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ABSTRACT

White-tailed deer (*Odocoileus virginianus*) impact the ecological integrity of eastern deciduous forests by modifying plant community composition and structure. Previous studies have shown that overabundant deer can negatively impact the recruitment and persistence of both woody and herbaceous plants. However, the strength and nature of these interactions can depend on habitat context. Forest edges provide favorable habitat for deer along with many introduced plant species, and have the potential to modify the nature of deer impacts. Here, we explore whether forest edges shape the impacts of deer on plant communities within the forest landscape. Specifically, we excluded deer, or, alternatively, allowed deer access, in plots along the edge and within the interior of two northern hardwood forests. Background deer abundance in these forests was approximately 6–12 individuals per km^2. After eight years of exclusion, we surveyed plant communities within plots to assess the impacts of deer on plant community composition across the forested landscape. We found that the impacts of deer were robust across habitat context within the forest, with relatively weak impacts on cover and richness of both native and introduced species. Edge habitat, on the other hand, had strong impacts on cover of both native and introduced species, as well as woody and herbaceous species, but the magnitude of these impacts was variable across the two forest sites. This work suggests that deer can have modest impacts when at relatively low densities, and that these effects can be consistent across forest habitat types, while forest fragmentation and subsequent generation of edge habitat can be an important driver of composition in the forest understory.

Index terms: deer; forest edge; herbivory; introduced species; plant community

INTRODUCTION

High densities of *Odocoileus virginianus* (white-tailed deer) can negatively impact the ecological integrity of eastern deciduous forests by altering plant community composition and productivity (Russell et al. 2001; Côté et al. 2004). Deer herbivory influences the plant community through preferential browsing of certain plant species, which can directly depress those species while indirectly affecting co-occurring species via habitat modification, seed dispersal, and food web interactions (Rooney and Waller 2003). Deer-driven decreases in native plant cover, and subsequent increases in bare ground, can favor the establishment of introduced species (Knight et al. 2009). However, while deer are often overabundant within many forests in North America, and research has suggested that overabundant deer can have myriad impacts on plant communities, deer do not always exist at such high abundances (Anderson and Katz 1993; Balgooyen and Waller 1995; Averill et al. 2018). That said, our understanding of the ecological impacts of deer at more moderate abundances (i.e., 2–4 deer/km^2), such as those mirroring levels likely prior to European settlement (Alverson et al. 1988), is more limited (Royo et al. 2010).

While many studies show that survival and growth of both herbaceous and woody plants are negatively affected by high levels of deer herbivory, more information about the context dependencies of these relationships is needed (Goetsch et al. 2011; Hurley et al. 2012). Proximity to forest edge, for example,

has the potential to modify the ecological impacts of deer. Habitat edges make up the area between adjacent ecosystems (e.g., between a closed forest canopy and open field habitat) and often contain microclimates and habitat characteristics that differ from the interior of either system (Chen et al. 1999). Forest edges typically have higher light levels, higher soil temperatures, lower humidity, less accumulation of leaf litter, and increased human and natural disturbance in comparison to the forest interior, contributing to differences in vegetation (Feeley 2004; Magnago et al. 2015; Valladares et al. 2016). In fragmented landscapes, deer are shown to be most active near forest edges, which coincides with greater dispersal of introduced plants that take advantage of the resources found in these areas (Guiden 2017). Additionally, the increase in edge habitat due to forest fragmentation has contributed to the overabundance of deer in eastern North America (Alverson et al. 1988).

Edge-tolerant plant species (which include a disproportionate number of introduced species) outcompete less tolerant (often native) species for resources found in exposed edges (McDonald and Urban 2006). Deer can further enhance introduced species while depressing native species through selective browsing, especially in forest edge habitats (Ruzicka et al. 2010; Kalisz et al. 2014; Averill et al. 2018; Gorchov et al. 2021). The propensity of deer to forage at different intensities across edge and interior habitats, and the influence of their selective browsing in plant communities across forest contexts, suggest that deer and edge have strong potential to interact to shape plant communities.

