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Impacts of Deer Herbivory on Vegetation in Rock Creek Park, 2001-2014

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ON THE COVER
Photograph of paired fenced plot and unfenced control plot in Rock Creek Park, Washington, D.C., July 2013. The vegetation sampling apparatus used for point intercept cover estimates is shown set up in the unfenced control plot on the left.
Photograph courtesy of Ken Ferebee

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Abstract

Starting in 2001, vegetation data were collected annually in 16 study modules consisting of paired (1×4 m) fenced plots and unfenced control plots located in the upland forests of Rock Creek Park, Washington, D.C. Vegetation data collected from 2001-2014 were analyzed to determine impacts of herbivory by *Odocoileus virginianus* (white-tailed deer) on vegetation in the park. Differences between fenced plots and unfenced control plots were analyzed for the following variables: cover provided by various groups of species (woody, herbaceous, native, non-native, trees, shrubs, and woody vines), as well as by individual dominant species, vegetation thickness (a measure of percent cover projected horizontally that provides information on the vertical distribution of vegetation), and species richness overall and for groups of species (woody, herbaceous, native, non-native, trees, shrubs, and woody vines). The annual collection of tree seedling count data began in 2010, allowing analysis of both tree seedling counts by height class and stocking rate (an index that assesses the adequacy of numbers of tree seedlings present to achieve forest regeneration under different deer density scenarios). The analyses were performed using repeated measures analysis of variance (ANOVA) and associated tests. Vegetation in plots protected from deer herbivory for 14 years showed significantly greater vegetative cover compared to plots not protected from deer herbivory. This effect was most pronounced for woody cover, shrub cover, and cover by one of the native shrub dominants, *Viburnum acerifolium* (mapleleaf viburnum). With respect to vegetation thickness, results indicate that protection from deer herbivory produced significantly greater levels of vegetation in the fenced plots compared to the unfenced control plots for all height classes in at least some of the years, with the strongest effects observed for the low (0-30 cm) and middle (30-110 cm) height classes. Protection from deer herbivory has led to higher overall species richness and higher species richness for woody species, natives, and shrubs compared to plots not receiving protection. Species richness for herbaceous species, non-native species, and woody vines showed little to no significant impacts from protection from deer herbivory. Tree seedlings in the 0-10 cm height class showed a negative effect associated with protection from deer herbivory (perhaps due to increased competition from a more well-developed understory), but this negative effect did not persist beyond the lowest height class. A significant positive effect was observed for tree seedlings in the 25-50 cm height range. Stocking rate did not show any significant differences between fenced and unfenced plots, and all means were below the 67% minimum stocking rate recommended to insure adequate forest regeneration. Recommendations were made regarding future sampling.

Keywords

Herbivory, fenced exclosures, vegetation thickness, *Odocoileus virginianus,* white-tailed deer, stocking rate, Rock Creek Park, Washington, D.C.

Introduction

Long-term vegetation monitoring conducted at Rock Creek Park in Washington, D.C., from 1991 through the present has shown significant degradation of the quality of the Park's interior upland forest over this time (Hatfield and Krafft 2009). Woody cover and species richness in the understory have decreased significantly. Tree seedling numbers have decreased significantly over time (except for the lowest height class of 0-10 cm), accompanied by significant decreases in stocking rates. Stocking rates for the Park are all below the 67% rate recommended by Stout (1998) to provide adequate forest regeneration. In addition, twig browse has increased significantly over the same timeframe. All of these long-term monitoring results are consistent with browsing by *Odocoileus virginianus* (white-tailed deer) and suggest deer browsing had negative impacts on the forest understory at Rock Creek Park.

Impacts of deer browsing on forest vegetation in the Eastern United States have been demonstrated through the use of both deer enclosures and exclosures, typically made of wire fencing. Tilghman (1989) used enclosures to document deer impacts to forests in northwestern Pennsylvania, adding known densities of deer to 65-ha forested sites. She found that at the end of 5 years, plots with the highest deer densities experienced decreases in woody stem height, density, and species composition. The significance of these differences depended on factors such as level of disturbance (typically, significant for areas that had been clearcut and not significant for uncut areas), height class, and species sensitivity to deer browse. In a similar 65-ha enclosure study in northwestern Pennsylvania, Horsley et al. (2003) observed over the course of 10 years that deer herbivory altered the trajectory of vegetation development. As deer densities increased, tree species richness decreased, as did heights and densities of a number of preferred forage species. Species avoided by deer actually increased with increasing deer densities. More recently, Abrams and Johnson (2012) analyzed data from 30 paired fenced and unfenced (2×2 m) plots in Valley Forge National Historical Park, Pennsylvania, that had been in place for 18 years. They found significantly higher plant diversity (Shannon diversity index and species richness), tree seedling density, and shrub and vine cover in the fenced plots that had been protected from deer herbivory for 18 years compared to the unfenced plots. There were no significant differences for herbaceous cover overall, although the stand where the invasive non-native grass *Microstegium vimineum* (Japanese stiltgrass) was abundant showed significantly greater *M. vimineum* cover in the unfenced plots compared to the fenced plots, possibly due to the high shrub cover in the fenced plots. The authors also noted that very few tree saplings (≥ 1.5 m in height and >1 cm diameter breast height) were present in the paired plots, and suggested that this may have reflected increased competition caused by the dense vegetation in the relatively small fenced plots, especially for *Quercus* seedlings, which are only moderately shade tolerant.

In order to document experimentally whether deer herbivory is causing the detrimental impacts to forest vegetation in Rock Creek Park, a series of herbivory study modules consisting of paired fenced plots and unfenced control plots, each measuring 1×4 m, was installed in the summer of 2000. Sixteen of the herbivory study modules have been monitored annually since 2001. An analysis of the first 4 years of data (Rossell et al. 2007) documented significant negative impacts of deer herbivory on woody and native cover and species richness, as well as vegetation thickness (vertical structure) less than 1 m in height. Our earlier report (Krafft and Hatfield 2011), which analyzed 2001-2009 data, showed continued effects of deer herbivory on various categories of cover, species richness, and vegetation thickness. The current report extends the period of analysis to 14 years (2001-2014), and examines the data from the standpoints of tree, shrub, woody vines, and dominant species, as well as the groups (woody, herbaceous, native, and non-native) analyzed by Rossell et al. (2007). It also reports results of analyses of tree seedling counts by height class and stocking rate, based on tree seedling data collected since 2010. Active deer management was initiated at Rock Creek Park in the winter of 2012/2013, with an extremely limited program in its first year. Given that the full deer management program had only been in effect one winter prior to the most recent year of data analyzed in this report, we did not attempt to draw conclusions regarding possible impacts of the deer management program on Park vegetation.

Methods

This study was conducted in the upland forests of the approximately 1,211-ha Rock Creek Park administrative unit located within Washington, D.C. Mapping conducted by The Nature Conservancy (TNC 1998) indicates that upland forest covers 923 ha of the administrative unit. Most of the upland forest is characterized as *Fagus grandifolia-Quercus alba*/*Podophyllum peltatum* (American beech-white oak/mayapple) forest, with a canopy dominated by *Fagus grandifolia*, *Quercus alba*, and *Liriodendron tulipifera* (tuliptree). TNC (1998) lists *Ilex opaca* (American holly) and *Cornus florida* (eastern dogwood) as sub-canopy dominants in this forest type, and describes a shrub layer dominated by *Viburnum acerifolium* (mapleleaf viburnum) and a fairly diverse herbaceous layer that is sparse to dense depending on soil type, disturbance history and moisture level. Two variants were noted (TNC 1998) for this forest association in Rock Creek Park, a mixed oak/beech variant on drier sites and a beech-tulip poplar variant on more mesic sites.

This study uses a paired plot design in which deer are excluded from the fenced study plots, whereas the control plots remain unfenced and vulnerable to deer herbivory. During the summer of 2000, 20 herbivory study modules were established (Figure 1) at random locations in the park’s interior upland forest habitat (Rossell et al. 2007). Each module consists of two 1×4 m study plots. In each module, one plot is surrounded by a 1.5×4.6 m welded wire fence (14 gauge) with a mesh size of 5×10 cm. The fence is 2.4 m tall with occasional openings where it is not in contact with the uneven ground surface, thereby excluding deer, but not small herbivores. A gate at one end of the exclosure allows access for sampling. The paired unfenced control plot is located approximately 0.3 m from the exclosure, on the side where vegetation most closely resembled that in the exclosure at the time of installation. Since a small buffer exists between the 1×4 m fenced study plot and the exclosure, the distance between the unfenced control study plot and the fenced study plot is approximately 0.6 m.

Sampling was conducted annually in the study modules since 2001, primarily during the months of July and August. Over the course of the study, four modules were abandoned for various reasons (e.g., module plots were positioned too close to a stream bank and eroded away, or the exclosure was crushed by a fallen tree). Analyses were conducted on data collected from the remaining 16 study modules. Three principal types of quantitative data were collected during the herbivory study: cover data, vegetation thickness (a horizontal projection of cover used to estimate vertical distribution of vegetation), and tree seedling heights.

Cover data were collected using the point intercept method (Elzinga et al. 1998). The sampling apparatus used for cover data consisted of two wooden spreaders with 10 4-m sections of tape measure, one attached every 10 cm (as shown in the cover photograph). One end of each tape measure was attached permanently to one of the spreaders. The other end of the tape measure could be threaded through the vegetation and then clicked into place in a notch on the opposite spreader and attached with a snap to hold it in place. The sampling apparatus provided 10 parallel 4-m lengths of tape measure. The benefit of using this apparatus rather than a more fixed sampling frame was that it provided the flexibility needed to set up in areas of varying plant density and height. Reproducibility of spreader location from year to year was addressed by equipping spreaders with a ring bolt at each end that could be slipped onto fixed sections of rebar marking the study plot corners opposite the exclosure gate. The opposite spreader was positioned temporarily at the same distance from the exclosure fence using surveyor’s chaining pins. Cover data were collected by lowering a plumb bob from 2 m above ground downward through the layers of vegetation. Any species (or nearest identifiable taxon) touched by the vertical string (or the tip of the plumb bob for prostrate vegetation) was recorded as a hit at that location. For locations with no living vascular vegetation, the first substrate cover class encountered by the plumb bob (e.g., litter, soil, wood) was recorded. Vegetation was measured in this way every 20 cm along each of the 10 tape measures for a total of 200 locations per study plot. Percent cover was calculated for each species by dividing the total number of hits for that species by 200 and multiplying by 100 to obtain a percentage. Two minor method updates occurred in 2013 and 2014. In 2013 the old spreader system was replaced with a new more efficient version that used 10 retractable metric tape measures rather than 10 sections cut from a reel-style tape measure. In 2014 the use of surveyor’s chaining pins to temporarily position the third and fourth corners of the sampling apparatus was obviated when permanent rebar were installed instead of the pins.

Plant identifications were made using Brown and Brown (1984, 1999). However, final nomenclature follows the U.S. Department of Agriculture PLANTS database (USDA, NRCS 2015). Species classifications regarding origin (native versus non-native) and life form (tree, shrub, woody vine, and herbaceous) generally follow the PLANTS database, except where it was possible to use Brown and Brown or the comprehensive Rock Creek Park plant species list (Fleming and Kanal 1995) to obtain more local information. Data were summarized for seven groupings of species (i.e., woody, herbaceous, native, non-native, tree, shrub, and woody vine) to determine impacts of protection from deer herbivory on different components of the forest vegetation. Dominant species were identified for further analysis as all species providing at least 5% cover (arithmetic mean) during at least one sampling event.

Vegetation thickness used in our study was a horizontal projection of cover designed to provide estimates of the vertical distribution of vegetation, which can be useful in assessing the ability of habitat to provide cover for wildlife (Rossell et al. 2007). It is also referred to as horizontal cover or foliage volume (Nudds 1977; Noon 1981). Vegetation thickness was estimated for three height classes, low (0-30 cm), middle (30-110 cm) and high (110-190 cm). Estimates were obtained using a drop cloth of clear acetate marked with a 10×10 cm grid 8 squares wide by 19 squares high (Noon 1981). The drop cloth was used by attaching it vertically with binder clips to the exclosure fence between the fenced plot and the unfenced control plot. Cover estimates were made by an observer kneeling 1 m away from the study plot, looking through the vegetation in the plot and estimating to the nearest eighth what fraction of each square on the drop cloth was obscured by vegetation. The sum of squares obscured by vegetation was recorded for each height class. The grid was positioned at 5 adjacent locations along the plot's long side, allowing vegetation thickness data to be obtained for the entire plot. Vegetation thickness estimates were obtained for each height class by adding together the sum of squares obscured by vegetation in each of the five drop cloth locations, dividing by the total number of possible squares in that height class, and multiplying by 100 to obtain a percentage. Vegetation thickness estimates were obtained in this way for both the fenced plot and the unfenced control plot within each module. For both types of plots the drop cloth was attached to the section of fence between the fenced plot and the unfenced control plot. For the fenced plots it was necessary to look through the fence to obtain the cover estimates.

Species richness was determined from the cover data for each study plot, and represents the number of species (or taxa not otherwise represented in the study plot) providing cover during that sampling event.

Tree seedling data were collected annually starting in 2010 to allow the analysis of tree seedling counts by height class and the calculation of stocking rates. Stocking rate is an index that assesses the adequacy of numbers of tree seedlings present to achieve forest regeneration under different deer density scenarios (McWilliams et al. 1995; Stout 1998). The height of each tree seedling in the study plots was measured and recorded by species or nearest known taxon. Tree seedling data were collected within four square-meter quadrants within the 1×4 m study plots, which allowed the calculation of a stocking rate for each study plot. Height classes were defined based on those used in the Rock Creek long-term monitoring study (Hatfield and Krafft 2009): height class 1 (0-10 cm), height class 2 (10-25 cm), height class 3 (25-50 cm), height class 4 (50-75 cm), height class 5 (75-100 cm), height class 6 (100-125 cm), height class 7 (125-150 cm), and height class 8 (>150 cm). A cut-off of 2.54 cm dbh (diameter at breast height) was used for height class 8, based on stocking rate guidelines (McWilliams et al. 1995). The tree seedling data provide useful information, although ideally these data would have been collected since the start of the study and included 2001 baseline data.

To calculate tree seedling stocking rates, we followed the recommendations of Stout (1998). We performed this analysis both for Stout's (1998) low deer density recommendation (10 weighted tree seedlings per 3.14 m^2 plot) and her high deer density recommendation (30 weighted tree seedlings per 3.14 m^2 plot). In the tree seedling stocking rate calculations, the number of tree seedlings is weighted by height class, and Stout (1998) recommends a weighting of 1 for seedling heights 5-30 cm, 2 for heights 30-100 cm, 15 for heights 100-150 cm, and 30 for heights > 150 cm. Since stocking rate calculations for the Rock Creek long-term monitoring report (Hatfield and Krafft 2009) included two modifications (tree seedlings < 5 cm in height are included and a weighting of 2 is used for tree seedlings 25-100 cm in height rather than 30-100 cm) stocking rate calculations were performed two ways to determine whether the modifications impacted the statistical significance of the results.

