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Effects of Browsing by Captive Elk (Cervus canadensis) on a Midwestern Woody Plant Community

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ABSTRACT.—Elk (*Cervus canadensis*) can significantly alter plant community composition and reduce plant biodiversity, mass, seedling numbers and sapling growth. Yet, few studies have examined the interactions of reintroduced elk with woody plant communities in eastern North America. To test the hypothesis that elk herbivory would reduce woody plant diversity and recruitment and also change woody plant community composition when compared to deer, we evaluated herbivory effects of a captive elk herd and a free-roaming white-tailed deer (*Odocoileus virginianus*) population in Land Between the Lakes National Recreation Area in western Kentucky. Elk and deer herbivory did not differ in their effects upon overall woody plant diversity. However, elk browsing significantly altered woody plant community composition ($F_{1,15} = 2.27$, $P = 0.005$), reduced stem heights of *Quercus* and *Cornus* genera ($Ps < 0.036$) and reduced frequencies of *Quercus, Nyssa,* and *Sassafras* ($Ps < 0.045$) when compared to deer. Our results suggest elk herbivory pressure on *Quercus,* as well as other tree and shrub species, will affect eastern forest regeneration and thus managing the growth and distribution of reintroduced elk populations will be important for the viability of eastern and midwestern deciduous forests within restoration zones.

INTRODUCTION

Reintroductions of formerly extirpated species have gained increased public support, government funding, and media coverage in recent years, often with a goal of restoring historical and healthy ecosystems (*e.g.,* Hayward *et al.,* 2007; Morrison *et al.,* 2007). For example, over the past several decades multiple eastern and midwestern states have reintroduced elk (*Cervus canadensis*) into large tracts of their former range (Larkin *et al.,* 2003). Some states such as Kentucky and Tennessee began their reintroductions in the 1990s, while other states such as North Carolina, Virginia, and Missouri have just begun reintroduction programs. Western herds often serve as the source populations for these reintroductions, but some states are using elk from adjacent or nearby eastern states with well-established reintroduced herds. In western Kentucky, Land Between the Lakes National Recreation Area (LBL; 36.8569°N, 88.0747°W) is taking part in these elk restoration efforts. The captive population at the Elk and Bison Prairie at LBL has served as a source for elk releases in eastern Tennessee and western North Carolina (F. C. Fowler, Land Between the Lakes, U.S.D.A. Forest Service, pers. comm.).

Although many studies have been published on the behavior and genetics of reintroduced elk (*e.g.,* Larkin *et al.,* 2003; Wichrowski *et al.,* 2005), few have examined the impacts of this large herbivore on its relatively new eastern habitat. This data gap leaves land managers and citizens near the restoration areas unprepared to understand or deal with the consequences, beneficial and deleterious, of reintroducing a large herbivore into an environment greatly altered from its historic character, such as through the absence of major predators and an increased level of human activity. The benefits of reintroduction are obvious: the beginnings of ecosystem restoration and increased ecotourism and hunting

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revenues in reintroduction areas (Donovan and Champ, 2009). In contrast, the possible positive and negative consequences on the surrounding ecosystem have thus far escaped scrutiny, although studies of western elk provide some insight.

Western elk populations can significantly alter plant community composition and reduce biodiversity, including the loss of shrub species richness (Johnson and Cushman, 2007), reduction of tree and shrub mass and frequency (Schreiner *et al.*, 1995; Riggs *et al.*, 2000; Endress *et al.*, 2012), and reduction in tree seedling numbers and sapling growth (Kuiters and Slim, 2002; Schoenecker *et al.*, 2004). Woody browse is a major component of elk diet and is often negatively affected by elk foraging (reviewed in Toweill *et al.*, 2002; Huffman and Moore, 2003; Johnson and Cushman, 2007). Dietary analysis has shown that eastern elk select woody browse more than other forage types (Murphy, 1963; Schneider *et al.*, 2006; Lupardus *et al.*, 2011) and thus have the potential to impact woody plant communities in similar fashion to their western counterparts.

Given the findings of studies from western elk populations, we hypothesized that elk herbivory would alter the composition of woody plant communities by reducing diversity, stem heights, and relative abundance of genera when compared to the impacts of white-tailed deer (*Odocoileus virginianus*) herbivory. We tested these hypotheses by studying the effects of LBL's captive elk herd on woody plants and comparing these effects to an area subject only to white-tailed deer browse.