Here, we explore whether the impacts of deer on plant community composition are contingent on forest context. Specifically, we test whether the impacts of deer are more intense near the forest edge relative to the forest interior. To accomplish this, we compare abundance, richness, diversity, and composition within plant communities inside and outside of 8-year-old deer exclosures along the edge and within the interior of two northern hardwood forests.

METHODS

Study Site

Research was conducted in two mature second-growth hardwood forests—Firman Forest and Bole Woods—located at The Holden Arboretum (41.610048, −81.3156624) in Lake County, Ohio. Deer are managed on site through game hunting and culling, maintaining densities at 6–12 deer/km^2 across Holden's 3500-acre property over the course of this study. Aerial IR surveys from 2003, 2004, and 2008 show deer densities were on average ∼10.0 deer/km^2 in Firman Forest and 7.6 deer/km^2 in Bole Woods. The two forest sites are ∼1.9 km apart and dominated by mature beech-maple forest communities. Both forests border old fields with a hard edge maintained with annual mowing regimes. In the field adjacent to Firman's northern border, a horse pasture is separated from the forest edge by 30 m of mowed old field. Firman Forest exhibits greater topographic variation with elevation sloping down from the field. Bole Woods experiences human foot traffic as it is bisected by a hiking trail. Bole Woods is surrounded by Holden Arboretum property along three sides and a residential area on the fourth side, while Firman Forest is surrounded on three sides by a residential area and the Holden Arboretum on the fourth. Notably, all adjacent residential areas are low density and support a closed tree canopy. Understory plant communities differ slightly among the two sites. The most common woody plants in Bole Woods include *Acer saccharum*, *Parthenocissus quinquefolia*, and *Fagus grandifolia*, while the herbaceous layer is dominated by *Allium tricoccum*, *Polygonatum pubescens*, and *Podophyllum peltatum*. Common woody plants in Firman Forest include *Acer saccharum*, *Fraxinus americana*, *Lindera benzoin*, and *Carya cordiformis*, while common herbaceous plants are *Allium tricoccum* and *Cardamine concatenata*.

Field Methods

In 2005, we established forty-one 10 m × 10 m plots to test for interactive effects of deer herbivory and forest edge on understory plant communities. In a fully factorial design, each 10 m × 10 m plot either excluded deer or allowed access by deer within the forest interior or in forest edge habitat. Deer exclusion plots were fenced with 2.5 m high polypropylene mesh with 2.5 × 2.5 cm holes. This exclusion fencing eliminated deer access within 10 m × 10 m plots, while allowing access by small mammals and birds. Deer access plots were left unfenced and accessible to background deer densities. Edge plots were located within 25 m of forest edge while interior plots were 60–100 m from the forest edge. We chose these distances as edge effects are shown to occur 30–60 m from forest edge (Matlack 1993, 1994; Harper et al. 2005). Twenty-two of these plots were located in

Firman Forest (8 deer access – edge, 5 deer access – interior, 4 deer exclusion – edge, 5 deer exclusion – interior), and the remaining 19 plots were located in Bole Woods (4 deer access – edge, 5 deer access – interior, 5 deer exclusion – edge, 5 deer exclusion – interior).

Understory plant communities were surveyed in 2013, 8 y after plot establishment. In each 10 m × 10 m plot, we placed two transects oriented perpendicular to the forest edge with transects run in the interior of each plot. Transects were 3 m from plot's edge. Along each transect, plant cover was recorded within nine 0.25 m^2 frames spaced at 1 m intervals. Frames alternated orientation along the transect. Within the 0.25 m^2 frames, we visually estimated cover (0.5–100%) for each plant species present. To ensure our surveys captured both early- and late-season plants we surveyed in spring and again in late summer. Spring sampling was done in April–May and included spring ephemerals and herbaceous plants. Summer sampling was done in August–September and included herbaceous and woody species. Woody species were only included if they were less than 1 m in height.

