RESTORATION ECOLOGY

Yellowstone's free-moving large bison herds provide a glimpse of their past ecosystem function

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Although momentum is building to restore bison across North America, most efforts focus on small, managed herds, leaving unclear how large, migrating herds shape landscapes and whether their effects enhance or degrade ecosystems. We assessed carbon and nitrogen dynamics across the northern Yellowstone ecosystem, where one of the last remaining large migratory populations resides. Bison stabilized net aboveground production while accelerating nitrogen turnover, increasing aboveground nitrogen pools while carbon pools remained stable, which improved landscape nutritional quality. Effects were strongest in wet, nutrient-rich habitats that received higher bison densities and grazing than is recommended in rangeland management, while soil and plant conditions suggested landscape resilience. Restoration should embrace heterogeneity in densities and effects across habitats and spatial scales beyond those guiding most current recovery efforts.

Migratory bison are, for all practical purposes, functionally extinct across their former range in North America (*1*, *2*). Bison were driven to near extinction in the late 1800s by market hunting, US military campaigns, and policies aimed at undermining Indigenous communities by destroying their primary food source. It is difficult to imagine the scale of the migrating herds before their decline. Historical accounts provide some illustration—Lewis and Clark estimated a herd of 20,000 bison in South Dakota in 1806, Thomas Farnham described a herd covering 3500 km^2 on the Santa Fe Trail in 1839, Colonel Richard H. Dodd encountered a herd of 3 million animals stretching 24 km wide by 40 km long along the Arkansas River in 1871, and Lakota oral histories measured herd size by the number of days it took them to pass (*3*, *4*). Today, there are about 400,000 bison, 95% of which are privately owned and raised for production, with an average herd size of 175 animals (*5*). The remainder exist in conservation herds averaging around 300 individuals, almost universally managed in constrained areas with strict limits on numbers and movements.

Research focused specifically on bison demonstrates that they can increase habitat heterogeneity, shape plant communities, and influence ecosystem functions such as nutrient cycling and productivity (*6–10*). But their role in large, migrating herds across broader landscapes remains poorly understood because today's bison are largely confined to ranches, refuges, reservations, and parks. Restoring this role would require recognizing that migratory bison systems operate differently than conventional grazing management frameworks. These frameworks regulate the timing and intensity of grazing to improve soil carbon storage and maintain desired plant communities (*11–15*). By contrast, historic bison migrations likely acted as a major ecological force, interacting with fire to create spatial and temporal heterogeneity (*7*). A bison-dominated North America was likely a heterogeneous landscape with highly concentrated impacts that might be perceived as degraded when viewed through the lens of modern grazing management (*16*, *17*).

Research from the Serengeti ecosystem, supported by plot-level experiments in North American tall and shortgrass prairies, African savannahs, and Tibetan alpine meadows, shows that grasslands are resilient to intensive grazing by native herbivores (*18–25*). This resilience arises from complex interactions among grazers, plants, and soil microbes that alter plant stoichiometry, primary production, nutrient cycling, and plant composition (*26–33*). Moreover, migratory animals move intentionally to exploit ephemeral foods (*34*, *35*), and the timing and amount of grazing in these areas may play a critical role in shaping animal feedbacks on soil and plant conditions (*36*). One notable trait of aggregate grazers, such as bison and wildebeest, is their propensity to create grazing lawns—heavily grazed areas characterized by short, nutritious vegetation that supports a diverse array of plant and animal species (*7*, *37*).

Restored bison migration enables analysis of grazing and nutrient dynamics

Restored bison migrations in the northern Yellowstone ecosystem now offer a rare opportunity to study how large herbivores shape grazing patterns and nutrient dynamics across a heterogeneous landscape. For more than 150 years, the Yellowstone area has served as a model for ecosystem restoration amid geographical, political, and societal constraints. It spans approximately 90,000 km^2 in the western United States. Through a series of evolving management strategies—including extirpation, reintroductions, control, and land use practices such as cultivation, hay production, and feeding wildlife—top predators and large herbivores such as wolves and bison (now occupying about 10% of the area) were restored to this landscape. Large herbivore populations, particularly elk and bison, fluctuated in response to these strategies (*38*). Since the 1960s, management within the park emphasized minimal human intervention, culminating in the restoration of a full predator guild by the late 1990s. Over recent decades, large herbivore biomass shifted from elk to bison (Fig. 1A). Bison numbers recently reached a stable winter population size because seasonal migrations (Fig. 1, B to D) out of the park have exposed them to hunting and federal removal efforts aimed at limiting range expansion (*39*).

