ARTICLE

Can grazing by elk and bison stimulate herbaceous plant productivity in semiarid ecosystems?

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Abstract

Plant communities in rangeland ecosystems vary widely in the degree to which they can compensate for losses to herbivores. Ecosystem-level factors have been proposed to affect this compensatory capacity, including timing and intensity of grazing, and availability of soil moisture and nutrients. Arid ecosystems are particularly challenging to predict because of their high degree of temporal variability in moisture inputs. We used a replicated herbivore exclusion experiment to evaluate herbaceous plant responses to grazing by large ungulates to test current theory and identify constraints on plant compensation in a dryland ecosystem. We measured nitrogen (N) yield and herbaceous production in three plant communities: meadows, willow-associated herbaceous communities, and riparian communities. We implemented grazing exclusion treatments from 2005 to 2008 in areas with elk and bison and areas with only elk. Grazing by large ungulates increased herbaceous production and N yield in herbaceous riparian communities. In willow communities, herbaceous plants displayed equal compensation in response to grazing in total aboveground production and N yield. Our results support the idea that plant compensation in this semiarid system is contingent on soil moisture availability, wherein the most productive sites (that received substantial moisture inputs from subsurface flow) exhibited overcompensation. Although the herbaceous riparian communities we studied are isolated patches of productive grassland in an otherwise shrub-dominated and minimally productive semiarid landscape, grazing by a combination of bison and elk removed only 44%–53% of aboveground net primary productivity (ANPP) during the growing season, and 25%–38% of production over winter. Consumption by ungulates was a positive linear function of herbaceous production, similar to reported patterns from other temperate and tropical grazing ecosystems. The slope of

this relationship was affected by the analytical method used to calculate ANPP and consumption rates, but, regardless of the method, was lower or similar to reported slopes for other intensively grazed systems (Yellowstone, Serengeti, Laikipia) that have sustained high ungulate densities for decades to centuries. Given that the vegetation communities exhibited equal or overcompensation in terms of total herbaceous ANPP in both years, elk and bison population levels during our study period did not appear to occur at densities leading to degradation of herbaceous communities.

INTRODUCTION

Herbivory has profound effects on vegetation production and structure (Augustine & McNaughton, 1998; Hobbs, 1996; Wisdom et al., 2006), and influences both directly and indirectly ecosystem processes aboveground and belowground (Bardgett & Wardle, 2010; Frank et al., 1998, 2002; Knapp et al., 1999; Schoenecker et al., 2004). The degree to which ungulate herbivores influence and potentially induce long-term degradation of the vegetation that supports their populations has long been of interest to ecologists, land managers, and agriculturalists. Mammalian vertebrate grazers evolved about 300 million years ago (Sues, 2000), and grazer–graminoid coevolution tracked the advent of grasslands in North America ~20 million years ago (Janis, 1989; McFadden, 1997). The concept that due to this coevolution, grazing may enhance the productivity of vegetation in some way was proposed by Ellison (1960) in a botanical review of grazing on rangelands. This potential effect was later described by the herbivore optimization hypothesis, which predicts an increase in aboveground net primary productivity (ANPP) at moderate grazing intensities up to some optimum, and a decrease with continued increases in grazing intensity (Dyer, 1975; Hilbert et al., 1981; McNaughton, 1979). McNaughton (1983) outlined the complexity of physiological and ecological mechanisms underlying responses to herbivory and concluded that based on available literature at the time "providing there is an intervening period of growth, removal of vegetative tissues to a certain proportion of their initial level is rarely translated into a commensurate proportional reduction in the final yield" (p. 331). The lack of such a commensurate proportional reduction in yield has been termed plant "tolerance" or "compensation." Plant overcompensation occurs when grazed plants produce significantly greater ANPP or have higher nitrogen (N) yield than ungrazed plants, equal compensation occurs when ANPP or N yield does not differ between grazed and ungrazed plants, and undercompensation occurs when grazed plants have significantly lower ANPP or N yield than ungrazed plants (Maschinski & Whitham, 1989; McNaughton, 1983).

Field experiments conducted in rangelands worldwide over the past half-century show that grazing by large mammalian herbivores can lead to equal- or overcompensation in herbaceous communities over a wide range of conditions (e.g., Augustine & McNaughton, 2006; Bagchi & Ritchie, 2011; Frank et al., 2002, 2016; Knapp et al., 2012; McNaughton, 1985). Understanding factors controlling the potential for plants to compensate for herbivory has major implications for the sustainable management of both wild and domestic large herbivores in these ecosystems. Maschinski and Whitham (1989) developed the compensatory continuum hypothesis, positing that increasing resource availability enhances potential for overcompensation in response to herbivory. This concept is consistent with a large body of ecological theory and research on plant resistance to herbivory (Coley, 1987; Milchunas & Lauenroth, 1993; Stamp, 2003). Both field and glasshouse studies provide empirical support that grasses can often replace tissue lost to herbivory where resources such as water, light, and nutrients are abundant and readily available, but not under conditions of low resource availability (Augustine & McNaughton, 2006; Chapin & McNaughton, 1989; Frank, 2007; Hamilton III et al., 1998). However, other studies indicate that plant response to herbivory is plastic and can potentially vary depending on multiple environmental conditions and resource limitations (Hawkes & Sullivan, 2001; Wise & Abrahamson, 2005). Wise and Abrahamson's limiting resource model predicts conditions under which plants compensate for herbivory by focusing on specific resources limiting plant fitness and the precise tissues that are damaged by herbivory. In addition, grazing preference by elk

and bison may contribute to herbaceous species composition differences, which influence how herbaceous vegetation responds to grazing (Frank et al., 2016).

