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Over-browsing in Pennsylvania creates a depauperate forest dominated by an understory tree: Results from a 60-year-old deer exclosure

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Kain, M. (Department of Biological Sciences, University of Pittsburgh, A234 Langley Hall, Pittsburgh, PA 15260), L. Battaglia (Department of Plant Biology, University of Southern Illinois Carbondale, 0411 Life Science II, Carbondale, IL 62901), A. A. Royo (USDA Forest Service, Northern Research Station, Forestry Sciences Lab, P.O. Box 267, Irvine, PA 16329-0267), and W. P. Carson (Department of Biological Sciences, University of Pittsburgh, A234 Langley Hall, Pittsburgh, PA 15260). Over-browsing in Pennsylvania creates a low density, depauperate forest dominated by an understory tree: results from a 60-year-old deer exclosure. J. Torrey Bot. Soc. 138: 322–326. 2011.—We evaluated the impact of long-term over-browsing by white-tailed deer on the diversity and density of trees in a forest in the Allegheny High Plateau region of central Pennsylvania. We compared tree diversity and density inside a 60 year-old deer exclosure to an adjacent reference site. Browsing caused a 55–100% decline in density of four tree species (*Prunus serotina*, *Acer saccharum, Betula lenta, Cornus alternifolia*) and created a forest dominated ($>$ 70% of all stems) by *Acer pensylvanicum*, an understory tree that is known to be highly browse-tolerant. The total density of trees that are capable of ascending into the canopy (i.e., non subcanopy tree species) declined by 85%. Browsing caused a significant decline in both mean species richness and Shannon diversity and created communities that contrasted significantly in tree species composition (ANOSIM, $R = 0.8105$, $P < 0.0001$). Our results suggest that long-term over-browsing can create low density, depauperate communities where dominance is concentrated in only a few browse-resistant species (*Acer pensylvanicum* and *Fagus grandifolia*; 82% of all individuals vs. 37% inside the exclosure). We suggest that this may lead to novel forest dynamics in the event of a large canopy disturbance because these two species were never co-dominant in this region and the beech saplings (typically root sprouts) will likely succumb to future bouts of beech bark disease. Our results combined with those of many other studies call for the long-term reduction in the size of the deer herd throughout this region.

Key words: *Acer pensylvanicum*, *Cornus alternifolia*, *Fagus grandfolia*, over browsing, white-tailed deer.

White-tailed deer (*Odocoileus virginianus*) have been overabundant throughout much of the Eastern Deciduous Forest since the 1930s (Horsley et al. 2003, Quality Deer Management Association 2011). Recent estimates indicate populations exceed 12 deer km^{-2} in more than half of the counties east of the Mississippi river (Quality Deer Management Association 2011). Over-browsing is often responsible for dramatic declines in the diversity and abundance of woody species (Rooney 2001, Russell et al. 2001, Côté et al. 2004). In addition, deer also change key growth and mortality relationships, which are often used to parameterize forest simulation models that predict future canopy composition (Long et al. 2007, Krueger et al. 2009).

Because white-tailed deer are often overabundant over vast regions, it can be difficult to fully gauge their impact because areas where deer are closer to historic levels are uncommon. One way to circumvent this difficulty is to find areas that serve as refugia from deer. For example, Banta et al. (2005) found that tree species richness and density in the Allegheny National Forest of Pennsylva-

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nia were much higher on the tops of large boulders that precluded deer access. A number of refugia have now been identified (e.g., treefall tip-up mounds, slash piles, areas around highly unpalatable species, and deer-free islands) and all confirm that numerous species are vulnerable to browsing and are far more abundant within these refugia (Grisez 1960, Long et al. 1998, Borgmann et al. 1999, Banta et al. 2005, Comisky et al. 2005, Stockton et al. 2005, Krueger and Peterson 2006). An alternative approach to evaluate the long-term impacts of over-browsing is to exclude deer by erecting fences but maintaining these fences for long periods is logistically difficult and thus there are few deer exclosures older than 25 years. Here we evaluate the long-term impact of deer browsing by quantifying the density, diversity, and composition of trees inside a 60-year old deer exclosure versus that of an adjacent reference site. To our knowledge, this is the oldest deer exclosure in the eastern US.

Methods. We conducted our study in north-central Pennsylvania on State Game Lands #30 (41°, 38′ N, 78°,19′ W) which lies within the Allegheny High Plateau region and is part of the Hemlock-Northern Hardwood Association (Whitney 1990). This region receives an average of 106.7 cm of precipitation a year and has an annual mean temperature of 7.8° C (Whitney 1990). For the past few decades deer densities in this area have ranged from 10–15 deer km^{-2}. However, deer densities were much higher from 1950–1980 (McCain 1939, Horsley et al. 2003). The region is characterized by second and third-growth hardwood forests with the predominant tree species being black cherry (*Prunus serotina* Ehrh.), sugar maple (*Acer saccharum* Marshall), red maple (*Acer rubrum* L.), American beech (*Fagus grandifolia* Ehrh.), and birch (*Betula* spp.) (Sundquist et al. 1990, nomenclature follows USDA, NRCS. 2010). For further information on the region and its climate see Hough and Forbes (1943) and Bjorkbom and Larson (1977).

