14 Years of Deer Browsing Shapes a Mesic Forest Understory in Southwestern CT

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Large herbivores are inseparable from – and often shape – the ecosystems in which they occur. In parts of East Africa, vegetation has shifted from woodland to grassland depending, in large part, on the density of elephants (Laws 1970). Similarly, at the end of the last ice age, large mammal extinctions are believed to have changed the vast mammoth steppe grassland into a mossy tundra (Zimov 2005).

In eastern temperate forests like those in Connecticut, large herbivores have comparatively minor effects on their habitat – white-tailed deer don't convert forests to savannahs or shrublands – but their effects on forest understories are still notable. An abundance of unpalatable plants, few tree seedlings, and noticeable browse lines are often characteristic of forests in parts of the state where deer are most abundant. The effect of deer herbivory on forest understories has consequently garnered much attention among land managers, ecologists, and botanists in recent decades (Waller and Alverson 1997, Rawinski 2008); however, surprisingly few studies have directly examined the effects of deer on herbaceous and overall plant diversity.

In 1998, Highstead, an ecological research and conservation center in southwestern CT, built a 1 acre deer exclosure in its mesic red maple-white ash forest as a demonstration experiment. Approximately half the fenced and adjacent unfenced area is on poorly drained soils vegetated with trees ~50 years old, while the other half occurs on moderately well drained soils with larger trees ~90 years old. Between 1998 and 2012, Highstead's forest supported deer densities estimated to be between 24 and 38 km^{-2} (60-100 $mile^{-2}$; Kilpatrick 2009 and personal observations of Highstead staff).

In 2012, we established a grid of 25 subplots in each of the soil type/forest age environments in both fenced and unfenced areas to assess plant diversity and density. Paired (fenced/unfenced) sampling grids in the young forest were approximately 75 meters apart from sampling grids in the old forest. With the help of consulting botanical expert, Bill Moorhead, we sampled woody and herbaceous plants in each of the two fenced and unfenced areas. Although in strict scientific terms these plots are all part of one exclosure and do not constitute two distinct sampling areas, for practical purposes they are far enough apart and occur in different enough sites to be considered two separate plots.

Results

Fourteen years of deer exclusion has revealed a dramatic change in the vertical structure of the forest understory. In unfenced plots, upright woody plants were predominantly below 0.5 meters in height, and the density of stems between 0.5 and 2 meters was reduced by a factor of seven (Fig. 1). The sprawling, invasive, and unpalatable *Berberis thunbergii* dominated the 0.5-2 meter height range and was two to three times more abundant in the unfenced plots than in the fenced plots (Fig. 2). Interestingly, *Fraxinus americana* seedlings grew almost exclusively among clumps of *Berberis*, an example of "associational resistance", whereby a palatable tree receives protection from herbivory by growing near an unpalatable and often thorny neighbor (Vera et al. 2006).

In contrast to the unfenced plots, the fenced plots were characterized by a relatively thick and vertically well-distributed woody plant layer dominated by *Lindera benzoin* (43% of stems) and the invasive *Euonymus alatus* (26% of stems; Figs. 1 and 2). No *E. alatus* stems grew above 0.5 meters in the unfenced plots. Hence, one dominant invasive shrub (*B. thunbergii*) was promoted by deer browsing, while a second dominant invasive (*E. alatus*) was promoted by deer exclusion.

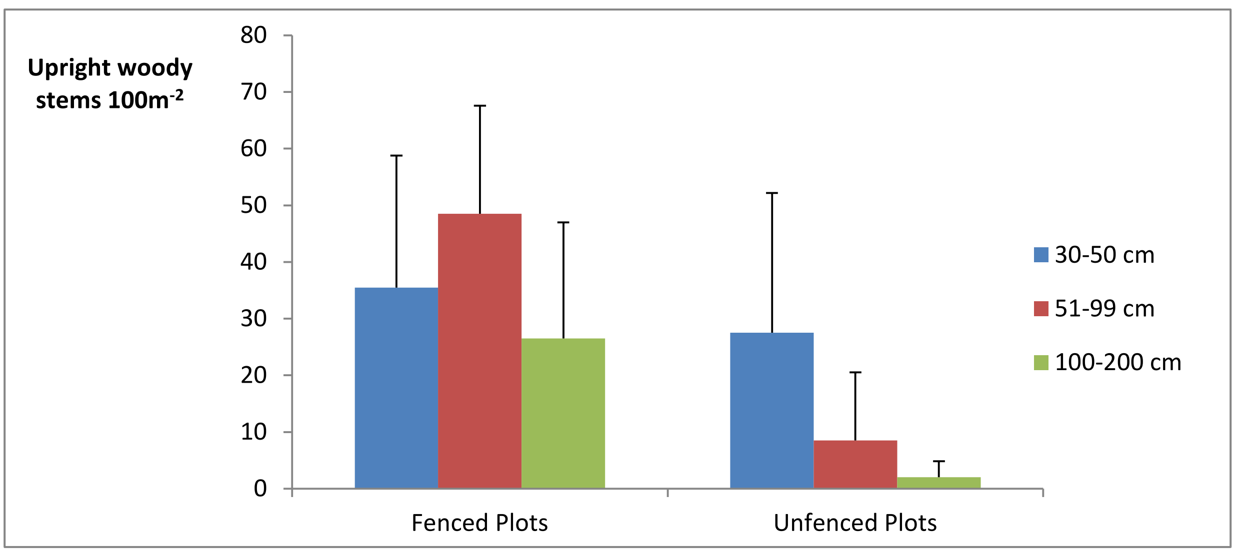

Figure 1. The response of three size classes of upright woody plants to deer herbivory after 14 years in Highstead's red maple-white ash forest

Native tree regeneration was more prolific inside the exclosure than outside by a factor of four, demonstrating the ability of deer to reduce tree seedlings under an intact forest canopy (Gill 2006). After 14 years of protection from deer, the average height of tree seedlings inside the fence (49.5 cm) was surprisingly similar to the average height outside the fence (41 cm). Although free from herbivory, tree seedlings inside the fence were exposed to greater competition and shade from the thick shrub layer, which apparently suppressed their height growth almost as much as herbivory.

