PNAS COMMENTARY

Bison outperform cattle at restoring their home on the range

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High-diversity grasslands are increasingly recognized as "old-growth" communities, having assembled over at least millennia, and often much, much longer (1, 2). Human-caused disturbance frequently disassembles such communities, reducing them to lower-diversity states (3). A substantial challenge to conservationists interested in habitat restoration is to reassemble high-diversity communities that have been degraded by anthropogenic disturbance. Although we know that certain North American grasslands have the potential for very high diversity of plants and other organisms (1, 4), we know relatively little about the historic influences of extirpated large native herbivores, which can be keystone species in the communities they inhabit (5). Among the reasons for our ignorance are the geographic extent and nature of degradation of grassland ecosystems: Many have been extensively plowed, the natural fire regime has been altered, and large native grazers have long been absent from most (1–3, 5). In the case of native grazer removal, one of the most important unknowns is how well the effects of these missing animals can be matched by similar nonnative stand-ins. These considerations bear on broader questions in conservation biology about "rewilding" and the restoration potential of influential species of all sorts. In PNAS, Ratajczak et al. (6) share evidence that reintroduced American bison (*Bison bison*) more effectively diversified a Great Plains plant community—from which bison had long been extirpated—than did their nonnative counterparts, cattle.

The US westward expansion of the 19th century caused bison numbers to crash and cattle numbers to soar. However, without unmodified reference sites it has been difficult to fully understand the extent to which these anthropogenic disturbances disassembled previously intact tallgrass prairie communities (5). Ratajczak et al. (6) studied the influence of native bison and domesticated cattle at the Konza Prairie Biological Station (KPBS) in Kansas, part of the Flint Hills ecoregion, which contains the largest remaining tract of unplowed tallgrass prairie (Fig. 1). For 29 y they compared vegetation among sites with bison, cattle, or neither large herbivore. During the long-term experiment, clear and consistently different trajectories characterized the three treatments. Ungrazed sites changed relatively little through time. In contrast, bison caused native plant species richness to increase compared to ungrazed sites during the nearly three-decade period, culminating in 103% higher species richness at the 10-m^2 plot scale and 86% higher richness at the larger catchment scale (each catchment was >18 ha and sampled with 20 noncontiguous plots). At the two respective scales, cattle caused modest 41% and 30% increases in native plant species richness compared to ungrazed sites. Relatively few nonnative plants were present in any of their sites. Bison concomitantly reduced combined cover of the four dominant grass species and increased forb cover, whereas dominant grass cover in sites grazed by cattle remained at intermediate levels between the relatively low dominant grass cover with bison and the relatively high grass cover in ungrazed sites. Fire is a key process in the tallgrass prairie ecosystem (5), but prescribed fire frequency (1- to 4-y return intervals) did not qualitatively change the observed outcomes with respect to grazer treatments.

To foster thoughtful conservation and restoration, Aldo Leopold (7) developed the Land Ethic—his philosophy concerning humans' responsibility toward nature. One of his metaphorical dictums was "to keep every cog and wheel is the first precaution of intelligent tinkering" (8). Even so, a general principle of community ecology is that some species play outsized roles in the ongoing process of community assembly. Keystone species wield large and disproportionately large influences relative to their abundances (9, 10). Foundation species form structurally dominant populations around which the rest of their community's species assemble (11, 12). Ecosystem engineers create, maintain, or modify habitat by physically altering environmental materials (13). With respect to community assembly, these various species of unusual effect (SUEs) are especially important "cogs and wheels." To remove any of these species from an intact community generally has substantial consequences for species composition, diversity, and often ecosystem function; to add one back to a community from which it was previously removed could have a similarly large effect on reversing those consequences.

By increasing plant species richness relative to ungrazed sites in the Konza Prairie experiment (6), it could be argued that both bison and cattle can play keystone roles in this tallgrass ecosystem. A previous smaller-scale, shorter-term experiment at KPBS found that both bison and cattle had a diversifying influence on the prairie vegetation (14). However, within the longer-term experiment, the bison effect on native plant species richness was more than double the cattle effect at the plot scale (6). In addition, sites with bison were more resilient to extreme drought (6). During the 20th and 21st years of the study, the Konza Prairie experienced one of its most severe droughts since the Dust Bowl of the 1930s. Although the drought reversed the steady increase in species richness that had occurred before the drought in

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Fig. 1. KPBS (site of the Konza Prairie Long-Term Ecological Research program): reintroduced native bison (*Top*), the prairie landscape with bison and prescribed fire (*Middle*), and narrow-leaved purple coneflower (*Echinacea angustifolia*), a native forb species (*Bottom*). All images courtesy of Eva Horne (Division of Biology, Kansas State University).

the bison-grazed catchments, species richness relatively rapidly recovered to meet a linear extrapolation of its predrought, steadily increasing trend. In contrast, postdrought species richness with cattle oscillated but resulted in no net change at the end of the study. In other words, reintroduced native bison are substantially more effective keystone species for diversifying the community than are domesticated cattle.

The relatively sustained increase in plant species diversity when bison were added back to the community supports the parsimonious conclusion that bison also had a diversifying influence before they were extirpated. We may never know whether the bison effect in the current study fully aligns catchments with the community compositions and biodiversity properties that existed prior to the 1800s, but higher diversity clearly benefits tallgrass prairie conservation. With so little relatively untouched, old-growth grassland remaining, any tract of high native species diversity is valuable (3, 5). Besides, bison also need habitat in which to roam!