We assessed grazing and nutrient dynamics across the northern migratory landscape from 2015 to 2022 by monitoring 16 sites representing three main habitats: valley bottoms (lawn-forming), adjacent hillsides (dry), and high-elevation topographically wet habitats (tables S1 and S2). Dry habitats were grazed in spring, fall, and winter depending on snowpack; lawn-forming habitats were grazed throughout the growing season; and high-elevation habitats were grazed from mid-season through season-ending frost. At each site, we compared natural grazing with grazing exclusion treatments using a repeated measures analysis of variance (ANOVA) design (*40*). Camera-trap data confirmed that bison were the primary grazers at these sites, accounting for more than 99% of relative abundance in lawn-forming habitats, 93% in high elevation habitats, and 77% in dry habitats (fig. S1).

Bison intensively graze lawn-forming habitats without depleting plant nitrogen pools

Bison numbers averaged near 3500 across the northern migratory landscape, utilizing roughly 852 km^2 annually at an average density of 4.2 bison km^{-2} year^{-1}. However, bison densities demonstrated significant variation across the migratory landscape during the growing season (Fig. 2A). The landscape produced an estimated 68 million kg

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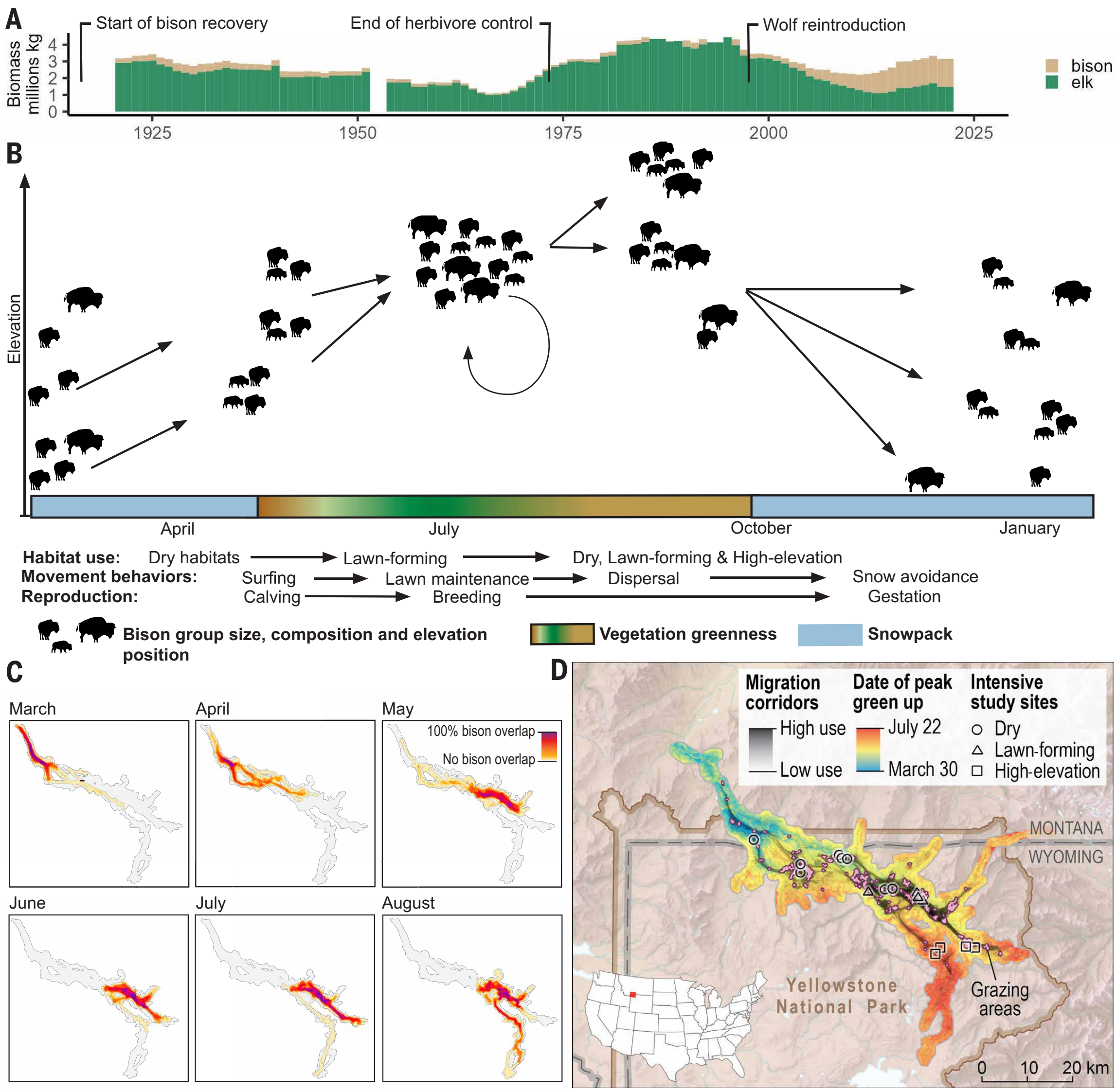

