

Hardwood tree decline following large carnivore loss on the Great Plains, USA

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In order to investigate long-term food web linkages and trophic cascades, we conducted a retrospective analysis of large carnivores, wild and domestic ungulates, human settlement, and hardwood trees from the late 1800s to the present at Wind Cave National Park in southwestern South Dakota. We measured diameters of all cottonwood (*Populus* spp) and bur oak (*Quercus macrocarpa*) trees within a large portion of the Park to assess long-term patterns of recruitment (growth of sprouts or seedlings into tall saplings or trees). Increment cores from a subset of these trees were used to determine tree age and to develop relationships between age and diameter. Resulting age structures indicated a lack of cottonwood and bur oak recruitment for more than a century, beginning in the 1880s and continuing to the present. This is attributable to high levels of browsing, initially by livestock and subsequently by wild ungulates, in the absence of large carnivores. Conversely, we found that hardwood trees had recruited to areas protected from browsing, such as inside fenced exclosures and within a small browsing refuge. Results indicate that Great Plains ecosystems may have been profoundly altered by mounting levels of ungulate herbivory following the removal of large carnivores.

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Hairston *et al.* (1960) set off a major debate when they proposed the “green world hypothesis”, which holds that predators maintain global plant biomass at high levels by limiting herbivore densities. Trophic cascades, as we now refer to them, occur when the presence of a top predator substantially affects consumer (herbivore) population size or habitat use and thereby alters producer (plant) abundance or spatial distribution. While current discussions on terrestrial food webs continue to question the relative strength of top-down forcing versus bottom-up controls (Terborgh *et al.* 1999; Polis *et al.* 2000), little work has been published on the role of large mammalian carnivores in terrestrial ecosystems (Borer *et al.* 2005).

In 1803, Lewis and Clark ventured into the northern Great Plains and found abundant bison (*Bison bison*), elk (*Cervus elaphus*), deer (*Odocoileus* spp), pronghorn (*Antilocapra americana*), gray wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and beaver (*Castor canadensis*). Since then, mammalian carnivore species have experienced substantial range contractions throughout the Great Plains relative to other North American biomes (Laliberte and Ripple 2004). Yet, long-term cascading effects involving the loss of large carnivores within this region are essentially unknown. To our knowledge, little work has been done on predator effects within the Great Plains biome, which occupies approximately 3.6 million square kilometers, or over one-third of the conterminous United States. Biological diversity is high on the Great Plains, with approximately 200 woody plant, 87 mammal, 457 bird, 67 reptile, 32 amphibian, 142 fish, and 20 000 invertebrate species (GPNC nd).

The objective of this study was to examine historical hardwood tree recruitment within the framework of trophic cascades theory. We hypothesize that the extirpation of large carnivores in the late 19th and early 20th centuries has resulted in increased ungulate herbivory and a subsequent decline in tree recruitment.

■ Study area

Wind Cave National Park (WCNP) is located along the southeastern foothills of the Black Hills of South Dakota. Elevations range from approximately 1100 m to over 1500 m. Annual precipitation averages 47 cm and occurs mostly in the spring and summer. Mixed-grass prairie (eg *Pascopyrum smithii*, *Bouteloua* spp, *Stipa* spp) covers approximately 75% of the Park, while the remainder is dominated by ponderosa pine (*Pinus ponderosa*) forest, with scattered groves of hardwood trees generally found in riparian areas. Recent estimates of ungulate populations within the Park (WCNP unpublished data) indicate approximately 800 elk (7 km⁻²), 450 bison (4 km⁻²), 150 mule deer (1.3 km⁻²; *Odocoileus hemionus*), 50 white-tailed deer (0.4 km⁻²; *O virginianus*), and 60 pronghorn (0.5 km⁻²; *Antilocapra americana*) reside there. Currently, coyotes (*Canis latrans*) are common and the cougar (*Puma concolor*) population is increasing from previously low levels (B Muenchau pers comm).

WCNP was originally established in 1903, encompassing 42.6 km², and expanded in 1935 to 47.4 km². In 1946, its area more than doubled, to 113.6 km², with inclusion of the adjacent Custer Recreational Demonstration Area (CRDA). Our study area (Figure 1) included only the CRDA portion of the Park (66.2 km²). Before purchase by the Federal Government in 1935, the CRDA area was used principally for livestock ranching (Beard 1942).