METHODS

The floral region that LBL occupies is characterized by oak-hickory (*Quercus-Carya*) forests and patches of native prairie (F.C. Fowler, pers. comm.), but the two study sites—the Elk and Bison Prairie and the Oak-Grassland Demonstration Area—varied considerably in habitat composition as well as the species of herbivores. The Elk and Bison Prairie (EBP; 36.7897°N, 88.0536°W) provides a unique opportunity for research on elk: built in 1996, it encloses 263 ha that is approximately 40% grassland, 30% woodland, and 30% forest. During the study (Oct. 2010 to Mar. 2011) the EBP contained approximately 28 elk, 47 bison, and no white-tailed deer, the latter having been removed since 2007. Elk densities have fluctuated throughout the EBP's existence from approximately 11–19/km^2 (F. C. Fowler, pers. comm.). The facility was originally stocked with 29 individuals in 1996, received six more in 1997, and 12 in 2002, all from Elk Island National Park, Alberta (F. C. Fowler, pers. comm.). The elk population has also been reduced through several exports: in 2001, 25 elk were relocated to Great Smokey Mountains National Park, followed by 31 in 2003, and 34 in 2008. Deer density within the EBP was not recorded before their extirpation, although they never reached densities observed outside the enclosure (*see below*) and were occasionally culled (dates of cullings were unavailable; F. C. Fowler, pers. comm.). Within the EBP, native prairie grasses have been reintroduced, creating prairie, oak-savannah, and woodland habitats, and managers apply prescribed fire on a 2 y cycle.

The unenclosed Oak-Grassland Demonstration Area (OGDA; 36.8080°N, 88.0348°W) is located immediately north of the EBP border fence, and provided a similar landscape that has also been regularly burned using fire management but differed from EBP by the presence of deer (8–9/km^2) and the absence of elk or bison (F. C. Fowler, pers. comm.). Historical deer densities for the OGDA were not available as population studies have only been conducted since 2010. In contrast to the EBP, the OGDA is approximately 80% forest, 10% woodland, 5% grassland, and 5% cropland, with substantially more contiguous forest than the EBP. Prior ungulate browsing and detailed woody plant community data were not available for reference for either the OGDA or EBP.

To compare differences in the plant communities of the two areas, 11 quarter-hectare plots were randomly selected at each site in forest, woodland, and shrub habitats. To measure woody plant communities within these plots, three 4 × 50 m belt transects were sampled at 25 m intervals, and three 4 m diameter circular subplots were evenly spaced along the transects (Magurran, 2004). We recorded woody plant species presence in each subplot. We then selected ten stems <2.5 m, the maximum browse height for elk, which were closest to the center point of each subplot to measure species frequency, stem height, and stem browse history (Baker *et al.*, 1997). We measured browse history using the plant architecture method for the year's growing season (Keigly and Frisna, 1998; Keigly *et al.*, 2003). Because tree cover has been shown to affect understory plant growth and diversity (Jenkins and Chambers, 1989; Gillet *et al.*, 1999), we measured tree density and diameter at breast height (DBH), which is directly related to tree crown cover, for all trees within the belt transect (Gery and May, 1995). We also quantified scat event frequency by herbivore species within each transect to directly compare ungulate area use to woody plant community composition (Fuller, 1991; Thompson *et al.*, 1998). Twelve transects in the EBP with bison scat were removed from analysis so bison foraging did not bias our results. Ungulate area usage was also compared with the magnitude of their effects upon woody plants.

To determine overall effects of browsing on alpha diversity in woody plant communities, we calculated Shannon diversity indices for woody species <2.5 m in the EBP and OGDA and tested the null hypothesis of no difference in the measures with bootstrapping using the R statistical language (R Development Core Team, 2013). In order to address the impact of browsing on the richness and abundance of plant species, permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001; Sitzia *et al.*, 2012) was used to test for differences in woody plant <2.5 m species composition between the EBP and OGDA sites. Since the PERMANOVA method is sensitive to relative dispersion within groups, we employed a permutational analysis of multivariate dispersions (PERMDISP; Anderson *et al.*, 2006; Sitzia *et al.*, 2012) to determine whether a difference found in community composition would be within or between sites. Both of these analyses were performed with the 'vegan' package in R (Oksanen *et al.*, 2013; R Development Core Team, 2013). Elk and deer area use and browse percentages were compared to the Shannon indices using linear regression. Browse percentage was calculated as browse events divided by plant species abundance ×100. We also used linear regression to compare elk and deer use to stem heights. We calculated Ivlev's electivity index to compare differences in elk and deer foraging behavior (Lechowicz, 1982). Stem heights and percent of stems browsed were compared between the EBP and OGDA using multivariate ANOVA. Although we recorded species for each stem, we did not have a large enough sample size to compare stem heights, percent browsed, and Ivlev indices between species within a genus; and thus we compared across genera. We also compared stem frequencies for species browsed at both sites, the difference in tree DBH between sites, and the difference in tree density between sites with a one-tailed student's *t*-test.