Figure 2. Unfenced plot (left) and fenced plot (right) in young red maple-white ash forest. Note the abundance of *Berberis thunbergii* in the unfenced plot and the more developed tall shrub layer and pink foliage of *Euonymus alatus* in the fenced plot.

The shrub layer inside the exclosures appeared to limit native forb composition as well. The density of native forb species was similar inside the fence (1.8 species m^{-2}) to outside the fence (1.9 species m^{-2}), although the forbs exposed to deer were much smaller in size than those protected from deer. Inside the fence, the forb layer was dominated by species characteristic of undisturbed woods such as *Impatiens capensis*, *Circaea canadensis*, and *Arisaema triphyllum,* whereas the unfenced plots were dominated by species characteristic of disturbed habitats such as *Persicaria sagittata*, *Maianthemum canadense*, and *Viola sororia* (New England Wildflower Society 2013). *M. canadense*, a purported browse sensitive indicator species (Rooney 2001), occurred more than three times as frequently outside the fence as inside.

Overall, the browsed plots trended toward higher species diversity (8.7 species m^{-2}) than the fenced plots (6.4 species m^{-2}; Fig. 3), with an increase in graminoid species contributing to much of the difference. By trampling and browsing woody plants, large herbivores can increase germination sites, reduce plant competition, and allow more light to reach the forest floor, frequently promoting plant diversity in relatively nutrient-rich sites (like our maple-ash forest); in nutrient poor sites, herbivores are more apt to maintain or reduce diversity (Hester et al. 2006). Deer are also prolific seed dispersers via their dung and fur (Williams and Ward 2008) and undoubtedly transported seeds into these unfenced plots.

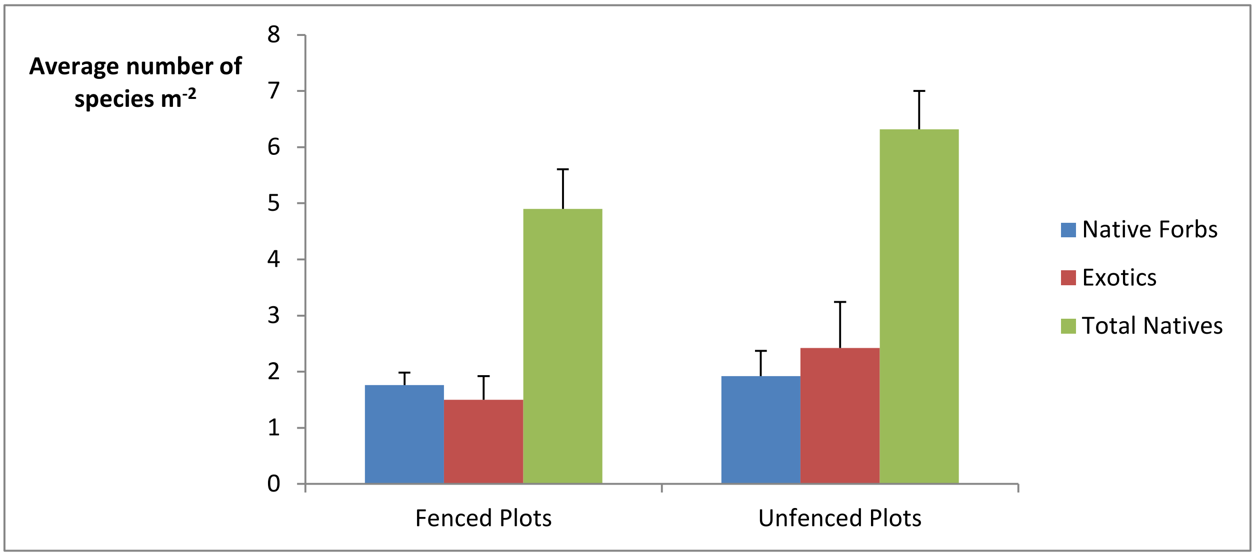

Figure 3. The response of plant diversity to deer herbivory after 14 years in Highstead's red maple-white ash forest

The trend toward greater diversity in the unfenced plots was true for both native and exotic species (Fig. 3), which runs counter to the assumption that promotion of exotic species by deer invariably leads to a decline in natives. In fact, the conditions that promote exotic species frequently promote native plants as well (Gilbert and Lechowicz 2005).

Concluding Thoughts

The results from this long-term deer exclosure experiment at Highstead show that deer-forest interactions, like most ecological phenomena, are more complex than many people realize. Our results also highlight the resilience of Connecticut's forests to disturbance, whether it is wind and ice storms, insect outbreaks, or deer herbivory. As such, our data exemplify the importance of using long-term monitoring and data collection rather than anecdote to explain the ever changing dynamics in our forests. We will continue to monitor vegetation structure, composition, and
diversity at this exclosure experiment every five years into the future.

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