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Source: The Journal of the Torrey Botanical Society, 144(1):1-14.

Published By: Torrey Botanical Society

DOI: <http://dx.doi.org/10.3159/TORREY-D-15-00066.1>

URL: <http://www.bioone.org/doi/full/10.3159/TORREY-D-15-00066.1>

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Response of spring flora to nearly two decades of deer exclusion and resurgent woody understories within exclosures¹

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Abstract. Exclosure studies have illustrated the profound effects overabundant populations of white-tailed deer can have on forest plant communities. However, complete exclusion of deer creates an artificial condition in most forests, and examining the long-term response of plant species composition and diversity to exclusion can provide valuable insight into the historic role of deer herbivory in forests. In 2014, we resampled spring flora and woody regeneration in a series of exclosure and control plots established in Great Smoky Mountains National Park in 1996. By comparing our data to regeneration data from 2002 and spring flora data from 2004, we were able to examine differences in vegetation at 6–8 and 18 yrs after deer exclusion. We observed a significant ($P < 0.001$) increase in the density of woody stems between 2002 and 2014 across all sites, with significantly more stems found within exclosures ($P < 0.001$). This increase in woody stem abundance within exclosures was associated with a decline in the abundance of some small-stature, spring herbaceous species. However, large-stature (taller) herbs, when present, tended to increase in abundance between sampling periods. Nonmetric multidimensional scaling ordinations supported this relationship between woody regeneration and herbaceous species composition. Shifts observed in spring flora composition along dominant ordination axes were correlated with the density of woody regeneration. Although our study further illustrates the negative effects of overabundant deer populations on plant communities, it also highlights the context-dependent nature of these effects and the potential consequences of long-term exclusion of herbivory on compositional diversity.

Key words: Cades Cove, endogenous disturbance, Great Smoky Mountains National Park, herbaceous layer, *Odocoileus virginianus*, southern Appalachian Mountains

¹ We thank Eric Fabio, Paul Allyn, Janice Pelton, Heather MacCulloch, Meryl Rose, Dana Soehn, Jennifer Tietjen, Katie Crosthwaite, Hanni Muerdter, Art vonLehe, Erika Choberka, Hope Hornbeck, Margie Mulligan, Eric Holzmüller, and Warren Reuschel for their assistance with data collection and entry associated with the 2002 regeneration data. We also thank Rick Varner, Chuck Hester, Bill Stiver, and Kim Delozier for constructing the exclosures. Keith Langdon provided invaluable input on this project. This research was supported by the Inventory and Monitoring Program of the National Park Service, the School of Forest Resources and Environmental Science at Michigan Technological University, and the Department of Forestry and Natural Resources, Purdue University.

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doi: 10.3159/TORREY-D-15-00066.1

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Received for publication October 13, 2015, and in revised form April 4, 2016; first published December 7, 2016.

Abundant populations of forest ungulates can have profound effects on native plant communities (for comprehensive reviews, see Russell *et al.* 2001, Rooney and Waller 2003, Côté *et al.* 2004). One of the most common approaches for documenting these effects is the construction of herbivore exclosures. Excluding mammalian herbivores, especially members of the deer family (Cervidae), from areas in which they are perceived to be affecting vegetation typically results in dramatic surges in the abundance and stature of browse-sensitive plants (*e.g.*, Frankland and Nelson 2003, Kraft *et al.* 2004, Rossell *et al.* 2005, Casabon and Pothier 2008); however, low understory-light levels and/or recalcitrant understory layers (*sensu* Royo and Carson 2006) of native and/or exotic plant species may delay or dampen responses (Horsley and Marquis 1983; Webster *et al.* 2005a, 2008; Collard *et al.* 2010).

One of the most consistent responses following deer exclusion is a significant increase in woody

regeneration (e.g., Nomiya *et al.* 2003, Griggs *et al.* 2006, Long *et al.* 2007, Tremblay *et al.* 2007, Collard *et al.* 2010, Abrams 2013). Woody plants have a number of traits that aid their recovery within deer exclosures and in areas in which herbivore numbers have been reduced (Holmes and Webster 2010, Jenkins *et al.* 2015). These include persistence in the understory as advance regeneration, propagule inputs from long-lived overstory trees beyond the reach of browsers, and mid- to long-distance seed dispersal by animals and wind. Recovery of dispersal-limited, forest, herbaceous species, on the other hand, is often limited to species that have been able to persist under high browsing pressure in either reduced growth forms, refugia, or the seed bank (Webster *et al.* 2005a, Collard *et al.* 2010, Royo *et al.* 2010). Consequently, their reinvasion of exclosures is unlikely if herbivory remains high in the surrounding matrix (Webster *et al.* 2005a) or residual densities are low resulting in Allee effects (Knight 2003, 2004).

Given the expense and difficulty of maintaining deer exclosures under forest canopies (Urbanek *et al.* 2011), replicated, long-term studies (decadal or longer) are comparatively rare (Abrams and Johnson 2012). More commonly, longer-term studies, although often consistent with predictions based on short-term studies, are confounded by a lack of replication and/or subjective placement of exclosures (Forrester *et al.* 2006, Goetsch *et al.* 2011, McGarvey *et al.* 2013), because older deer exclosures, especially those in protected areas in which they are more likely to have been maintained, were often established for illustrative and educational, rather than research, purposes.

Cades Cove, a sheltered valley bottom entirely within Great Smoky Mountains National Park, provided an opportunity to assess the long-term effect of deer exclusion on forest herbs. This area has a long and well-documented history of deer overabundance (Bratton 1979; Bratton *et al.* 1980; Griggs *et al.* 2006; Webster *et al.* 2005a, b) and contains a well-maintained network of replicated deer exclosures and control plots, which were established during the fall of 1996 (Griggs *et al.* 2006). The results presented, herein, provide a decadal census of the spring flora of these plots (Webster *et al.* 2005a) and represent a total treatment period of 18 yr. Early flowering, spring herbs are an important group to monitor because they are highly sought after by foraging deer and

are particularly sensitive to herbivory (Frankland and Nelson 2003). Our specific objectives were to (a) examine the influence of long-term deer exclusion and access on community composition of spring-flowering herbaceous species, and (b) investigate the influence of resurgent woody plants within exclosures on species composition.