Since the paired plots are correlated, statistical analyses were conducted on the differences between the paired fenced plots and unfenced control plots rather than the actual plot values. Differences were calculated and analyzed for a variety of variables using mixed model repeated measures analysis of variance (SAS 2012, PROC MIXED) to compare data among years (2001-2014). Variables analyzed were: cover by seven groups of species (woody, herbaceous, natives, non-natives, trees, shrubs, woody vines) and individual dominant species, vegetation thickness, species richness overall and for species groups, tree seedling counts by height class, and stocking rates. Cover data (including vegetation thickness) and tree seedling count data were transformed prior to analysis using a natural log transformation to improve normality. Since the difference between fenced – unfenced control may be negative, it is necessary to perform the log transformation by taking the difference of the logs rather than the log of the differences. Four variance-covariance structures were modeled (compound symmetry, autoregressive, Toeplitz, and unstructured) and the best model selected via AIC_c comparisons (Littell et al. 1996). Post pairwise comparisons to determine whether the fenced – unfenced differences varied among years were made using Tukey's t-test of least squares means (family-wise error rate with α = 0.05). Inspection of the least square means and associated t-tests were used to determine the significance of mean differences between fenced and unfenced plots for each year (α = 0.05 after Bonferroni correction).

Results and Discussion

Results are provided in Table 1 of the ANOVAs conducted on the differences between fenced plots and unfenced control plots. *P*-values refer to whether the mean differences between fenced plots and unfenced control plots behave the same or differently depending on the year. They provide an indication of whether the mean differences in percent plant cover, vertical distribution of plant cover, species richness, tree seedling counts by height class, and stocking rate are increasing over time as the vegetation in the two types of plots diverges due to the reduction in deer herbivory pressure experienced by the fenced plots compared to the ambient deer herbivory pressure experienced by the unfenced control plots.

Table 2 provides means and standard errors for the differences between fenced and unfenced control plots, as well as Tukey test results indicating whether the mean differences vary significantly across years. For the cover and tree seedling count variables, back-transformation from the natural log produces an estimate of the ratio of (fenced+1)/(unfenced control+1), rather than the difference of fenced - unfenced control.

Of particular importance to this study are the associated least square means and t-tests that indicate the significance of mean differences between the fenced plots and unfenced control plots, since these reflect whether the treatment (protection from herbivory) is having a significant effect in any given year. Significance of the mean differences between fenced plots and unfenced control plots (α = 0.05 after Bonferroni correction) is indicated in Table 2 and Figures 2 through 6. Although the statistical tests were conducted on the differences between the paired plots rather than their actual values, the graphs in Figures 2 through 6 display the arithmetic means of the fenced plots and unfenced control plots (± 1 standard error) for ease of interpretation and to provide context.

A species list is provided in the Appendix. This list contains the 95 distinct taxa (88 species and 7 genera not otherwise represented by species) identified in the herbivory study plots from 2001-

2014.

Vegetative Cover

Cover data were analyzed for a number of different groups as well as individual dominant species to determine the impacts of deer herbivory on various components of the forest vegetation.

Woody Cover

Woody cover was provided by 59 distinct taxa, 44 (75%) of which are native, 13 (22%) are non-native, and 2 (3%) are of unknown origin (Appendix). Five woody species met the dominant species criterion of providing at least 5% cover in at least one sampling event: *F. grandifolia*, *V. acerifolium*, *Lindera benzoin* (northern spicebush), *Hedera helix* (English ivy) and *Viburnum dilatatum* (linden arrowwood).

In the baseline year of 2001, woody cover did not differ significantly between fenced plots and unfenced control plots (Figure 2a, Table 2). By the following year, however, there was significantly greater woody cover in the fenced plots than in the paired unfenced plots. Woody cover has remained significantly higher in the fenced plots through 2014, the most recent year for which vegetation data have been analyzed. Results of the ANOVA (Table 1, $P = 0.0079$) and Tukey tests (Table 2) indicate that differences in woody cover between fenced plots and unfenced control plots have increased significantly over time, indicating that not only are the means different for fenced plots and control plots, but they have also been diverging over time as a result of protection from deer herbivory. The mean difference in 2014 did not differ significantly from the 2001 baseline, however. More time is needed to determine whether this shift reflects normal variability in woody cover or the start of a recovery made possible by deer management.

Woody cover results indicate that protection of the fenced plots from deer herbivory has resulted in significantly greater woody cover than that achieved in the unfenced control plots, and that the fenced and unfenced control plots have diverged significantly over time with respect to woody cover.

Herbaceous Cover

Over the fourteen-year period during which the data for these analyses were collected, herbaceous cover was provided by 36 taxa, 28 (78%) of which are native, 6 (17%) are non-native, and 2 (6%) are of unknown origin (Appendix). None of the 36 provided sufficient cover to meet the dominant species threshold of at least 5% cover in at least one sampling event.

Although cover by herbaceous plants remains much lower than that of woody plants, sustained protection of the herbaceous layer in the fenced plots has produced significantly greater herbaceous cover in the fenced plots compared to the unfenced control plots for the most recent five years of sampling (Figure 2b, Table 2). ANOVA and Tukey results (Tables 1 and 2) indicate a weaker response than that exhibited by woody cover, however, since although the mean fenced plot – unfenced control plot differences increased over time, the increases have not become sufficient to achieve statistical significance (Table 1, $P = 0.4241$).

Herbaceous cover results indicate a significant treatment effect of protection from deer herbivory, with less of a divergence between fenced plots and unfenced control plots than observed for woody cover. The significant herbaceous cover effect observed in the exclosures in Rock Creek Park stands in contrast to the lack of significant impact to overall herbaceous cover observed in the long-term exclosure study conducted at Valley Forge National Historical Park in Pennsylvania (Abrams and Johnson 2012), where the only significant herbaceous cover effect observed was for the non-native invasive grass, *M. vimineum*, which produced significantly lower cover in the fenced plots compared to the unfenced plots. The authors suggest this suppression of the *M. vimineum* in the fenced plots may have been due to the fenced plot's higher levels of both shrub cover and low shade.

Native Cover

Native cover was provided by 72 (76%) of the 95 taxa identified in the study plots during the 14 years over which these data were collected. Three of the five species meeting the dominant species criterion, *F. grandifolia*, *V. acerifolium*, and *L. benzoin*, are native.

Cover by native species was significantly greater in the fenced plots than in the unfenced control plots for all years of data collection, 2001-2014 (Figure 2c, Table 2). Collection of data in 2000, the year in which the exclosures were installed, might have provided the baseline needed to draw stronger conclusions regarding the cause of the significant differences in native cover between fenced plots and unfenced control plots. ANOVA and Tukey results (Tables 1 and 2) indicate a weaker response than that exhibited by woody cover, however, since although the mean fenced plot – unfenced control plot difference estimates increased numerically over time, the increases have not become sufficient to achieve statistical significance (Table 1, $P = 0.1225$).

Non-Native Cover

Non-native cover was provided by 19 species, representing 20% of the 95 taxa identified in the study plots. Of the five species meeting the dominant species criterion by 2014, two were non-native, *H. helix* and *V. dilatatum*.

Cover by non-natives did not differ significantly between fenced plots and unfenced control plots for the 2001 baseline or for a number of years thereafter, but by 2009 and for five of the six most recent years of data collection, non-native fenced plot means were significantly greater than unfenced control plot means (Figure 2d, Table 2). Although the differences between fenced plots and unfenced plots have increased numerically over time, the results of the repeated measures ANOVA and Tukey tests (Tables 1 and 2) did not indicate that the change over time was statistically significant (Table 1, $P = 0.1493$).

The significantly greater cover means exhibited by non-natives in Rock Creek Park's exclosures is in contrast to the significant negative impact of protection from deer herbivory on fitness and density of the herbaceous non-native invasive *Alliaria petiolata* (garlic mustard) observed by Kalisz et al. (2014) during a 6-year demographic study conducted in southwestern Pennsylvania. Possible contributors to these differences include differences in methods, analyses, and woody versus herbaceous non-natives (since the dominant non-natives observed in the Rock Creek Park exclosures were woody, compared to the herbaceous *Alliaria petiolata*).

Tree Cover
Data were also analyzed separately for trees, shrubs, and woody vines in an effort to provide a richer understanding of the results for woody cover.

Tree cover during 2001-2014 was provided by 32 taxa, 27 (84%) of which were native, 3 (9%) non-native, and 2 (6%) of unknown origin (Appendix). Only one tree species, *F. grandifolia,* provided sufficient cover to meet the dominant species threshold. *F. grandifolia* was analyzed separately and is addressed further in the section on cover by individual dominant species.

The tree data indicate that prolonged protection from deer herbivory has had a positive impact on tree cover, with significantly greater tree cover means in the fenced plots compared to the unfenced control plots for five of the seven most recent years (Figure 2e, Table 2). Although the 2014 results showed a lack of significance for the fenced plot – unfenced control plot mean differences, more time is needed to determine whether this may be the beginning of a recovery made possible by the deer management that was started by the National Park Service in the winter of 2012-2013, or simply normal year to year variability. Results of the ANOVA and Tukey tests (Tables 1 and 2) indicate that differences between fenced plots and unfenced control plots increased numerically over time for tree cover, although this increase was not statistically significant (Table 1, $P = 0.5843$).

Tree cover results indicate a significant treatment effect of protection from deer herbivory, with less of a divergence between fenced plots and unfenced control plots than observed for woody cover overall.

Shrub Cover
Shrub cover was provided by 17 species, 12 (71%) of which were native, and the remaining 5 (29%) were non-native (Appendix). Three shrub species, *V.acerifolium, L.benzoin*, and *V. dilatatum*, provided at least 5% cover in at least one sampling event, and are addressed further in the results for dominant species.

Statistically, the shrub cover data exhibited a pattern similar to that observed for woody cover. Differences between fenced plots and unfenced plots were not significant during the baseline year of the study (2001), but by the third year of the study and in all subsequent years, shrub cover was significantly greater in the fenced plots than in the unfenced plots (Figure 2f, Table 2). ANOVA and Tukey results for shrub cover (Tables 1 and 2) show a significant increase in the differences between fenced plots and unfenced plots over time with respect to 2001 (Table 1, $P = 0.0068$), reflecting a greater divergence and more pronounced impact between fenced plots and unfenced control plots than that observed for tree cover.

Woody Vine Cover
Woody vine cover was provided by 10 species, consisting of 5 (50%) native species and 5 (50%) non-native species (Appendix). The percentages of native and non-natives species for woody vines were distinctly different (there was a higher percentage of non-natives) from those observed for the other life forms, reflecting an issue Rock Creek Park has worked to address through herbicidal control of its non-native woody vines. One non-native vine species, *H. helix,*

met the dominant species criterion of at least 5% cover in at least one sampling event.

With respect to cover by woody vines, differences between fenced plots and unfenced plots did not become significant until 2004, the fourth year of the study. During the period of 2004 through 2014, fenced plots exhibited significantly greater woody vine cover compared to unfenced control plots (Figure 2g, Table 2). ANOVA and Tukey results for woody vine cover show that although differences between fenced plots and unfenced plots have increased numerically over time, these increases did not achieve statistical significance (Tables 1 and 2). These results indicate that protection of vegetation in the fenced plots has led to greater woody vine cover compared to the unprotected control plots, although the divergence between the fenced plots and unfenced control plots for this variable is more similar than for tree species, and not so pronounced as observed for overall woody and shrub cover.

Cover by Individual Dominant Species

Although narrowing down to the species level may be hindered by issues regarding variability and normality, five species meeting the dominant species criterion were considered for analysis: *F. grandifolia*, *V. acerifolium*, *L. benzoin*, *H. helix*, and *V. dilatatum*. The three native species, *F. grandifolia*, *V. acerifolium*, and *L. benzoin*, were all analyzed using ANOVA. The two non-natives, *H. helix* and *V. dilatatum*, were not analyzed due to extremely poor normality even after log transformation, but their cover means are displayed in the graphs and addressed below.

F. grandifolia and *L. benzoin* (Figures 2h and j) both showed fenced plot means that were numerically greater than the paired unfenced plot means, but none of the mean differences was significant for *F. grandifolia* in 2001-2014, and only one of the years (2013) was significant for *L. benzoin*. By contrast, *V. acerifolium* showed significantly greater cover in the fenced plots than in the unfenced plots starting in 2004 and continuing through 2014 (Figure 2i and Table 2). Of note, *V. acerifolium* was present in 10 of the 16 study modules in 2014, but was not observed in any of the unfenced plots of those modules.

For *H. helix*, mean cover in the fenced plots was slightly greater numerically than the means for the unfenced control plots, with lots of variability (Figure 2k). Inspection of the raw data provides insight into this high variability, since *H. helix* was present in only 3 of the 16 study modules in 2014. Unlike *V. acerifolium*, *H. helix* was present in a mix of fenced plots and unfenced control plots. For *V. dilatatum* (Figure 2l), however, there was a slow steady increase in fenced plot cover over time, rising from less than 1% cover in 2001 to meet the dominant criterion of 5% in 2012. *V. dilatatum* was present in 5 of the 16 study modules in 2014, representing a mix of fenced plots and unfenced control plots. Neither *H. helix* nor *V. dilatatum* were analyzed using ANOVA due to extremely poor normality even after log transformation.

ANOVA results (Table 1) indicate that the changes observed over time for fenced plot – unfenced control plot mean differences were significant for only one of the three dominant species analyzed, *V. acerifolium*.

Dominant species results indicate that protection of vegetation in the fenced plots for 14 years produced significant increases in cover for *V. acerifolium*, with the suggestion of improvements in cover by the other two native dominants, *F. grandifolia* and *L. benzoin*, but little to support it statistically. The significance of the mean difference between fenced and unfenced control plots for *L. benzoin* in 2013 may presage a stronger protection effect to come, however, given a significant protection effect exhibited by *L. benzoin* after 18 years of protection in the exclosures at Valley Forge National Historical Park (Abrams and Johnson 2012). Interpretation of the results for the two non-native dominants, *H. helix* and *V. dilatatum*, was hindered by their high variability and poor normality, but inspection of the annual averages for these two species suggests that they may be receiving some benefit from protection from deer herbivory.

Vegetation Thickness

Vegetation thickness provides an estimate of the vertical distribution of vegetation through a horizontal projection of cover, rather than the vertical projection typical for cover data. Analyses of the vegetation thickness data indicate significant responses to protection of vegetation in all height classes, with the strength of the response varying by height class.

For the low height class (0-30 cm) vegetation thickness did not differ significantly during the first two years of the study, but by the third year (2003) and in ten of the subsequent eleven years, vegetation thickness was significantly greater in the fenced plots than in the unfenced control plots (Figure 3a). In addition, ANOVA and Tukey test results (Tables 1 and 2) showed a steady and significant increase over time in fenced plot – unfenced control plot differences for vegetation thickness in the low height class.

Vegetation thickness in the middle height class (30-110 cm) started out with no significant differences between fenced plots and unfenced control plots for the first three years (Figure 3b). By the fourth year (2004) and in all subsequent years through 2014, vegetation thickness was significantly greater in the fenced plots than the unfenced control plots. Estimates for fenced plot – unfenced control plot differences in middle height class vegetation thickness provided in Table 2 show numerical increases over time. The statistical results for the middle height class were not so strong as for the low height class, however, since the increase in estimates was not accompanied by Tukey test results indicating a significant increase over time with respect to the baseline year of 2001.