The degree to which herbivores induce over- or under-compensation in grasslands is also linked to grazing intensity (Augustine & McNaughton, 1998; Briske & Richards, 1995; Milchunas & Lauenroth, 1993), and the way grazing pressure is distributed across the landscape in relation to variation in plant productivity (Augustine & McNaughton, 2006; Frank et al., 1998; McNaughton, 1985). Because ruminants face a trade-off between maximizing intake of high-quality forage and obtaining an adequate daily quantity of forage consumed, they are predicted to select grassland patches of intermediate biomass, with optimal patch biomass dependent on the ruminant's body size (Wilmshurst et al., 2000). Thus, all other factors being equal, plant communities of both low and high biomass are expected to experience lower grazing pressure than areas of intermediate biomass. In landscapes where highly productive grassland is widespread and herbivores occur at relatively low density, many high-ANPP patches may remain ungrazed early in the growing season. These patches can develop high standing biomass and correspondingly low digestibility later in the growing season, and therefore continue to experience low grazing intensity (e.g., Knapp et al., 1999). Under these conditions, we expect an arched relationship between ANPP and ungulate consumption. However, other conditions may allow herbivores to move spatially and temporally in response to the rate and timing of plant growth, resulting in a linear relationship between ANPP and herbivore consumption. These include migration of herbivores across spatiotemporal gradients of precipitation and soil nutrients (McNaughton, 1985) or temperature-controlled gradients of plant growth (Frank et al., 2016; Hebblewhite et al., 2008). In addition, localized responses of sedentary grazers to the patchy distribution of soil nutrients (Augustine et al., 2003; McNaughton, 1988) or other factors driving local variation in ANPP (e.g., soil moisture) could result in a linear relationship between ANPP and ungulate consumption. Understanding how grazing intensity varies in response to ANPP and factors controlling spatiotemporal variation in ANPP in different ecosystems is central to understanding mechanisms in which herbivores may induce under- or overcompensation.

Evaluating these ideas in dryland systems is particularly challenging because moisture availability can fluctuate dramatically, which has the potential to uncouple feedback between plants and herbivores (Ellis & Swift, 1988; Noy-Meir, 1973). However, where resources are predictable in space and time in portions of these dynamic ecosystems, such as riparian communities, intense grazing could still potentially lead to the feedback of herbivores to vegetation dynamics (Illius & O'Connor, 1999). Experimental field studies that quantify the intensity of grazing in relation to ANPP and the degree of compensatory plant response to grazing are needed to inform these competing perspectives on plant–herbivore interactions in semiarid ecosystems.

Here, we use a replicated herbivore exclusion experiment to evaluate herbaceous plant response to grazing by two large ungulates, bison (*Bison bison*) and elk (*Cervus elaphus*), in a semiarid ecosystem of western North America. We hypothesized that where both elk and bison coexist, grazing pressure would be sufficiently intense to result in plant undercompensation. In contrast, where bison are absent and elk are the sole large grazer, we hypothesized that plants would exhibit equal or overcompensation relative to areas with elk and bison. That is, the degree of compensation will depend on both resource availability (proxied by location) and amount of herbivore consumption (proxied by whether the site is elk only or elk + bison), and the extent of compensation will increase with an increase in productivity (shaped by water availability in this semiarid ecosystem). We applied two different analytical methods to calculate production and consumption to assess which was more appropriate (less biased) for water-limited systems. We compare our results with other well-studied temperate and tropical grazing ecosystems, in order to draw broader inferences about the capacity for plant communities to compensate for varying levels of grazing pressure and to provide a metric against which to compare offtake levels and sustainability of grazing in the Great Sand Dunes vegetation communities we studied.

MATERIALS AND METHODS

Study area

We conducted our study on the eastern region of the San Luis Valley of south-central Colorado, USA (Figure 1), within Great Sand Dunes National Park, the Baca National Wildlife Refuge, and The Nature Conservancy's Medano Ranch. The San Luis Valley is a semiarid, high-altitude (2300 m) intermountain basin just east of the Continental Divide, often referred to as a cold desert. Streams entering the southern portion form the headwaters of the Rio Grande, while the Closed Basin portion in the north is hydrologically closed. The Sangre de Cristo Mountains along the eastern boundary of the valley extend ~4000 m in elevation. Precipitation averages 280 mm annually and falls mostly during monsoonal rains in July through September. Summers are hot with daily maximum temperatures ranging from 33 to 28°C on the valley floor. Winters are cold and dry with minimum low temperatures ranging from −17 to −36°C. Eight
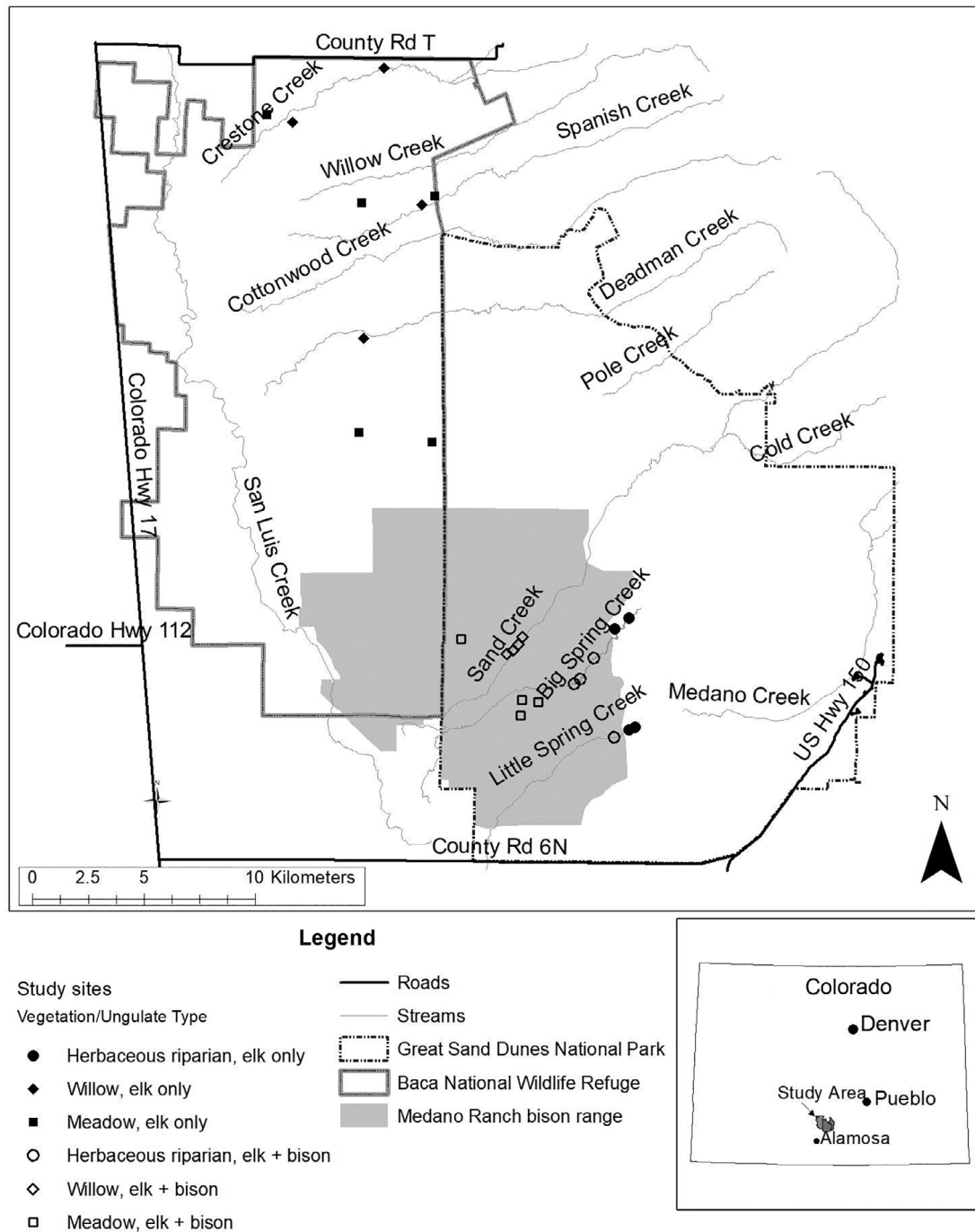
FIGURE 1 Map of exclosure locations in each vegetation community and ungulate stratum for plant compensation research conducted from 2005 to 2009 in the Great Sand Dunes National Park ecosystem of the San Luis Valley, Colorado, USA. Meadow communities had grazing cages, which are shown within elk-only and elk-bison sites, but not the large exclosures that were established in herbaceous riparian and willow communities