Analysis

To accommodate seasonal variability in cover, the maximum cover estimate between spring and summer sampling periods was used for herbaceous species in all analyses. We then summed cover across all eighteen 0.25 m^2 frames in each 10 m × 10 m plot separately for each group: introduced species, native species, woody species, and herbaceous species. Species classifications are given in Supplemental Table S1.

Cover: The relationship between deer, forest edge, and plant cover was examined using general linear models (function *glm*). In eight separate models we tested the average plant cover for cumulative native, introduced, woody, and herbaceous species as a function of deer (Allowed vs. Excluded) and habitat type (Edge vs. Interior), for each group (introduced, native, woody, and herbaceous) in each site (Bole vs. Firman). Interactions were not significant, and therefore excluded from analysis. Given non-normality of the data, significance of individual factors within the models was determined using Wald chi-square tests (function *Anova*, package *car*; Fox and Weisberg 2019). Individuals identified to functional group (rather than species) were excluded from analyses of native and introduced species (83 of 2081 total individuals).

Richness: We explored the impacts of deer and habitat type on the richness of native and introduced species. We used Chao II richness (function *Chao2*, package *fossil*; Vavrek 2011) to calculate incidence-based estimates of species richness for each 10 × 10 m^2 plot. Chao II richness uses incidence-based data to estimate probable species richness accounting for both observed and undetected species (Chao et al. 2020). In four separate models, we analyzed the relationship between native and (separately) introduced richness in each forest site (Bole vs. Firman) as a function of deer (Allowed vs. Excluded) and habitat type (Edge vs. Interior) using general linear models (function *glm*) with site (Firman vs. Bole) included as a random effect. Significance of individual factors within the models was determined using Wald chi-square tests due to lack of normality of the data (function *Anova*, package *car*). There was no
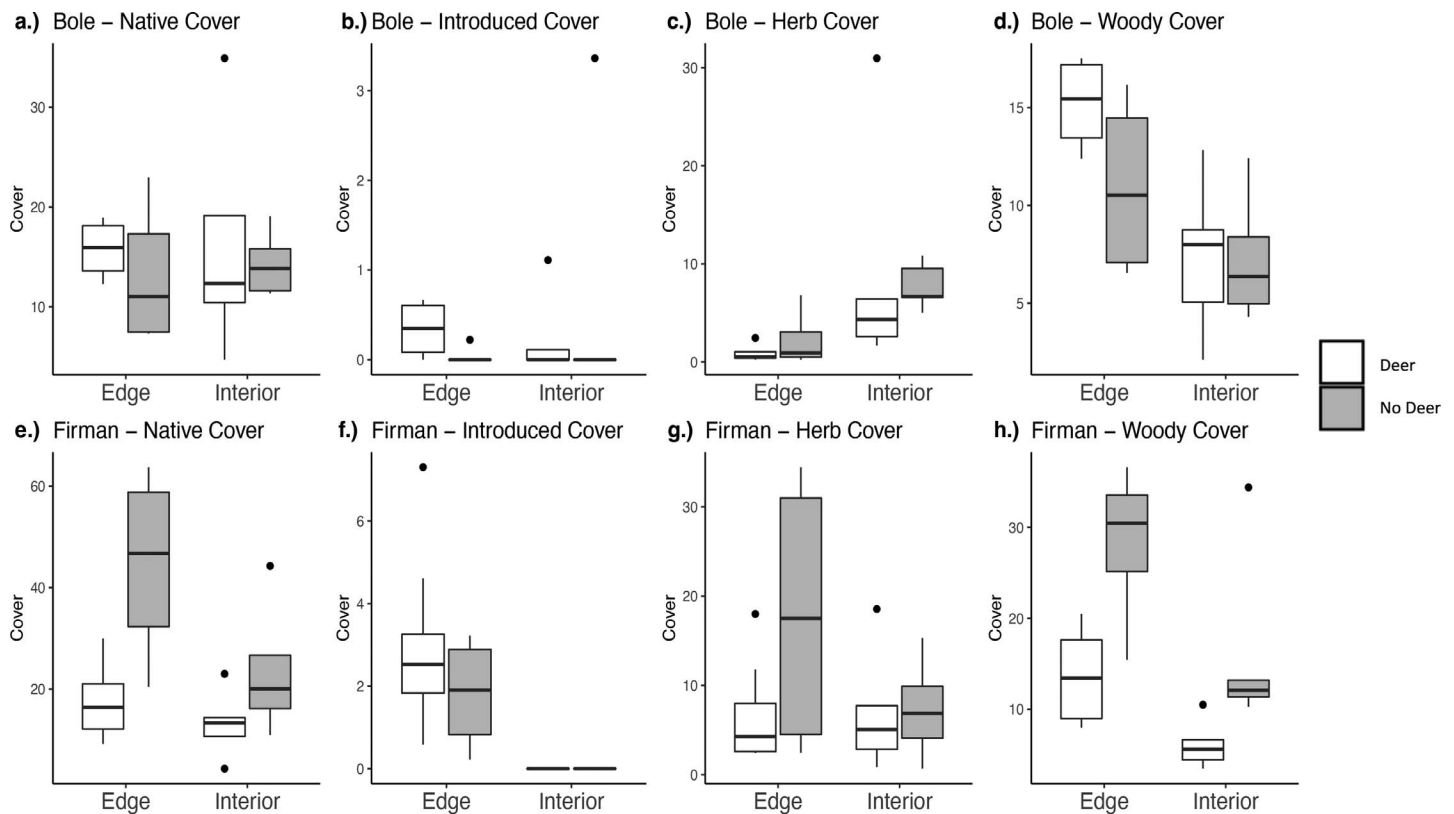
Figure 1.—Average vegetative cover as a function of deer access and forest edge after 8 y of deer exclusion for native, introduced, herbaceous, and woody species separated by each forest site.