Vegetation thickness in the high height class (110-190 cm) was significantly greater in the fenced plots than in the unfenced control plots in three years, 2007, 2013, and 2014 (Figure 3c, Table 2). Although modest increases in the estimates for fenced plot – unfenced control plot differences are shown in Table 2, the Tukey test results do not indicate any significant differences in the estimates between years.

Mean differences among height classes were statistically significant in only three years. In 2006 vegetation thickness in the low and middle height classes was significantly greater than in the high height class; in 2009 and 2011 vegetation thickness in the low height class was still significantly greater than the high height class, but vegetation thickness in the middle height class was no longer significantly greater than that in the high height class.

The vegetation thickness data analyses indicate that protection of the fenced plots from deer herbivory has to date produced the strongest revegetation in the low height class, with a somewhat less pronounced effect in the middle height class, and a limited statistically significant effect in the high height class. Continued monitoring should reveal to what extent the revegetation continues to work its way up the understory.

Species Richness

Species richness is defined for this study as the number of species (or distinct taxa) observed per 1×4 m study plot. It is used in conjunction with estimates of plant cover to provide insights into the health of the forest understory. Overall species richness and subgroups were analyzed to determine whether any observed impacts were driven by particular subgroups or represented a cumulative effect across subgroups.

Overall Species Richness

Overall species richness reflects the total number of species (distinct taxa) identified per study plot. In the baseline year of 2001, there was no significant difference in overall species richness between fenced plots and unfenced control plots (Figure 4a, Table 2). By 2002, and in all subsequent years through 2014, however, overall species richness was significantly greater in the fenced plots than in the unfenced controls. Results of the repeated measures ANOVA show that the fenced plot – unfenced plot differences in overall species richness varied significantly over time (Table 1, $P = 0.0358$). Estimates of the fenced plot – unfenced control plot differences for overall species richness (Table 2) have increased over time with respect to the baseline, although these differences were statistically significant in only two years, 2005 and 2012.

Woody Species Richness

Fenced plot and unfenced control plot arithmetic means are quite similar to those exhibited by overall species richness, indicating that most of the overall species richness has been contributed by the woody species, with a relatively small contribution from herbaceous species. Woody species richness showed no significant differences between fenced plots and unfenced control plots in the 2001 baseline, but by 2004 and in all subsequent years up to and including 2014, woody species richness was significantly greater in the fenced plots than in the unfenced control plots (Figure 4b and Table 2). Similar to overall species richness, the repeated measures ANOVA and Tukey tests (Tables 1 and 2) for woody species richness showed a significant year effect for the fenced plot – unfenced control plot differences, with the significance of the increases with respect to the 2001 baseline varying by year. Results indicate a somewhat more pronounced effect for woody species richness than overall, given a lower P-value (0.0016 compared to 0.0358) and the fact that three of the pairwise comparisons were significant (2001 compared to 2005, 2008, and 2012), compared to only two for overall species richness.

In an effort to determine whether the strong response observed for woody species richness was based on one woody component or represented a cumulative effect across multiple components, species richness for trees, shrubs, and woody vines were also analyzed separately. Results of those analyses are presented below.

Herbaceous Species Richness

Unlike the herbaceous cover data, which showed significantly greater cover in the fenced plots compared to the unfenced control plots for the five most recent years of data (2010-2014), the results for herbaceous species richness have not shown any significant differences between fenced plot and unfenced control plot means (Figure 4c, Table 2). In addition the fenced plot – unfenced control plot differences for herbaceous species richness have not changed significantly over time (Table 1, P = 0.9264). Herbaceous species richness results indicate that protection from herbivory has had little effect on this variable.

Native Species Richness

Native species richness results indicate that species richness for natives has been significantly greater in the fenced plots than in the unfenced control plots for all 13 years following the 2001 baseline, when means between the fenced and unfenced plots did not differ significantly (Figure 4d, Table 2). Tukey test results (Table 2) show that all of the mean fenced plot – unfenced control plot differences for 2002-2014 were numerically greater than the 2001 baseline values, although, as for overall species richness, statistical significance of the baseline comparisons was restricted to two years, 2005 and 2012. ANOVA results were marginally insignificant (Table 1, P = 0.0596) indicating that the strength of the divergence over time between the fenced plots and the unfenced control plots was less strong for native species richness than for woody species or overall species richness.

Non-Native Species Richness

Unlike overall species richness, woody species richness and native species richness, non-native species richness did not differ significantly between fenced plots and unfenced control plots in any of the 14 years from 2001-2014 (Figure 4e, Table 2). Repeated measures ANOVA and Tukey test pairwise comparisons of the differences did not show any significant changes over time (Table 1, P = 0.2132; Table 2). Protection of vegetation from deer herbivory appears to have had little impact on non-native species richness.

Tree Species Richness

Tree species richness was significantly greater in the fenced plots than the unfenced control plots in 5 of the last 10 years (Figure 4f, Table 2), indicating that protection of vegetation from deer herbivory has produced a positive effect on tree species richness in the fenced plots. The effect on tree species richness was positive, but less pronounced than for woody species richness, where species richness in the fenced plots significantly exceeded that in the unfenced control plots in 11 of the 13 years post-baseline. The absence of statistical significance in the repeated measures ANOVA results (Table 1, P = 0.1065) and the Tukey results indicate that although protection from herbivory has significantly increased tree species richness, plot means between fenced and unfenced control plots have not diverged significantly over time.

Shrub Species Richness

Statistical results for shrub species richness indicate that protection from deer herbivory has had a fairly strong impact on shrub species richness, with fenced plot means significantly exceeding unfenced control plot means in 6 years, including 5 of the last 7 years (Figure 4g and Table 2). Repeated measures ANOVA results for shrub species richness (Table 1) indicate a significant year effect for fenced plot –unfenced control plot differences (P = 0.0051). Richness increased over time for fenced plot –unfenced control plot differences with respect to the baseline (Table

2), and was statistically significant in three years (2008, 2012, and 2014). Taken together these results indicate that protection from herbivory has resulted in significant increased shrub species richness, with the difference between fenced plot and unfenced plot means diverging significantly over time. The fact that fenced plot – unfenced control plot mean differences were significant for 11 of 13 years post-baseline for woody species richness, compared to only 6 of 13 for shrub species richness indicates that although shrub species richness has benefited from herbivory protection, it is not the sole contributor to/benefactor of the strong positive effect observed for woody species richness.

Woody Vine Species Richness

Results indicate little impact of protection from deer herbivory on the species richness of woody vines in the fenced plots compared to the unfenced control plots. Woody vine species richness in the fenced plots significantly exceeded levels in the unfenced control plots in only 1 of the 9 years of data analyzed (Figure 4h, Table 2), repeated measures ANOVA (Table1) showed no significant year effect (P = 0.6598), and Tukey test results (Table 2) indicate that none of the fenced plot – unfenced control plot estimates differed significantly from the 2001 baseline.

Tree Seedlings

Tree seedling count data analyzed by height class showed significant differences between fenced plot and unfenced control plot means for only two height classes, height class 1 (0-10 cm) and height class 3 (25-50 cm). Height class 1 unfenced control plot means were significantly greater than fenced plot means for all five years in which tree seedlings were measured (Figure 5a, Table 2). By contrast, height class 3 fenced plot means were numerically greater than unfenced control plot means in all years measured (Figure 5c, Table 2). These differences were statistically significant in four of the five years measured (2010-2012 and 2014).

For the remaining height classes, fenced plot means were all numerically greater than unfenced control plot means in all years measured, but none of the differences was statistically significant. Given that, from the stocking rate standpoint, for a study plot 4 m^2 in size the combination of one seedling >150 cm and one seedling 100-150 cm in height would be sufficient to consider the plot fully stocked for regeneration even at high deer density (Stout 1998), it is probably unrealistic to think that a statistically significant difference would develop between fenced and unfenced control plot means for tree seedling counts in the upper height classes.

Pairwise comparisons between height classes within years (Table 2) show that for each of the years measured (2010-2014) the fenced plot – unfenced control plot mean for height class 3 was significantly greater than that for height class 1, indicating a more positive impact from protection from herbivory in height class 3 compared to height class 1**.** In two of the five years measured, 2011 and 2013, the mean differences for all of the other height classes were also significantly greater than that for height class 1, indicating a positive response from these height classes to protection from herbivory, albeit less strong than that experienced by height class 3.

In summary, the analyses of the tree seedling count data indicate that although in the lowest height class (0-10 cm) there were significantly more tree seedlings in the unfenced control plots, this did not persist as tree seedlings grew out of the lowest height class. In fact the reverse was true for height class 3 (25-50 cm), where there were significantly more tree seedlings in the fenced plots compared to the unfenced control plots. From the regeneration standpoint, tree seedlings in the 25-50 cm height range are more valuable than those in the 0-10 cm height range due to the high mortality levels experienced in the lowest height range (Stout 1998; Hatfield and Krafft 2009). This value difference is reflected in differential weight counts and the exclusion of seedlings in the 0-5 cm height range during standard stocking rate calculations (Stout 1998). The tree seedling analysis results suggest a positive influence from protection from deer herbivory on all tree seedling height classes greater than 1, although the influence was less pronounced for the other tree seedling height classes than for height class 3. Greater numbers of seedlings in the 0-10 cm height class in the unfenced control plots compared to the fenced plots may be the result of more open space and less shade and competition provided by woody plants in the unfenced control plots.

Stocking Rate

Annual mean stocking rates calculated for fenced plots (2010-2014) using the Stout (1998) method were numerically greater than the unfenced control plot means in the same year (Figures 6a and b, Table 2). For the low deer density results annual numerical stocking rate means for the fenced plots ranged from 39 ± 8% to 25 ± 6% stocked compared to a range of 27 ± 9% to 16 ± 7% for the unfenced control plots. These numbers suggest that stocking rate in the fenced plots may have experienced some recovery during the years of protection from deer herbivory, although it should be noted that the mean differences between fenced plots and unfenced plots were not statistically significant (Figures 6a and b and Table 2). The repeated measures ANOVA results indicate that the mean difference between fenced plots and unfenced control plots did not change significantly over the five years that tree seedlings were measured (Table 1, $P = 0.2156$), but given that tree seedling counts were not made during the first 9 years of protection from deer herbivory, a lack of change in the mean difference for years 10 through 14 should perhaps not be surprising. For the high deer density results annual numerical stocking rate means for the fenced plots ranged from 8 ± 3% to 6 ± 3% stocked compared to a range of 6 ± 4% to 2 ± 2% for the unfenced control plots, with again no statistical significance in any of the five years measured, and no significant change in the mean differences over time (Table 1, $P = 0.4449$). Results using the second stocking rate method were included to allow comparison between the standard stocking rate calculations (Stout 1998) and the rate that was used for the Rock Creek long-term monitoring report (Hatfield and Krafft 2009). Results were similar between the two methods and did not differ in significance (Figures 6a, b, c and d, and Tables 1 and 2). The only curious result was for high deer density using the Hatfield and Krafft (2009) method (Figure 6d), where the stocking rate mean for the unfenced control plots in 2011 was numerically greater than the mean for the fenced plots, presumably due to seedlings in the < 5 cm height range that were included in the Hatfield and Krafft (2009) method, but discarded using the standard (Stout 1998) method. It appears that seedlings in the 25-30 cm height range, which would have received a weight of 1 using the standard (Stout 1998) method but a weight of 2 using the Hatfield and Krafft (2009) stocking rate method, did not play a role in increasing the total weight count of the control plots in 2011, since all of the tree seedlings in that height range in 2011 appeared in the fenced plots.

In summary, the stocking rate results indicate that, although the numerical means are greater for the fenced plots than the unfenced control plots and may suggest some recovery from 14 years of protection from herbivory, the results are not statistically significant.

Conclusions

Data from the first 14 years of the Rock Creek Park herbivory study indicate that deer herbivory is having significant negative impacts on forest vegetation in the park.

Cover results show protection from deer herbivory for 14 years resulted in significantly greater plant cover in the fenced plots compared to the unfenced control plots for woody species, herbaceous species, native species, non-native species, trees, shrubs, and woody vines. The most pronounced impacts of protection from deer herbivory on cover were exhibited by woody cover and shrub cover. Differences between fenced and unfenced control plots have increased significantly over time with respect to 2001 data for cover by woody species and shrub species. These results indicate that for woody and shrub species, protection from deer herbivory has not only produced significant differences, but the differences are increasing over time with continued protection. The remaining groups showed no significant changes over time with respect to the 2001 baseline.

Five species met the dominant species criterion of providing at least 5% cover in at least one sampling event. These included one tree species (*F. grandifolia*), three shrub species (*V. acerifolium*, *L. benzoin*, and *V. dilatatum*), and one woody vine (*H. helix*). Of these, three are native (*F. grandifolia*, *V. acerifolium*, and *L. benzoin*) and two are non-native (*H. helix* and *V. dilatatum*). Statistical analyses showed a strong positive effect of protection from deer herbivory on *V. acerifolium*, with consistently greater cover in the fenced plots compared to the unfenced control plots, as well as significant divergence between the two groups over time. The other two natives showed results that were of extremely limited significance (*L. benzoin*) or no statistical significance (*F. grandifolia*). The two non-natives were not analyzed statistically due to extremely poor normality even after log transformation. The graphs suggest that protection from deer herbivory may be conferring some cover benefit to these two non-native dominants as well, which would be consistent with the positive but statistically limited response exhibited for cover by the larger group, non-natives.

Results for vegetation thickness showed some evidence for significantly more vegetation present in the fenced plots compared to the unfenced control plots for all height classes, with the strength of the response decreasing with increasing height class. Differences between fenced plots and unfenced control plots showed steady, significant increases over time for the low height class (0-30 cm). Significant, but less pronounced increases were observed in the middle height class (30-110 cm), with no significant increases in the differences between fenced plots and unfenced control plots observed in the high height class (110-190 cm).

Species richness has shown significantly greater means in fenced plots than unfenced control plots for overall species richness as well as for woody species, natives, trees, and shrubs. The response was most pronounced for overall species richness, woody species, shrub species, and natives, all of which showed significant divergence over time between the fenced plots and unfenced control plots, as well as showing significantly greater richness in fenced plots compared to unfenced control plots in individual years. Herbaceous and non-native species richness showed no significant response to protection from deer herbivory, and the response from woody vine species richness was of extremely limited statistical significance.

Tree seedling counts by height class showed significant opposite results in two of the height classes. For height class 1 (0-10 cm), unfenced control plot means were significantly greater than fenced plot means. This is in contrast to height class 3 (25-50 cm), where fenced plot means were significantly greater than unfenced plot means. Means for fenced plot and unfenced control plots did not differ significantly for any of the other height classes. Stocking rate procedures can provide some insight into these results, suggesting that the smallest tree seedlings are of relatively low value from the regeneration standpoint, and that counts in the highest height classes would be expected to be fairly small, even under fully stocked conditions.