streams in the study area flow east to west, all of which have limited flow during the year and frequently disappear underground at their lower reaches.

This landscape contains the highest sand dunes in North America (229 m) with associated vegetation. Creeks and ephemeral wetlands run through the area, supporting riparian woody vegetation (Figure 1), as well

as localized patches of riparian herbaceous vegetation that can be substantially more productive than the upland plant communities that occur across the majority of the landscape. Our study focused on three herbaceous plant communities: meadows, herbaceous riparian, and willow understory communities. Willow communities were the driest sites based on depth-to-water table,

followed by meadows, with herbaceous riparian communities comprising the wettest sites (Appendix S1: Figure S1). Soil type and soil drainage classification varied by ungulate strata and vegetation community but was mostly comprised of poorly drained soils with medium site productivity potential, although willow communities in elk-only strata were the highest in productivity potential based on soil composition, despite being the driest community (Appendix S1: Table S1).

Meadow communities comprise roughly 10% of the study area and are interspersed across the landscape between the more linear riparian communities occurring along major drainages (Figure 1). Meadows typically exhibit seasonally saturated soils but lack the large seasonal and interannual water-table fluctuations characteristic of riparian herbaceous communities. Wet meadow soils are mineral soils, but they have significantly more organic matter than soils in the surrounding upland, which may cause them to drain and dry more readily than riparian herbaceous communities (Schweiger et al., 2015). Vegetation is largely dominated by native species forming a moderately dense-to-dense herbaceous layer. Graminoids typically dominate the herbaceous layer including *Carex praegracilis*, *Distichlis spicata*, *Hordeum jubatum*, *Juncus balticus*, *Leymus triticoides*, *Muhlenbergia asperifolia*, *M. wrightii*, *Pascopyrum smithii*, *Poa fendleriana*, *Puccinellia nuttalliana*, *Sporobolus airoides*, and forbs such as *Argentina anserina*, *Cleome multicaulis*, *Iris missouriensis*, and *Potentilla hippiana*. Scattered rabbitbrush (*Ericameria nauseosa*) or other shrubs may be present (Salas et al., 2011; Zeigenfuss & Schoenecker, 2015).

Herbaceous riparian communities comprise <1% of the study area but are among the most productive. The main characteristic of riparian areas is the presence of unidirectional moving water and a connection to surficial hydrology, although this connection may be seasonal (Schweiger et al., 2015). Vegetation is dense and dominated by sedges (*Carex aquatilis*, *C. simulata*, and *C. utriculata*), *Eleocharis acicularis*, *E. palustris*, *J. balticus*, and *Schoenoplectus pungens*. Forb species include *A. anserina*, *Berula erecta*, *C. multicaulis*, *Epilobium brachycarpum*, *Mimulus guttatus*, and *Veronica anagallis-aquatica* (Salas et al., 2011; Schoenecker, 2012). No shrubs are present. Soils tend to have a higher amount of organic matter than meadow communities, which allows them to hold water for a longer time.

Willow communities comprise less than 0.1% of the study area. Coyote willow (*Salix exigua*) is the predominant willow type within the study area. Other willow species (*S. ligulifolia* and *S. lucida* ssp. *caudata*) may also be found in these sites. Scattered trees, such as cottonwood, may also be present, and the understory ranges from barren to abundant forb and graminoid species (Salas et al., 2011). Understory herbaceous species include graminoids such as *Achnatherum hymenoides*, *C. utriculata*, *E. acicularis*, *J. balticus*, *L. triticoides*, and *M. asperifolia*, and forb species such as *Oenothera albicaulis*, *Psoralidium lanceolatum*, and *Senecio spartioides* var. *multicapitatus*; however, the majority of our willow study sites have low herbaceous productivity (Schoenecker, 2012; Zeigenfuss & Schoenecker, 2015).