Materials and Methods. **STUDY AREA.** Located within the Tennessee portion of Great Smoky Mountains National Park (GSMNP), Cades Cove contains a mosaic of woodlots and fallow fields, which are almost entirely surrounded by mountains. Open fields are maintained for cultural heritage purposes, with the forests becoming contiguous with increasing elevation above the valley floor. This portion of GSMNP has a long and well-documented history of white-tailed deer (*Odocoileus virginianus* Zimmermann) abundance and vegetation impact (Bratton 1979; Bratton *et al.* 1980; Webster *et al.* 2005a, b; Griggs *et al.* 2006). The highest deer densities in Cades Cove occurred during a period of irruptive cycles in the late 1970s (43 deer km⁻²; Kinningham 1980, Wathen and New 1989). Population estimates are not available for the contemporary deer herd, which appears to have stabilized below peak abundance (B. Stiver, personal communication). Nevertheless, the contemporary deer population of Cades Cove remains the greatest concentration of deer within GSMNP and is sufficient to produce pronounced impacts on vegetation (Fig. 1; Jenkins *et al.* 2007, Thiemann *et al.* 2009, Webster and Jenkins 2014, Webster *et al.* 2015). A detailed history of deer abundance in Cades Cove is provided in Griggs *et al.* (2006).

Exclosures were constructed during the fall of 1996 at three sites: Abrams Creek, Hyatt Lane, and John Oliver. Exclosure and control plots (five of each) were arrayed randomly within a 0.5-ha area. Plots were 10 m × 10 m, and exclosures were constructed to completely contain the plot and provide a 1-m buffer on all sides between the plot edge and the fence. Exclosures were constructed from heavy gauge fencing and were approximately 2.4 m tall.

The exclosure sites are located in two of the most common forest types found within the Cades Cove. The John Oliver and Hyatt Lane sites are located within *Quercus alba* L. (*Quercus rubra* L., *Carya* Nutt. spp.) forest (White *et al.*, 2003). Overstory vegetation at both sites is dominated by *Q. alba*, *Liriodendron tulipifera* L., and *Tsuga*

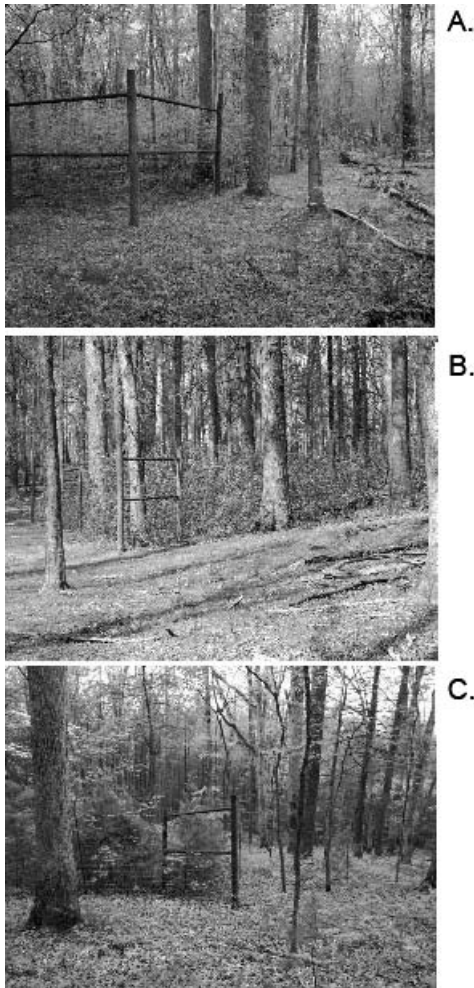


FIG. 1. Representative enclosure and control plots at (A) Abrams Creek, (B) Hyatt Lane, and (C) John Oliver study sites in Cades Cove, Great Smoky Mountains National Park, TN. Photos were taken in the spring of 2012. Photo credit: C. R. Webster.

canadensis (L.) Carrière. The Abrams Creek site is located within *Liquidambar styraciflua* L. (*Acer rubrum* L.) seasonally flooded forest (White *et al.*, 2003). The overstory of this floodplain site is dominated by *L. styraciflua*, *L. tulipifera*, *A. rubrum*, and *Pinus strobus* L. All three sites are located in the intensive deer impact area of Cades Cove described by Bratton (1979).

Cades Cove ranges in elevation from 518 m to 610 m, with landscape features consisting of the Abrams Creek floodplain, colluvial fans, and stream terraces. According to the most recent survey (NRCS 2009), soils within Cades Cove consist of very deep and well-drained silt loams

that were derived from deep alluvium and/or colluvium deposits that overlay limestone bedrock. Although the limestone bedrock is evident as scattered outcrops and karst features (NRCS 2009), it has minimum influence on most soils within Cades Cove because of these deep deposits (Mathis 2005, NRCS 2009).

FIELD TECHNIQUES. Within each 10 m × 10 m control and enclosure plot, we counted the number of individuals of spring-flowering herbaceous species. Each plot was divided into sectors with fiberglass tapes to facilitate sampling. For *Claytonia virginica* L., which was especially numerous, density was estimated from five systematically placed 1 m × 1 m quadrats. Sampling was conducted in early April 2014 and mirrored our 2004 survey of these same plots (Webster *et al.* 2005a), except that we did not assess flowering status because many species were at a slightly earlier phenological stage than during the previous survey. Spring-flowering herbs were not sampled within the enclosures before 2004. Species nomenclature follows the US Department of Agriculture Plants Database (USDA 2015).

To examine the influence of woody plants on spring-flowering herbaceous species, we counted all woody regeneration ≥ 0.5 m in height but < 5 cm diameter at breast height (DBH) within one 3.2 m × 3.2 m subplot. These subplots were established at the time the enclosures were constructed and were permanently marked with rebar. We compared our counts to a 2002 census of these plots.

STATISTICAL APPROACH. To examine changes in species composition between enclosures and controls through time, we conducted a study-wide and individual site-level nonmetric multidimensional scaling ordinations (NMS). Ordinations were performed with PC-ORD version 6.08 (McCune and Mefford 2011) using the Autopilot Mode with slow and thorough settings. The PC-ORD Autopilot Mode is an automated search procedure, which determines the appropriate dimensionality and evaluates statistical significance based on multiple runs with real and randomized data (250 runs each; McCune and Grace 2002). This procedure uses a Sørensen (Bray-Curtis) distance measure, a random starting configuration, and a Monte Carlo test ($P \leq 0.05$) to select the final dimensionality by comparing final stress values among best solutions to randomized

runs (McCune and Grace 2002, McCune and Mefford 2011). A zero adjustment for denuded assemblages was applied to the species matrices (main matrices) before analysis because control plots were sometimes devoid or nearly devoid of spring-flowering species (Clarke *et al.* 2006). This adjustment has a homogenizing effect on dissimilarities between empty or near-empty samples, which would otherwise be undefined or tend toward erratic behavior, but has little effect on nondenuded samples (Clarke *et al.* 2006, Thiemann *et al.* 2009). Because one of our primary goals was to investigate herbaceous-layer composition in association with increased woody regeneration density, 2014 woody regeneration stem density (≥ 0.5 m in height but < 5 cm DBH) was included in our environmental matrices (second matrix) as a quantitative variable. Categorical variables in these matrices included sampling period, treatment, and site (in the study-wide ordination only).