Stocking rate results (graphs) suggest that prolonged protection from deer herbivory may have afforded some limited benefit from the regeneration standpoint, but none of the results were statistically significant. With highest annual mean stocking rates of 39 ± 8% for the fenced plots and 27 ± 9% for the unfenced control plots, even under low deer density conditions, both sets of plots fall short of the 67% recommended by Stout as adequately stocked.

The 14-year exclusion of deer from the fenced plots in Rock Creek Park has resulted in significantly greater cover, vegetation thickness, and species richness for vegetation in the fenced plots compared to that in the unfenced control plots that received no protection from deer herbivory. Results have been most pronounced for: cover by woody species, shrubs, and *V. acerifolium*; species richness overall and for woody, natives, and shrubs; and vegetation thickness for the low height class. In each case, results included both evidence for significantly higher levels in the fenced plots compared to unfenced control plots, as well as significant evidence for the divergence of the vegetation in the fenced plots and unfenced control plots over time. Analysis of the tree seedling count data collected since 2010 show significant positive impacts of protection from deer herbivory to an intermediate height class, in contrast to negative impacts to the lowest height class. Stocking rate differences between fenced plots and unfenced control plots were not significant; all were below the 67% stocking rate recommended by Stout (1998) as adequate for regeneration.

With respect to the future, continued monitoring of the deer herbivory study modules in Rock Creek Park is recommended. Now that deer populations are being managed, differences between the fenced plots and unfenced plots would be expected to decrease over time as vegetation in the unfenced control plots experiences a reduction in pressure from deer herbivory. Continued monitoring would document any changes that occur. The timeframe over which these changes might occur is unknown. Periodic monitoring of exclosure integrity is recommended so that damaged exclosures can be repaired or reconstructed as needed. Since the number of herbivory study modules has already decreased from 20 to 16 (due to causes such as fallen trees and streambank erosion), every effort should be made to avoid further losses.

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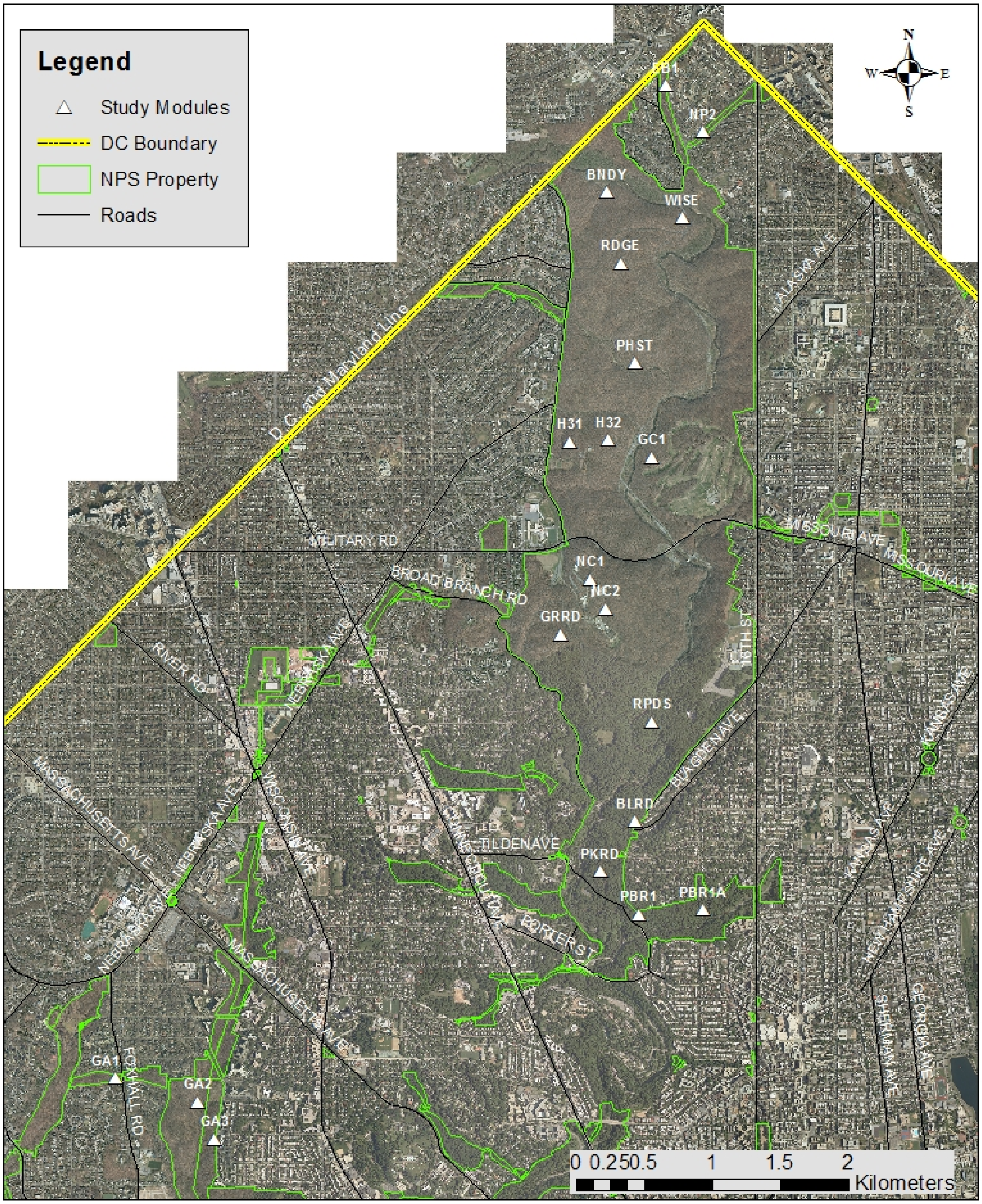


Figure 1. Location of the herbivory study modules in Rock Creek Park, Washington, D.C. Four study modules (EB1, NP2, PBR1, and PBR1A) abandoned between 2001 and 2004 were not included in this analysis.

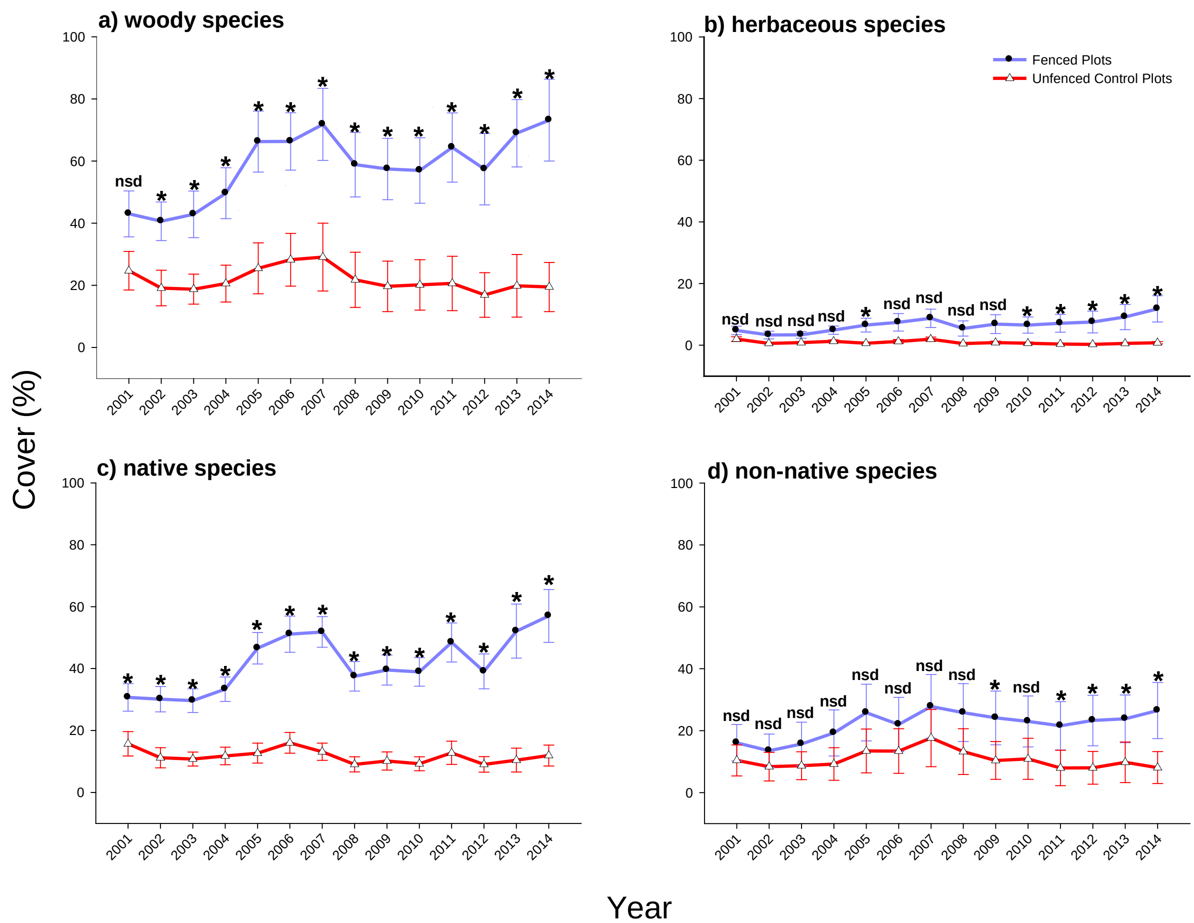


Figure 2. Cover by a) woody species, b) herbaceous species, c) native species, d) non-native species, e) trees, f) shrubs, g) woody vines, h) *F. grandifolia*, i) *V. acerifolium*, j) *L. benzoin*, k) *H. helix* and l) *V. dilatatum* in the herbivory study plots at Rock Creek Park. Data points represent arithmetic means ± 1 SE. An * indicates a significant difference between the means of the paired fenced plots and unfenced control plots within that year. No significant difference within a year is denoted by nsd. Analyses were not performed on *H. helix* or *V. dilatatum* due to extremely poor normality even after log transformation.

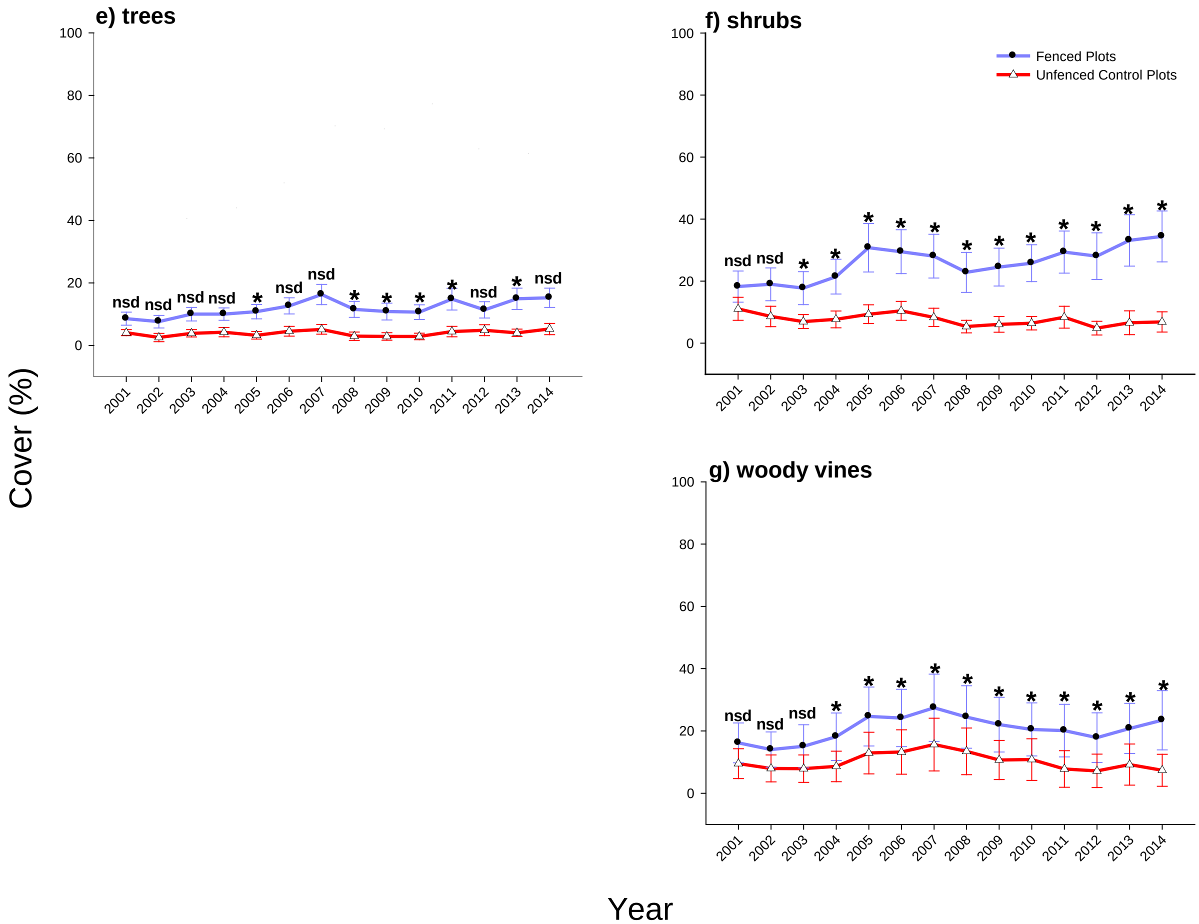


Figure 2 (continued). Cover by a) woody species, b) herbaceous species, c) native species, d) non-native species, e) trees, f) shrubs, g) woody vines, h) *F. grandifolia*, i) *V. acerifolium*, j) *L. benzoin*, k) *H. helix* and l) *V. dilatatum* in the herbivory study plots at Rock Creek Park. Data points represent arithmetic means ± 1 SE. An * indicates a significant difference between the means of the paired fenced plots and unfenced control plots within that year. No significant difference within a year is denoted by nsd. Analyses were not performed on *H. helix* or *V. dilatatum* due to extremely poor normality even after log transformation.

