 | 0.00164 | 0.00161 | 0.00399 | 0 | 0 |
| <i>Sphagnum platyphyllum</i> (Lindb. ex Braithw.) Sull. ex Warnst. | 0.0026 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Symphotrichum</i> sp. | 0 | 0.00206 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Thelypteris noveboracensis</i> (L.) Nieuwl. | 0 | 0 | 0 | 0.04562 | 0.00993 | 0 | 0 | 0 | 0.23647 | 0.05938 |
| <i>Toxicodendron radicans</i> (L.) Kuntze | 0 | 0 | 0 | 0 | 0.00445 | 0 | 0 | 0 | 0 | 0.01035 |
| <i>Trientalis borealis</i> Raf. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.00499 | 0 | 0 |
| <i>Trillium grandiflorum</i> (Michx.) Salisb. | 0 | 0.00206 | 0.0015 | 0.00152 | 0.00015 | 0 | 0 | 0 | 0 | 0.00452 |
| <i>Triodanis</i> sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0.00161 | 0.00599 | 0 | 0 |
| <i>Urtica dioica</i> L. | 0 | 0 | 0 | 0 | 0 | 0 | 0.00482 | 0.00449 | 0 | 0 |
| <i>Uvularia perfoliata</i> L. | 0.0086 | 0.02469 | 0.07669 | 0.03558 | 0 | 0.01636 | 0.00963 | 0.01995 | 0.01296 | 0 |
| <i>Veronica officinale</i> L. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.00075 |
| <i>Viola</i> spp. | 0.04836 | 0.02675 | 0.06316 | 0.02768 | 0 | 0.10926 | 0.12199 | 0.13468 | 0.1362 | 0.0159 |