RESULTS

EBP ($H' = 3.00$) and the OGDA ($H' = 3.03$) did not differ significantly in Shannon diversity (bootstrapped $t = 0.025$, $P = 0.68$). The PERMANOVA showed a significant community dissimilarity between sites ($F_{1,15} = 2.27$, $P = 0.005$), and the PERMDISP was not significant, indicating no evidence for a lack of homogeneity within the sites ($F_{1,15} = 0.05$, $P = 0.83$). These results indicate that communities were different between sites but not within

TABLE 1.—Species present at each site. "X" indicates species presence

Species	EBP	OGDA
Acer rubrum		X
Amelanchier arborea	X	X
Aralia spinosa	X	X
Carya glabra		X
Carya tomentosa	X	X
Cercis canadensis	X	X
Cornus florida	X	X
Corylus americana		X
Crataegus sp.	X	
Eleagnus umbellata	X	X
Fagus grandifolia		X
Fraxinus pennsylvanica	X	X
Gleditsia triancanthos		X
Ilex decidua	X	X
Juniperus canadensis	X	X
Ligustrum vulgare	X	
Liquidambar styraciflua	X	
Lonicera japonica	X	X
Nyssa sylvatica	X	X
Ostrya virginiana		X
Pinus taeda	X	X
Prunus serotina	X	X
Quercus alba	X	X
Quercus coccinea	X	X
Quercus falcata		X
Quercus imbricaria	X	
Quercus marilandica	X	X
Quercus rubra	X	X
Quercus stellata	X	X
Rhus alata	X	X
Rosa multiflora	X	
Rubus allegheniensis	X	X
Rubus sp.	X	X
Sassafras albidum	X	X
Smilax rotundifolia	X	X
Symphoricarpos orbiculatus	X	X
Toxicodendron radicans		X
Ulmus alata	X	X
Vaccinium sp.	X	X
Vitus sp.	X	X

sites, suggesting that community differences between sites were significant (Sitzia *et al.*, 2012). The EBP sampling revealed 32 woody plant species with five unique species whereas the OGDA had 35 species with eight unique species (Table 1). Regression relationships between elk and deer use and diversity of the woody plant communities as well as elk and deer browse percentages and diversity of the woody plant communities were not significant ($Fs < 2.42$, $Ps > 0.15$).

Stem heights varied significantly across sites ($F_{3,19} = 4.4$, $P = 0.016$), with *Quercus* and *Cornus* stems lower in the EBP than in the OGDA ($Ps < 0.036$). Percentage browsed was

TABLE 2.—Genera browsed, the percent of each genus browsed, and resulting Ivlev electivity indices for each site

	EBP		OGDA	
Genus	Percent browsed	Ivlev index	Percent browsed	Ivlev index
Acer	—	—	0	−1
Amelanchier	0	−1	0	−1
Aralia	0	−1	0	−1
Carpinus	—	—	0	−1
Carya	7.78	0.244	0	−1
Cercis	0	−1	0	−1
Cornus	50	0.151	50	0.559
Corylus	0	−1	0	−1
Crataegus	0	−1	—	—
Eleagnus	0	−1	0	−1
Fagus	—	—	0	−1
Fraxinus	50	0.341	0	−1
Gleditsia	—	—	0	−1
Ilex	0	−1		
Juniperus	—	—	0	−1
Ligustrum	0	−1	—	—
Liquidambar	27.3	0.638	—	—
Lonicera	0	−1	0	−1
Nyssa	29.44	0.567	15.89	0.847
Pinus	0	−1	—	—
Prunus	31.25	−0.141	0	−1
Quercus	18.71	0.185	1.64	−0.0621
Rhus	0	−1	0.89	0.0612
Rosa	0	−1	—	—
Rubus	9.25	0.341	0.85	−0.207
Sassafras	15.28	0.0343	1	0.0815
Smilax	0	−1	0	−1
Symphoricarpos	8.07	0.104	0	−1
Toxicodendron	—	—	0	−1
Ulmus	6.91	−0.215	1.25	−0.268
Vaccinium	0	−1	1.59	0.103
Vitus	0	−1	0	−1