How does a single species of large herbivore change the processes of community assembly so drastically, sustaining nearly three decades of diversifying influence and doubling small-scale plant diversity? Why are bison so much better at it than cattle? Ratajczak et al. (6) acknowledge that their large-herbivore treatments represent two different, albeit typical, land-use types that differ for a variety of reasons beyond grazer identity. In their experiment, grazing seasonality and stocking density differed between the two species. Bison and cattle also behave differently; e.g., bison generally selectively consume a higher percentage of dominant native grasses, create wallows, and exhibit their own distinctive individual and collective grazing-patch dynamics, resulting in particular patterns of microdisturbances (e.g., trampling) and nutrient redistribution (e.g., deposition of dung and urine) (5, 6). Whether the hyperdiversifying effect of bison results directly from increased fine-scale environmental heterogeneity owing to their idiosyncratic behaviors, indirectly through competitive release of high-diversity forbs, or some other cause, understanding the potential mechanisms for the observed pattern of vegetation differences among treatments would help resolve one of the most elusive problems in ecology: the maintenance of diversity in high-diversity communities (e.g., ref. 15). The mechanistic explanation could also help identify management options for cattle (e.g., stocking certain breeds or altering their husbandry) to render their effects more like those of bison and to diversify working grassland landscapes at an even broader scale to include areas where bison are unlikely to be added. In addition, further comparisons between native SUEs and analog species will help clarify the circumstances under which "rewilding" with functionally similar substitutes for native taxa differentially influences native biodiversity.

Restoration ecologists generally agree that it is usually favorable to bring back lost elements (native species, natural processes, etc.) when restoring a community (16, 17). This may be especially true for SUEs. For example, what would a tallgrass prairie be without its foundational guild of dominant C_4 grasses (5)? Similarly, Ripple et al. (18) recommend rewilding apex predatory wolves and ecosystem engineering beavers in US western states. They marshaled evidence that bringing back those focal species across selected landscapes could substantially help achieve the goal of the Conserving and Restoring America the Beautiful initiative codified in President Biden's Executive Order 14008—to conserve at least 30% of our national lands and waters by 2030. The study by

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Ratajczak et al. (6) further supports the ecosystem management rule of thumb that SUEs in natural communities can be unusually effective at diversifying anthropogenically disturbed communities, with great potential to meet the challenging policy objectives that face us as we continue to strive to create a sustainably diverse planet.

1. R. F. Noss *et al.*, How global biodiversity hotspots may go unrecognized: Lessons from the North American Coastal Plain. *Divers. Distrib.* **21**, 236–244 (2015).
2. A. N. Nerlekar, J. W. Veldman, High plant diversity and slow assembly of old-growth grasslands. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 18550–18556 (2020).
3. E. Buisson, S. Archibald, A. Fidelis, K. N. Suding, Ancient grasslands guide ambitious goals in grassland restoration. *Science* **377**, 594–598 (2022).
4. J. B. Wilson *et al.*, Plant species richness: The world records. *J. Veg. Sci.* **23**, 796–802 (2012).
5. A. K. Knapp *et al.*, The keystone role of bison in North American tallgrass prairie. *Bioscience* **49**, 39–50 (1999).
6. Z. Ratajczak *et al.*, Reintroducing bison results in long-running and resilient increases in grassland diversity. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2210433119 (2022).
7. A. Leopold, *A Sand County Almanac and Sketches Here and There* (Oxford University Press, 1949).
8. A. Leopold, *Round River: From the Journals of Aldo Leopold*, L. B. Leopold, Ed. (Oxford University Press, 1993).
9. R. T. Paine, A note on trophic complexity and community stability. *Am. Nat.* **103**, 91–93 (1969).
10. M. E. Power *et al.*, Challenges in the quest for keystones. *Bioscience* **46**, 609–620 (1996).
11. P. K. Dayton, "Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica" in *Proceedings of the Colloquium on Conservation Problems in Antarctica*, B. C. Parker, Ed. (Allen Press, Lawrence, KS, 1972) pp. 81–96.
12. A. M. Ellison *et al.*, Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* **3**, 479–486 (2005).
13. C. G. Jones, J. H. Lawton, M. Shachak, Organisms as ecosystem engineers. *Oikos* **69**, 373–386 (1994).
14. E. G. Towne, D. C. Hartnett, R. C. Cochran, Vegetation trends in tallgrass prairie from bison and cattle grazing. *Ecol. Appl.* **15**, 1550–1559 (2005).
15. P. Chesson, Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Evol. Syst.* **31**, 343–366 (2020).
16. A. D. Bradshaw, Underlying principles of restoration. *Can. J. Fish. Aquat. Sci.* **53** (suppl. 1), 3–9 (1996).
17. K. N. Suding, Toward an era of restoration in ecology: Successes, failures, and opportunities ahead. *Annu. Rev. Ecol. Evol. Syst.* **42**, 465–487 (2011).
18. W. J. Ripple *et al.*, Rewilding the American West. *Bioscience*, 10.1093/biosci/biac069 (2022).

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