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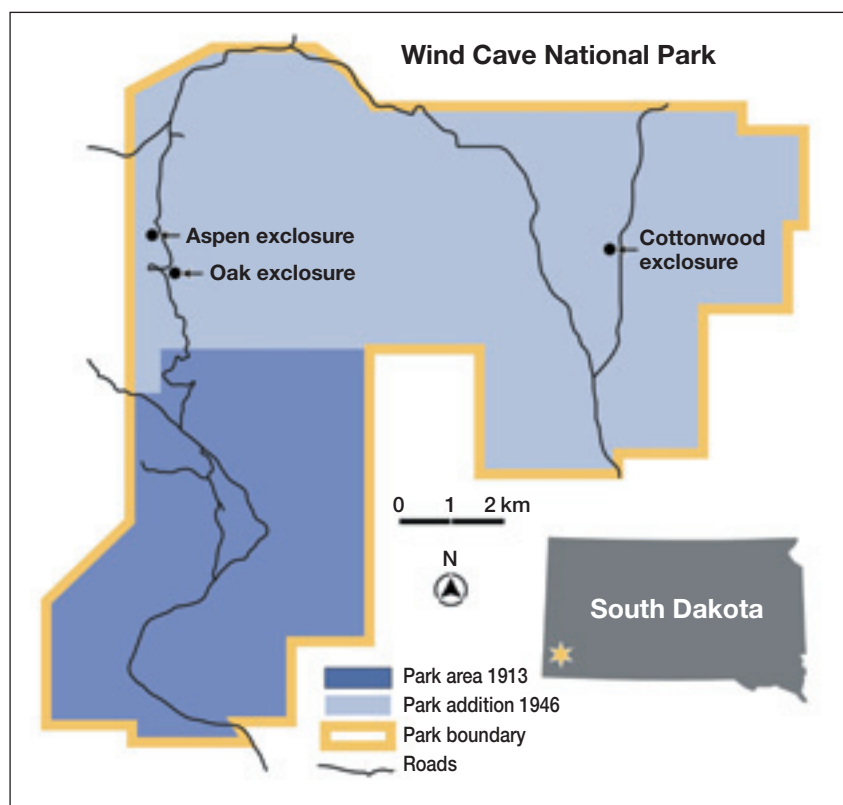


Figure 1. Map of Wind Cave National Park in southwestern South Dakota. Our study area comprised the entire northern part of the Park (light blue). This 66.2 km²-area was originally the Custer Recreational Demonstration Area, added to the Park in 1946.

Methods

We obtained information on human exploration and settlement, livestock grazing, land use, large carnivores, and ungulates from the late 1800s to the present from published books, articles, and government documents. In May 2005, we conducted a search for all cottonwoods (*Populus* spp) and bur oaks (*Quercus macrocarpa*) within the study area that were ≥ 1 cm in diameter at breast height (DBH). We also measured the height and browsing status of up to five cottonwood root sprouts associated with each tree.

For a subset of the measured trees, we extracted increment cores to determine tree age and develop relationships between tree DBH and age. These relationships were used to estimate establishment dates of individual trees and to develop frequency distributions of tree numbers by age (Beschta 2005). We also measured the diameter of all trees ≥ 1 cm DBH within a 2-ha cottonwood enclosure established in 1991 and a 0.2-ha bur oak enclosure established in 1977.

Results

Pre-settlement era

Historically, WCNP was a traditional hunting ground of the Lakota Sioux. In the summer of 1874, George A

Custer led a military and scientific expedition to the Black Hills and found a region with recent evidence of wildfire, plentiful forage, and abundant large carnivores and ungulates. In contrast to post-settlement fire suppression, pre-settlement fires may have occurred as frequently as every 10–12 years (Brown and Sieg 1999), a process that created plentiful forage and open, park-like settings, as illustrated by Custer Expedition photographs (Progulske 1974). Naturalist George Bird Grinnell, of the Custer Expedition, recorded the presence of elk, mule deer, white-tailed deer, pronghorn, beaver, wolves, grizzly bears, black bears (*Ursus americanus*), and cougars, but no coyotes and only limited signs of bison (Ludlow 1875). Grinnell wrote, “I found the gray wolf one of the most common animals in the Black Hills and hardly a day passed without seeing several . . . Their howlings were often heard at night” (Ludlow 1875). Grinnell also saw indications of large numbers of grizzly bears during his travels in the region (Ludlow 1875). He reported that beaver were numerous in this area and noted, “Almost all the streams which we passed were dammed in many places by beaver

and fresh tracks and signs were very plenty.” The expedition’s botanist, Aris Donaldson, documented an abundance of berry-producing shrubs and numerous wildflower species (Krause and Olson 1974).