We used multiresponse permutation procedures (MRPP) to test for overall (study-wide) and site-level differences in species composition among exclosure and control plots in 2004 and 2014. This nonparametric test was conducted using the Sørensen (Bray-Curtis) distance measure in PC-ORD version 6.08 (McCune and Mefford 2011).

Changes in the abundance of woody regeneration were evaluated with general linear mixed models (GLMM) that contained exclosure treatment and year, with site as a random effect. The GLMM procedure was performed in Minitab version 16 (Minitab Statistical Software Inc., State College, PA). Overall changes in the total abundance of spring-flowering herbaceous species at each site within exclosures and controls between the two time periods were compared using paired t tests. Changes in absolute and relative density of individual spring-flowering herbaceous species are presented in summary and tabular format (Table 1, 2) but were not compared statistically. We chose this approach to emphasize community-level patterns and biologically interesting changes in absolute and relative abundance between two nearly complete censuses of the spring flora on our study plots.

Results. All three study areas (Abrams Creek, Hyatt Lane, and John Oliver) experienced significant increases in the abundance of woody regeneration (≥ 0.5 m in height but < 5 cm

DBH) within deer exclosures as compared with controls (Fig. 1, 2). A general linear model that included exclosure treatment, site, and year identified significant differences between years ($F_{1, 59} = 40.8$, $P < 0.001$) and exclosures and controls ($F_{1, 59} = 37.5$, $P < 0.001$). No significant differences were found among sites ($F_{2, 59} = 0.88$, $P = 0.419$). Stem densities of woody plants within exclosures averaged 32.5 ± 13.8 stems per 100 m^2 during a 2002 inventory (sixth growing season following exclosure construction) but had increased to 343 ± 35.0 stems per 100 m^2 by spring 2014. No stems within this size class were observed on control plots during the 2002 inventory. By the spring of 2014, the abundance of this size class on control plots was 39.7 ± 19.8 stems per 100 m^2 , with 47% of plots containing no stems of this size class. When regeneration was present on control plots, it was typified by browse tolerant and/or less palatable tree species, such as *A. rubrum* and *L. styraciflua*. Regeneration within exclosures was typified by a mixture of midtolerant and shade-tolerant hardwood species. Regeneration of conifer species (*T. canadensis* and *P. strobus*) was present within exclosures at all three sites, and accounted for approximately 18% of woody stems at John Oliver but $\leq 1\%$ of woody stems at Abrams Creek and Hyatt Lane.

Absolute densities of spring-flowering plants displayed marginally significant increases at Abrams Creek in both exclosures (from $3,318.4 \pm 1,308.7$ to $10,744.6 \pm 3,654.4$ plants m^{-2} ; $t = -2.64$, $P = 0.058$) and controls (from 939.4 ± 472.6 to $3,803.4 \pm 1,526.8$ plants m^{-2} ; $t = -2.42$, $P = 0.073$). These increases were attributable to large increases in both the absolute and relative abundance of *C. virginica* (Table 1, 2). At Hyatt Lane, the absolute density of spring-flowering plants was less within deer exclosures during the second inventory (down from 355.2 ± 210.2 plants m^{-2} in 2004 to 151.4 ± 96.7 plants m^{-2} in 2014), but the change was not statistically significant ($t = 1.75$, $P = 0.155$). More plants were observed in control plots at this site during the second inventory (from 316.8 ± 228.7 to 821.6 ± 721.4 plants m^{-2}), but the change was also not statistically significant ($t = -0.67$, $P = 0.537$). The increased density in control plots was associated with the presence of *C. virginica* on two plots in which it was not observed previously. The absolute density of other spring-flowering plants on control plots actually declined between 2004 and 2014

Table 1. Mean relative density (\pm SE) of spring-flowering, herbaceous species at Abrams Creek, Hyatt Lane, and John Oliver study sites within Cades Cove, Great Smoky Mountains National Park, TN.^a