Bison, elk, mule deer (*Odocoileus hemionus*), and pronghorn antelope (*Antilocapra americana*) were native to the area until about the 1840s when ungulates were mostly extirpated. Elk and pronghorn likely moved into the area from surrounding populations to the north and south, and mule deer populations have varied through time. Bison were returned to the landscape by private producers. The former Luis Marie "Baca" Ranch, which makes up the northern part of Great Sand Dunes National Park and all the Baca National Wildlife Refuge, was grazed by cattle (*Bos taurus*) until 2004. A population of bison ranging in size from approximately 1200–1500 individuals inhabited the 16,000-ha fenced Medano Ranch during our study period and were managed with annual gathers and removals. A population of approximately 4500 elk inhabit and move freely across the entire ~120,000-ha study area (Schoenecker & Lubow, 2016).

Sampling design

We selected plant communities that varied in moisture and grazing intensity. Riparian herbaceous and willow communities comprise only ~2% of the landscape but are the most important for native species biodiversity (Schulz & Leininger, 1990) owing to the structure they provide across the landscape for nesting birds, porcupines (*Erethizon dorsatus*), and a host of other small- and medium-sized mammals. The meadow community is more widespread (~10% of landscape) and important in providing much of the forage supply for large grazers. We evaluated each community in relation to two strata of ungulate use: elk as the primary grazer ("elk only"), and elk and bison together ("elk + bison"). Mule deer and pronghorn are also present in the study area, but are not considered primary herbivores due to their smaller body size (45 kg for pronghorn and 68 kg for mule deer, vs. 567 kg for bison and ~365 kg for elk; Wassink, 1993) and lower forage intake based on their density in the study area. Mule deer density was 0.03/ha (1.8 kg/ha) (CDOW, 2008a) during our study period, pronghorn density was 0.02/ha (0.8 kg/ha) (CDOW, 2008b), bison density was 0.08/ha (47.9 kg/ha) (Schoenecker, 2012), and elk density was 0.04/ha (13.7 kg/ha) (Schoenecker & Lubow, 2016). Ungulates have an average forage demand of

~2% of their body weight/day (Cordova et al., 1978; Holechek & Pieper, 1992), so the larger-bodied elk and bison have greater forage demands than deer and pronghorn.

In herbaceous riparian and willow communities, we established permanent exclosures to measure herbaceous productivity in the absence of ungulate grazing and additionally used movable grazing cages to measure herbaceous production and the amount consumed by ungulates. In meadow communities, we used movable exclosures to measure herbaceous production and consumption by ungulates, but we did not establish permanent exclosures. All exclosures were established in 2005, and measurements inside exclosures and movable grazing cages were conducted during 2006 and 2008.

We selected study sites for willow and herbaceous riparian communities from a group of randomly generated points within target communities in the two ungulate strata (Figure 1). We evaluated each point to ensure that there was enough area for a 0.4-ha grazed plot that could contain five grazing cages within the vegetation type. These small, movable cages protected ~1-m² areas from grazing for short periods. We established four replicate study sites in riparian herbaceous and willow communities, within each ungulate stratum (elk-only and elk + bison). At both sites, two plots were selected, and a coin flip determined which would be the 0.4-ha size exclosure versus the 0.4-ha grazed plot. Exclosures had 2.4-m-height fences and were either square or rectangular in shape. The willow communities in elk–bison areas differed from those in elk-only areas in terms of willow and herbaceous species composition, water regime, and soil type. For this reason, we did not compare elk–bison with elk-only willow community responses to herbivory. We established five grazing cages in nine meadow communities (four in elk-bison and five in elk only). Current-plus previous-year annual water year precipitation was 232 mm in 2005 + 2006 and 383 mm in 2007 + 2008 (Colorado Climate Center, http://climate.colostate.edu/wy_data.html; accessed 8 October 2021).

Data collection

Herbaceous production

We used five 1-m² movable cages on grazed controls adjacent to each treatment exclosure. Cages protected enclosed plants from ungulate grazing for several weeks, until we moved them based on peak phenology of C3 and C4 plants, to capture regrowth of grazed plants and measure total consumption for the season. We sampled annual aboveground herbaceous production by clipping all vegetation within 0.25-m² circular plots inside and outside cages, which were then randomly moved for the next sampling following McNaughton et al. (1996), McNaughton (1985), and Bonham (1989). Grazing cages were put in place in April 2006 and 2008, and then clipped and moved in June, July, and August/September. To estimate overwinter consumption, we clipped grazed plots and vegetation inside cages in April 2007. We clipped all graminoids, forbs, and subshrubs within plots at ground level, stored samples in paper bags, oven-dried samples at 55°C for 48 h, and then weighed them. We sorted a subsample of plots to separate live and dead plant materials, separating current-year production from previous-year dead material. On all sampling dates, we conducted the same measurements within permanent exclosures in willow and herbaceous riparian communities, randomly placing and clipping five circular plots inside exclosures. Data are available at https://doi.org/10.5066/P9961IKS.