The exclosure (0.4 ha), which excludes deer but is large enough to allow smaller vertebrates through (e.g., woodchucks, *Marmota monax* L.), was constructed in the late 1940s by Roger Latham and Stanley Forbes (Stout 1998; J. Dzemyan pers. comm.) and has been maintained thereafter by the Pennsylvania Game Commission (for other studies developed using this exclosure see Goetsch et al. In Press, and Kirschbaum 2005). We censused all trees (> 2.0 cm DBH) in seven randomly placed 10 × 30 m plots stratified throughout the exclosure and an adjacent reference site in May 2010. This site is a second-growth forest that was logged in the early 1940s prior to the building of the exclosure (J. Dzemyan pers. comm.). A 5 m buffer area adjacent to the fence was not sampled to avoid edge effects. The fence was not replicated and we used subpots ($n = 7$) as replicates (pseudoreplicates *sensu* Hurlbert 1984); thus, our results should be interpreted with caution. We used t-tests to compare species abundances between the exclosure and control and calculated species richness and also diversity using the Shannon-Wiener index. All univariate statistical tests were conducted using SAS version 9.1 (2004). When necessary, we used the Satterthwaite method to account for unequal variances (Satterthwaite 1946).

We used non-metric multidimensional scaling (NMDS) to examine patterns of community composition in the reference site and exclosure. NMDS is highly effective for ordination of community data (Minchin 1987). Dissimilarities based on density data were calculated using the Bray-Curtis index (Bray and Curtis 1957), which is recommended for community ordination (Faith et al. 1987). We performed NMDS in one to six dimensions, in each case using 100 random initial configurations. We used Analysis of Similarities (ANOSIM) (Clarke 1993) to test whether there were statistically significant differences in composition between the two sites. All multivariate analyses were performed using the DECODA package (Minchin 1989).

Results. Chronic deer browsing significantly reduced total tree species richness and species diversity (Table 1). The density of larger trees (> 25 cm DBH, either total or for individual species) did not differ statistically between the exclosure versus the reference site (density in exclosure = 626.7 ± 39.0, density in reference site 466.7 ± 17.2; t-test, $P = 0.193$). Although the total density of all species > 2.0 cm DBH did not differ between the two sites, when the density of the two subcanopy species, striped maple (*Acer pensylvanicum*) and dogwood (*Cornus alternifolia*) was excluded, total density of tree species that reach canopy size was nearly three times higher inside the exclosure

Table 1. Species richness, Shannon diversity and density (per hectare) of trees (stems > 2 cm DBH) in the exclosure and adjacent reference site ($n = 7$). *Acer Pensylvanicum* and *Cornus alternifolia* were excluded in one comparison because these are both subcanopy tree species.

Species	Exclosure (se)	Reference (se)	*P*
Acer pensylvanicum L.	128.57 (51.65)	752.38 (140.46)	0.0018
Acer rubrum L.	42.86 (18.85)	14.29 (9.91)	0.106
Acer saccharum Marsh.	152.38 (32.48)	57.14 (9.52)	0.013
Betula lenta L.	66.67 (29.1)	0	0.031
Betula nigra L.	19.05 (12.3)	0	0.086
Cornus alternifolia L.f.	252.38 (88.45)	0	0.016
Fagus grandifolia Ehrh.	309.52 (105.34)	104.76 (61.9)	0.063
Fraxinus americana L.	0	9.52 (6.15)	0.086
Magnolia acuminata (L.) L.	4.76 (4.76)	0	0.178
Prunus serotina Ehrh.	214.29 (40.41)	95.24 (22.34)	0.020
Total Tree Density	1190.48 (127.18)	1033.33 (154.65)	0.242
Total Tree Density minus A*cer pensylvanicum* and *Cornus alternifolia*	809.52 (122.09)	280.95 (71.96)	0.017
Total number of species per site	9	6	
Mean number of species per plot	6.43 (.30)	3.86 (.34)	0.0002
Shannon Diversity Index	1.62 (.13)	.75 (.11)	0.0001

(Table 1). The density of sugar maple, dogwood, black cherry and yellow sweet birch (*Betula lenta* L.) were each significantly higher inside the exclosure. The density of striped maple was more than 5 times higher *outside* the exclosure.

A two-dimensional NMDS ordination solution (stress = 0.101) was accepted as an adequate summary of the community composition of the plots, based on species specific relative tree density (Figure 1). The ordination revealed clear differences in community composition and the ANOSIM confirmed that the species composition differed significantly between the two sites ($R = 0.8105$, $P < 0.0001$).