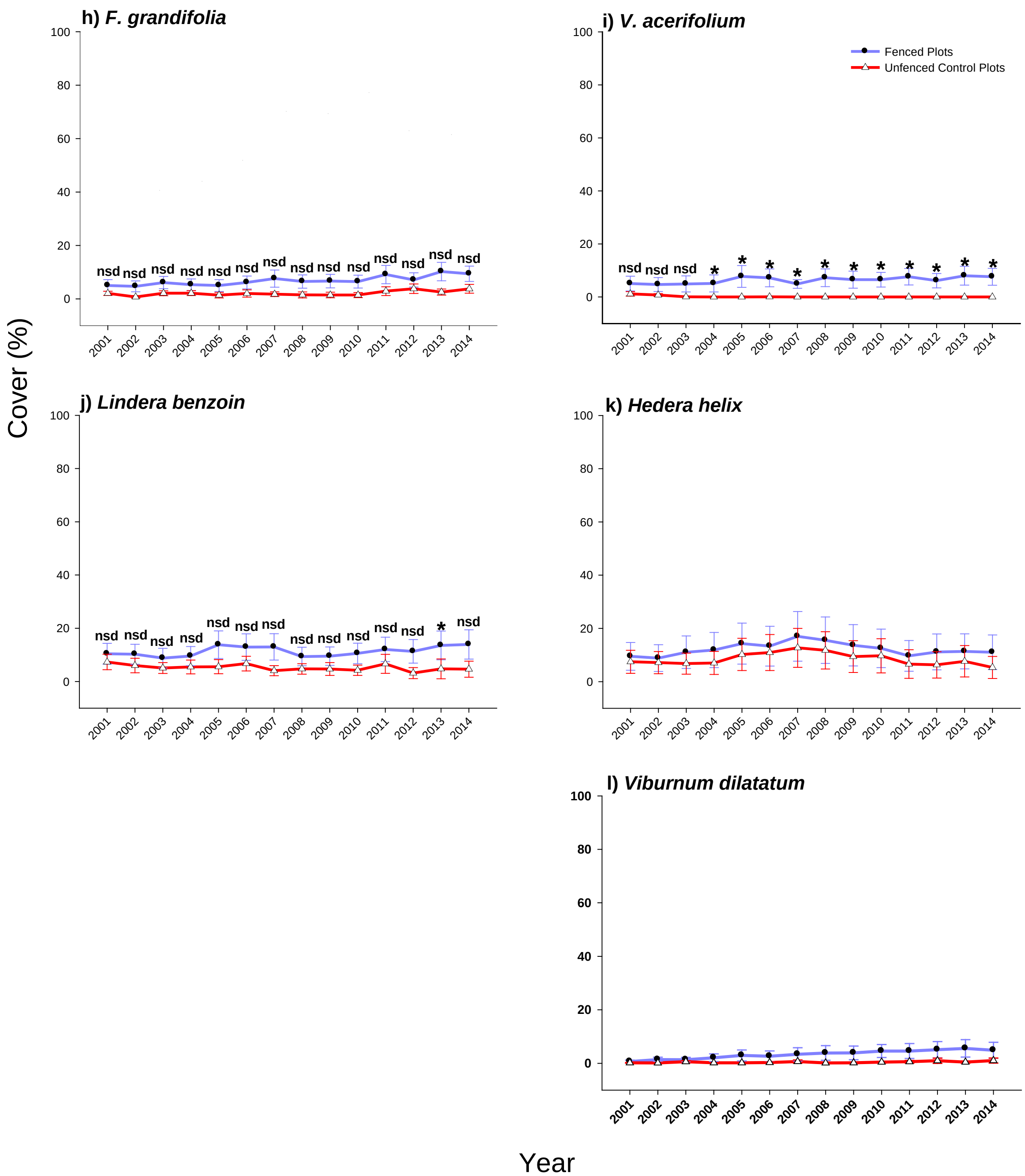


Figure 2 (continued). Cover by a) woody species, b) herbaceous species, c) native species, d) non-native species, e) trees, f) shrubs, g) woody vines, h) *F. grandifolia*, i) *V. acerifolium*, j) *L. benzoin*, k) *H. helix* and l) *V. dilatatum* in the herbivory study plots at Rock Creek Park. Data points represent arithmetic means ± 1 SE. An * indicates a significant difference between the means of the paired fenced plots and unfenced control plots within that year. No significant difference within a year is denoted by nsd. Analyses were not performed on *H. helix* or *V. dilatatum* due to extremely poor normality even after log transformation.

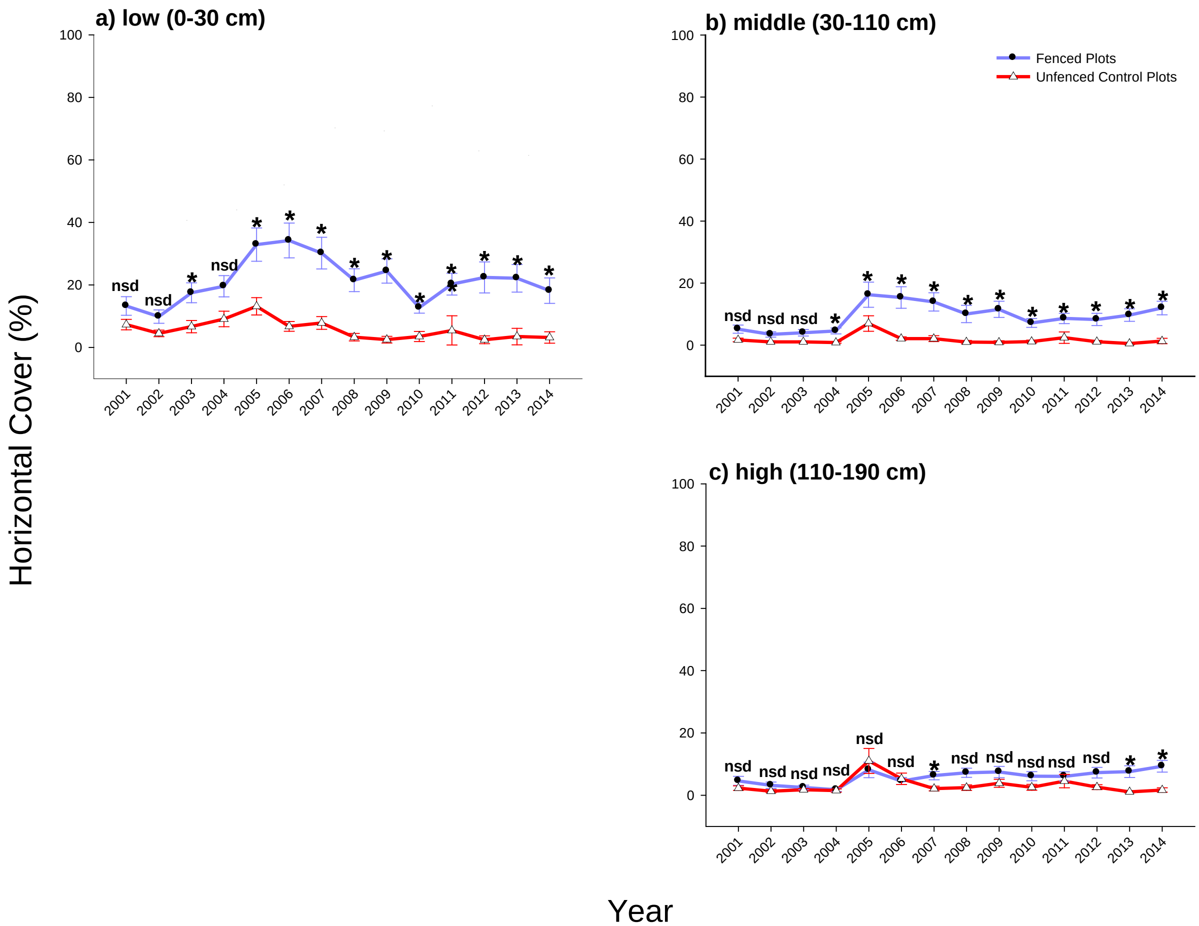


Figure 3. Vegetation thickness (cover projected horizontally) in a) low (0-30 cm), b) middle (30-110 cm), and c) high (110-190 cm) height classes in the herbivory study plots at Rock Creek Park. Data points represent arithmetic means ± 1 SE. An * indicates a significant difference between the means of the paired fenced plots and unfenced control plots within that year. No significant difference within a year is denoted by nsd.

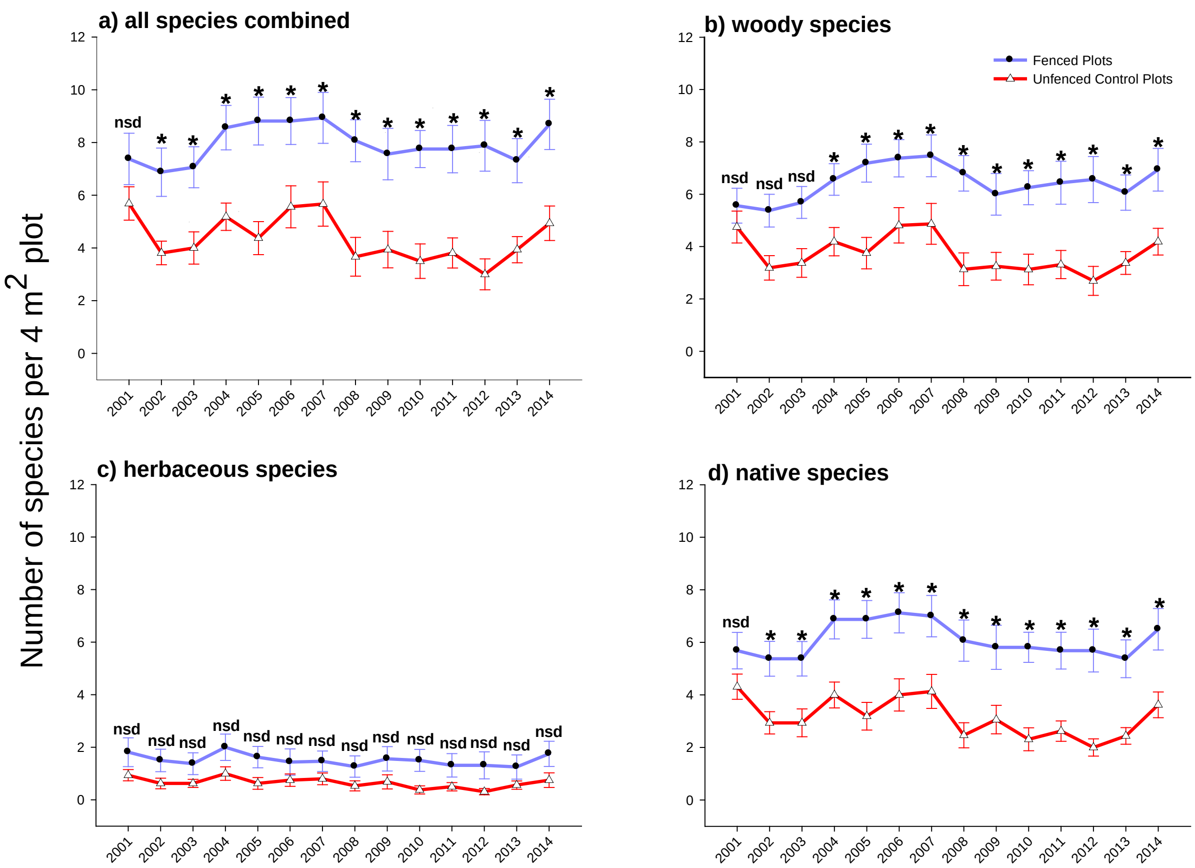
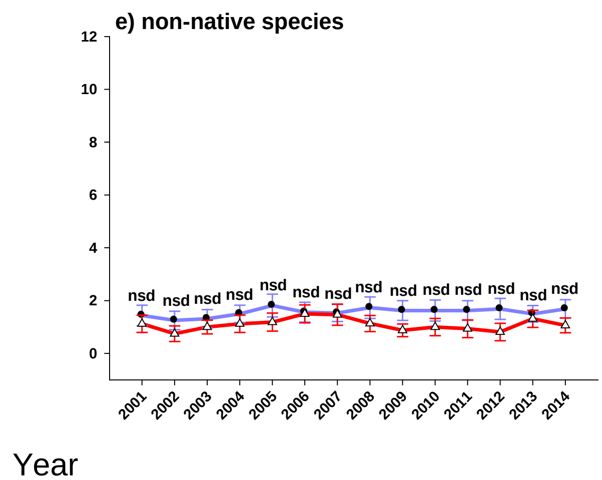


Figure 4. Species richness for
a) all species combined, b) woody species, c) herbaceous species, d) native species, e) non-native species, f) trees, g) shrubs, and h) woody vines in the herbivory study plots at Rock Creek Park. Data points represent arithmetic means ± 1 SE. An * indicates a significant difference between the means of the paired fenced plots and unfenced control plots within that year. No significant difference within a year is denoted by nsd.



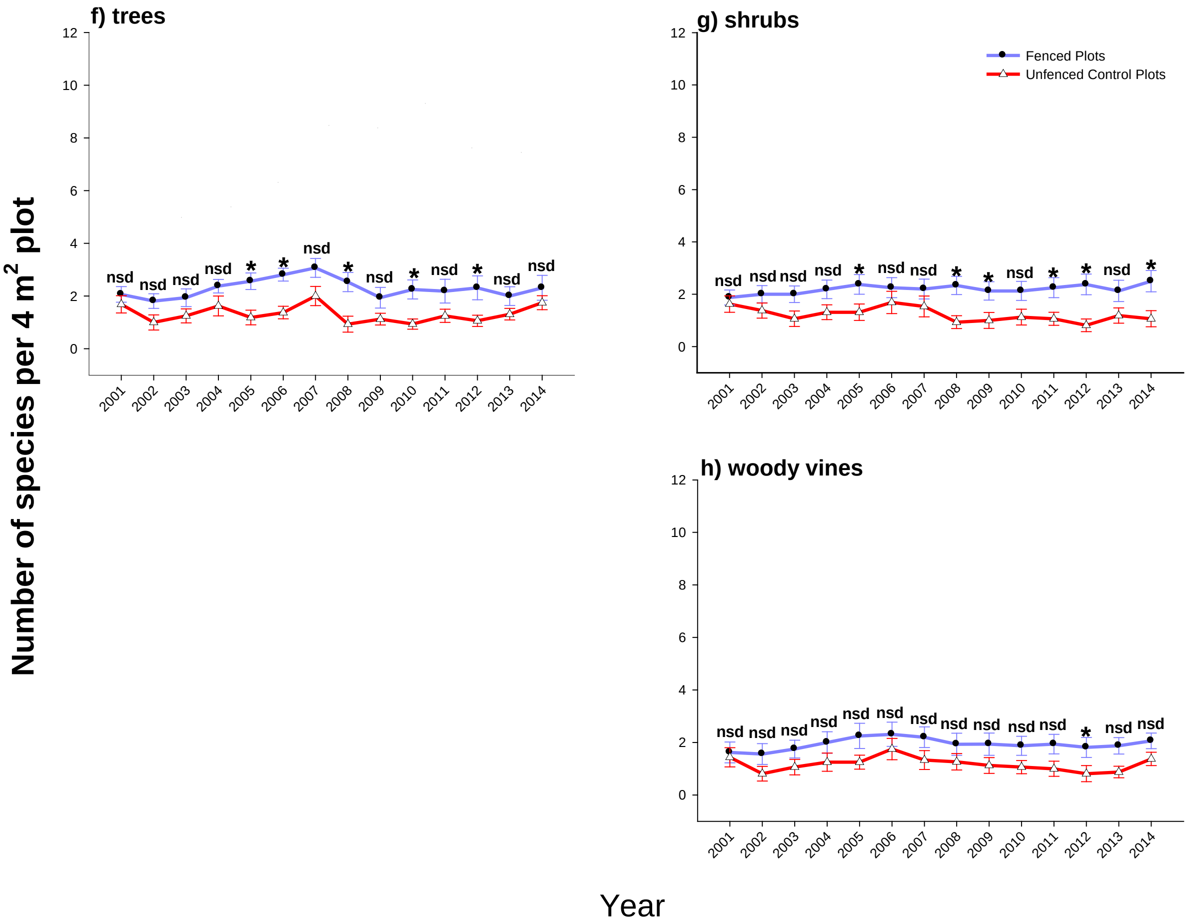


Figure 4 (continued). Species richness for a) all species combined, b) woody species, c) herbaceous species, d) native species, e) non-native species, f) trees, g) shrubs, and h) woody vines in the herbivory study plots at Rock Creek Park. Data points represent arithmetic means ± 1 SE. An * indicates a significant difference between the means of the paired fenced plots and unfenced control plots within that year. No significant difference within a year is denoted by nsd.