Location and species	Exclosure			Control		
	2004	2014	% Change	2004	2014	% change
Abrams Creek						
<i>Claytonia virginica</i> L.	79.3 \pm 15.8	97.3 \pm 4.2	17.9	78.0 \pm 40.1	98.8 \pm 1.4	20.8
<i>Houstonia serpyllifolia</i> Michx.	t	...	—	...	t	+
<i>Oxalis violacea</i> L.	6.2 \pm 12.4	2.6 \pm 4.2	-3.6	17.6 \pm 39.4	0.1 \pm 0.3	-17.5
<i>Ranunculus hispidus</i> Michx.	...	t	+
<i>Viola blanda</i> Willd.	14.5 \pm 17.7	0.1 \pm 0.2	-14.4	4.4 \pm 2.5	1.0 \pm 1.5	-3.4
Hyatt Lane						
<i>Cardamine hirsuta</i> L.*	23.2 \pm 29.8	0.6 \pm 0.9	-22.6	27.1 \pm 37.4	5.7 \pm 12.4	-21.4
<i>Claytonia virginica</i> L.	1.6 \pm 3.6	5.0 \pm 11.1	3.3	...	19.8 \pm 44.3	19.8
<i>Oxalis stricta</i> L.	1.3 \pm 2.9	0.1 \pm 0.2	-1.2	4.2 \pm 5.7	1.5 \pm 3.0	-2.6
<i>Polygonatum biflorum</i> (Walter) Elliott	...	t	+	3.1 \pm 6.9	0.8 \pm 1.7	-2.3
<i>Ranunculus abortivus</i> L.*	2.8 \pm 6.2	1.9 \pm 3.4	-0.9	0.1 \pm 0.1	...	-0.06
<i>Stellaria media</i> (L.) Vill.*	27.0 \pm 41.1	...	-27.0	10.4 \pm 14.2	21.2 \pm 44.1	10.8
<i>Viola bicolor</i> Pursh*	...	2.2 \pm 3.9	2.2	...	t	+
<i>Viola sororia</i> Willd.	24.1 \pm 27.4	70.2 \pm 41.5	46.2	35.2 \pm 48.3	30.8 \pm 44.1	-4.4
<i>Viola triloba</i> Schwein.	0.2 \pm 0.5	0.2
John Oliver						
<i>Antennaria plantaginifolia</i> (L.) Richardson	4.7 \pm 9.3	4.7
<i>Cardamine concatenata</i> (Michx.) Sw.	1.3 \pm 3.0	1.4 \pm 3.1	0.04
<i>Claytonia virginica</i> L.	0.2 \pm 0.5	0.2
<i>Houstonia serpyllifolia</i> Michx.
<i>Hypoxis hirsuta</i> (L.) Coville	2.2 \pm 4.6	...	-2.2	13.8 \pm 30.1	11.5 \pm 23.3	-2.3
<i>Iris cristata</i> Aiton	1.0 \pm 2.2	2.2 \pm 5.0	1.27	1.6 \pm 3.5	6.5 \pm 14.1	4.9
<i>Isotria verticillata</i> Raf.	...	0.1 \pm 0.2	0.07
<i>Maianthemum racemosum</i> (L.) Link	0.2 \pm 0.4	0.1 \pm 0.2	-0.11	0.2 \pm 0.4	...	-0.2
<i>Oxalis stricta</i> L.	t	...	—
<i>Oxalis violacea</i> L.	55.6 \pm 36.5	37.3 \pm 23.5	-18.4	41.9 \pm 40.8	28.2 \pm 36.2	-13.7
<i>Polygonatum biflorum</i> (Walter) Elliott	3.6 \pm 6.7	33.6 \pm 28.6	30	4.5 \pm 6.3	3.9 \pm 4.7	-0.6
<i>Ranunculus hispidus</i> Michx.	0.4 \pm 0.7	0.4
<i>Stellaria pubera</i> Michx.	...	0.3 \pm 0.6	0.3	...	1.7 \pm 2.5	1.7
<i>Thalictrum dioicum</i> L.	t	+
<i>Thalictrum thalictroides</i> (L.) Eames & B. Boivin	0.1 \pm 0.3	3.6 \pm 7.9	3.4	0.1 \pm 0.3	0.5 \pm 1.1	0.4
<i>Trillium catesbaei</i> Elliott	t	3.9 \pm 8.7	3.8	0.7 \pm 1.2	0.3 \pm 0.3	-0.4
<i>Trillium luteum</i> (Muhl.) Harbison	0.2 \pm 0.3	4.3 \pm 9.6	4.1	0.5 \pm 1.0	0.3 \pm 0.7	-0.2
<i>Viola hastata</i> Michx.	0.1 \pm 0.2	...	-0.1
<i>Viola sororia</i> Willd.	28.8 \pm 30.7	13.7 \pm 13.1	-15.2	23.7 \pm 25.8	27.4 \pm 29.0	3.8
<i>Viola triloba</i> Schwein.	8.0 \pm 9.7	1.0 \pm 0.7	-7.08	11.7 \pm 9.7	13.0 \pm 12.4	1.3

^a Abbreviations: * = introduced exotic species, — = decrease, + = increase, ... = absent, t = trace (relative density < 0.1).

(from 316.8 ± 228.7 to 89.6 ± 59.4 plants m^{-2}), but again the change was not statistically significant ($t = 0.95$, $P = 0.396$) because of the small sample size and the large variance. At John Oliver, the absolute density of spring-flowering plants declined significantly within exclosures (from 471.6 ± 95.1 to 222.0 ± 45.0 plants m^{-2} ; $t = 3.98$, $P = 0.016$), but not in control plots (from 887.2 ± 638.9 to 763.6 ± 358.1 plants m^{-2} ; $t = 0.29$, $P = 0.786$).

A three-dimensional, NMS ordination solution was found for the spring-flora overall (study-wide). Following 66 iterations, the final solution had a stress of 9.65 and instability of < 0.00001 , and it explained 66.3% of the variation in species composition. Axis 1 explained the most variation ($R^2 = 26.5\%$) followed by axis 2 ($R^2 = 26.4\%$) and 3 ($R^2 = 13.5\%$). Axes 1 and 2 displayed weak correlations ($r = 0.090$ and -0.092 , respectively) with the abundance of woody regeneration. Axis 3

Table 2. Absolute density (mean plants per 100 m² ± SE) of spring-flowering, herbaceous species at Abrams Creek, Hyatt Lane, and John Oliver study sites within Cades Cove, Great Smoky Mountains National Park, TN.^a

