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Chronic over browsing and biodiversity collapse in a forest understory in Pennsylvania: Results from a 60 year-old deer exclusion plot

Chandra Goetsch and Jennifer Wigg

Department of Biological Sciences, University of Pittsburgh, A234 Langley Hall, Pittsburgh, PA 15260

Alejandro A. Royo and Todd Ristau

USDA Forest Service Northern Research Station, Forestry Sciences Lab, P.O. Box 267, Irvine, PA 16329-0267

Walter P. Carson[1]

Department of Biological Sciences, University of Pittsburgh, A234 Langley Hall, Pittsburgh, PA 15260

GOETSCH, C., J. WIGG (Department of Biological Sciences, University of Pittsburgh, A234 Langley Hall, Pittsburgh, PA 15260), A. A. ROYO, T. RISTAU (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, Pittsburgh, PA 15260). Chronic over browsing and biodiversity collapse in a forest understory in Pennsylvania: results from a 60-year-old deer exclusion plot. J Torrey Bot. Soc. 138: 220–224. 2011.—We evaluated the impact of chronic deer over browsing on the diversity and abundance of understory forbs and shrubs within a forest stand in the Allegheny High Plateau Region of Pennsylvania by comparing vegetation inside a 60-year-old exclosure to vegetation within an adjacent reference site. This is the oldest known exclosure in the Eastern Deciduous Forest. Browsing caused the formation of an extremely low diversity herbaceous understory dominated by a single fern species, caused the local extirpation of shrubs, and drove forbs to extremely low abundance ($< 0.2\%$ cover m^{-2} vs. 43% inside the exclosure). Our results confirm previous findings that demonstrate that browsing has caused 60–80% declines in herb and shrub richness regionally. Because many of these species have low dispersal and reproductive rates, we predict long-term legacy effects if deer numbers are ever reduced. Our results combined with other studies provide information on shrub and herb abundance in the absence of browsing that may serve as a baseline to compare potential community recovery in the future.

Key words: biodiversity, herbivory, herbs, over browsing, white-tailed deer.

Over browsing by white-tailed deer (*Odocoileus virginianus*, Boddaert) has caused major changes in plant species composition and dramatically reduced diversity across broad regions within Eastern Deciduous Forest in Pennsylvania and elsewhere (Rooney 2001, Russell et al. 2001, Horsley et al. 2003, Côte et al. 2004). For example, over browsing was apparently responsible for dramatic declines in herbaceous species richness (59 and 80%) between 1929–1995 in two hemlock dominated old-growth stands in north central PA (Rooney and Dress 1997). Understory shrubs and herbs are particularly vulnerable to over browsing because they seldom reach a size refuge (Miller et al 1992, Anderson 1994, Augustine and Frelich 1998, Singleton et al 2001) and many herbs have short dispersal distances, limited reproduction and growth, and long generation times (e.g., Beattie and Culver 1981, Bierzychudek 1982, Matlack 1994, Ruhren and Handel 2003). Once locally extirpated they may be very slow to recolonize former habitat (Flinn and Velland 2005) and consequently understory herbs are prone to legacy effects where over browsing leads to low diversity herb and shrub communities that remain depauperate even if ungulate populations are brought under control (Banta et al. 2005, Webster et al. 2005, de la Cretaz and Kelty 1999).

It is difficult to fully gauge the impacts of chronic over browsing because it has typically occurred for decades across entire states and physiographic provinces (Rooney 2001, Côte et al. 2004) potentially causing widespread legacy effects. One way to circumvent this problem is to find natural refugia from deer (e.g., surfaces of large boulders $>$ 2m) and compare vegetation or performance of species on these refugia to surrounding areas (Grisez 1960, Rooney 1997, Long et al. 1998, Borgmann, 1999, Comisky 2005, Banta et al. 2005, Stockton et al. 2005, Krueger and Peterson 2006). These studies demonstrate that browsing has created depauperate communities

[1] Author for correspondence: E-mail: walt@pitt.edu

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dominated by a few unpalatable species compared to these natural refugia, some of which have been termed "Rock Refugia Gardens" (Comisky et al. 2005). A critique of this approach is that these refugia may support high species diversity for reasons other than browsing (Banta et al. 2005). For example, large tree tip-up mounds provide newly disturbed soil in addition to being refugia from deer. Another approach is to maintain fenced exclosures for long periods but because of logistical challenges few have remained intact for periods > 20 years. Consequently, we have few true reference areas that might reveal what understories might look like if not overbrowsed for decades.

Here we compare the diversity, species richness, and abundance of herbs and shrubs inside a 60 year old fenced exclosure with that of an unfenced adjacent site in north central Pennsylvania. To our knowledge, this is the oldest permanently maintained deer exclosure in the eastern US. As such it provides a unique window into the impact of more than a half century of overbrowsing.