Discussion. After 60 years, chronic overbrowsing led to the formation of a low density, depauperate forest stand dominated by an understory tree, striped maple (Table 1). These types of impoverished stands are common in the region and also contain depauperate herbaceous and shrub layers (Comisky et al. 2005, Banta et al. 2005, Royo and Carson 2006, Royo et al. 2010, Goetsch et al. in press). It is important to point out however, that when deer herd sizes are much smaller and more similar to levels thought to have occurred prior to European colonization, deer browsing can promote diversity by reducing the dominance of dense shrub layers (Royo et al. 2010).

Overall, our results confirm many previous studies that over-browsing can create low-density, depauperate stands (Rooney 2001, Russell et al. 2001, Horsley et al. 2003, Côte et al. 2004). Our results go one step further because they suggest that in this region long-term over-browsing is particularly deleterious because it creates stands dominated by striped maple, with American beech the second most abundant species (Table 1). This trend has significant ramifications for forest dynamics of the region. Beech bark disease complex has killed the vast majority of adult beech in this region (Runkle 2007). Indeed, no adult beech trees (> 30 cm DBH) were found either inside or outside the exclosure though smaller individuals were abundant (Table 1). As beech saplings reach larger size classes, they become vulnerable to the disease complex (Houston 1994). Additionally, beech saplings in this region are typically root sprouts arising from formerly healthy tall individuals (Jones and Raynal 1996). Because these root sprouts are clonally identical to their parents any potential for resistant populations of beech to develop as saplings is dramatically reduced. Although speculative, we suggest that if a large canopy disturbance occurred in such a depauperate site, it would create novel forest dynamics because the advance regeneration layer capable of regenerating after a disturbance would be dominated by beech root sprouts and an understory tree, striped maple. Thus, forest regeneration would be controlled by the degree that the advance regeneration layer is browse or disease tolerant and less so by shade tolerance (Long et al. 2007, Krueger et al. 2009).

Both striped maple and beech were able to persist in the understory in spite of decades of

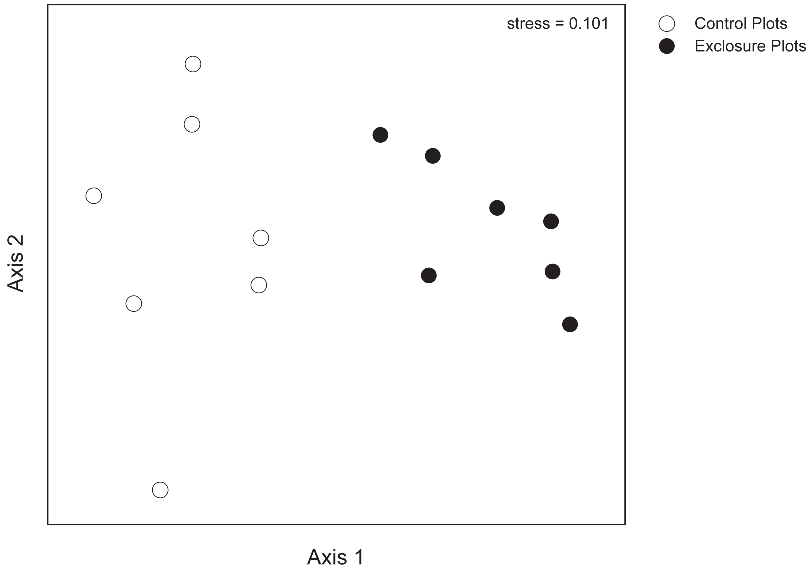

FIG. 1. Two-dimensional ordination (non-metric multidimensional scaling) comparing the community composition of the control plots vs. the exclosure plots ($n = 7$). The placement of white circles (control plots) and black circles (exclosure plots) reflects the similarity of communities. Stress indicates the badness-of-fit in rank order between the original Bray-Curtis dissimilarities and the distance in the ordination.

heavy browsing. Thus not only are these two species shade-tolerant (Hewitt 1998, Humbert et al. 2007) they are also browse-tolerant (Liang and Seagle 2002, Horsley et al. 2003). The mechanism of browse tolerance appears to be different for the two species. We suggest that striped maple is browse tolerant because its stems are photosynthetic and thus even severe defoliation by browsers leaves the tree with photosynthetic tissue (Cullina 2002). Small beech saplings that remain clonally integrated to larger individuals that have reached a size refuge from deer may continue to receive carbon from below ground connections (Jones and Raynal 1986) and thus may persist in the face of heavy defoliation. These contrasting mechanisms remain to be verified via experimental studies. Overall, we argue that persistence in forest understories where deer are over-abundant requires that species have two key traits: high shade tolerance and high browse tolerance. Although hemlock is highly shade-tolerant, it is not browse-tolerant and thus saplings have become uncommon in this region (Hough 1965) or are forced into refugia (Long et al. 1998). Overall, our findings call for a long-term (> 10 yr) reduction in the size of the deer population in this region and other parts of Pennsylvania. Indeed, the legacy of over-browsing has recently been show to cascade back up though trophic levels thereby reducing both insect and avian densities (Nuttle et al. 2011).

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