significant interaction between deer and habitat type and so interaction terms were dropped from the models.

Composition: We assessed variation in community composition (package *vegan*; Oksanen et al. 2019) using a three-way permutational analysis of variance (PERMANOVA) based on a Bray-Curtis dissimilarity index of species abundance. Compositional differences were tested as a function of the interaction between deer (Allowed vs. Excluded) and habitat type (Edge vs. Interior), separately for each forest site (Bole vs. Firman). We used nonmetric multidimensional scaling (NMDS) to display community structure across treatments. All analyses were conducted in the statistical programming language R 1.3.1093.

RESULTS

We surveyed a total of 69 plant species across our 41 study plots. Of these, 61 species were present in deer accessible plots and 51 were present in deer exclusion plots. Forty-two species were common to both deer treatments (access and exclusion). Fifty-nine species were found in forest edge plots while 40 species were present in forest interior plots. Thirty species were common to both edge and interior plots.

Cover: We found both deer and edge habitat to be important drivers of vegetation cover, although these impacts varied across the two forests. In Bole Woods, average vegetative cover of native species was unaffected by both deer ($\chi^2 = 0.478$, $P = 0.489$; Figure 1a) and edge ($\chi^2 = 0.067$, $P = 0.796$; Figure 1a). Deer ($\chi^2 = 0.052$, $P = 0.819$; Figure 1b) and edge ($\chi^2 = 0.568$, $P = 0.451$;