Location and species	Exclosure			Control		
	2004	2014	Change	2004	2014	Change
Abrams Creek						
<i>Claytonia virginica</i>	2,935.2 ± 1,264.5	10,356.0 ± 3,532.2	7,420.8	832.2 ± 481.8	3,784.0 ± 1523.1	2,951.8
<i>Houstonia serpyllifolia</i>	189.4 ± 145.2	363.4 ± 231.0	174.0	70.8 ± 70.8	10.4 ± 10.4	-60.4
<i>Oxalis violacea</i>	+
<i>Ranunculus hispidus</i>	193.6 ± 82.4	25.0 ± 18.3	-168.6	36.4 ± 16.3	8.0 ± 4.1	-28.4
<i>Viola blanda</i>	3,318.4 ± 1,308.7	10,744.6 ± 3,654.4	7,426.2	939.4 ± 472.6	3,803.4 ± 1,526.8	2,864.0
Total						
Hyatt Lane						
<i>Cardamine hirsuta</i> *	185.0 ± 118.5	0.6 ± 0.4	-184.4	219.4 ± 170.4	6.0 ± 4.6	-213.4
<i>Claytonia virginica</i>	17.2 ± 17.2	25.4 ± 25.4	8.2	...	732.0 ± 732.0	732.0
<i>Oxalis stricta</i>	1.4 ± 1.4	t	-1.0	8.2 ± 7.2	4.8 ± 3.2	-3.4
<i>Polygonatum biflorum</i>	...	t	+	1.2 ± 1.2	2.4 ± 2.4	-1.2
<i>Ranunculus abortivus</i> *	3.2 ± 3.0	1.4 ± 0.9	-1.8	t	...	-
<i>Stellaria media</i> *	46.4 ± 27.7	...	-46.4	78.8 ± 58.2	2.0 ± 1.2	-76.8
<i>Viola bicolor</i> *	...	9.4 ± 9.2	9.4	...	t	+
<i>Viola sororia</i>	102.0 ± 51.9	114.0 ± 65.0	12.0	9.0 ± 5.5	74.0 ± 58.5	65.0
<i>Viola triloba</i>	t	+
Total	355.2 ± 210.2	151.4 ± 96.7	-203.8	316.8 ± 228.7	821.6 ± 721.4	504.8
John Oliver						
<i>Antennaria plantaginifolia</i>	19.6 ± 12.8	19.6
<i>Cardamine concatenata</i>	46.0 ± 46.0	24.2 ± 24.2	21.8
<i>Claytonia virginica</i>	t	+
<i>Houstonia serpyllifolia</i>
<i>Hypoxis hirsuta</i>	9.8 ± 9.3	...	-9.8	80.4 ± 79.9	164.2 ± 160.7	83.8
<i>Iris cristata</i>	4.0 ± 4.0	4.4 ± 4.4	0.4	9.2 ± 9.2	97.0 ± 96.5	87.8
<i>Isotria verticillata</i>	...	t	+
<i>Maianthemum racemosum</i>	...	t	-	t	...	-
<i>Oxalis stricta</i>	t	...	-
<i>Oxalis violacea</i>	315.2 ± 109.2	97.4 ± 28.4	-217.8	674.6 ± 617.0	332.2 ± 301.3	-342.4
<i>Polygonatum biflorum</i>	15.6 ± 13.6	64.0 ± 31.7	48.4	3.8 ± 2.3	6.6 ± 2.3	2.8
<i>Ranunculus hispidus</i>	t	+
<i>Stellaria pubera</i>	...	t	+	...	4.2 ± 2.2	4.2
<i>Thalictrum dioicum</i>	t	+
<i>Thalictrum thalictroides</i>	1.0 ± 1.0	10.0 ± 10.0	9.0	4.4 ± 4.4	8.4 ± 8.4	4.0
<i>Trillium catesbaei</i>	t	11.0 ± 11.0	10.8	3.8 ± 3.3	2.6 ± 1.9	-1.2
<i>Trillium luteum</i>	1.0 ± 0.8	12.2 ± 12.2	11.2	t	t	+

Table 2. Continued.

Location and species	Exclosure			Control		
	2004	2014	Change	2004	2014	Change
	<i>Viola hastata</i>	t	...	-
<i>Viola sororia</i>	93.0 ± 30.4	20.0 ± 5.4	-73.0	41.0 ± 14.2	66.0 ± 19.5	25
<i>Viola triloba</i>	30.6 ± 16.6	1.8 ± 0.6	-28.8	23.2 ± 6.4	37.0 ± 12.0	13.8
Total	471.6 ± 95.1	222.0 ± 45.0	-249.6	887.2 ± 638.9	763.6 ± 358.1	-123.6

^a Abbreviations: * = introduced exotic species, - = decrease, + = increase, ... = absent, t = trace (relative density < 1.0 plants per 100 m²).

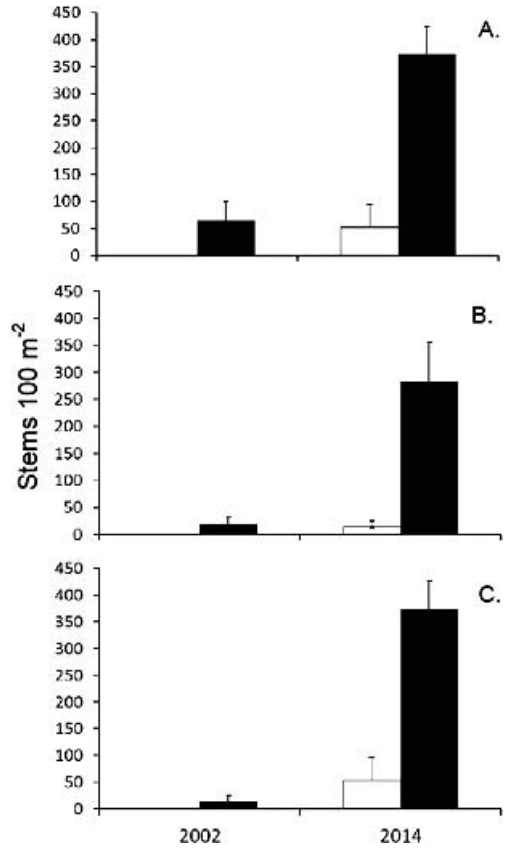


FIG. 2. Mean (\pm SE) density of woody regeneration (≥ 0.5 m in height but < 5 cm diameter at breast height [DBH]) at (A) Abrams Creek, (B) Hyatt Lane, and (C) John Oliver study sites in Cades Cove, Great Smoky Mountains National Park, TN. Open bars indicate control plots, and solid bars indicate exclosures.

was negatively correlated with the abundance of woody regeneration ($r = -0.321$). Two exotic species, *Stellaria media* (L.) Vill. ($r = 0.573$) and *Cardamine hirsuta* L. ($r = 0.566$), displayed the strongest positive correlations with axis 3, whereas *Oxalis violacea* L. ($r = -0.351$) and *Polygonatum biflorum* (Walter) Elliott ($r = -0.290$) displayed the strongest negative correlations (Table 3). The MRPP results suggested that, in both 2004 and 2014, species compositions did not vary significantly between exclosures and controls (2004: $A = -0.004$, $P = 0.572$; 2014: $A = -0.004$, $P = 0.578$), when plots from all sites were combined. Species composition, however, did vary significantly between sites during both surveys (2004: $A = 0.168$, $P < 0.001$; 2014: $A = 0.182$, $P < 0.001$),

Table 3. Correlations (r) of individual species and the environmental gradient in woody regeneration abundance with nonmetric multidimensional scaling ordination axes for study-wide and site-specific ordinations of spring-flowering plant communities within Cades Cove, Great Smoky Mountains National Park, TN.^a