Methods for estimating herbaceous production from the sequential sampling of plant biomass over time have been discussed (McNaughton et al., 1996; Sala et al., 1988), but not effectively resolved. Summing all positive increments of biomass can introduce an overestimation bias because random errors can produce both artificial peaks and troughs in biomass, even if no growth has occurred during an interval. We used two different analytical methods to estimate herbaceous production and consumption, which avoid this bias in different ways. We compare results of both methods, discuss how they affect our estimation of ANPP and grazing intensity, and address how methodology may affect comparisons of our results with other grazing ecosystems. The first method, described by Bonham (1989), estimates total herbaceous production using:

$$\text{ANPP}_g = P_1 + \sum_{i=1}^{T} \left(P_{c(i+1)} - P_{ui} \right),$$

where ANPP_g is the total aboveground net herbaceous production in the presence of grazers, $P_{c(i+1)}$ is the average amount of biomass in caged plots at time $i + 1$, and P_{ui} is the amount of biomass outside cages at time i. For the first time interval, $P_1 = P_{ci}$. We summed both positive and negative increments (hereafter referred to as the SPNI method) in biomass for each interval with the initial caged biomass to determine production. For each sampling period, we also calculated the difference in biomass inside versus outside cages, and we calculated total growing-season ungulate consumption (CPN) as the sum of all differences, whether positive or negative. We calculated total aboveground net herbaceous production in the ungrazed exclosures (ANPP_{ug}) as the sum of the average biomass clipped at the end of the first time period plus

the differences (whether positive or negative) in average biomass between each succeeding time period (Appendix S1: Figure S2). Inclusion of negative differences in the summed total avoids overestimation bias because the estimate of ANPP includes both positive and negative random errors. However, if there is substantial senescence of biomass during one interval of the growing season, this can result in an underestimate of total production. However, our field observations of plant phenology indicated no notable periods of senescence during our growing-season sampling periods in 2006 or 2008.

The second method avoids random errors by summing only those positive biomass increments that are statistically significant at a $p < 0.05$ or $p < 0.1$ level (referred to hereafter as the SSPI method; e.g., Augustine & McNaughton, 2006; Frank et al., 2002, 2016). Here, we used $p < 0.1$ given the low power of our tests due to limited sample sizes. For $ANPP_g$, we statistically compared biomass in uncaged plots at time i versus caged plots at time $i + 1$; for $ANPP_{ug}$, we compared biomass inside exclosures at time i and time $i + 1$; and for CPN, we compared biomass inside versus outside cages at time $i + 1$ across sites within each ungulate stratum (Appendix S1: Figure S2). A strength of SSPI is that it prevents random sampling errors from influencing estimates of ANPP and CPN. However, given the low sample sizes used at each site, it is possible that small amounts of plant growth or ungulate consumption in a given time interval would not be detected at a statistically significant level. Particularly if this happens over multiple time intervals, SSPI could underestimate ANPP and/or CPN. As a result, this method is most suited to systems where both growth and consumption occur in large pulses, but not where it occurs at low rates over multiple sampling intervals.

Herbaceous nitrogen yield

We collected graminoid and forb samples for N analyses in June, July, and August/September 2008 from the ungrazed (exclosed) treatments and grazed controls. We sorted samples by plant functional group, vegetation type, ungulate stratum, and grazing treatment. We took a representative subsample of plant material from each sample using all parts of the plant, and we combined them to form composites with three plots/composite. We ground composites in a Wiley Mill using a 20-gauge mesh screen to form a homogeneous mixture and processed them on a LECO C/N analyzer. A 0.10- to 0.11-g aliquot of each subsample was weighed, recorded, and placed into the autosampler. The LECO C/N analyzer uses combustion and an inert carrier gas (He) to process samples. Percent N is measured using a thermal conductivity detector. All samples were bracketed in increments of 10 with a blank and a known standard to ensure instrument accuracy. We calculated N yield by multiplying graminoid and forb production/site derived from the SPNI method by the corresponding %N for that functional group and site.

Statistical analyses

We analyzed data using the SAS statistical analysis software v9.2 (SAS Institute, Cary, NC). We analyzed herbaceous production data using a mixed linear model procedure (PROC MIXED) that is a generalization of the standard linear model designed to analyze data generated from several sources of variation. We tested for main effects and interaction effects of ungulate stratum, grazing treatment, and year (2006 and 2008) within each vegetation type with the effects of random sites and grazing treatments nested within an ungulate stratum. We collected pretreatment data in 2005 prior to fencing to ensure grazed and ungrazed sites did not differ. We determined plant response as overcompensation, equal compensation, or undercompensation by comparing production and N yield of herbaceous vegetation in grazed versus ungrazed treatments following Maschinski and Whitham (1989).

Comparing grazing ecosystems

To place our results in context with other grazing ecosystems, we compared our regressions for ANPP versus ungulate consumption from both elk-only and elk–bison strata to published regressions from three other grazing ecosystems: (1) grasslands in Yellowstone National Park grazed by elk and bison (Frank et al., 2016); (2) savannas of the Serengeti ecosystem in northern Tanzania and southern Kenya where grazing fauna is dominated by wildebeest (*Connochaetes taurinus*), plains zebra (*Equus quagga*), and Thompson's gazelles (*Eudorcas thomsonii*; McNaughton, 1985); and (3) savannas of the Laikipia Plateau in central Kenya where grazing fauna is dominated by impala (*Aepyceros melampus*), cattle (*B. taurus*), and plains zebra (Augustine & McNaughton, 2006).

RESULTS

When we examined differences in $ANPP_g$ estimates by the SPNI versus the SSPI method, and whether that difference varied by year, ungulate strata, or vegetation type, we found no differences by year or strata ($p > 0.06$),

but we found a significant interaction between method and vegetation type ($p = 0.039$). Contrast testing for a difference between methods in each vegetation type showed no difference for riparian herbaceous ($p = 0.15$) or willow communities ($p = 0.21$; Table 1), but the SPNI method estimated $ANPP_g$ for meadow communities to be greater (364 g/m^2 averaged across years and strata) than the SSPI method (299 g/m^2; $p = 0.043$). For estimates of $ANPP_{ug}$, we found no difference between methods that depended on year, strata, or vegetation type ($p > 0.26$ for all interaction terms), and no overall difference between methods ($p = 0.44$). Thus, estimates of both $ANPP_g$ and $ANPP_{ug}$ were largely similar across years, strata, and vegetation types, with the exception of lower estimates of $ANPP_g$ in meadow communities via SSPI. Hence, our estimates of the magnitude of over- or undercompensation were unaffected by method. Lower estimates based on SSPI in meadow communities reflect the slow rate of biomass increase in meadow sites over each measurement interval each growing season, such that some of these increments were not statistically significant.