Figure 1b) also did not impact introduced cover in Bole Woods. In Firman Forest, native cover was higher in areas where deer were excluded ($\chi^2 = 0.131$, $P < 0.001$; Figure 1e), as well as near the forest edge ($\chi^2 = 4.524$, $P = 0.033$; Figure 1e). Introduced cover in Firman, however, was unaffected by deer ($\chi^2 = 0.869$, $P = 0.351$; Figure 1f), but, as with native species, was higher near the forest edge compared to the interior ($\chi^2 = 15.721$, $P < 0.001$; Figure 1f). Notably, introduced species were a relatively small component of the plant community in Firman forest. In Bole Woods, deer did not impact herbaceous cover nor woody cover (herbaceous: $\chi^2 = 0.002$, $P = 0.965$; Figure 1c; woody: $\chi^2 = 1.404$, $P = 0.236$; Figure 1d), while edge habitat drove higher cover of both functional groups (herbaceous: $\chi^2 = 5.148$, $P = 0.023$; Figure 1c; woody: $\chi^2 = 10.861$, $P < 0.001$; Figure 1d). In Firman Forest, herbaceous cover was unaffected by deer ($\chi^2 = 2.391$, $P = 0.122$; Figure 1g) and edge ($\chi^2 = 1.181$, $P = 0.278$; Figure 1g), while woody cover was higher in the absence of deer ($\chi^2 = 17.171$, $P < 0.001$; Figure 1h) and near the forest edge ($\chi^2 = 10.01$, $P < 0.01$; Figure 1h).

Richness: Richness of both introduced and native species was unaffected by deer across both forests (native richness in Firman: $\chi^2 = 1.526$, $P = 0.217$; Figure 2a; introduced richness in Firman: $\chi^2 = 2.098$, $P = 0.146$; Figure 2b; native richness in Bole: $\chi^2 = 0.039$, $P = 0.843$; Figure 2c; introduced richness in Bole, $\chi^2 = 0.303$, $P = 0.582$; Figure 2d). Richness of native ($\chi^2 = 10.812$, $P < 0.01$; Figure 2a) and introduced ($\chi^2 = 95.943$, $P < 0.001$; Figure 2b) species was higher near the forest edge relative to the interior in Firman Forest, while neither native ($\chi^2 = 1.328$, $P = 0.250$;
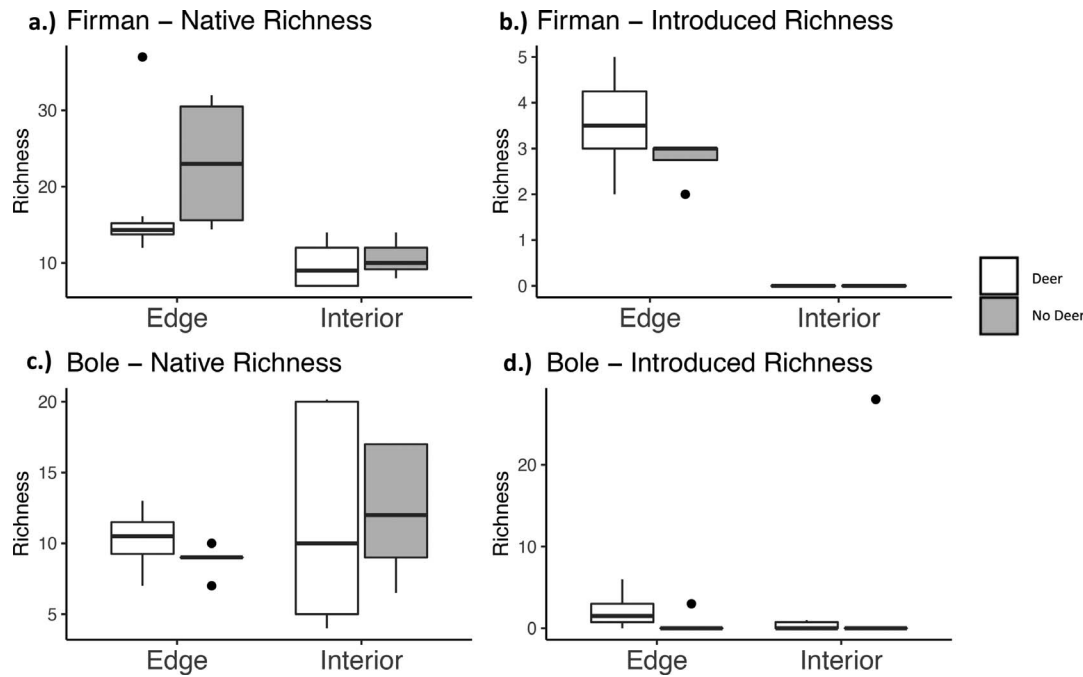
Figure 2.—Chao II richness of (a) native species in Firman, (b) introduced species in Firman, (c) native species in Bole, and (d) introduced species in Bole as a function of deer access and forest edge after 8 y of deer exclusion.