Fig. 1. Bison migration is a medley of moving in tempo with plant emergence, sustaining grazing lawns and escaping snow. (**A**) Bison now account for the majority of herbivore biomass on Yellowstone's northern range, which has a complete guild of migratory herbivores and their carnivores. (**B**) Beginning in spring at lower elevations in the West, bison move in dispersed groups, calving on the move and following the "green wave" of emerging vegetation (*36*). (**C**) As they ascend, they gather in larger, coordinated groups on floodplains and wet grasslands, forming grazing lawns crucial for nurturing calves (*36*). The longevity of high-quality food on these lawns depends on snowmelt and early summer moisture, and as they dry, many bison shift to higher elevations and subalpine meadows, exploiting the last of the emerging spring vegetation in Yellowstone. By fall, bison move westward to escape accumulating snow, pausing at productivity hotspots dictated by terrain. They typically migrate only as far as necessary, often not reaching the lowest elevations and delaying their arrival in the westernmost areas until late winter (*58*). (**D**) The main migratory route in Yellowstone covers about 100 km from west to east in the northern part of Yellowstone, influenced by varying moisture, productivity, and phenology gradients shaped by the region's topography.

of net aboveground production (NAP) per year, or ~19,000 kg of NAP per bison. Bison foraged at varying intensities across their migratory landscape, because consumption increased linearly with density [table S3; coefficient of determination (R^2) = 0.77]. Growing season net consumption was notably higher in lawn-forming habitats (table S4), averaging 135 ± 20.8 grams per square meter per season ($n = 12$) compared with 19.4 ± 3.1 ($n = 20$) in dry habitats and 66.9 ± 20.5 ($n = 7$) in high-elevation habitats. We defined "month" as the number of 30-day intervals since snowmelt at each site, thereby approximating the phenological stage of plant development. Using this definition, we found a significant interaction between habitat and month when comparing daily consumption rates across habitats (table S5). Pairwise comparisons revealed that daily consumption rates were similar across habitats in the first month, were higher in lawn-forming and high-elevation habitats in the second month, and remained higher in lawn-forming compared with dry habitats thereafter (fig. S2 and table S5). Bison consumed more in areas with greater NAP (grams per square meter per year), according to a mixed-effects model relating seasonal net consumption to NAP (Fig. 2B and table S6). The slope of this relationship was higher in lawn-forming habitats [0.64 ± 0.09; credible interval (CrI): 0.48 to 0.83] than in dry habitats (0.39 ± 0.19; CrI: 0 to 0.74) and high-elevation (0.44 ± 0.14; CrI: 0.20 to 0.73) habitats.