Estimates of CPN were more strongly influenced by method, as reflected in a significant interaction between method, year, and vegetation type ($p = 0.012$). Consumption estimates were similar for riparian herbaceous and willow communities in 2006 ($p > 0.15$), but significantly lower based on SSPI than on SPNI for meadow communities in 2006 and for all three community types in 2008 ($p < 0.001$ for all four contrasts; Table 1). Both methods yielded very similar results for riparian herbaceous communities, where vegetation was productive and the most heavily grazed. SSPI detected few instances of significant differences in biomass inside versus outside cages for a given measurement interval for willow and meadow communities, and even estimated zero consumption in

all willow communities in both ungulate strata and both years. We observed signs of grazing at most study sites during the growing season, including bites on grasses, presence of dung and tracks, and direct observation of ungulates using sites. This was particularly evident in all three plant communities in the elk + bison strata, yet the SSPI method did not detect any significant intervals of grazing for willow sites in either ungulate strata. For this reason, the SPNI method appears to provide a less biased estimate of CPN, whereas SSPI was unable to capture the temporal pattern of low-intensity grazing that occurred in willow and meadow communities. Therefore, we present the analysis of overcompensation and consumption patterns hereafter based on SPNI. We note that none of the results for plant compensation were affected by method, and results for consumption patterns would only change if we had used SSPI by giving estimates of consumption in meadow and willow communities that were so low as to contradict field observations.

Herbaceous production and consumption

A generalized mixed model examining the influence of grazing treatment, ungulate strata, vegetation type, and year on herbaceous ANPP (estimated via the SPNI method) indicated that the effect of grazing treatment varied by ungulate strata and vegetation type (3-way interaction; $p = 0.061$) and also by year (2-way interaction; $p = 0.016$), so we examined contrasts between grazed versus ungrazed ANPP for each stratum, vegetation type, and year separately. In 2006, elk-only grazing enhanced ANPP 1.8-fold in riparian herbaceous sites ($p = 0.009$) and had no effect on ANPP in willow communities ($p = 0.28$), while grazing by elk and bison

TABLE 1 Comparison of estimates of ANPP in the presence and absence of grazing ($ANPP_g$ and $ANPP_{ug}$) and the amount of biomass consumed by grazers during the growing season (CPN) based on two different estimation methods (see "Methods" for a detailed description of methods)

Strata	Community	Sum of all positive and negative increments (SPNI)			Sum of all significant positive increments (SSPI)		
		$ANPP_g$	$ANPP_{ug}$	CPN	$ANPP_g$	$ANPP_{ug}$	CPN
Elk only	Herbaceous riparian	717 (54)	372 (23)	264 (66)	701 (63)	344 (40)	242 (68)
	Willow	269 (43)	233 (17)	44 (17)	309 (32)	222 (27)	0 (0)
	Meadow	412 (85)		76 (41)	339 (71)		33 (33)
Elk and bison	Herbaceous riparian	449 (44)	322 (24)	217 (44)	382 (53)	335 (23)	154 (52)
	Willow	76 (12)	57 (10)	38 (9)	109 (28)	52 (10)	0 (0)
	Meadow	329 (53)		147 (32)	267 (78)		40 (26)

Note: All values are in g/m^2, and values in parentheses show 1 SE based on 2 years of measurements at each of four sites per community in each ungulate stratum.

Abbreviation: ANPP, aboveground net primary productivity.

combined had no effect on ANPP in either community ($p > 0.28$; Figure 2). In 2008, elk-only grazing again enhanced ANPP in riparian herbaceous sites (2.1-fold; $p = 0.003$) and had no effect on herbaceous vegetation in willow communities ($p = 0.10$). In 2008, grazing by bison and elk enhanced ANPP in both riparian herbaceous (1.6-fold; $p = 0.032$) and willow communities (1.8-fold;
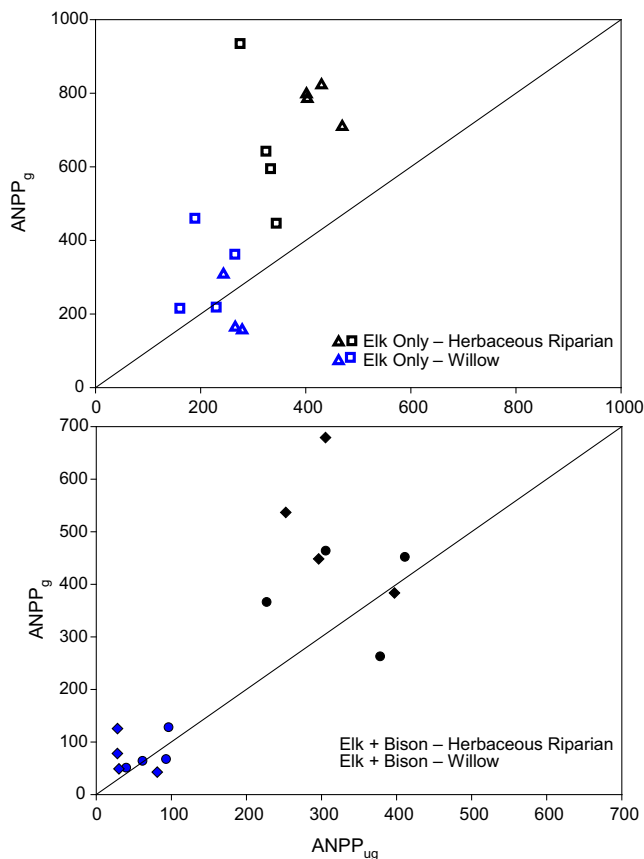