While in the Black Hills, Custer’s expedition discovered gold, which triggered a rush of miners into the region and sparked the last major Indian war of the Great Plains. Custer lost his life in a battle in 1876. Soon afterward, the US cavalry suppressed Indian resistance and a treaty with the Sioux in 1877 opened the Black Hills to Euro-American settlement and livestock grazing.

Livestock era

In 1878, cattle were driven into the Black Hills to establish open-range ranching. Rewards were offered to settlers for the “taking of wolves and other large carnivores” (Palais 1942). By the early to mid-1880s, the Black Hills contained at least 500 000 head of cattle and approximately 85 000 head of sheep. Depleted range conditions were widely reported soon thereafter, due to the high stocking and continuous grazing of livestock. Thus, “. . . by 1885 the beaver had begun to disappear and their dams began to let go” (Palais 1942). By the end of the 1880s, homesteaders arrived and began replacing much of the open-range ranching with fenced-pasture ranching. As a result, bison, elk, pronghorn, and grizzly bears were

extirpated from the Black Hills by the late 1800s.

Park Service era

Bison were reintroduced into the relatively new WCNP in 1913 and 1916, and pronghorn in 1914. Elk were reintroduced to WCNP from Yellowstone National Park between 1911 and 1916. The WCNP superintendent's report for 1914 states, "Coyotes are common and an occasional gray wolf has been seen". Again in 1915, the superintendent's report notes, ". . . an occasional gray wolf seen in the park". The last wolf recorded in the vicinity of WCNP was killed in 1920 (Beard 1942).

After the 1946 WCNP expansion, the elk herd increased dramatically in size. By 1952, the elk population was estimated at over 1200 individuals (11 km^{-2}) and bison numbered over 400 animals (4 km^{-2}). Out of concern for impacts on herbaceous and woody vegetation, the Park Service has periodically removed elk and bison since the mid-1940s. However, their populations have undergone repeated periods of rapid increase following herd reductions, apparently because little predation occurs in the Park (Wydeven 1977). Since 1946, the Park Service has culled a total of 3200 elk and 3790 bison (mean annual removal of 54 elk and 64 bison; WCNP unpublished data).

Field studies

For trees of $\geq 1 \text{ cm}$ DBH within the study area and outside fenced exclosures, we found and measured 64 plains cottonwood (*P. deltoides*), 16 lanceleaf cottonwood (*P. acuminata*), and 56 bur oak trees. Root sprouts of plains cottonwood averaged 35 cm in height (range 4 to 99 cm; $n = 35$) with 86% browsed within the last year, while those of lanceleaf cottonwood averaged 50 cm (range 15 to 82 cm; $n = 38$) with 68% browsed within the last year.

We obtained 16 readable cores from cottonwoods and 18 readable cores from bur oaks. Based on estimated establishment dates from our tree diameter and age relationships, recruitment of plains cottonwoods and bur oaks peaked in the 1870s, diminished during the 1880s, and was essentially non-existent from the 1890s to the present (Figure 2). A small number of lanceleaf cottonwoods ($n = 12$) originated between 1900 and the 1920s, with no recruitment since the 1920s. It appears that none of the measured bur oaks originated before the 1860s. In a small site ($< 0.05 \text{ km}^2$), we found an additional 54 bur oaks encompassing size classes ranging from $< 1 \text{ cm}$ to