Higher bison densities and consumption per unit NAP for lawn-forming habitats suggest use of lawn-forming habitats beyond expectations from plant productivity. To understand why, we assessed carbon

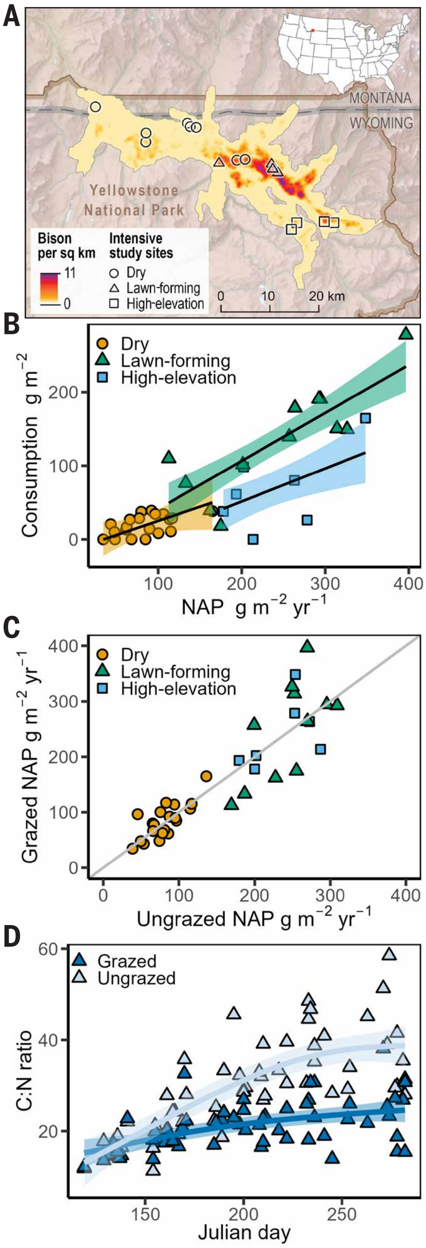

Fig. 2. Bison did not alter plant growth rate through their grazing but decreased whole-plant leaf C:N ratios. (**A**) Bison densities during the growing season were concentrated in lawn-forming habitats ranging from 5 to more than 10 bison per square kilometer per season. Bison densities were estimated from GPS collar and aerial count data. Growing season net consumption (grams per square meter per season) increased linearly with density (table S3; $R^2 = 0.77$). (**B**) Bison consumed more seasonally per unit net aboveground production (NAP; grams per square meter per year). A mixed-effects model showed that the slope of the consumption-NAP relationship was significantly higher in lawn-forming habitats (0.64 ± 0.09) than in dry (0.39 ± 0.19) or high-elevation habitats (0.44 ± 0.14). The 95% credible intervals are shown, based on a random intercept and slope linear model based on habitat. (**C**) NAP in grazed and ungrazed areas followed a 1:1 relationship across all production levels ($R^2 = 0.81$). In (B) and (C), points show annual values for each site (*40*). (**D**) Whole-plant carbon to nitrogen ratios were consistently lower in grazed treatments ($F_{1,52} = 18.52$, $P < 0.001$; table S11). Points show subsamples from each site across years for lawn-forming habitats, where effects were the strongest. Trend line was fitted using a generalized linear model assuming a Gamma distribution.

and nitrogen pools across different grazing areas. We calculated aboveground plant pools by multiplying total aboveground biomass by nutrient percentages. A significant three-way interaction among habitat, grazing treatment, and month affected the aboveground carbon pool size (table S7). This interaction was primarily driven by lawn-forming habitats, where high grazing significantly reduced the aboveground carbon pool size starting in the second month of the growing season (fig. S3 and table S7). Other habitats remained unaffected. However, grazing did not similarly impact the aboveground nitrogen pool size (table S8). Despite substantial bison consumption of plant material in these habitats, the nitrogen pool size in the remaining tissue of grazed plants was comparable to that of ungrazed plants throughout the summer in all habitats (fig. S4).