highest for *Cornus* and *Fraxinus,* with averages of 50% browsed (Table 2). Due to resource and ungulate browsing variability across sites, we were not able to conduct statistical analyses on the Ivlev indices but can illustrate several disparities between sites. More genera had positive Ivlev indices at the EBP than the OGDA (Table 2) and elk exhibited positive electivity for *Quercus* at the EBP (0.185) versus a negative electivity in the presence of deer foraging at the OGDA (−0.0621). We also observed a trend of higher electivity for *Cornus* at the OGDA (0.559) than the EBP (0.151) and similar electivities for *Nyssa* and *Sassafras* at both sites (Table 2). Although percent browsed values tended to be higher in the EBP, they were only marginally different ($F_{2,19} = 2.95$, $P = 0.076$). Browsed stem frequencies between sites differed significantly for *Quercus* ($t = -1.88$, 10 df, $P = 0.045$), *Nyssa* ($t = -3.15$, 10 df, $P = 0.005$), and *Sassafras* ($t = -3.97$, 10 df, $P = 0.001$), and all these genera were less numerous at the EBP than the OGDA. Tree DBH ($t = 0.381$, 9 df, $P = 0.67$) and density ($t = 1.484$, 9 df, $P = 0.086$) did not differ between sites.

DISCUSSION

Elk browsing did not affect woody plant diversity differently than deer browsing during our study; however, elk herbivory did alter the frequencies and growth of certain genera, resulting in significant differences in woody plant community composition between sites. Our results are consistent with numerous other studies that have shown differences in composition but not diversity of woody plant communities when experiencing elk and other ungulate browse pressure (Ammer, 1996; Hobbs, 1996; Moser and Witmer, 2000; Peinetti *et al.*, 2001; Rooney and Waller, 2003; Sankaran *et al.*, 2008; *but see* Johnson and Cushman, 2007; Beschta and Ripple, 2008). Elk foraging is also known to reduce tree sapling and seedling density, biomass, and regeneration (McPherson, 1993; Scheiner *et al.*, 1995; Baker *et al.*, 1997; Zeigenfuss *et al.*, 2002; Endress *et al.*, 2012) and shrub biomass and regeneration (Scheiner *et al.*, 1995; Singer and Renkin, 1995; Huffman and Moore, 2003; Johnson and Cushman, 2007). White-tailed deer appear to affect woody plant communities similarly (Rooney and Waller, 2003). However, we know of no previous studies that have directly compared the effects of elk and white-tailed deer on woody plant communities (Bellhouse and Rosatte, 2007).

The reduced stem heights and frequencies of multiple genera of woody plants in response to elk herbivory that we observed have the potential to slow or inhibit regeneration and alter woody plant community structure (Beschta and Ripple, 2008). Elk are expected to have a proportionally greater per capita effect on plant communities than deer because the consumption rate of an adult elk is approximately three times that of an adult white-tailed deer (Habitat Monitoring Committee, 1996). This suggests that, over time and given similar population densities, elk herbivory should have a much greater effect on woody plant community structure and the abundance of certain preferred genera than deer. Although elk might influence woody plant communities in multiple, interactive ways (*e.g.*, through nutrient additions), our results suggest that impacts from elk foraging on eastern and midwestern forests are likely to be substantial as restoration efforts expand.

One of the largest impacts that elk could have on eastern deciduous forests is by affecting the regeneration of *Quercus* (Lupardus *et al.*, 2011), one of the most dominant tree genera in the east (Dyer, 2001). The reduction of both stem heights and frequencies of *Quercus* by elk in our study supports this hypothesis and is consistent with controlled simulated mammalian herbivory experiments, studies on elk dietary preference, and historical accounts of elk habitat use in eastern North America. McPherson (1993) and Meiners and Handel (2000) found that *Quercus* seedlings showed increased mortality when clipped by simulated herbivory. Likewise, a study on white oak (*Quercus alba*) seedlings' responses to herbivory found seedling height growth and shoot elongation reduced due to herbivory (Adams and Rieske, 2000). Elk have also been found to select for *Quercus* species in studies of eastern and western elk diets, both as woody browse and as mast (*e.g.*, Baldwin and Patton, 1938; Murphy, 1963; reviewed in Toweill *et al.*, 2002; Schneider *et al.*, 2006; Lupardus *et al.*, 2011). Historically, oak savannah was a major habitat type in Kentucky and probably used by elk, although the nature of their interaction with that habitat is uncertain (Schneider *et al.*, 2006; Lupardus *et al.*, 2011). However, the tendency of ungulate herbivory to maintain savannah plant community structure by reducing woody plant biomass and frequency has been well documented (Sankaran *et al.*, 2008).