Species	Study-wide			Hyatt Lane		John Oliver	
	Axis 1 ($R^2 = 0.265$)	Axis 2 ($R^2 = 0.264$)	Axis 3 ($R^2 = 0.135$)	Axis 1 ($R^2 = 0.499$)	Axis 2 ($R^2 = 0.124$)	Axis 1 ($R^2 = 0.497$)	Axis 2 ($R^2 = 0.336$)
Woody regeneration (≥ 0.5 m in height but < 5 cm DBH)	0.090	-0.092	-0.321	-0.187	0.259	-0.155	0.533
<i>Antennaria plantaginifolia</i>	-0.144	-0.191	0.110			0.198	-0.344
<i>Cardamine concatenata</i>	-0.021	-0.337	-0.234			-0.675	-0.208
<i>Cardamine hirsuta</i>	-0.102	0.021	0.566	0.438	-0.635		
<i>Claytonia virginica</i>	0.626	-0.189	-0.124	0.514	0.252	0.096	-0.006
<i>Houstonia serpyllifolia</i>	0.234	0.028	0.084				
<i>Hypoxis hirsuta</i>	-0.149	-0.241	0.272			0.307	-0.726
<i>Iris cristata</i>	-0.119	-0.206	0.239			0.252	-0.628
<i>Isotria verticillata</i>	-0.086	-0.09	-0.208			-0.079	0.356
<i>Maianthemum racemosum</i>	-0.144	-0.22	-0.122			-0.108	0.050
<i>Oxalis stricta</i>	-0.056	0.098	0.374	0.364	-0.314	-0.164	-0.158
<i>Oxalis violacea</i>	0.060	-0.485	-0.351			-0.782	-0.206
<i>Polygonatum biflorum</i>	-0.209	-0.199	-0.290	0.174	0.363	-0.087	0.531
<i>Ranunculus abortivus</i>	-0.197	0.014	0.181	0.125	0.019	0.349	-0.487
<i>Ranunculus hispidus</i>	-0.036	-0.167	0.178				
<i>Stellaria media</i>	-0.109	0.043	0.573	0.41	-0.682		
<i>Stellaria pubera</i>	-0.170	-0.173	-0.030			0.144	-0.018
<i>Thalictrum dioicum</i>	-0.100	-0.183	0.226			0.229	-0.589
<i>Thalictrum thalictroides</i>	-0.089	-0.322	-0.234			-0.514	-0.024
<i>Trillium catesbaei</i>	-0.129	-0.200	-0.098			-0.047	0.000
<i>Trillium luteum</i>	-0.085	-0.129	-0.190			-0.146	0.235
<i>Viola bicolor</i>	0.013	-0.021	0.127	0.230	0.300		
<i>Viola blanda</i>	0.445	-0.018	0.025				
<i>Viola hastata</i>	-0.134	-0.060	0.097			0.267	-0.151
<i>Viola sororia</i>	-0.349	-0.284	0.458	0.538	0.322	0.354	-0.647
<i>Viola triloba</i>	-0.303	-0.409	0.050	0.045	-0.035	0.181	-0.534

^a Coefficients of determination describe the amount of variation in the species composition explained by the ordination axis. See text for complete ordination diagnostics. A stable nonmetric multidimensional scaling ordinations solution could not be found for the Abrams Creek study site. See Table 1 for full species nomenclature. Abbreviation: DBH = diameter at breast height.

confirming differences in species composition between the three sites.

Two-dimensional solutions were found for the individual site ordinations of spring herbaceous communities at Hyatt Lane and John Oliver (Fig. 3; Table 3). PC-ORD was unable to converge on a stable solution for the Abrams Creek site. The MRPP results for the Abrams Creek site indicated that species composition did not vary significantly between exclosures and control plots in either 2004 ($A = 0.022$, $P = 0.153$) or 2014 ($A = 0.048$, $P = 0.313$).

The final NMS solution for Hyatt Lane had a stress of 6.16 and instability of < 0.00001 following 59 iterations, and it explained 62.3% of the variance in species composition. Axis 1 explained the most variation ($R^2 = 49.9\%$),

followed by axis 2 ($R^2 = 12.4\%$). The abundance of woody regeneration was negatively associated with axis 1 ($r = -0.187$) and was positively associated with axis 2 ($r = 0.259$). The species with the strongest associations with axis 1 were *Viola sororia* Willd. ($r = 0.538$) and *C. virginica* ($r = 0.514$), whereas *S. media* ($r = -0.682$) and *C. hirsuta* ($r = -0.635$) displayed the strongest associations with axis 2 (Table 2). The MRPP results suggested that, in both 2004 and 2014, species compositions did not vary significantly between exclosures and controls (2004: $A = -0.052$, $P = 0.858$; 2014: $A = -0.054$, $P = 0.901$)

The final NMS solution for John Oliver had a stress of 8.22 and instability of < 0.00001 following 96 iterations, and it explained 83.3% of the variance in species composition. Axis 1

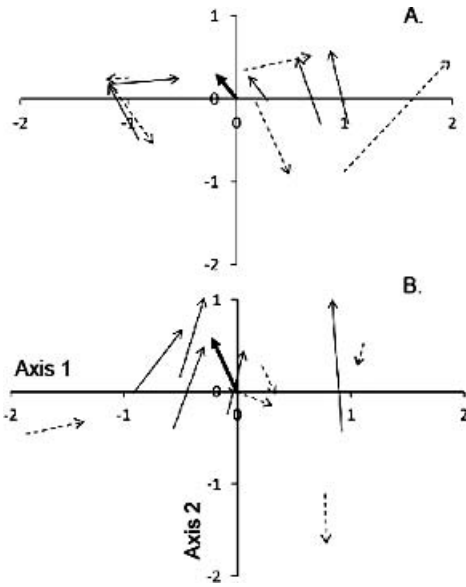


FIG. 3. Nonmetric multidimensional scaling ordinations of spring-flowering, herbaceous plant communities at (A) Hyatt Lane, and (B) John Oliver study sites in Cades Cove, Great Smoky Mountains National Park, TN. Vectors illustrate movement of plots through time (2004 to 2014) in the ordination space. Solid lines represent enclosure plots, and dashed lines represent controls. The bold arrow in each panel indicates the direction and strength of the correlation between woody regeneration density and each ordination axis.

explained the most variation ($R^2 = 49.7\%$) followed by axis 2 ($R^2 = 33.6\%$). The abundance of woody regeneration was negatively associated with axis 1 ($r = -0.155$) and positively associated with axis 2 ($r = 0.533$). The species with the strongest associations (Table 3) with axis 1 were *O. violacea* ($r = -0.782$) and *Cardamine concatenata* (Michx.) Sw. ($r = -0.675$). *Hypoxis hirsuta* (L.) Coville ($r = -0.726$) and *V. sororia* ($r = -0.647$) displayed the strongest associations with axis 2 (Table 2). The MRPP results from 2004 indicated that species composition did not vary significantly between enclosure and control plots ($A = 0.026$, $P = 0.201$). However, MRPP results from the 2014 survey revealed a significant difference in species composition between the treatment groups ($A = 0.082$, $P = 0.006$), indicating that the composition of the spring flora within these treatments had diverged significantly since the 2004 survey.