FIGURE 3 Relationships between aboveground net primary production and ungulate consumption rates for the portion of the study area supporting elk only and for the portion supporting both elk and bison. Both areas showed a linear relationship with nearly identical slope, but the intercept was significantly greater with both elk and bison than with elk only. Symbols on the left versus the right in the legend show results from 2006 to 2008, respectively. ANPP, aboveground net primary productivity

FIGURE 2 Relationships between aboveground net primary production of herbaceous communities when they were ungrazed ($ANPP_{ug}$) versus when they were grazed ($ANPP_g$) in the Great Sand Dunes (GRSA) ecosystem of southern Colorado. In the portion of GRSA grazed by elk only (upper panel), all herbaceous riparian sites were substantially more productive when grazed, that is, exhibited significant overcompensation. In contrast, for the portion of GRSA grazed by elk and bison, one herbaceous riparian site exhibited undercompensation (falling below the 1:1 line) in both 2006 and 2008, while the remainder showed overcompensation; averaged across sites, the magnitude of overcompensation was not significantly different from zero. For willow communities, which were less productive and also grazed less than hebaceous riparian sites, $ANPP_g$ was more similar to $ANPP_{ug}$ across sites in both herbivore strata. Averaged across sites and years, the magnitude of overcompensation in willow communities was not significantly different from zero. Symbols on the left versus right in the legends show 2006 and 2008, respectively. Meadow sites had no permanent exclosures, so only two communities are presented. ANPP, aboveground net primary productivity
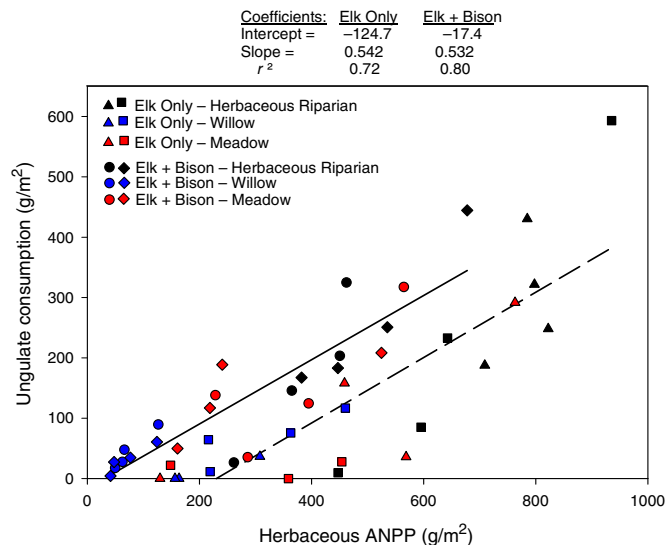
$p = 0.010$; Figure 2). Thus, elk-only grazing consistently resulted in overcompensation in riparian herbaceous and equal compensation in willows in both years. In contrast, grazing by elk plus bison resulted in equal compensation in both communities in 2006 and enhanced ANPP in both communities in 2008.

Ungulate consumption rates increased linearly with ANPP in both ungulate strata (Figure 3). Although the slope of this relationship was similar for elk-only and elk–bison strata, the intercept was significantly lower for elk–bison, meaning that grazing was more intense for any given level of ANPP, particularly in the willow and meadow communities (Figure 3). In the elk-only strata, we estimated ungulates consumed 33%, 13%, and 14% of ANPP in herbaceous riparian, willow, and meadow communities, respectively. In the elk–bison strata, we estimated ungulates consumed 45%, 46%, and 45% of ANPP in those three communities, respectively.

Herbaceous nitrogen yield

In elk–bison communities, herbaceous plants showed mostly equal compensation in response to herbivory; N yield did not differ between grazed and ungrazed treatments in both vegetation communities with the exception of grazed graminoids in willow communities, which

TABLE 2 Nitrogen (N) yield (g/m^2; mean with SE in parentheses) of herbaceous vegetation in herbaceous riparian (HR) communities and willow (W) communities grazed by elk only or elk and bison in the San Luis Valley, Colorado

Date by location	Veg class	Elk and bison			Elk only			Both strata pooled		
		Grazed	Ungrazed	p	Grazed	Ungrazed	p	Grazed	Ungrazed	p
HR										
Jul	F	0.51 (0.07)	0.53 (0.22)	0.917	0.49 (0.33)	0.76 (0.39)	0.628	0.50 (0.15)	0.63 (0.19)	0.728
	G	4.52 (0.82)	3.33 (0.31)	0.137	5.94 (0.56)	2.95 (0.74)	0.049	5.23 (0.54)	3.14 (0.38)	0.013
Sep	F	0.24 (0.14)	0.16 (0.11)	0.535	2.16 (1.55)	1.22 (0.68)	0.429	1.06 (0.71)	0.62 (0.34)	0.542
	G	3.55 (0.66)	3.52 (0.78)	0.912	4.20 (0.77)	3.88 (0.62)	0.418	3.88 (0.48)	3.70 (0.47)	0.796
W										
Jul	F	nd	nd	...	0.94 (0.54)	0.91 (0.54)	0.540	0.84 (0.43)	0.91 (0.54)	0.547
	G	nd	nd	...	3.82 (0.91)	2.21 (0.39)	0.153	3.11 (1.00)	2.21 (0.39)	0.994
Sep	F	1.30	0.11 (0.05)	...	1.23 (0.44)	0.55 (0.26)	0.026	1.24 (0.34)	0.30 (0.14)	a
	G	0.56 (0.08)	0.38 (0.14)	0.002	2.82 (0.07)	2.20 (0.27)	0.229	1.85 (0.46)	1.29 (0.37)	a

Note: Nitrogen samples were collected in 2008 from forb (F) and graminoid (G) species. The collection date was July to early August (Jul) or late August to September (Sep). There were no permanent exclosures in meadow communities, so samples were not collected from meadow sites. nd, not determined.
[a]Comparison not made due to site differences between strata.

displayed overcompensation in response to grazing (Table 2). In elk-only communities, N yield was higher in grazed riparian herbaceous graminoids than in ungrazed graminoids ($p = 0.013$), and higher in grazed forbs than in ungrazed forbs in elk-only willow communities (Table 2).