Elk herbivory in our study also significantly affected several other genera of woody plants common to eastern and midwestern forests, including *Nyssa, Sassafras,* and *Cornus.* Although *Nyssa* has not been previously observed in elk diets (Murphy, 1963; reviewed in Toweill *et al.*, 2002; Schneider *et al.*, 2006; Lupardus *et al.*, 2011), we observed a strong positive electivity by both elk and deer and reduced stem frequency by elk, suggesting that elk browsing has a greater negative effect than deer on this genus. Similarly, *Sassafras* stem frequency was significantly reduced by elk browsing, but unlike *Nyssa, Sassafras* has been documented in elk diets in eastern Tennessee (Lupardus *et al.*, 2011).

Cornus is a major woody forage for elk in eastern Kentucky (Schneider *et al.*, 2006) and in the west (reviewed in Toweill *et al.*, 2002), but it was not a major component of elk diet in other eastern studies (*e.g.*, Murphy, 1963; Lupardus *et al.*, 2011). This difference may be due to variability in the relative abundance of *Cornus* or other more palatable species in different regions of the country. Within our study, browse percentages for *Cornus* were some of the highest of any genera at both sites (Table 2), but stem frequencies were similar across sites. Nevertheless, elk foraging reduced *Cornus* stem heights while deer browsing did not, which contrasts with the electivities calculated for elk and deer on this genus (0.151 vs. 0.559, respectively). Although these electivity values could not be evaluated for statistical significance, our observation of increased preference for *Cornus* among deer when compared to elk is inconsistent with the reduced stem heights due to elk browse. It is likely the similarly high browse percentages on *Cornus* at both sites and the greater consumption rate of elk (Lupardus *et al.*, 2011) may exert a strong impact on *Cornus* stem height.

It is possible that the small deer population that persisted in the EBP until 2007 may have created additive browsing pressure with the elk and thereby altered the woody plant community structure in the EBP before our study took place. However, the deer population within the enclosure was always small, and the population was occasionally culled to maintain that low population size (F. C. Fowler, pers. comm.). Our electivity indices also indicated elk and deer diets were sufficiently different so that any additive browse pressure by deer within the EBP may not have significantly affected any one genus, except perhaps *Nyssa* that was strongly selected by both elk and deer (Table 2). *Sassafras* was not strongly selected by deer, and although *Cornus* was selected more strongly by deer, only stem heights were different between sites, suggesting that deer and elk herbivory did not have long-term effects on the genus (Table 2). The electivity data also suggested that as *Quercus* was avoided by deer and selected by elk, so it is unlikely that the deer within the EBP significantly affected *Quercus* regeneration (Table 2). Given these results, previous studies that have shown minimal effects of low densities of ungulates on plant communities (Olff and Ritchie, 1998; Stewart *et al.*, 2009), and other studies that have shown low winter dietary overlap between elk and *Odocoileus* species (Hobbs *et al.*, 1983; Gogan and Barrett, 1995), it appears unlikely the small, historical deer population within the EBP had a substantial impact on our results.

As wildlife agencies continue to restore elk and other species in the eastern and midwestern U.S., scientists will need to further explore the community consequences of such reintroductions to better understand the effects of restored species on their new environment. Our results suggested elk browsing pressure on oaks and other woody species are likely to be substantial throughout elk restoration areas, and management plans for these reintroduced elk populations should carefully consider the impacts of elk on woody plant communities and long-term forest viability.

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LITERATURE CITED

ADAMS, A. S. AND L. K. RIESKE. 2001. Herbivory and fire influence white oak (*Quercus alba* L.) seedling vigor. *Forest Sci.*, **47**:331–337.

AMMER, C. 1996. Impact of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. *For. Ecol. Manage.*, **88**:43–53.

ANDERSON, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral. Ecol.*, **26**:32–46.

———, K. E. ELLINGSEN, AND B. H. MCARDLE. 2006. Multivariate dispersion as a measure of beta diversity. *Ecol. Lett.*, **9**:683–693.

ARMOUR, C., S. BUNTING, AND L. NEUENSCHWANDER. 1984. Fire intensity effects on the understory in ponderosa pine forests. *J. Range Manage.*, **37**:44–49.