Figure 2c) nor introduced ($\chi^2 = 0.310$, $P = 0.577$; Figure 2d) richness was affected by edge habitat in Bole Woods.

Composition: Deer did not drive significant differences in community composition in Bole Woods ($F_{1,18} = 1.041$, $P = 0.381$; Figure 3) or Firman Forest ($F_{1,21} = 0.142$, $P = 0.147$; Figure 3b). Plant community composition differed significantly between edge and interior plots across the two forest sites (Bole: $F_{1,18} = 5.843$, $P < 0.001$; Firman: $F_{1,21} = 16.211$, $P < 0.001$). There was no interaction between deer and edge habitat, therefore this term was dropped from the model.

DISCUSSION

Following 8 y of exclusion, we found deer to have relatively modest impacts on the plant community. Further, these effects were robust across edge and interior habitats, with no strong interactions between deer and proximity to forest edge. However, context dependencies were clearly important in driving differences in the impacts of deer across the two study forests. Specifically, deer decreased both native and woody cover within Firman Forest, while having no impact on plant cover in Bole Woods. Deer did not have an effect on the cover of introduced or herbaceous species, nor did they impact species richness, within either forested site.

Edge habitat was a significant driver of plant community composition, simultaneously driving differences in cover of both native and introduced plants, as well as woody and herbaceous species. Edge also influenced the richness of both native and introduced species, but only in one of the two forests (Firman Forest), with higher richness of introduced species near the forest edge.

While deer and forest edge were both drivers of various aspects of plant community composition, counter to expectations, we did not observe the ecological impacts of deer to be contingent on proximity to edge. Nevertheless, this study made clear that the impacts of deer can be context dependent, as evidenced by differences in the magnitude of deer effects across the two study forests. This finding is similar to others who have found important context dependencies in the impacts of deer on forest communities (Royo et al. 2017). The slightly higher deer density in Firman Forest relative to Bole Woods may be one factor driving the more pronounced response to deer within Firman Forest. Both forests in this study were adjacent to annually mowed fields and, more distantly, low-density residential areas. However, in Firman Forest, this old-field habitat was relatively narrow with a horse pasture just beyond, while Bole Woods's adjacent old field was much more extensive. Bole Woods, however, was bisected by a walking trail that may serve as a corridor for invasive species establishing in the forest interior. Perhaps as a result of this hiking trail, or perhaps for other reasons, the abundance of introduced species was markedly higher in the interior of Bole Woods relative to Firman Forest. Further study in this and other systems will be critical in determining how nuanced differences within forested habitats drive responses to deer herbivory within the plant community (Habeck and Schultz 2015).