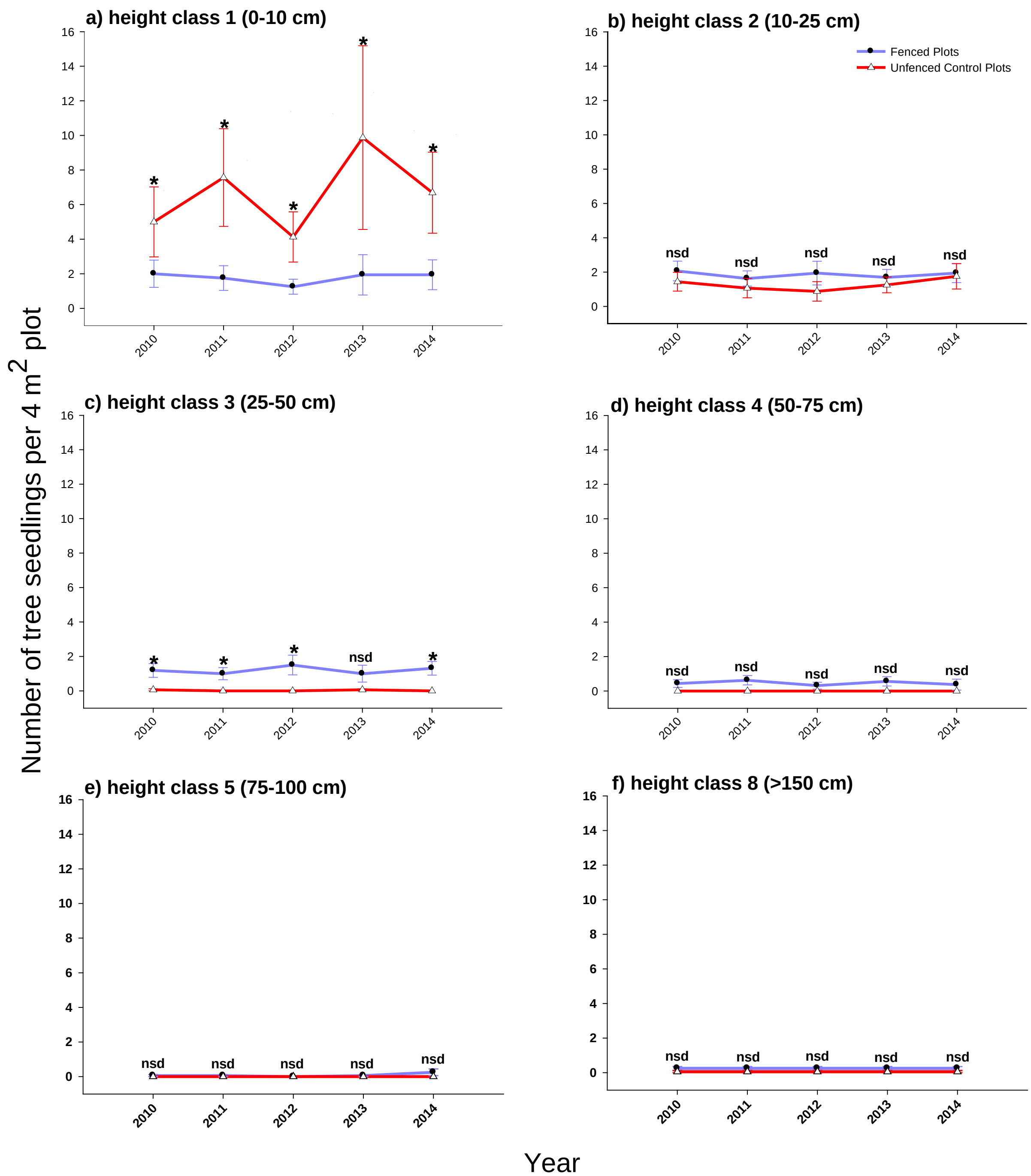


Figure 5. Tree seedling counts by height class: a) 1 (0-10 cm), b) 2 (10-25 cm), c) 3 (25-50 cm), d) 4 (50-75 cm), e) 5 (75-100 cm), 8 (>150 cm). Height classes 6 and 7 had no seedlings so were not included in the analysis. An * indicates a significant difference between the means of the paired fenced plots and unfenced control plots within that year. No significant difference within a year is denoted by nsd.

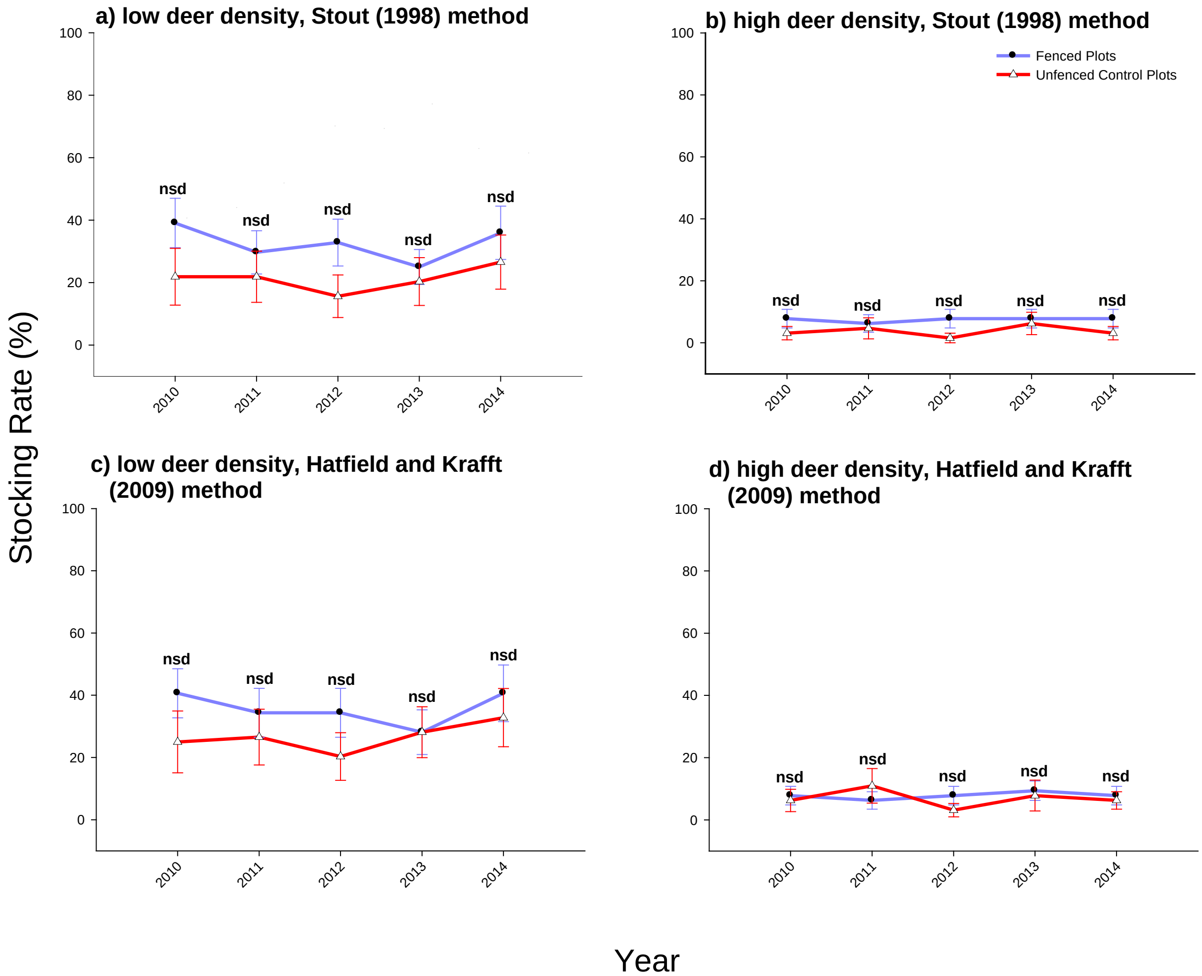


Figure 6. Stocking rates for a) low deer density, Stout (1998) method; b) high deer density, Stout (1998) method; c) low deer density, Hatfield and Krafft (2009) method; and d) high deer density, Hatfield and Krafft (2009) method. The Hatfield and Krafft (2009) method includes tree seedlings < 5 cm in height (unlike the Stout [1998] method), and one of the height class breaks occurs at 25 cm (not 30 cm as for the Stout [1998] method). This is the same modification to stocking rate that was used in the analysis of the Rock Creek long-term vegetation monitoring plots (Hatfield and Krafft 2009). An * indicates a significant difference between the means of the paired fenced plots and unfenced control plots within that year. No significant difference within a year is denoted by nsd.

Table 1. Summary statistics (*F*-values and *P*-values) from the repeated measures analysis of variance (ANOVA) for each variable. See text for descriptions of the vegetation variables and for details concerning the ANOVA models.

	Fixed Effects Terms in ANOVA Model					
	Year[1]		Height Class[2]		Year × Height Class	
Variable[3]	*F*	*P*	*F*	*P*	*F*	*P*
Difference (Fenced − Unfenced Control) in:						
Log Woody Cover (%)[4]	2.45	0.0079				
Log Herbaceous Cover (%)[4]	1.04	0.4241				
Log Native Cover (%)[5]	1.49	0.1225				
Log Non-Native Cover (%)[4]	1.49	0.1493				
Log Tree Cover (%)[4]	0.87	0.5843				
Log Shrub Cover (%)[4]	2.59	0.0068				
Log Vine Cover (%)[4]	1.10	0.3748				
Log *Fagus grandifolia* Cover (%)[4]	1.52	0.1341				
Log *Lindera benzoin* Cover (%)[4]	1.52	0.1464				
Log *Viburnum acerifolium* Cover (%)[5]	1.87	0.0356				
Log Vegetation Thickness (%)[6]	9.44	< 0.0001	56.82	< 0.0001	1.17	0.2535
Overall Species Richness[4]	1.97	0.0358				
Woody Species Richness[4]	3.02	0.0016				
Herbaceous Species Richness[4]	0.49	0.9264				
Native Species Richness[4]	1.72	0.0596				
Non-Native Species Richness[4]	1.34	0.2132				
Tree Species Richness[6]	1.54	0.1065				
Shrub Species Richness[4]	2.63	0.0051				
Vine Species Richness[4]	0.80	0.6598				

Table 1 (continued). Summary statistics (*F*-values and *P*-values) from the repeated measures analysis of variance (ANOVA) for each variable. See text for descriptions of the vegetation variables and for details concerning the ANOVA models.

	Fixed Effects Terms in ANOVA Model					
	Year[1]		Height Class[2]		Year × Height Class	
Variable[3]	*F*	*P*	*F*	*P*	*F*	*P*
Difference (Fenced – Unfenced Control) in:						
Log Tree Seedling Counts[4]	1.17	0.3400	9.53	< 0.0001	0.99	0.4809
Stocking Rate, Low Deer Density, Stout (1998) Method (%)[5]	1.49	0.2156				
Stocking Rate, High Deer Density, Stout (1998) Method (%)[7]	1.00	0.4449				
Stocking Rate, Low Deer Density, Hatfield and Krafft (2009) Method (%)[5,8]	0.80	0.5314				
Stocking Rate, High Deer Density, Hatfield and Krafft (2009) Method (%)[7,8]	1.82	0.1903				

[1]Fourteen years (2001 - 2014) for all variables except tree seedling counts and stocking rates, which were measured during five years (2010 – 2014).

[2]Three height classes for vegetation thickness (Low: 0-30 cm; Middle: 30-110 cm; High: 110-190 cm). Six height classes for tree seedling counts (1: 0-10 cm; 2: 10-25 cm; 3: 25-50 cm; 4: 50-75 cm; 5: 75-100 cm; 6: 100-125 cm; 7: 125-150 cm; 8: >150 cm). Height classes 6 and 7 were deleted for this analysis since they were empty and deleting them improved the fit of the model.

[3]The transformation natural log (Fenced+1) - natural log (Unfenced Control+1) was used to improve normality where indicated.

[4]Variable was analyzed using Toeplitz variance-covariance structure, based on AIC_c comparisons.

[5]Variable was analyzed using autoregressive variance-covariance structure, based on AIC_c comparisons.

[6]Variable was analyzed using compound symmetry variance-covariance structure, based on AIC_c comparisons.

[7]Variable was analyzed using the unstructured variance-covariance structure, based on AIC_c comparisons.

[8] Hatfield and Krafft (2009) stocking rate method uses the same modification to stocking rate as for the Rock Creek long-term vegetation monitoring plots, where tree seedlings < 5 cm in height are included (unlike the Stout [1998] method), and one of the height class breaks occurs at 25 cm (not 30 cm as for the Stout [1998] method). For more details, please refer to the Methods section.

Table 2. Results of Tukey's multiple comparison procedure for least square means (standard error in parentheses) from repeated measures analysis of variance (ANOVA) of the difference between fenced and unfenced controls, and associated Tukey's t-test of least squares means. Within each row, means with the same lower case letter superscript are not significantly different among years ($P > 0.05$). Within each column, vegetation thickness means with the same upper case letter superscript are not significantly different among height classes ($P > 0.05$). Within each column, tree seedling count means with the same upper case letter superscript are not significantly different among height classes ($P > 0.05$). Species richness and stocking rate estimates represent the mean difference of fenced – unfenced control. Cover, vegetation thickness and tree seedling count estimates received a natural log transformation to improve normality. Back-transformed estimates are presented for variables that were log transformed for analysis, resulting in a ratio of (fenced+1)/(unfenced control+1). Inspection of the least square means and associated t-tests were used to determine the significance of mean differences between fenced and unfenced control plots for each year ($\alpha = 0.05$ after Bonferroni correction). Red italicized text indicates the unfenced control mean was numerically greater than the fenced mean; in all other cases the fenced mean was numerically greater than the unfenced control mean. Bolding indicates the mean difference of fenced – unfenced control was significant.