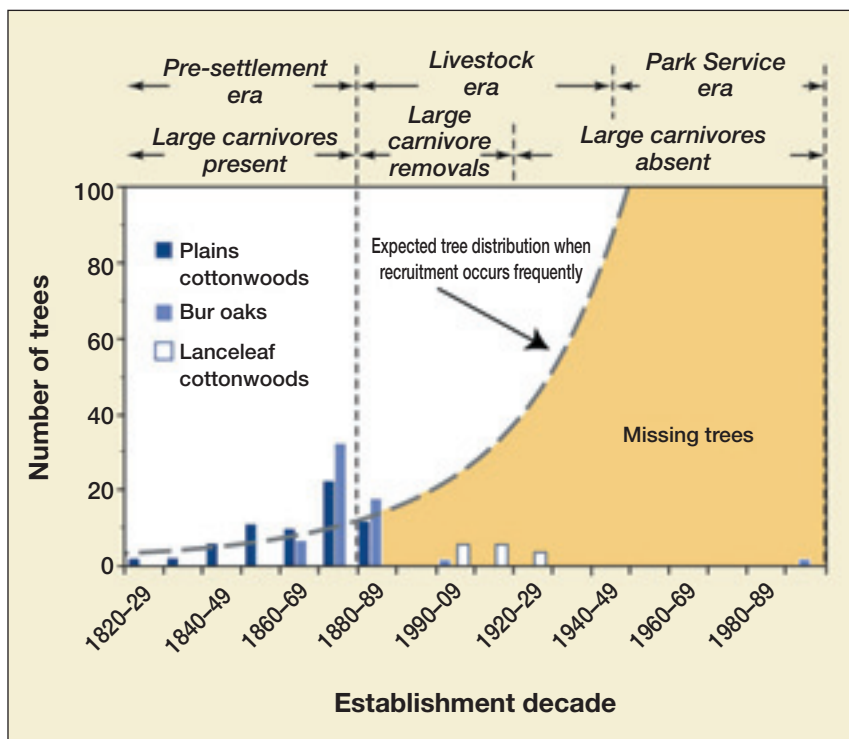


Figure 2. Estimated tree establishment dates in WCNP study area for plains cottonwood, lanceleaf cottonwood, and bur oak trees growing outside of fenced exclosures. Few trees have originated since the 1880s. The dashed line shows the expected pattern of tree numbers if recruitment occurred from the 1880s to the present. With natural stand dynamics, there should be exponentially more small young trees than large old trees (Beschta 2005).

51 cm DBH. These trees are relatively protected from ungulate browsing (refuge) since they were located in and around a pigtail bridge (a road bridge formed when the road curls around and passes over itself), as well as between the highway and a cliff. These features serve as physical barriers to ungulate movement. Our tree inventory data from inside the cottonwood and oak exclosures indicate a dramatic increase in recruitment of these species after the exclosure fences were constructed (Figure 3).

Discussion

Our data confirm a major gap in cottonwood and bur oak age structure at WCNP from the 1880s to the present (Figure 2). This lack of hardwood tree recruitment coincides temporally with large carnivore removals and the rapid increase in livestock numbers during the 1880s, and continues through the history of wild ungulate management by the Park Service.

Plains cottonwoods within the Park are near the end of their normal life span and are on the verge of local extirpation (Figure 4a). Without new recruitment, other hardwood species will also be extirpated within the Park in areas accessible to ungulates. For example, even though relatively prolific aspen recruitment is occurring within an exclosure (Figure 4b), there are only a few large-stem aspens growing across the entire Park. Other than within

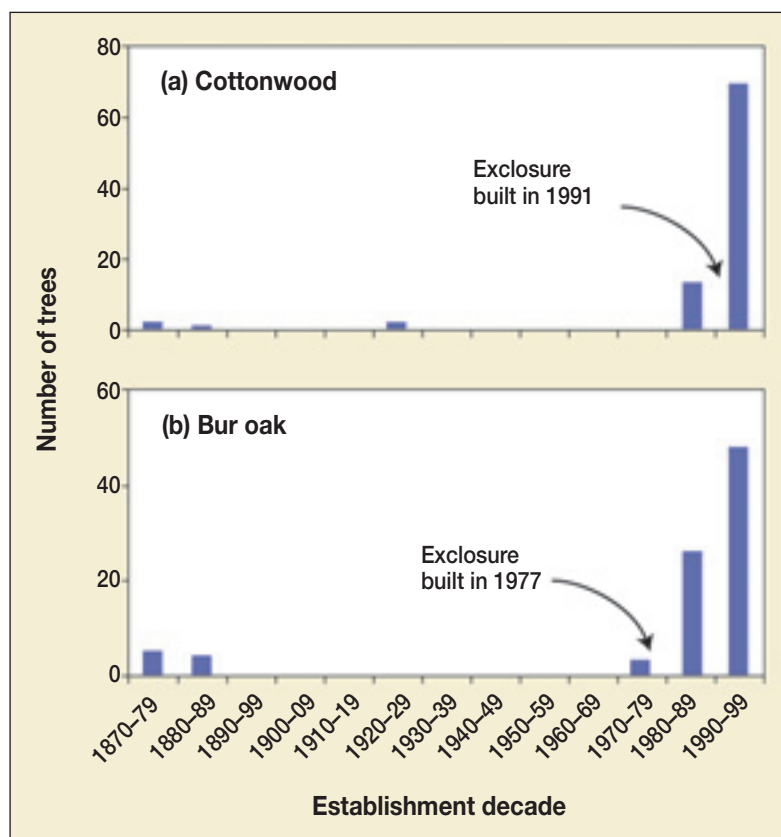


Figure 3. Estimated tree establishment dates inside ungulate exclosures for (a) cottonwoods (lanceleaf cottonwoods plus three plains cottonwood trees originating between 1870 and 1889) and (b) bur oak.

an exclosure, bur oaks were found recruiting to only a single small browsing refuge. Such small-scale, isolated refugia can often be found in broader landscapes heavily impacted by browsing (Beschta 2005).