AUGUSTINE, D. J. AND S. J. MCNAUGHTON. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *J. Wildl. Manage.*, **62**:1165–1183.

BAKER, W., J. MUNROE, AND A. HESSEL. 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. *Ecography*, **20**:155–165.

BALDWIN, W. AND C. PATTON. 1938. A preliminary study of food habits of elk in Virginia. Trans. North American Wildlife Conference, **3**:747–755.

BARNES, T. AND D. VAN LEAR. 1998. Prescribed fire effects on advanced regeneration in mixed hardwood stands. *Southern J. Appl. Forestry*, **22**:138–142.

BELLHOUSE, T. AND R. ROSATTE. 2005. Assessment of the potential for negative interaction between re-introduced elk (*Cervus elaphus*) and resident white-tailed deer (*Odocoileus virginianus*) in their wintering areas in Ontario, Canada. *Mammalia mamm*, **69**:35–56.

BESCHTA, R. L. AND W. J. RIPPLE. 2008. Wolves, trophic cascades, and rivers in the Olympic National Park, USA. *Ecohydrology*, **1**:118–130.

BOYD, R. 1970. Elk of the White River Plateau, Colorado. Tech. Bull. 25. Denver: Colorado Div. Game, Fish, and Parks. 126 p.

BROOKSHIRE, J. E., B. J. KAUFFMAN, D. LYTJEN, AND N. OTTING. 2002. Cumulative effects of wild ungulate and livestock herbivory on riparian willows. *Oecologia*, **132**:559–566.

DONOVAN, G. AND P. CHAMP. 2009. The economic benefits of elk viewing at the Jewell Meadows Wildlife Viewing Area in Oregon. *Hum. Dimens. Wildl.*, **14**:51–60.

DYER, J. M. 2001. Using witness trees to assess forest change in southeastern Ohio. *Can. J. Forest Res.*, **31**:1708–1718.

ENDRESS, B., M. WISDOM, M. VAVRA, C. PARKS, B. DICK, B. NAYLOR, AND J. BOYD. 2012. Effects of ungulate herbivory on aspen, cottonwood, and willow development under forest fuels treatment regimes. *For. Ecol. Manage.*, **276**:33–40.

FULLER, T. 1991. Do pellet counts index white-tailed deer numbers and population change? *J. Wildl. Manage.*, **55**:393–396.

GERING, L. AND D. MAY. 1995. The relationship of diameter at breast height and crown diameter for four species groups in Hardin County, Tennessee. *Southern J. Appl. Forestry*, **19**:177–181.

GILLET, F., B. MURISIER, A. BUTTLER, J. GALLANDAT, AND J. GOBAT. 1999. Influence of tree cover on the diversity of herbaceous communities in subalpine wooded pastures. *Appl. Veg. Sci.*, **2**:47–54.

GOGAN, P. J. AND R. H. BARRETT. 1995. Elk and deer diets in a coastal prairie-scrub mosaic, California. *J. Range Manage.*, **48**:327–335.

HABITAT MONITORING COMMITTEE. 1996. Procedures for environmental monitoring in range and wildlife habitat management. *BC Ministry of Environment, Lands and Parks, and BC Ministry of Forests, Victoria, BC.* 225 p.

HANBERRY, B., D. DEY, AND H. HE. 2012. Regime shifts and weakened environmental gradients In open oak and pine ecosystems. *PLOS ONE*, **7**:e41337.

HAYWARD, M., J. ADENDORFF, J. OBRIEN, A. SHOLTO-DOUGLAS, C. BISSETT, L. MOOLMAN, P. BEAN, A. FOGARTY, D. HOWARTH, R. SLATER, AND G. KERLEY. 2007. Practical considerations for the reintroduction of large, terrestrial, mammalian predators based on reintroductions to South Africa's Eastern Cape Province. *Open Conservat. Biol. J.*, **1**:1–11.

HESSEL, A. 2002. Aspen, elk, and fire: the effects of human institutions on ecosystem processes. *BioScience*, **52**:1011–1022.

HOBBS, N. T. 1996. Modification of ecosystems by ungulates. *J. Wildl. Manage.*, **60**:695–713.

———, D. L. BAKER, AND R. B. GILL. 1983. Comparative nutritional ecology of montane ungulates during winter. *J. Wildl. Manage.*, **47**:1–16.

HOLZMUELLER, E., S. JOSE, AND M. JENKINS. 2009. The response of understory species composition, diversity, and seedling regeneration to repeated burning in southern Appalachian oak-hickory forests. *Nat. Area. J.*, **29**:255–262.