Individual species responses (absolute and relative abundance) were idiosyncratic among

treatments and sites (Table 1), but some general trends were apparent. For example, members of the lily family tended to increase in both absolute and relative abundance within enclosures, whereas small-statured species, including *O. violacea*, *Viola triloba* Schwein., and *V. sororia*, often declined (Table 1, 2; see Appendix 1 for information on plant stature and growth habit). In control plots, however, most small-statured species increased in both absolute and relative abundance, with the exception of *O. violacea*, which declined in both absolute and relative abundance (Table 1, 2; 50% decline in absolute abundance study wide).

Abrams Creek contained the fewest herbaceous species, and its spring flora, which was dominated by *C. virginica*, varied little between enclosure and control plots (Table 1, 2). Hyatt Lane contained more spring-flowering species but also contained the greatest complement of exotic species (Table 1, 2). Enclosures experienced a decline in the relative density of two exotic species, *S. media* and *C. hirsuta*. The native *V. sororia* displayed the greatest increase in relative density. *Polygonatum biflorum*, a browse-sensitive lily, which was not observed within enclosures during the 2004 inventory, was recorded during the 2014 survey. The relative density of this species declined on control plots. In fact, the relative density of most species declined within control plots in response to large increases in the relative abundance of *C. virginica* and *S. media*. John Oliver contained the greatest number of spring-flowering species and the most members of the lily family (Table 1, 2). Three lily species (*Trillium luteum* (Muhl.) Harbison, *Trillium catesbaei* Elliott, and *P. biflorum*), which accounted for < 4% of the spring flora of enclosures during the 2004 inventory, accounted for nearly 42% of the spring flora during the 2014 survey. This increase was associated with an increase in the absolute abundance of these species (17.6 ± 14.1 stems m^{-2} vs. 87.4 ± 32.3 stems m^{-2}) and declines in the relative density of many small-statured species (see Appendix 1 for information on stature and growth form), including *Viola* spp., *O. violacea*, and *H. hirsuta*. Compositional changes within control plots reflected a general increase in the representation of small-statured species and across the board declines in the relative density of members of the lily family (Table 1).

Discussion. Our results highlight the difficulty of contextualizing herbaceous species response to

herbivory and long-term deer exclusion. Individual species and community responses were highly context specific because, in large part, of the patchy nature of spring herbs and potentially persistent legacies of low species richness and abundance at the time the study was initiated. Exclosures were built in response to high deer abundance, dramatic declines in the abundance of browse-sensitive herbs, and the appearance of browse lines (Bratton 1979, Bratton *et al.* 1980, Griggs *et al.* 2006). As illustrated by Griggs *et al.* (2006), and this study, woody regeneration has increased significantly within exclosures. The response of the herbaceous layer has been more nuanced and is likely confounded by the “ghost of herbivory past” (*sensu* Banta *et al.* 2005).

Abundant deer populations have been shown to produce persistent legacy effects in forest plant communities (*e.g.*, Royo *et al.* 2010a, Nuttle *et al.* 2011, Frerker *et al.* 2014, Nuttle *et al.* 2014). Our results, however, also illustrate the idiosyncratic and context-dependent nature of the effects and plant community recovery across different forest types, which vary in spring-flora species composition and diversity. Cades Cove has a well-documented history of deer overabundance and deleterious impacts to local plant communities (*e.g.*, Bratton 1979, Bratton *et al.* 1980, Griggs *et al.* 2006). Previous comparisons with reference sites in GSMNP and historic accounts suggest that the herbaceous layer in the Cades Cove is less diverse and more homogenous than it was when initially incorporated into GSMNP about 1940 (Thiemann *et al.* 2009, Webster *et al.* 2005a). Correspondingly, the level of differentiation between control and exclosure plots was strongly influenced by the abundance and composition of spring-flowering herbs during our previous survey in 2004. Exclosures at our most species-rich site, John Oliver, displayed the greatest change and convergence through time in species composition and differentiation from control plots. These changes were apparent in our NMS plot and were confirmed by MRPP. At the next most species-rich site, Hyatt Lane, exclosures exhibited fewer idiosyncratic patterns of change than control sites, but were not clearly differentiated from controls in ordination space or compositionally, even after nearly two decades of deer exclusion. Species composition at Abrams Creek, the site with the most species-poor spring flora, displayed little, if any, differentiation between exclosures and con-

trols through time, and a stable ordination was not obtained. Our MRPP also failed to find significant compositional differences between the treatments. Similarly, Nuttle *et al.* (2014) found that reductions in species richness associated with exposure to elevated deer densities during early stand development persisted for decades in Pennsylvania forests, even after deer densities were reduced and equalized across sites. The duration of high deer abundance, however, may be an important factor because it can influence the level of species loss and degradation experienced by the plant community (Augustine and deCalesta 2003). For example, results presented by Jenkins *et al.* (2014) suggested a strong recovery of herbaceous plant communities after 17 yr of deer reductions in Indiana state parks, where hunting programs were initiated relatively soon (in most cases) after widespread impacts were observed (Mitchell *et al.* 1997, Webster *et al.* 2001).

At the individual plant level, abundance and apparency influence herbivore foraging behavior and subsequent impacts on individual plants, populations, and communities. Augustine *et al.* (1998) noted that differences in the abundance of the late-flowering herb *Laportea canadensis* (L.) Weddell had a strong, nonmonotonic influence on the rate of consumption by deer, in which the proportion of individuals browsed declined with increasing plant abundance, once a minimum abundance was reached. Similarly, Fletcher *et al.* (2001) found that deer browsed a greater proportion of *Lilium superbum* L. plants emerging in small *vs.* large patches. In our study, large-statured herbs generally declined in abundance on control plots but increased in abundance within exclosures. These species tended to be rare at the outset of the study in both exclosures and controls. Nonconcurrent phenology between spring flora and woody plants may have reduced competition among these species and woody plants in exclosures, whereas many smaller-statured species, which likely compete more directly with larger spring herbs, declined within exclosures.

Small-statured, super-abundant species, such as *C. virginica*, tended to increase in abundance regardless of deer access. This perennial, in particular, has a short, vernal growing season, which may allow it to counter losses to herbivory with a brief, but synchronous, population-wide cycle of emergence, flowering, and senescence (“masting”; see also Frankland and Nelson 2003).