Grazing accelerates nitrogen cycling through plant regrowth and microbial feedbacks

To understand how plants maintained aboveground nitrogen pools despite intense, repeated grazing, we assessed growth rates and energy and nutrient flow in both grazed and ungrazed plants across the growing season. Grazed plants grew at the same rate as ungrazed plants (Fig. 2C and table S9). Growth rates varied by habitat and month of the growing season, with faster growth in lawn-forming and high-elevation habitats and slower growth in dry habitats (fig. S5 and table S9). Water availability is the primary limiting factor for plant growth in C3 ecosystems such as Yellowstone (*41*). Soil moisture levels were similar between grazed and ungrazed treatments (table S10), allowing soils to sustain essential growth processes such as exudation, microbial activity, and nutrient and water absorption (*42*, *43*). Consequently, as grazed and ungrazed plants grew at similar rates, the tissue removed by grazing was replaced with nitrogen-rich tissue (*41*, *44*). This led to an increase in the proportion of nitrogen in aboveground plant tissue in grazed treatments (Fig. 2D and table S11).

To understand the source of additional nitrogen, we examined microbial processes that mineralize organic matter into plant-available forms (*30*, *31*, *45*) for at least one 30-day period before peak biomass for a subset of sites. Grazing significantly increased microbial mass and ammonia-oxidizing bacteria (Fig. 3, A and B, and tables S12 and S13). This was accompanied by higher nitrogen availability, as measured by ion-exchange membranes that integrate nitrogen flux over time (Fig. 3C and table S14). However, mineralized nitrogen in soil cores was similar between grazing treatments at the start and end of the 30-day period (table S15), indicating rapid plant uptake. Total soil nitrogen—including both organic and mineralized forms—and soil carbon pools were also similar between treatments (tables S16 and S17). Taken together, these findings suggest that grazing enhanced nitrogen cycling without altering total soil nutrient stocks.

Bison grazing enhances crude protein availability across the migratory landscape

By considering the cumulative carbon and nitrogen consumed and reintegrating these nutrients into aboveground plant pools, we found that bison increased the aboveground plant nitrogen pool (Fig. 3D and table S18), while the concentration of carbon in the aboveground pool remained stable (table S19). The increase in the aboveground nitrogen pool was most pronounced at the peak of the growing season in lawn-forming habitats, as indicated by a significant three-way interaction among grazing treatment, habitat, and month (table S18). Established correlations between aboveground plant nitrogen and dietary crude protein for herbivores (*46*) show that when the aboveground plant nitrogen pool peaked, grazing provided 156% more crude protein in lawn-forming habitats, 119% more in dry habitats, and 155% more in high-elevation habitats.

Classic work by McNaughton and others demonstrated that herbivores could enhance nutrient cycling and create nutritional hotspots