Variable	*2001*	*2002*	*2003*	*2004*	*2005*
Plant Cover (%)					
Woody [1]	2.01^{b} (1.27)	**3.18^{ab} (1.28)**	**2.96^{ab} (1.28)**	**3.19^{ab} (1.28)**	**4.31^{ab} (1.28)**
Herbaceous [1]	1.60^{a} (1.30)	1.80^{a} (1.30)	1.66^{a} (1.30)	2.09^{a} (1.30)	**2.64^{a} (1.30)**
Native [1]	**2.33^{a} (1.29)**	**3.57^{a} (1.29)**	**3.34^{a} (1.29)**	**3.51^{a}(1.29)**	**4.90^{a} (1.29)**
Non-Native [1]	1.59^{a} (1.35)	1.72^{a} (1.35)	1.48^{a}(1.35)	2.17^{a} (1.35)	2.07^{a} (1.35)
Tree [1]	1.60^{a} (1.40)	2.65^{a} (1.40)	2.25^{a} (1.40)	2.45^{a} (1.40)	**2.85^{a} (1.40)**
Shrub [1]	1.71^{c} (1.28)	2.14^{bc} (1.29)	**2.64^{abc} (1.29)**	**3.17^{ab} (1.29)**	**3.83^{ab} (1.29)**
Woody Vine [1]	1.53^{a} (1.23)	1.84^{a} (1.23)	1.77^{a} (1.23)	**2.10^{a} (1.23)**	**2.02^{a} (1.23)**
Fagus grandifolia [1]	1.28^{a}(1.42)	2.00^{a}(1.42)	1.50^{a}(1.42)	1.36^{a} (1.42)	1.71^{a}(1.42)
Lindera benzoin [1]	1.26^{a} (1.30)	1.34^{a}(1.29)	1.41^{a} (1.29)	1.54^{a} (1.29)	1.76^{a} (1.30)
Viburnum acerifolium [1]	1.83^{bc} (1.32)	1.88^{c} (1.32)	2.36^{abc}(1.32)	**2.46^{abc}(1.32)**	**3.35^{a} (1.32)**
Vegetation Thickness (%) [1,2]					
Low	1.67^{bA} (1.34)	1.76^{bA} (1.32)	**2.56^{abA} (1.32)**	2.30^{bA}(1.32)	**3.03^{abA}(1.32)**
Middle	2.15^{aA} (1.34)	1.89^{aA} (1.32)	2.23^{aA} (1.32)	**2.56^{aA} (1.32)**	**2.43^{aA} (1.32)**
High	1.53^{aA} (1.34)	1.66^{aA} (1.32)	1.10^{aA} (1.32)	1.11^{aA} (1.32)	1.01^{aA} (1.32)

Table 2 (continued). Results of Tukey's multiple comparison procedure for least square means (standard error in parentheses) from repeated measures analysis of variance (ANOVA) of the difference between fenced and unfenced controls, and associated Tukey's t-test of least squares means. Within each row, means with the same lower case letter superscript are not significantly different among years ($P > 0.05$). Within each column, vegetation thickness means with the same upper case letter superscript are not significantly different among height classes ($P > 0.05$). Within each column, tree seedling count means with the same upper case letter superscript are not significantly different among height classes ($P > 0.05$). Species richness and stocking rate estimates represent the mean difference of fenced – unfenced control. Cover, vegetation thickness and tree seedling count estimates received a natural log transformation to improve normality. Back-transformed estimates are presented for variables that were log transformed for analysis, resulting in a ratio of (fenced+1)/(unfenced control+1). Inspection of the least square means and associated t-tests were used to determine the significance of mean differences between fenced and unfenced control plots for each year ($\alpha = 0.05$ after Bonferroni correction). Red italicized text indicates the unfenced control mean was numerically greater than the fenced mean; in all other cases the fenced mean was numerically greater than the unfenced control mean. Bolding indicates the mean difference of fenced – unfenced control was significant.

Variable	*2001*	*2002*	*2003*	*2004*	*2005*
Species Richness					
Overall	1.53^{b} (0.84)	**3.15^{ab} (0.84)**	**2.97^{ab} (0.84)**	**3.37^{ab} (0.84)**	**4.38^{a} (0.84)**
Woody	0.79^{b} (0.74)	2.18^{ab} (0.74)	2.27^{ab} (0.74)	**2.38^{ab} (0.74)**	**3.34^{a} (0.74)**
Herbaceous	0.92^{a} (0.37)	0.84^{a} (0.37)	0.76^{a} (0.37)	1.02^{a} (0.37)	0.96^{a} (0.37)
Native	1.38^{b} (0.68)	**2.44^{ab} (0.68)**	**2.44^{ab} (0.68)**	**2.88^{ab} (0.68)**	**3.69^{a} (0.68)**
Non-Native	0.28^{a} (0.37)	0.54^{a} (0.37)	0.27^{a} (0.37)	0.38^{a} (0.37)	0.62^{a} (0.37)
Tree	0.38^{a} (0.39)	0.81^{a} (0.39)	0.69^{a} (0.39)	0.75^{a} (0.39)	**1.38^{a} (0.39)**
Shrub	0.22^{c} (0.33)	0.61^{abc} (0.33)	0.94^{abc} (0.33)	0.86^{abc} (0.33)	**1.05^{abc} (0.33)**
Woody Vine	0.14^{a} (0.32)	0.78^{a} (0.32)	0.63^{a} (0.32)	0.80^{a} (0.32)	0.96^{a} (0.32)

Table 2 (continued). Results of Tukey's multiple comparison procedure for least square means (standard error in parentheses) from repeated measures analysis of variance (ANOVA) of the difference between fenced and unfenced controls, and associated Tukey's t-test of least squares means. Within each row, means with the same lower case letter superscript are not significantly different among years ($P > 0.05$). Within each column, vegetation thickness means with the same upper case letter superscript are not significantly different among height classes ($P > 0.05$). Within each column, tree seedling count means with the same upper case letter superscript are not significantly different among height classes ($P > 0.05$). Species richness and stocking rate estimates represent the mean difference of fenced – unfenced control. Cover, vegetation thickness and tree seedling count estimates received a natural log transformation to improve normality. Back-transformed estimates are presented for variables that were log transformed for analysis, resulting in a ratio of (fenced+1)/(unfenced control+1). Inspection of the least square means and associated t-tests were used to determine the significance of mean differences between fenced and unfenced control plots for each year ($\alpha = 0.05$ after Bonferroni correction). Red italicized text indicates the unfenced control mean was numerically greater than the fenced mean; in all other cases the fenced mean was numerically greater than the unfenced control mean. Bolding indicates the mean difference of fenced – unfenced control was significant.

Variable	*2006*	*2007*	*2008*	*2009*
Plant Cover (%)				
Woody [1]	**4.11^{ab} (1.28)**	**4.23^{ab} (1.28)**	**4.78^{ab} (1.28)**	**5.51^{a} (1.28)**
Herbaceous [1]	2.12^{a} (1.30)	2.00^{a} (1.31)	1.97^{a} (1.31)	2.16^{a} (1.30)
Native [1]	**4.12^{a} (1.29)**	**4.65^{a} (1.29)**	**5.05^{a} (1.29)**	**5.49^{a}(1.29)**
Non-Native [1]	1.84^{a} (1.35)	2.14^{a} (1.35)	2.50^{a} (1.35)	**2.67^{a} (1.35)**
Tree [1]	2.72^{a} (1.40)	2.78^{a} (1.40)	**3.34^{a} (1.40)**	**2.89^{a} (1.40)**
Shrub [1]	**3.02^{abc} (1.29)**	**3.97^{ab} (1.29)**	**4.04^{ab} (1.29)**	**4.52^{ab} (1.29)**
Woody Vine [1]	**2.29^{a} (1.23)**	**2.14^{a} (1.24)**	**2.13^{a} (1.24)**	**2.31^{a} (1.23)**
Fagus grandifolia [1]	1.73^{a} (1.42)	1.74^{a} (1.42)	1.95^{a} (1.42)	2.10^{a} (1.42)
Lindera benzoin [1]	1.34^{a} (1.30)	1.76^{a} (1.30)	1.54^{a} (1.30)	1.73^{a} (1.30)
Viburnum acerifolium [1]	**3.34^{abc} (1.32)**	**3.74^{ab} (1.32)**	**3.42^{abc} (1.32)**	**3.34^{abc} (1.32)**
Vegetation Thickness (%) [1,2]				
Low	**5.79^{abA} (1.32)**	**4.95^{abA} (1.33)**	**5.93^{abA} (1.33)**	**9.11^{aA} (1.32)**
Middle	**4.70^{aA} (1.32)**	**5.18^{aA} (1.33)**	**4.69^{aA} (1.33)**	**5.72^{aAB} (1.32)**
High	1.11^{aB} (1.32)	**2.38^{aA} (1.33)**	2.34^{aA} (1.33)	1.78^{aB} (1.32)

Table 2 (continued). Results of Tukey's multiple comparison procedure for least square means (standard error in parentheses) from repeated measures analysis of variance (ANOVA) of the difference between fenced and unfenced controls, and associated Tukey's t-test of least squares means. Within each row, means with the same lower case letter superscript are not significantly different among years ($P > 0.05$). Within each column, vegetation thickness means with the same upper case letter superscript are not significantly different among height classes ($P > 0.05$). Within each column, tree seedling count means with the same upper case letter superscript are not significantly different among height classes ($P > 0.05$). Species richness and stocking rate estimates represent the mean difference of fenced – unfenced control. Cover, vegetation thickness and tree seedling count estimates received a natural log transformation to improve normality. Back-transformed estimates are presented for variables that were log transformed for analysis, resulting in a ratio of (fenced+1)/(unfenced control+1). Inspection of the least square means and associated t-tests were used to determine the significance of mean differences between fenced and unfenced control plots for each year ($\alpha = 0.05$ after Bonferroni correction). Red italicized text indicates the unfenced control mean was numerically greater than the fenced mean; in all other cases the fenced mean was numerically greater than the unfenced control mean. Bolding indicates the mean difference of fenced – unfenced control was significant.

Variable	*2006*	*2007*	*2008*	*2009*
Species Richness				
Overall	**3.19^{ab} (0.84)**	**3.22^{ab} (0.85)**	**4.15^{ab} (0.85)**	**3.67^{ab} (0.84)**
Woody	**2.54^{ab} (0.74)**	**2.57^{ab} (0.74)**	**3.47^{a} (0.74)**	**2.80^{ab} (0.74)**
Herbaceous	0.74^{a} (0.37)	0.58^{a} (0.38)	0.69^{a} (0.38)	0.88^{a} (0.37)
Native	**3.13^{ab} (0.68)**	**2.78^{ab} (0.69)**	**3.35^{ab} (0.69)**	**2.75^{ab} (0.68)**
Non-Native	0.06^{a} (0.37)	0.16^{a} (0.38)	0.58^{a} (0.38)	0.75^{a} (0.37)
Tree	**1.44^{a} (0.39)**	1.05^{a} (0.40)	**1.48^{a} (0.40)**	0.81^{a} (0.39)
Shrub	0.53^{bc} (0.33)	0.74^{abc} (0.34)	**1.29^{ab} (0.34)**	**1.14^{abc} (0.33)**
Woody Vine	0.61^{a} (0.32)	0.78^{a} (0.33)	0.69^{a} (0.33)	0.80^{a} (0.32)

Table 2 (continued). Results of Tukey's multiple comparison procedure for least square means (standard error in parentheses) from repeated measures analysis of variance (ANOVA) of the difference between fenced and unfenced controls, and associated Tukey's t-test of least squares means. Within each row, means with the same lower case letter superscript are not significantly different among years ($P > 0.05$). Within each column, vegetation thickness means with the same upper case letter superscript are not significantly different among height classes ($P > 0.05$). Within each column, tree seedling count means with the same upper case letter superscript are not significantly different among height classes ($P > 0.05$). Species richness and stocking rate estimates represent the mean difference of fenced – unfenced control. Cover, vegetation thickness and tree seedling count estimates received a natural log transformation to improve normality. Back-transformed estimates are presented for variables that were log transformed for analysis, resulting in a ratio of (fenced+1)/(unfenced control+1). Inspection of the least square means and associated t-tests were used to determine the significance of mean differences between fenced and unfenced control plots for each year ($\alpha = 0.05$ after Bonferroni correction). Red italicized text indicates the unfenced control mean was numerically greater than the fenced mean; in all other cases the fenced mean was numerically greater than the unfenced control mean. Bolding indicates the mean difference of fenced – unfenced control was significant.

Variable	*2010*	*2011*	*2012*	*2013*	*2014*
Plant Cover (%)					
Woody [1]	**5.17^{a} (1.28)**	**5.12^{a} (1.28)**	**5.45^{a} (1.28)**	**6.01^{a} (1.28)**	**5.57^{ab} (1.27)**
Herbaceous [1]	**2.58^{a} (1.30)**	**2.64^{a} (1.30)**	**2.50^{a} (1.30)**	**2.37^{a} (1.30)**	**3.54^{a} (1.30)**
Native [1]	**5.52^{a} (1.29)**	**5.18^{a} (1.29)**	**5.36^{a} (1.29)**	**6.55^{a}(1.29)**	**5.85^{a} (1.29)**
Non-Native [1]	2.58^{a} (1.35)	**3.17^{a} (1.35)**	**3.31^{a} (1.35)**	**2.78^{a} (1.35)**	**3.22^{a} (1.35)**
Tree [1]	**3.21^{a} (1.40)**	**3.02^{a} (1.40)**	2.38^{a} (1.40)	**2.92^{a} (1.40)**	2.76^{a} (1.40)
Shrub [1]	**3.99^{ab} (1.29)**	**4.19^{ab} (1.29)**	**5.16^{a} (1.29)**	**5.65^{a} (1.29)**	**5.76^{a} (1.28)**
Woody Vine [1]	**2.11^{a} (1.23)**	**2.80^{a} (1.23)**	**2.88^{a} (1.23)**	**2.57^{a} (1.23)**	**3.17^{a} (1.23)**
Fagus grandifolia [1]	2.05^{a}(1.42)	1.96^{a}(1.42)	1.40^{a}(1.42)	2.17^{a} (1.42)	1.90^{a}(1.42)
Lindera benzoin [1]	1.70^{a} (1.30)	1.71^{a}(1.29)	2.25^{a} (1.29)	**2.34^{a} (1.29)**	2.17^{a} (1.30)
Viburnum acerifolium [1]	**3.52^{abc} (1.32)**	**3.60^{abc} (1.32)**	**3.27^{abc}(1.32)**	**3.65^{abc} (1.32)**	**3.69^{abc} (1.32)**
Vegetation Thickness (%) [1,2]					
Low	**5.14^{abA} (1.32)**	**7.69^{aA} (1.32)**	**7.37^{aA} (1.32)**	**9.03^{aA} (1.32)**	**6.74^{aA} (1.32)**
Middle	**3.59^{aA} (1.32)**	**4.19^{aAB} (1.32)**	**3.76^{aA} (1.32)**	**5.90^{aA} (1.32)**	**6.30^{aA} (1.32)**
High	2.03^{aA} (1.32)	1.88^{aB} (1.32)	2.20^{aA} (1.32)	**3.09^{aA} (1.32)**	**3.68^{aA} (1.32)**

Table 2 (continued). Results of Tukey's multiple comparison procedure for least square means (standard error in parentheses) from repeated measures analysis of variance (ANOVA) of the difference between fenced and unfenced controls, and associated Tukey's t-test of least squares means. Within each row, means with the same lower case letter superscript are not significantly different among years ($P > 0.05$). Within each column, vegetation thickness means with the same upper case letter superscript are not significantly different among height classes ($P > 0.05$). Within each column, tree seedling count means with the same upper case letter superscript are not significantly different among height classes ($P > 0.05$). Species richness and stocking rate estimates represent the mean difference of fenced – unfenced control. Cover, vegetation thickness and tree seedling count estimates received a natural log transformation to improve normality. Back-transformed estimates are presented for variables that were log transformed for analysis, resulting in a ratio of (fenced+1)/(unfenced control+1). Inspection of the least square means and associated t-tests were used to determine the significance of mean differences between fenced and unfenced control plots for each year ($\alpha = 0.05$ after Bonferroni correction). Red italicized text indicates the unfenced control mean was numerically greater than the fenced mean; in all other cases the fenced mean was numerically greater than the unfenced control mean. Bolding indicates the mean difference of fenced – unfenced control was significant.