Methods. STUDY SITE. We conducted our study in north central Pennsylvania on Game Lands #30 in southeastern McKean County (41°38′N, 78°19′W) within the Allegheny High Plateau Region. The region (as well as our specific site, Kain et al. unpublished manuscript) is part of the Hemlock-Northern Hardwoods Association (Whitney 1990) and is now composed of second and third growth hardwood forest dominated by black cherry (*Prunus serotina* Ehrh.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and birch (*Betula* L. spp.; nomenclature follows USDA, NRCS. 2010). The region has a cool, humid climate with an average annual temperature of 7.8 °C and receives an average of 106.7 cm of precipitation per year. The elevation ranges from 457–597 m above sea level. Further descriptions of the flora, climate, and geology can be found in Hough and Forbes (1943) and Bjorkbom and Larson (1977). Deer have been overabundant in the area since the 1930s (Rooney and Dress 1997, Horsley et al. 2003) and densities have ranged between 10–15 deer km^{-2} for the past few decades but were typically higher from 1950 through the 1980s (Horsley et al 2003).

We compared the understory vegetation within a fenced deer exclosure (0.4 ha) to that of an adjacent unfenced reference site of the same size. Both sites were well developed 60–80 year old second growth closed canopy forests with similar tree species composition and no signs of recent large-scale disturbances. The exclosure (often called the Latham Plot) was erected by Roger Latham circa 1940 (Stout 1998) and has been regularly maintained ever since by the Pennsylvania Game Commission. The mesh size of the fence excludes deer but is large enough to allow smaller mammals to pass through (e.g., woodchucks, *Marmota monax* L.).

SAMPLING DESIGN AND VEGETATION ANALYSIS. We arrayed 29, 1 m^2 plots randomly throughout each site in a stratified fashion. All plots were at least 8 m apart and located at least 2 m from the fence to minimize edge effects. We visually estimated the percent cover of all herbs and shrubs in each plot on May 17, 2007. We also measured the height and flowering percentage for two indicator species, *Trillium erectum* L. and *Medeola virginiana* L. (e.g., Kirshbaum and Anacker 2005). We haphazardly selected 30 individuals by walking throughout each site and pointing a meter stick to the ground while looking away. We then selected the individual nearest the tip of the meter stick (Carson and Root 2000). Finally, we performed a meander survey (Goff et al. 1982) by walking throughout each site for 30 minutes to identify species that did not occur within the subplots.

DATA ANALYSIS. We used the non-parametric Wilcoxon-Mann Whitney two sample z-test procedure to compare percent cover (total, forb, shrub, fern, and individual species), species richness, and species diversity (Shannon Diversity Index) between the exclosure and the control ($n = 29$). For the two indicator species, we compared plant height and leaf width with a *t*-test and used a Chi-square test to compare the percent of individuals that had infloresences. Because the exclosure was not replicated our analyses were necessarily based on the 29, 1 m^2 plots within each site (pseudoreplicates *sensu* Hurlbert 1984), thus our results need to be interpreted in light of this caveat.

Results. PLANT COVER. Long-term over browsing decreased the cover of forbs by more than 99% and eliminated shrubs (Table 1). Ferns, particularly *Dennstaedtia punctilobula*

Table 1. The mean percent cover (per m^2) of understory herbs and shrubs in the exclosure and adjacent reference site. Asterisks (*) indicate statistically significant differences ($P < 0.01$). Dashes (-) indicate the species was not observed in the site. Trace (T) indicates the species was observed only in the meander search and not used to estimate cover.

Species	Exclosure ± SE	Reference ± SE	*P*
Forbs			
Actaea pachypoda Ell.	T	-	
Arisaema triphyllum (L.) Schott	0.07 ± 0.05	-	
Carex sp.L.	T	-	
Epifagus virginiana (L.) W. Bart.	-	T	
Maianthemum canadense L.*	18.21 ±4.11	T	< 0.0001
Mainthemum racemosa (L.) Link*	10.90 ± 2.58	-	< 0.0001
Medeola virginianum L.	2.52 ± 1.23	0.07 ± 0.07	
Panax quinquefolius L.	T	-	
Polygonatum pubescens (Willd.) Pursh	0.83 ± 0.39	-	
Polygonum cilinode Michx.	0.24 ± 0.18	-	< 0.0001
Solidago rugosa P. Mill.	T	-	
Trientalis borealis Raf.	0.28 ± 0.16	-	
Trillium erectum L.*	9.17 ± 2.55	0.10 ± 0.10	< 0.0001
Trillium undulatum Willd.	0.21 ± 0.15	T	
Urtica dioica L.	T	-	
Viola blanda Willd.	0.10 ± 0.08	T	
Viola macloskeyi Lloyd	0.11 ± 0.06	T	
Forbs Total *	42.63 ± 6.10	0.17 ± 0.12	< 0.0001
Ferns			
Botrychium virginianum (L.) Sw.	0.03 ± 0.03	-	
Dennstaedtia punctilobula (Michx.) T. Moore*	3.87 ± 0.99	7.59 ± 1.18	< 0.008
Dryopteris intermedia (Muhl. ex Willd.) Gray	2.69 ± 1.28	0.14 ± 0.11	
Thelypteris noveboracensis (L.) Nieuwl.	0.17 ± 0.17	T	
Ferns Total	6.76 ± 1.76	7.73 ± 1.19	
Shrubs			
Cornus alternifolia L. f.	2.31 ± 1.07	-	
Mitchella repens L	0.31 ± 0.31	-	
Rubus allegheniensis Porter*	8.07 ± 1.59	-	< 0.0001
Rubus idaeus L.	0.17 ± 0.11	-	
Sambucus racemosa L.	0.59 ± 0.37	-	
Shrubs Total*	11.45 ± 2.10	0.00 ± 0.00	< 0.0001
Total Plant Cover*	63.42 ± 6.10	9.28 ± 1.55	< 0.0001
Total Plant Cover minus *Dennstaedria punctilobula*	59.55	1.69	< 0.0001
Total number of species per site	25	10	
Mean number of species per plot*	6.2	1.1	< 0.0001
Shannon Diversity Index*	3.75	1.14	< 0.005