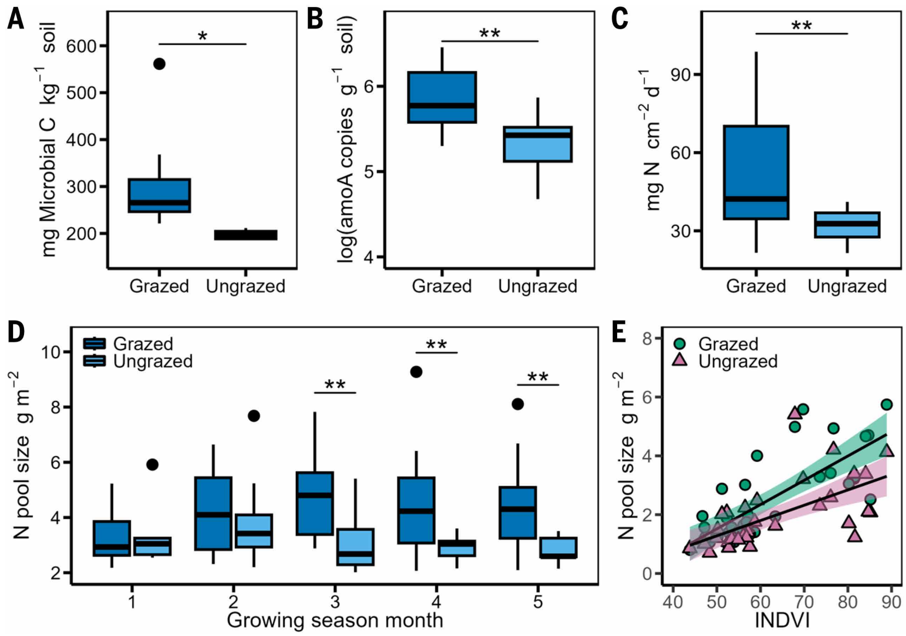

Fig. 3. Bison increased the size of the aboveground nitrogen pool through belowground linkages between microbes and plants. (**A**) Microbial mass increased in grazed treatments after periods of bison grazing (milligrams of microbial carbon per kilogram of soil; $F_{1,10} = 6.702$, $P = 0.027$; table S12). (**B**) Grazing increased the abundance of nitrogen cycle ammonia-oxidizing bacteria, which are responsible for converting soil ammonium into nitrite ($F_{1,20} = 10.678$, $P = 0.004$; table S13). Abundance was measured as the number of gene copies per gram of soil on the log scale of the ammonia monooxygenase (amoA) gene in *Eubacteria* quantified by quantitative polymerase chain reaction (*59*). (**C**) This, in turn, led to an increase in soil-plant available inorganic nitrogen (milligrams of nitrogen per square centimeter per day; $F_{1,18} = 8.208$, $P = 0.010$; table S14). (**D**) Plants in grazed treatments exhibited elevated nitrogen concentration in aboveground tissue ($F_{1,52} = 18.52$, $P < 0.001$; Fig. 2D and table S11), which was then consumed by bison (Fig. 2B and fig. S2). Reintegrating consumed nitrogen into aboveground plant pools resulted in higher aboveground plant nitrogen in grazed treatments as summer progressed, indicated by a three-way interaction among grazing treatment, habitat, and month ($F_{3.04,157.83} = 8.063$, $P = <0.001$; table S14). Adjusted N pool size is shown for lawn-forming habitats only. (**E**) Adjusted N pool size per unit of landscape greenness measured with integrated normalized difference vegetation index (INDVI) was higher in grazing treatments [table S20 (*40*)]. The relationship in (D) suggested that crude protein provided by the migratory landscape was doubled under grazing. In (A) to (D), the boxes represent the interquartile range, and asterisks (**P* < 0.05, ***P* < 0.01) indicate significant differences based on post hoc tests of treatment (grazed, ungrazed) effects from ANOVA analysis (*40*).

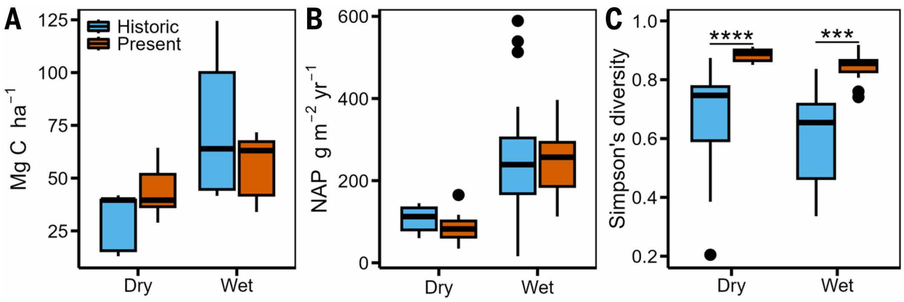

Fig. 4. The migratory landscape maintained soil carbon levels and herbaceous plant production, while plant communities became more diverse over several decades. (**A**) Soil carbon levels per hectare measured in the 1990s to 2000s (*45*,*48*) and (**B**) net aboveground plant production (NAP) measured in the 1980s to 1990s (*41*,*49*) were consistent with the conditions observed during 2015–2021. (**C**) However, plant diversity increased from the 1960s (*50*) to 2017–2021 (table S21). Soil and plant measurements were taken at different sites among periods generally reflecting dry and wet habitats across the migratory landscape. In each panel, the box represents the interquartile range, and asterisks (****P* < 0.001, *****P* < 0.0001) indicate significant differences based on pairwise comparisons.