Custer Expedition journal records suggest that the current flora and fauna conditions within WCNP starkly contrast with what might have been present in 1874. Members of the Custer Expedition described abundant large carnivores, ungulates, beaver, berry-producing shrubs, and wildflowers. For example, serviceberry, a browse species, was commonly observed: “The serviceberry is very abundant, both in the form of low bushes in open, dry, sparse copses and as thickets in the valleys, growing about as high as a man’s head. It furnished the most abundant berry met with by the expedition” (Ludlow 1875). More recently, Smith (unpublished) undertook a field study of rare trees and shrubs in WCNP and concluded, “The fact that red osier dogwood (*Cornus stolonifera*), serviceberry (*Amelanchier* spp), and sapling aspens (*Populus tremuloides*) are found only in secluded and inaccessible areas, combined with the fence-line differences in buffaloberry (*Shepherdia canadensis*) and bearberry (*Arctostaphylos uva-ursi*) numbers, suggest that browse utilization in the study area is intense.”

It is also noteworthy to contrast the contemporary abundance of coyotes and absence of wolves with the lack of coyotes and abundance of wolves as documented by

the Custer Expedition. Current coyote abundance may be the result of a mesocarnivore release, whereby the removal of large carnivores results in the overabundance of smaller predators, which may have different ecosystem impacts (Crooks and Soule 1999).

While beaver colonies currently exist outside WCNP on National Forest Service lands, there have been no active beaver colonies documented in WCNP since the early 1900s (B Muenchau pers comm). Since high-density ungulate populations can heavily browse woody plants in riparian areas, thus reducing forage available to beaver (Baker *et al.* 2005), the present lack of beaver within WCNP – which contrasts starkly with the abundance observed by Custer in 1874 – may well be a result of ungulate browsing.

Our results indicate a continuing lack of tree recruitment, even after the Park Service took control of these lands – a period characterized by the presence of wild ungulates and absence of domestic livestock. Furthermore, tree recruitment failed, even with long-term attempts by the Park Service to manage elk and bison populations through culling. Sport hunting or periodic removal by humans is not ecologically equivalent to persistent predation associated with large carnivores (Berger 2005). In addition to direct killing, the mere

presence of large carnivores can affect woody plant recruitment through predation risk, which influences spatial patterns of ungulate movement and herbivory (Ripple and Beschta 2004).

Our results from WCNP indicate that Great Plains ecosystems may have been profoundly altered by high levels of herbivory by wild or domestic ungulates after the removal of large carnivores. While WCNP currently has a complete wild ungulate guild, it has not had a complete large carnivore guild for many decades. In other national parks with incomplete carnivore guilds or low densities of large carnivores, significant impacts on deciduous woody species have also been documented (Berger *et al.* 2001; Hebblewhite *et al.* 2005).

Overall, the results of this study are consistent with recent tree ring research that examined the role of large carnivores in trophic cascades in other areas of the western US (Ripple and Larsen 2000; Beschta 2005; Binkley *et al.* 2006). Researchers have also documented altered river channel dynamics (Beschta and Ripple 2006), loss of beaver (Baker *et al.* 2005), reduction in abundance and diversity of birds (Berger *et al.* 2001), and reduction in berry-producing shrubs, followed by black bear extirpation (Côté 2005), in areas without wolves and with abundant ungulate populations.