Variable	*2010*	*2011*	*2012*	*2013*	*2014*
Species Richness					
Overall	**4.30^{ab} (0.84)**	**4.00^{ab} (0.84)**	**4.96^{a} (0.84)**	**3.39^{ab} (0.84)**	**3.86^{ab} (0.84)**
Woody	**3.16^{ab} (0.74)**	**3.19^{ab} (0.74)**	**3.94^{a} (0.74)**	**2.70^{ab} (0.74)**	**2.89^{ab} (0.74)**
Herbaceous	1.11^{a} (0.37)	0.83^{a} (0.37)	0.99^{a} (0.37)	0.70^{a} (0.37)	1.00^{a} (0.37)
Native	**3.50^{ab} (0.68)**	**3.06^{ab} (0.68)**	**3.69^{a} (0.68)**	**2.94^{ab} (0.68)**	**2.88^{ab} (0.68)**
Non-Native	0.65^{a} (0.37)	0.68^{a} (0.37)	0.90^{a} (0.37)	0.19^{a} (0.37)	0.68^{a} (0.37)
Tree	**1.31^{a} (0.39)**	0.94^{a} (0.39)	**1.25^{a} (0.39)**	0.69^{a} (0.39)	0.56^{a} (0.39)
Shrub	1.03^{abc} (0.33)	**1.20^{abc} (0.33)**	**1.59^{a} (0.33)**	0.92^{abc} (0.33)	**1.45^{ab}(0.33)**
Woody Vine	0.85^{a} (0.32)	0.91^{a} (0.32)	**1.02^{a} (0.32)**	0.98^{a} (0.32)	0.73^{a} (0.32)
Tree Seedling Counts[1,3]					
Height Class 1	***0.64^{aB} (1.19)***	***0.40^{aB} (1.19)***	***0.61^{aB} (1.19)***	***0.39^{aB} (1.19)***	***0.53^{aB} (1.19)***
Height Class 2	1.24^{aAB} (1.19)	1.35^{aA} (1.19)	1.55^{aA} (1.19)	1.22^{aA} (1.19)	1.15^{aAB} (1.19)
Height Class 3	**1.69^{aA} (1.19)**	**1.66^{aA} (1.19)**	**1.95^{aA} (1.19)**	1.53^{aA} (1.19)	**1.88^{aA} (1.19)**
Height Class 4	1.27^{aAB} (1.19)	1.39^{aA} (1.19)	1.19^{aAB} (1.19)	1.35^{aA} (1.19)	1.17^{aAB} (1.19)
Height Class 5	1.04^{aAB} (1.19)	1.04^{aA} (1.19)	1.00^{aAB} (1.19)	1.04^{aA} (1.19)	1.14^{aAB} (1.19)
Height Class 8	1.14^{aAB} (1.19)	1.14^{aA} (1.19)	1.14^{aAB} (1.19)	1.14^{aA} (1.19)	1.14^{aAB} (1.19)

Table 2 (continued). Results of Tukey's multiple comparison procedure for least square means (standard error in parentheses) from repeated measures analysis of variance (ANOVA) of the difference between fenced and unfenced controls, and associated Tukey's t-test of least squares means. Within each row, means with the same lower case letter superscript are not significantly different among years (*P* > 0.05). Within each column, vegetation thickness means with the same upper case letter superscript are not significantly different among height classes (*P* > 0.05). Within each column, tree seedling count means with the same upper case letter superscript are not significantly different among height classes (*P* > 0.05). Species richness and stocking rate estimates represent the mean difference of fenced – unfenced control. Cover, vegetation thickness and tree seedling count estimates received a natural log transformation to improve normality. Back-transformed estimates are presented for variables that were log transformed for analysis, resulting in a ratio of (fenced+1)/(unfenced control+1). Inspection of the least square means and associated t-tests were used to determine the significance of mean differences between fenced and unfenced control plots for each year ($\alpha = 0.05$ after Bonferroni correction). Red italicized text indicates the unfenced control mean was numerically greater than the fenced mean; in all other cases the fenced mean was numerically greater than the unfenced control mean. Bolding indicates the mean difference of fenced – unfenced control was significant.

Variable	*2010*	*2011*	*2012*	*2013*	*2014*
Stocking Rate, Low Deer Density, Stout (1998) Method (%)	17.19^{a} (7.48)	7.81^{a} (7.48)	17.19^{a} (7.48)	4.69^{a} (7.48)	9.38^{a} (7.48)
Stocking Rate, High Deer Density, Stout (1998) Method (%)	4.69^{a} (4.09)	1.56^{a} (4.82)	6.25^{a} (3.61)	1.56^{a} (4.82)	4.69^{a} (3.40)
Stocking Rate, Low Deer Density, Hatfield and Krafft (2009) Method (%)[4]	15.63^{a} (9.00)	7.81^{a} (9.00)	14.06^{a} (9.00)	*0.00^{a} (9.00)*	7.81^{a} (9.00)
Stocking Rate, High Deer Density, Hatfield and Krafft (2009) Method (%)[4]	1.56^{a} (5.34)	*-4.69^{a} (6.54)*	4.69^{a} (3.40)	1.56^{a} (6.24)	1.56^{a} (3.59)

[1]Back-transformed from natural log (fenced+1) – natural log (unfenced control+1).
[2]Three height classes for vegetation thickness (Low: 0-30 cm; Middle: 30-110 cm; High: 110-190 cm).
[3]Six height classes for tree seedling counts (1: 0-10 cm; 2: 10-25 cm; 3: 25-50 cm; 4: 50-75 cm; 5: 75-100 cm; 6: 100-125 cm; 7: 125-150 cm; 8: >150 cm). Height classes 6 and 7 were deleted for this analysis since they were empty and deleting them improved the fit of the model.
[4] Hatfield and Krafft (2009) stocking rate method uses the same modification to stocking rate as for the Rock Creek long-term vegetation monitoring plots, where tree seedlings < 5 cm in height are included (unlike the Stout [1998] method), and one of the height class breaks occurs at 25 cm (not 30 cm as for the Stout [1998] method). For more details, please refer to the Methods section.

Appendix A. Species list from Rock Creek Park herbivory study plots, 2001-2014. List consists of 88 species and 7 genera not otherwise represented by species.

Scientific Name[1]	***Common Name[1]***	***Origin[2]***	***Form[2]***
Acer negundo L.	Boxelder	native	tree
Acer palmatum Thun.	Japanese maple	non-native	tree
Acer platanoides L.	Norway maple	non-native	tree
Acer rubrum L.	red maple	native	tree
Acer saccharum Marsh.	sugar maple	native	tree
Actaea racemosa L. var. *racemosa*[3]	black bugbane	native	herbaceous
Alliaria petiolata (M. Bieb.) Cavara & Grande	garlic mustard	non-native	herbaceous
Amphicarpaea bracteata L. (Fernald)	American hogpeanut	native	herbaceous
Ailanthus altissima (Mill.) Swingle	tree of heaven	non-native	tree
Amelanchier arborea (Michx. F.) Fernald	common serviceberry	native	tree
Ampelopsis brevipedunculata (Maxim.) Trautv.	Amur peppervine	non-native	woody vine
Arisaema triphyllum (L.) Schott	Jack in the pulpit	native	herbaceous
Asimina triloba (L.) Dunal	Pawpaw	native	tree
Aster L. spp.	aster	unknown	herbaceous
Berberis thunbergii DC.	Japanese barberry	non-native	shrub
Carya cordiformis (Wangenh.) K. Koch	bitternut hickory	native	tree
Carya glabra (Mill.) Sweet	pignut hickory	native	tree
Carya tomentosa (Lam.) Nutt.[4]	mockernut hickory	native	tree
Carex virescens Muhl. Ex Willd.	ribbed sedge	native	herbaceous
Celastrus orbiculatus Thunb.	Oriental bittersweet	non-native	woody vine
Circaea lutetiana L. ssp. *canadensis* (L.) Asch. & Magnus[5]	broadleaf enchanter's nightshade	native	herbaceous
Cornus florida L.	flowering dogwood	native	tree
Carpinus caroliniana Walter	American hornbeam	native	tree
Conopholis americana (L.) Wallr.	American cancer-root	native	herbaceous
Corallorhiza maculata (Raf.) Raf.	summer coralroot	native	herbaceous
Crataegus L. spp.	hawthorn	unknown	tree
Desmodium glabellum (Michx.) DC.	Dillenius' ticktrefoil	native	herbaceous
Desmodium nudiflorum (L.) DC.	nakedflower ticktrefoil	native	herbaceous
Dioscorea quaternata J.F.Gmel.	fourleaf yam	native	herbaceous
Dioscorea villosa L.	wild yam	native	herbaceous

Appendix (continued). Species list from Rock Creek Park herbivory study plots, 2001-2014. List consists of 88 species and 7 genera not otherwise represented by species.

Scientific Name[1]	***Common Name***[1]	***Origin***[2]	***Form***[2]
Duchesnea indica (Andrews) Focke	Indian strawberry	non-native	herbaceous
Euonymus alatus (Thunb.) Siebold	burningbush	non-native	shrub
Euonymus americanus L.	bursting-heart	native	shrub
Euonymus fortunei (Turcz.) Hand.-Maz.	winter creeper	non-native	woody vine
Eurybia divaricata (L.) G.L.Nesom[6]	white wood aster	native	herbaceous
Fagus grandifolia Ehrh.	American beech	native	tree
Fraxinus americana L.	white ash	native	tree
Fraxinus pennsylvanica Marsh.	green ash	native	tree
Galium triflorum Michx.	fragrant bedstraw	native	herbaceous
Gaylussacia baccata (Michx.) K. Koch	black huckleberry	native	shrub
Geum canadense Jacq.	white avens	native	herbaceous
Glechoma hederacea L.	ground ivy	non-native	herbaceous
Hamamelis virginiana L.	American witchhazel	native	tree
Hedera helix L.	English ivy	non-native	woody vine
Humulus japonicus Siebold & Zucc.	Japanese hop	non-native	herbaceous
Huperzia lucidula (Michx.) Trevis[7]	shining clubmoss	native	herbaceous
Ilex laevigata (Pursh) A. Gray	smooth winterberry	native	shrub
Ilex verticillata (L.) A. Gray	common winterberry	native	shrub
Ilex opaca Aiton	American holly	native	tree
Impatiens L. spp.	touch-me-knot	native	herbaceous
Kalmia latifolia L.	mountain laurel	native	shrub
Lindera benzoin (L.) Blume	northern spicebush	native	shrub
Liriodendron tulipifera L.	tuliptree	native	tree
Lonicera fragrantissima Lindl. & Paxton	sweet breath of spring	non-native	shrub
Lonicera japonica Thunb.	Japanese honeysuckle	non-native	woody vine
Luzula echinata (Small) F.J.Herm.	hedgehog woodrush	native	herbaceous

Appendix (continued). Species list from Rock Creek Park herbivory study plots, 2001-2014. List consists of 88 species and 7 genera not otherwise represented by species.

Scientific Name[1]	***Common Name***[1]	***Origin***[2]	***Form***[2]
Maianthemum racemosum L. Link ssp. r*acemosum*[8]	feathery false lily of the valley	native	herbaceous
Malus Mill. spp.	Apple	unknown	tree
Medeola virginiana L.	Indian cucumber	native	herbaceous
Microstegium vimineum (Trin.) A. Camus	Japanese stiltgrass	non-native	herbaceous
Mitchella repens L.	partridgeberry	native	herbaceous
Nyssa sylvatica Marsh.	blackgum	native	tree
Osmorhiza longistylis (Torr.) DC.	longstyle sweetroot	native	herbaceous
Ostrya virginiana (Mill.) K. Koch	hophornbeam	native	tree
Parthenocissus quinquefolia (L.) Planch.	Virginia creeper	native	woody vine
Pinus L. spp.	Pine	native	tree
Podophyllum peltatum L.	mayapple	native	herbaceous
Polystichum acrostichoides (Michx.) Schott	Christmas fern	native	herbaceous
Polygonatum biflorum (Walter) Elliot	smooth Solomon's seal	native	herbaceous
Polygonum perfoliatum L.	Asiatic tearthumb	non-native	herbaceous
Prunus serotina Ehrh.	black cherry	native	tree
Quercus alba L.	white oak	native	tree
Quercus prinus L.	chestnut oak	native	tree
Quercus falcata Michx.	southern red oak	native	tree
Quercus rubra L.	northern red oak	native	tree
Quercus velutina Lam.	black oak	native	tree
Rhododendron periclymenoides (Michx.) Shinners	pink azalea	native	shrub
Rubus allegheniensis Porter	Allegheny blackberry	native	shrub
Rubus flagellaris Willd.	northern dewberry	native	shrub
Rubus phoenicolasius Maxim.	wine raspberry	non-native	shrub
Sanguinaria canadensis L.	bloodroot	native	herbaceous
Sanicula canadensis L.	Canadian blacksnakeroot	native	herbaceous
Sassafras albidum (Nutt.) Nees	sassafras	native	tree

Appendix (continued). Species list from Rock Creek Park herbivory study plots, 2001-2014. List consists of 88 species and 7 genera not otherwise represented by species.

Scientific Name[1]	***Common Name[1]***	***Origin[2]***	***Form[2]***
Smilax glauca Walter	cat greenbrier	native	woody vine
Smilax rotundifolia L.	roundleaf greenbrier	native	woody vine
Stellaria pubera Michx.	star chickweed	native	herbaceous
Toxicodendron radicans (L.) Kuntze	eastern poison ivy	native	woody vine
Ulmus americana L.	American elm	native	tree
Uvularia L. spp.	bellwort	native	herbaceous
Vaccinium pallidum Aiton	Blue Ridge blueberry	native	shrub
Viburnum acerifolium L.	mapleleaf viburnum	native	shrub
Viburnum dentatum L.	southern arrowwood	native	shrub
Viburnum dilatatum Thunb.	linden arrowwood	non-native	shrub
Viola L. spp.	Violet	unknown	herbaceous
Vitis aestivalis Michx.	summer grape	native	woody vine

[1] Nomenclature follows the US Department of Agriculture PLANTS database (USDA, NRCS 2015).

[2] Species classifications regarding origin and life form are based on classifications in the PLANTS database.

[3] *Cimicifuga racemosa* (L.) Nutt. synonym.

[4] *Carya alba* (L.) Nutt., nom. utique rej.

[5] *Circaea quadrisulcata* (Maxim.) Franch. & Savigny var. c*anadensis* (L.) H. Hara synonym.

[6] *Aster divaricatus* L. synonym.

[7] *Lycopodium lucidulum* Michx. synonym.

[8] *Smilacina racemosa* (L.) Desf. synonym.

NPS XXXXXX, Month Year (The Fort Collins Support Office will fill out this line for you)

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