Given this species' rapid life cycle, some of its increase in abundance may also be attributable to subtle differences in phenological stage among the inventories, which could have enhanced its detectability in 2014. Small-statured herbs with longer or later growing seasons tended to decline in relative density within exclosures, possibly in response to competition from woody plants and large-statured herbs. On control plots, however, their comparative success and persistence may have been enhanced by their lower apparency compared with larger-statured herbs.

All of the exclosures in our study had dense stands of woody regeneration during our 2014 inventory, whereas woody regeneration remained comparatively uncommon on control plots (nearly 10-fold less abundant). Consequently, exclosures exhibited greater variability in the vertical and horizontal distribution of vegetation (Fig. 1). The woody regeneration layer, however, was slow to develop, even within the exclosures and, during a 2002 inventory, was slightly less dense than what was observed on control plots in 2014, which were devoid of regeneration during the 2002 inventory. Slow rates of recovery after deer exclusion have been observed elsewhere in undisturbed, deciduous forests and may be attributable to low understory light levels (Horsley *et al.* 2003, Collard *et al.* 2010). When present, large-statured herbs also tended to increase in abundance within exclosures, in spite of the increase in woody competition (*cf.* Collard *et al.* 2010). This is likely due to their earlier phenology compared with their predominately deciduous, woody competitors (Routhier and Lapointe 2002). In our study, however, "large-stature" appeared to be a somewhat relative term. For example, at the Hyatt Lane site, *V. sororia* increased in relative abundance within exclosures, where it was among the tallest spring-flowering herbs, whereas that species declined in relative abundance at the John Oliver site, which contained a greater abundance of even-taller herbs (*e.g.*, *T. luteum*, *T. catesbaei*, and *P. biflorum*). Consequently, changes in the abundance and vertical distribution of leaf heights in the herbaceous layer associated with continued browsing or deer exclusion likely have an important influence on competitive hierarchies (Givnish 1982).

Recolonization of our study sites was modest and likely reflects within-site dispersal and increased detectability of some species with deer

exclusion. For example, we first observed *P. biflorum* in an exclosure at Hyatt Lane during our 2014 survey. Previously, that species was found on a single control plot at that site. Some species that appeared to have colonized sample plots, such as *Antennaria plantaginifolia* (L.) Richardson, were noted near those plots during the 2004 survey. Others, however, may have simply been missed because of their small stature and rarity. For example, *C. virginica* and *Thalictrum dioicum* L. at the John Oliver site were represented by two and one individuals, respectively, during our 2014 survey. Consequently, additional monitoring and surveys of the surrounding forest matrix will be needed to clarify whether species have, indeed, colonized the area and whether those events are associated with long- or short-distance dispersal.

Complete exclusion of deer is likely a novel condition, which may have unexpected consequences for plant and animal communities that evolved with a compliment of native herbivores (Royo *et al.* 2010b, Cook-Patton *et al.* 2014). Consequently, although our results highlight the persistent legacy of abundant deer populations on forest understory communities through reduced abundance of woody regeneration and browse-sensitive species, they also hint at the beneficial, albeit context dependent, role of herbivores in forest understories. By reducing the dominance of large-statured herbs and woody plants, herbivory may promote compositional diversity (Royo *et al.* 2010b, Cook-Patton *et al.* 2014). Nevertheless, striking a balance between deleterious levels of ungulate abundance (*e.g.*, Frerker *et al.* 2014) and beneficial levels of herbivory presents a significant management quandary, especially for rare and/or browse-sensitive species. A greater understanding of the long-term consequences of herbivore abundance and exclusion on forest plant communities could help inform conservation efforts and provide insights into the role of herbivory in species coexistence.

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APPENDIX 1 Growth form and potential stature (height) of spring-flowering plant species observed on study plots in Cades Cove, Great Smoky Mountains National Park, TN. All descriptions are from Carman (2001), unless otherwise noted.

Species	Growth form/life history	Stature/height (cm)	Notes
<i>Antennaria plantaginifolia</i>	Colonial perennial with stolons	10–41	Plant height
<i>Cardamine concatenata</i>	Upright rhizomatous perennial	20–41	Stem length
<i>Cardamine hirsuta</i>	Weedy winter annual	10–41	Plant height
<i>Claytonia virginica</i>	Delicate perennial arising from a corm	10–30	Plant height
<i>Houstonia serpyllifolia</i>	Creeping perennial	10–20	Plant height
<i>Hypoxis hirsuta</i>	Grass-like perennial arising from a corm	5–60	Leaf length
<i>Iris cristata</i>	Perennial with curved, arching leaves	10–20	Leaf length
<i>Isotria verticillata</i>	Perennial arising from fleshy-fibrous roots	20–41	Stem height
<i>Maianthemum racemosum</i>	Arching, unbranched perennial	41–81	Plant height
<i>Oxalis stricta</i>	Cosmopolitan, weedy perennial	up to 41	Plant height
<i>Oxalis violacea</i>	Perennial with basal, long-stalked leaves	10–20	Flowering stalk height
<i>Polygonatum biflorum</i>	Perennial with erect to arching, unbranched stem	41–122	Stem length
<i>Ranunculus abortivus</i>	Erect annual	20–51	Plant height
<i>Ranunculus hispidus</i>	Perennial	up to 91	Plant height
<i>Stellaria media</i>	Annual to winter annual with decumbent or ascending stems	5–40	Stem length < http://www.efloras.org >
<i>Stellaria pubera</i>	Erect or ascending perennial	up to 41	Plant height
<i>Thalictrum dioicum</i>	Dioecious, erect perennial	30–71	Plant height
<i>Thalictrum thalictroides</i>	Perennial with long-stalked, basal leaves	10–30	Plant height
<i>Trillium catesbaei</i>	Erect single-stemmed perennial	15–41	Plant height
<i>Trillium luteum</i>	Erect single-stemmed perennial	20–41	Plant height
<i>Viola bicolor</i>	Annual	up to 30	Plant height < http://www.wildflower.org >
<i>Viola blanda</i>	Low perennial with creeping rhizomes and all basal leaves	2–10	Leaf length
<i>Viola hastata</i>	Causcescent perennial arising from a long branching rhizome	5–25	Plant height
<i>Viola sororia</i>	Acaulescent perennial arising from a stout horizontal rhizome	4–10	Leaf length
<i>Viola triloba</i>	Perennial arising from a low basal rosette	5–10	Petiole length < http://www.inaturalist.org >