While our results are consistent with trophic cascades theory, we nevertheless considered alternative scenarios

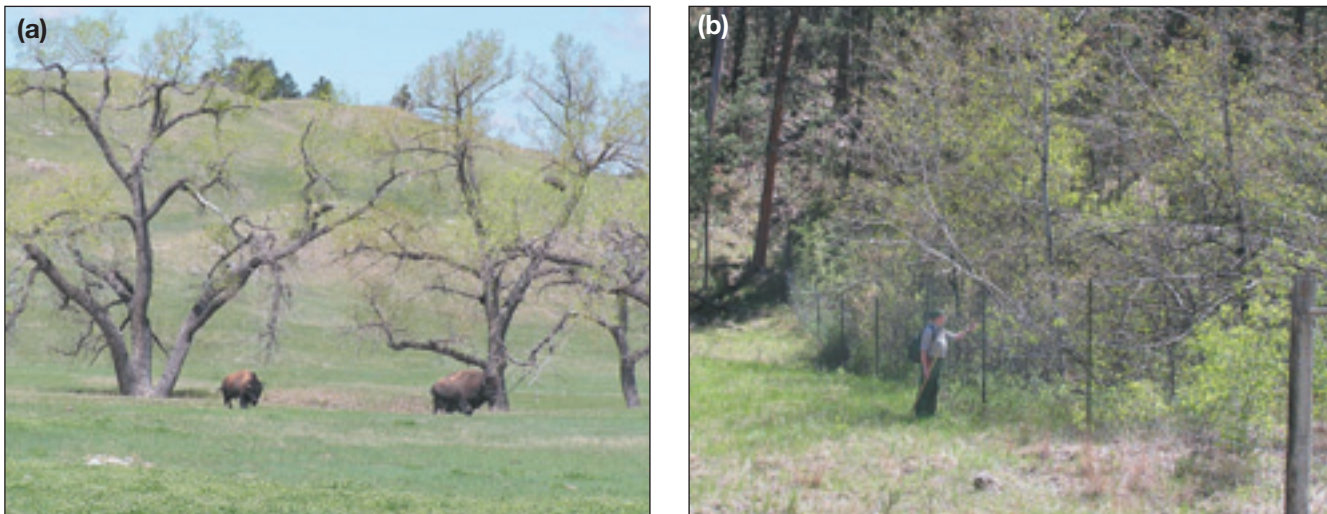


Figure 4. Photographs from May 2005. (a) Plains cottonwood trees and bison within the Wind Cave National Park study area. Note the lack of smaller tree size classes (ie recruitment gap). (b) Aspen enclosure built in 1978. Aspen inside the enclosure (right side of photo) were 4–6 m tall, while only small (<54 cm in height) aspen sprouts were found outside of the fence (left side of photo).

that might affect tree recruitment. Our data show no oak trees originating before the 1860s. Since bur oak was an important species for logging, the larger, older trees in our study area may have been cut by early settlers or loggers. Even if forest harvesting removed the larger trees, this does not explain the bur oak recruitment gap from the 1880s to the present. Furthermore, fire suppression and climate influences represent unlikely causes for the lack of tree recruitment, because enclosure data show excellent recruitment of multiple tree species immediately after fences excluded ungulate herbivory.

Potential confounding factors in this study include: (1) uncertainty associated with characterizations of historical large carnivore and ungulate populations; (2) different historical ungulate migration patterns, since those animals were not confined, as they are today, to the relatively small area enclosed by park fencing; (3) lack of randomization or replication for enclosure data due to limited availability of fenced enclosures within the Park; (4) the fact that Custer Expedition observations were made at least 25 km north of the current study area and may not be representative of the exact conditions within WCNP; and (5) our inability to estimate pre-settlement hunting pressure by the Sioux on ungulates and carnivores, as Native American hunting can affect these populations (Kay 1994; Laliberte and Ripple 2003).

Understanding the history of the WCNP study area was fundamental for our interpretation of present-day ecosystem structure. The legacy of human disturbances and alterations leading up to the present provided a necessary context for the realistic evaluation of ongoing effects. Using tree diameters and coring results, we were able to reach back over 150 years to assess stand structural dynamics of the hardwoods within WCNP. With the availability of fenced enclosures, we were also able to disentangle the potential effects of ungulate browsing from climate or other factors. Not surprisingly, perhaps, both

the hardwood tree recruitment gap and the enclosure data tend to confirm that ungulate herbivory represents a disturbance regime capable of having major effects on plant communities within the Great Plains biome.

Although various confounding factors are inevitable in any retrospective study of Great Plains ecosystems, our results are consistent with trophic cascades theory. Furthermore, the long-term inability of woody species to establish and grow over periods of multiple decades indicates that other plants and animals with much shorter life cycles than the trees studied herein may have been severely impacted or locally extirpated, thus reducing biodiversity. There is an important need for additional studies to identify potential biodiversity changes within the Great Plains biome that have resulted from long-term patterns of herbivory in the absence of large carnivores.

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