HUFFMAN, D. W. AND M. M. MOORE. 2003. Ungulate herbivory on buckbrush in an Arizona ponderosa pine forest. *J. Range Manage.*, **56**:358–363.

JENKINS, M. AND J. CHAMBERS. 1989. Understory light levels in mature hardwood stands after partial overstory removal. *For. Ecol. Manage.*, **26**:247–256.

——— AND P. WHITE. 2002. *Cornus florida* mortality and understory composition changes in western Great Smoky Mountains National Park. *J. Torrey Bot. Society*, **129**:194–206.

JOHNSON, B. AND J. CUSHMAN. 2007. Influence of a large herbivore reintroduction on plant invasions and community composition in a California grassland. *Conserv. Biol.*, **21**:515–526.

KEIGLEY, R. AND M. FRISINA. 1998. Browse evaluation by analysis of growth form, Vol. I: methods for evaluating condition and trend. Montana Fish Wildlife & Parks. Helena, MT. 153 p.

———, ———, AND C. FAGER. 2003. A method for determining the onset year of intense browsing. *J.Range Manage.*, **56**:33–38.

KIRCHHOFF, M. AND D. LARSEN. 1998. Dietary overlap between native Sitka black-tailed deer And introduced elk in southeast Alaska. *J. Wildl. Manage.*, **62**:236–242.

KUDDES-FISCHER, L. AND M. ARTHUR. 2002. Response of understory vegetation and tree regeneration to a single prescribed fire in oak-pine forests. *Nat. Area. J.*, **22**:43–52.

KUITERS, A., G. MOHREN, AND S. VAN WIEREN. 1996. Ungulates in temperate forest ecosystems. *For. Ecol. Manage.*, **88**:1–5.

——— AND P. SLIM. 2002. Regeneration of mixed deciduous forest in a Dutch forest-heathland, following a reduction of ungulate densities. *Biol. Conservat.*, **105**:65–74.

LARKIN, J., D. MAEHR, J. COX, D. BOLIN, AND M. WICHROWSKI. 2003. Demographic characteristics of a reintroduced elk population in Kentucky. *J. Wildl. Manage.*, **67**:467–476.

LECHOWICZ, M. 1982. The sampling characteristics of electivity indices. *Oecologia*, **52**:22–30.

LUPARDUS, J., L. MULLER, AND J. KINDALL. 2011. Seasonal forage availability and diet for reintroduced elk in the Cumberland Mountains, Tennessee. *Southeast. Nat.*, **10**:53–74.

MAGURRAN, A. E. 2004. Measuring biological diversity. Blackwell Publishing, Malden, MA. 264 p.

MCPHERSON, G. R. 1993. Effects of herbivory and herb interference on oak establishment in a semi-arid temperate savanna. *J. Veg. Sci.*, **4**:687–692.

MEINERS, S. J. AND S. N. HANDEL. 2000. Additive and nonadditive effects of herbivory and competition on tree seedling mortality, growth, and allocation. *Am. J. Bot.*, **87**:1821–1826.

MORRISON, J., W. SECHREST, E. DINERSTEIN, D. WILCOVE, AND J. LAMOREUX. 2007. Persistence of large mammal faunas as indicators of global human impacts. *J. Mammal.*, **88**:1363–1380.

MOSER, B. W. AND G. W. WITMER. 2000. The effects of elk and cattle foraging on the vegetation, birds, and small mammals of the Bridge Creek Wildlife Area, Oregon. *Int. Biodeter. Biodegr.*, **45**:151–157.

MURPHY, D. 1963. A captive elk herd in Missouri. *J. Wildl. Manage.*, **27**:411–414.

OKSANEN, J., F. G. BLANCHET, R. KINDT, P. LEGENDRE, P. R. MINCHIN, R. B. O'HARA, G. L. SIMPSON, P. SOLYMOS, M. H. H. STEVENS, AND H. WAGNER. 2013. vegan: Community ecology package. Rpackage version 2.0-7. URL: http://CRAN.R-project.org/package=vegan. Accessed Jun 28, 2013.

OLFF, H. AND M. E. RITCHIE. 1998. Effects of herbivores on grassland plant diversity. *Trends Ecol. Evol.*, **13**:261–265.

PEINETTI, H. R., R. S. MENEZES, AND M. B. COUGHENOUR. 2001. Changes induced by elk browsing in the aboveground biomass production and distribution of willow (*Salix monticola* Bebb): their relationships with plant water, carbon, and nitrogen dynamics. *Oecologia*, **127**:334–342.