The relatively weak negative impacts of deer on all species contrasts with studies that show pronounced negative effects of overabundant deer on the abundance of native plants (Tilghman 1989; Anderson and Katz 1993; Habeck and Schultz 2015; Nishizawa et al. 2016). There are several mechanisms that could drive the limited impacts of deer observed in this study. First, inconsistencies in the effect of deer exclusion across forests could be related to local environmental contingencies such as habitat
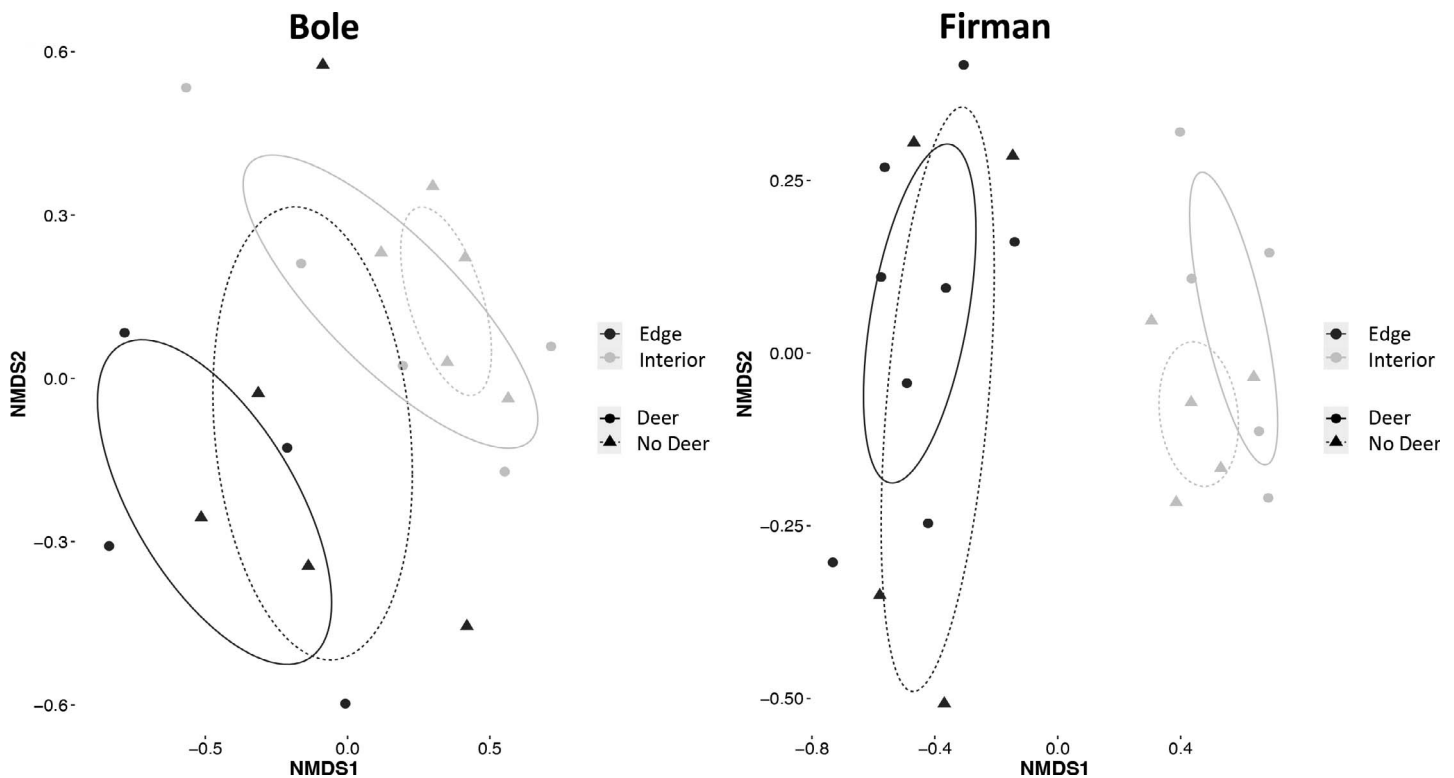
Bole

Firman

Figure 3.—Nonmetric multidimensional scaling (NMDS) plot representing community similarity for deer access and exclusion plots and edge and interior plots in (left) Bole Woods and (right) Firman Forest. Circles represent plots with deer access while triangles represent plots in which deer were excluded. Black represents plots near forest edges and gray represents plots within the forest interior. Ellipses represent 95% confidence limits, with dotted ellipses representing plots where deer were excluded and solid ellipses representing plots where deer were allowed to forage. Ordination stress across two dimensions is 0.22.