through grazing, particularly in ecosystems that support grazing lawns (*7*, *18*, *19*, *37*, *47*). We extended this concept to estimate how such effects scale across a large migratory landscape by developing a linear model relating aboveground plant nitrogen pools to the Landsat-derived integrated normalized difference vegetation index (INDVI) and grazing treatment. We fitted the model to plot-level data (Fig. 3E and table S20) and applied it to predict aboveground nitrogen pool size across the landscape under grazed and ungrazed conditions. When converted to crude protein (*46*), grazing increased crude protein availability from approximately 3.45 million to 6.67 million kg.

Our findings suggest that the return of freely moving bison is actively stimulating and transforming Yellowstone grasslands. Landscape heterogeneity governs these dynamics. Wet, nutrient-rich soils foster intense grazing and nutrient acceleration, whereas drier areas receive less grazing and exhibit weaker nutrient effects. This produces strong spatial variation in grazing patterns and ecosystem processes, beyond what climate or topography alone would generate. Our work shows that spatial heterogeneity is an intrinsic feature of the migratory bison system. As this system continues to change—with bison now dominating the large herbivore guild (Fig. 1A)—cross-sectional data across multiple decades indicate that the landscape remains resilient. Soil carbon and NAP measured in the 1990s to 2000s (*45*, *48*) and 1980s to 1990s (*41*, *49*), respectively, were consistent with observations from 2015 to 2021 (Fig. 4, A and B). Plant diversity increased from levels recorded in the 1960s (*50*) to those measured from 2017 to 2021 (Fig 4C). Bison appear to be sustaining a dynamic grassland system that challenges the conventional emphasis for managing toward fixed, desired plant communities.

We expect that in grazing lawn habitats where herbivore engineering is the strongest, additional influences may exist, such as top-down control over plant composition, fire suppression, and increased diversity of smaller animals. Such effects are well documented in systems with large herbivores, which exert outsized effects on ecosystems (*24*, *25*). Additionally, owing to the substantial overlap of bison with other migrating herbivores (fig. S6) and increased available crude protein, we suspect that interspecific interactions such as facilitation are occurring in Yellowstone, similar to those identified in Serengeti National Park (*51*), but this has not yet been determined.

The Serengeti provides a valuable reference point, where a fully protected migratory route supports wildebeest near carrying capacity (*21*) and relatively stable predator populations (*52*). By contrast, only part of the Yellowstone bison migration route is protected, and removals outside the park limit bison densities (*39*, *53*). Yet bison are reshaping nutrient flow, producing effects absent or weaker in more constrained systems where herbivores are tightly regulated or fenced (*20*, *54*–*56*).

The claim that large herbivores have outsized effects on ecosystems is true (*24*). However, our findings reinforce that it is not just body size that matters. Large numbers, high densities, and the freedom to move across expansive landscapes are all critical (*57*). Whether it is 1.2 million wildebeest that shape the 25,000-km^2 Serengeti ecosystem, or a half-million caribou migrating >1200 km annually in the Alaskan tundra, the ecological function of migratory herbivores depends fundamentally on their ability to move across landscapes.

To move forward with conserving migratory herbivores and grassland ecosystems, we must embrace landscape-scale heterogeneity—not at the scale of individual ranches or pastures, but at sizes that allow for thousands of migrating large herbivores to move freely across the landscape. Our findings emphasize that ecosystems with large native herbivores, such as bison, can function successfully in today's world. Although challenges remain because of habitat fragmentation and sociopolitical constraints, restoring bison at this scale is not only possible—it works.

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SUPPLEMENTARY MATERIALS

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Materials and Methods; Figs. S1 to S7; Tables S1 to S23; References (*61*–*70*); MDAR Reproducibility Checklist

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