PIERCE, A., W. BROMER, AND K. RABENOLD. 2008. Decline of *Cornus florida* and forest succession in a *Quercus–Carya* forest. *Plant Ecol.*, **195**:45–53.

R CORE TEAM. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org. Accessed on Jun 28, 2013.

RIGGS, R., A. TIEDEMANN, J. COOK, T. BALLARD, P. EDGERTON, M. VAVRA, W. KRUEGER, F. HALL, L. BRYANT, AND L. IRWIN. 2000. Modification of mixed-conifer forests by ruminant herbivores in the Blue Mountains ecological province. *U.S. Forest Service Research Paper PNW.*, **527**:1–77.

RITCHIE, M. E. AND M. L. WOLFE. 1994. Sustaining rangelands: application of ecological models to evaluate the risks of alternative grazing systems. USDA Forest Service General Technical Report RM-247, Fort Collins, CO. 328–336 p.

ROONEY, T. P. AND D. M. WALLER. 2003. Direct and indirect effects of white-tailed deer in Forest ecosystems. *For. Ecol. Manage.*, **181**:165–176.

SANKARAN, M., J. RATNAM, AND N. HANAN. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecol. Biogeogr.*, **17**:236–245.

SCHOENECKER, K., F. SINGER, L. ZEIGENFUSS, D. BINKLEY, AND R. MENEZES. 2004. Effects of elk herbivory on vegetation and nitrogen processes. *J. Wildl. Manage.*, **68**:837–849.

SCHNEIDER, J., D. MAEHR, K. ALEXY, J. COX, J. LARKIN, AND B. REEDER. 2006. Food habits of reintroduced elk in southeastern Kentucky. *Southeast. Nat.*, **5**:535–546.

SCHREINER, E., K. KRUEGER, P. HAPPE, AND D. HOUSTON. 1996. Understory patch dynamics and Ungulate herbivory in old-growth forests of Olympic National Park, Washington. *Can. J. Forest Res.*, **26**:255–265.

SINGER, F. J. AND R. A. RENKIN. 1995. Effects of browsing by native ungulates on the shrubs in big sagebrush communities in Yellowstone National Park. *West. N. Am. Naturalist*, **55**:201–212.

SITZIA, T., G. TRENTANOVI, M. DAINESE, G. GOBBO, E. LINGUA, AND M. SOMMACAL. 2012. Stand Structure and plant species diversity in managed and abandoned silver fir mature woodlands. *For. Ecol. Manage.*, **270**:232–238.

STEWART, K. M., R. T. BOWYER, J. G. KIE, B. L. DICK, AND R. W. RUESS. 2009. Population density of North American elk: effects on plant diversity. *Oecologia*, **161**:303–312.

THOMPSON, I., I. DAVIDSON, S. O'DONNELL, AND F. BRAZEAU. 1998. Use of track transects to measure the relative occurrence of some boreal mammals in uncut forest and regeneration stands. *Can. J. Zool.*, **67**:1816–1823.

TOWEILL, D., J. THOMAS, AND D. METZ. 2002. North American Elk: ecology and management, 1st ed. Smithsonian Institute Press, Washington D.C. 1128 p.

WANG, G., D. LEAR, AND W. BAUERLE. 2005. Effects of prescribed fires on first-year establishment of white oak (*Quercus alba* L.) seedlings in the Upper Piedmont of South Carolina, USA. *For. Ecol. Manage.*, **213**:328–337.

WHITE, M. A. 2012. Long-term effects of deer browsing: composition, structure and productivity in a northeastern Minnesota old-growth forest. *For. Ecol. Manage.*, **269**:222–228.

WICHROWSKI, M., D. MAEHR, J. LARKIN, J. COX, AND M. OLSSON. 2005. Activity and movements Of reintroduced elk in southeastern Kentucky. *Southeast. Nat.*, **4**:365–374.

WRIGHT, A., S. SCHNITZER, I. DICKIE, A. GUNDERSON, G. PINTER, S. MANGAN, AND P. REICH. 2013. Complex facilitation and competition in a temperate grassland: loss of plant diversity and elevated CO2 have divergent and opposite effects on oak establishment. kl *Oecologia.*, **171**:449–458.

ZEIGENFUSS, L. C., F. J. SINGER, S. A. WILLIAMS, AND T. L. JOHNSON. 2002. Influences of herbivory and water on willow in elk winter range. *J. Wildl. Manage.*, **66**:788–795.

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