heterogeneity. Increased edge density and fragmentation of forest cover has been shown to decrease the home range of deer, potentially impacting the magnitude of their ecological impacts (Walters et al. 2016). A meta-analysis of exclosure studies throughout North America found that local environmental factors, such as deer density and time since exclusion, can also influence the direction and magnitude of plant responses to deer (Habeck and Schultz 2015). Habeck and Schultz (2015) found deer density and time since exclusion drive positive relationships with woody plant communities, although not herbaceous plant communities. Deer densities were 6–12 individuals per km^2 in the vicinity of our study site. This is at the low end of regional deer abundances, which can be anywhere from 4 to 107 individuals per km^2 (Averill et al. 2018). The relatively low deer browse pressure in our forests could have muted any impacts of deer that we might have observed across our manipulations. That said, deer have been found to negatively impact plant communities at densities of less than 8 individuals per km^2 and tend to scale with increasing densities (Horsley et al. 2009). Historically high levels of deer density are also known to create legacy effects, or long-term impacts that suppress regeneration of both woody and herbaceous species as long as 60 y after reducing deer pressure (Goetsch et al. 2011; Pendergast et al. 2015). Legacy effects of deer could be influencing plant communities within our plots, possibly depressing the magnitude of the impact of deer on these plant communities. Such legacy effects may operate through changes in plant community composition

established well before experimental exclusion. For example, plant palatability can interact with deer density to drive plant community structure and composition and, as a result, low deer impact may also be driven by deer-resistant species (Arcese et al. 2014). Past accumulation of deer-resistant species in these forests could further limit responses to recent deer exclosure.

We found forest edge habitat to be an important driver of the plant community. Edge effects are known to promote the diversity and cover of forest vegetation (Fraver 1994; Marchand and Houle 2006; Alignier et al. 2014) as abiotic differences between the interior and edge of forests can drive variation in plant community composition. However, the specific nature of the habitat adjacent to the forest edge can mediate the extent of edge effects (Magnago et al. 2015). Introduced species, for example, thrive in these edge habitats, posing a threat to native species (Yates et al. 2004). We found both higher cover and richness of introduced species in edge habitat in Firman Forest, but no effects in Bole. Native cover, too, was higher in edge habitat, although only in one of our two study forests. Abiotic differences between the interior and edge of forests can drive differences in plant community composition between these two habitat types; although, importantly, the specific edge type or habitat adjacent to the forest edge can mediate the magnitude of edge effects (Magnago et al. 2015). It is evident that nuanced differences among the forests themselves can also play an important role in structuring the impact of edge on forest communities.

We found plant community composition to be sensitive to both deer and edge habitat. However, treatment effects on richness and cumulative plant cover by functional and origin (native vs. introduced) groupings were much more responsive to edge habitat than to deer exclusion. Further, we found the impacts of deer to be relatively robust across habitat context— within the forest interior and along the forest edge. As important drivers of ecosystem structure, added research detailing the long-term and interactive effects of forest edge and deer is needed to fully understand how these dynamics influence compositional changes to the forest landscape.

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Alexa Wagner is a PhD Candidate at Case Western Reserve University and the Holden Arboretum. For the past five years, she has studied the impacts of temperate forest management on understory plant demographics and species interactions with the goal of conveying this information to landowners and restoration practitioners.

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Mike Watson is the Conservation Biologist at Holden Forests and Gardens. Based at the Holden Arboretum in northeast Ohio, Mike has spent more than 15 years working on conservation monitoring and management projects, including a long-term deer study focused on the impacts of deer browse in forested systems.

David Burke is a research scientist and Vice President for Science and Conservation at Holden Forests and Gardens, which includes the Holden Arboretum and Cleveland Botanical Garden. His research focuses on the outcome of human disturbance on plant communities with a special focus on the interaction between plants and microorganisms.

Katharine Stuble is a community ecologist at the Holden Arboretum in northeastern Ohio. For the past six years, she and her team have been exploring how species interactions shape forested ecosystems, and how this knowledge can be used to inform best practices in restoration.

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