(Michx. T. Moore), dominated the reference site, however fern cover did not differ significantly between sites. Excluding deer increased total plant cover seven fold (Table 1). Browsing decreased the total cover of all species after subtracting the fern *D. punctilobula* from nearly 60% to 2% (Table 1). Browsing significantly reduced the cover of four herbs *Maianthemum canadense* L., *Maianthemum racemosum* (L.) Link, and *Trillium erectum* and one shrub (*Rubus allegheniensis* Porter, Table 1).

Species Richness, Diversity, and Plant Performance. Browsing decreased mean species richness m^{-2} and mean species diversity m^{-2} by 80% and 70%, respectively (Table 1). Browsing reduced the total number of understory species throughout the entire site by 60% (site meander survey). Browsing significantly decreased plant height by nearly 40% for both *Trillium erectum* and *Maianthemum virginiana* (*T. erectum*: Exclosure = 32.1 cm, Reference site = 19.5 cm, *t*-test, $P < 0.0001$; *M. virginiana*: Exclosure = 31.7 cm, Reference site = 19.8, *t*-test, $P < 0.0001$). Browsing also significantly reduced the percentage of individuals that produced inflorescences (*T. erectum*: Exclosure = 83.3%, Reference site = 42.9%, Chi-Square test, $P < 0.001$; *M. virginiana*: Exclosure = 66.6%, Reference site = 25.0%, Chi-Square test, $P < 0.001$).

Discussion. Decades of over browsing by deer caused the formation of a highly depauperate understory dominated by a single fern species. Browsing caused the site level extinction of shrubs and drove forbs to extremely low abundance ($< 0.2\%$ cover m^{-2}). Similarly, Rooney and Dress (1997) found that browsing was the likely cause of a $\sim$70% decline from 1928 to 1995 in the species richness of understory herbs and shrubs for two old-growth stands in the Allegheny National Forest. Rooney and Dress (1997) did not conduct meander surveys and considered a species "lost" if it did not occur in 1 m^2 plots that were arrayed and sampled in a similar manner in 1928 and then in 1995. Our meander surveys suggest that some herbs are not actually lost, but rather driven to extremely low abundance. Diversity losses in our study were 60% at the site scale (0.4 ha) versus 80% at the plot scale (1 m^2). Regardless, our findings parallel other studies showing that browsers have locally extirpated numerous understory species and driven many others to very low abundance throughout the Allegheny National Forest (Rooney and Dress 1997, Comisky et al. 2005, Banta et al. 2005). Moreover, our results show that those individuals that are present are smaller and less likely to flower (*Trillium erectum* and *Maianthemum virginiana*). Comisky et al (2005) found that the number of flowering individuals for all forb species combined was more than 100 times higher on tall boulders than on the soil surface. The genetic (e.g., inbreeding depression) and fitness related (e.g., pollen limitation) consequences of dramatically reducing the abundance and flowering of these formerly widespread and abundant species remains little studied but could be highly deleterious (Banta et al. 2005).

Overall, our findings, in combination with those that have investigated natural refugia (Comisky et al. 2005, Banta et al. 2005) and with those that have looked at species losses over decades at the same location (Rooney and Dress 1997) strongly suggest that over browsing by deer has converted what was once a species rich and lush understory of forbs and shrubs into a depauperate understory dominated by a few ferns, grasses, and browse resistant trees (e.g., *Fagus grandifolia* Ehrh.) throughout the region. Due to legacy effects, it may take decades or longer for many of these species to reclaim their former habitat and once again form lush understory layers. Taken together, all of these studies suggest what understories might have looked like without decades of over browsing, thus providing a yardstick by which to compare recovery should browsers be brought under control. One might argue that these areas are artificial and reflect understories where browsing has been completely eliminated and thus are not reliable barometers. This view, however, contrasts with recent experimental findings that deer at historical (lower) levels promote understory herb diversity by preferentially browsing fast growing clonal shrubs and early successional trees (Royo et al. 2010).

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