Comparing grazing ecosystems

Several prior studies quantified the relationship between herbaceous ANPP and ungulate consumption rates using methods comparable to our work in Great Sand Dunes (GRSA). Measurement of grasslands in Yellowstone National Park in the late 1980s when elk were abundant, bison were at low relative abundance, and both species migrated altitudinally during the growing season (Frank & McNaughton, 1992) shows a very similar relationship between ANPP and consumption as the area of GRSA grazed by elk and bison (Figure 4). In contrast, during the 2010s when bison had increased in abundance in Yellowstone and exhibited less migratory behavior, grazing intensity increased in Yellowstone, such that sites exceeding 200 g/m^2 experienced greater grazing intensity than riparian herbaceous communities in both strata of GRSA (Figure 4). Despite this higher level of grazing in the 2010s in Yellowstone, Frank et al. (2016) found that grazing still enhanced ANPP (i.e., resulted in overcompensation).

On the Laikipia Plateau of central Kenya, Augustine et al. (2003) quantified ungulate grazing intensity across a gradient of sites that varied in ANPP, where the most productive sites consisted of nutrient-enriched grassland patches that supported highly digestible and nutrient-rich grasses, and hence were used preferentially by both native and domestic grazers. Similarly, the most productive sites we studied in GRSA were small patches of
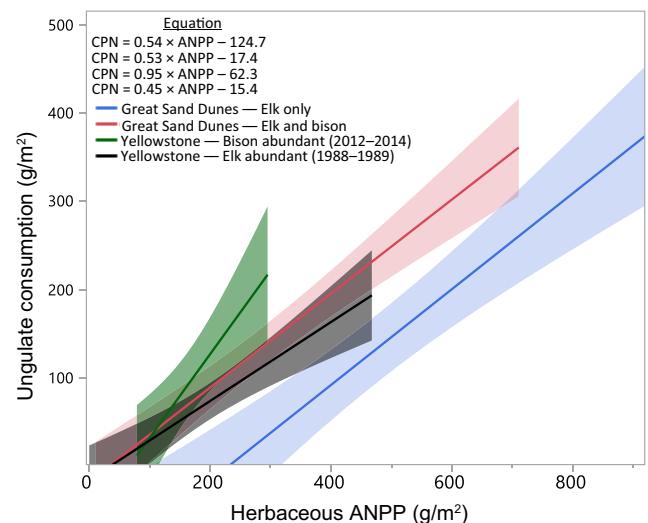

FIGURE 4 Comparison of the relationship between herbaceous aboveground net primary productivity (ANPP) and ungulate consumption in Yellowstone (Frank et al., 2016) and Great Sand Dunes (this study) ecosystems with varying abundances of elk and bison. Shaded areas surrounding each regression show 95% CIs. Recent measurements in Yellowstone (2012–2014), when bison had increased in abundance and become more sedentary in grazing distribution compared with the prior century, showed the steepest slope and hence highest grazing intensity, whereas slope and grazing intensity were lowest in the portion of Great Sand Dunes grazed only by elk. In all of these studies, experimental comparisons with ungrazed grassland showed no evidence that grazing suppressed herbaceous ANPP (Figure 2 of this study; figure 5 of Frank et al., 2016)

grassland receiving high water inputs from subsurface flow within a landscape of less productive plant communities. As with GRSA, the Laikipia ecosystem showed a strong linear relationship between ANPP and consumption, but with a significantly greater slope than both the elk-only and elk–bison strata of GRSA (Figure 5). For context, we compared these sites with the relationship between ANPP and consumption in the Serengeti ecosystem, which encompasses a much broader range of grassland ANPP driven by a precipitation gradient that includes sites substantially more mesic than GRSA and Laikipia (Figure 5). Grazing intensity in Serengeti was intermediate between that measured in Laikipia and the elk–bison strata of GRSA (Figure 5).

All studies depicted in Figures 4 and 5 additionally examined whether the level of grazing they documented could induce under- or overcompensation. All grazing
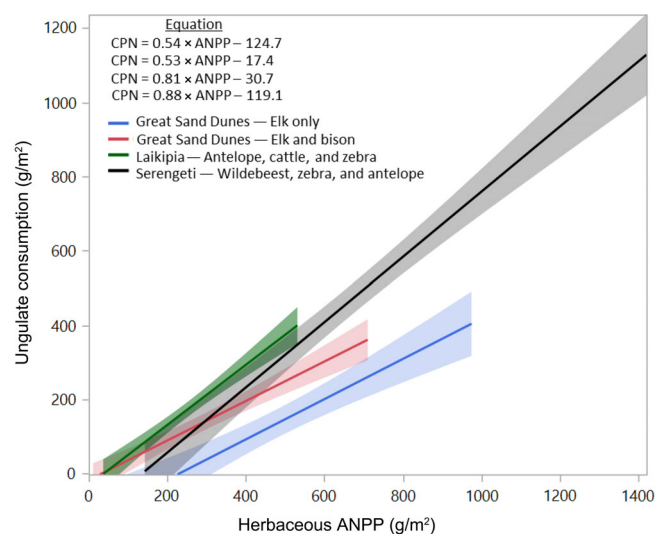

FIGURE 5 Comparison of the relationship between herbaceous aboveground net primary productivity (ANPP) and ungulate consumption in the Great Sand Dunes (GRSA) ecosystem with two tropical grazing ecosystems in Kenya and Tanzania. In both GRSA and the Laikipia Plateau, ungulates were primarily nonmigratory, and spatial variation in ANPP was associated with variation in either soil nutrients (Laikipia Plateau; created by patchy inputs of cattle manure from abandoned corrals; Augustine et al., 2003) or soil moisture (GRSA; created by subsurface flow to herbaceous riparian 'wet meadows'). In Serengeti, variation in productivity was due to a broad precipitation gradient, which included portions of the ecosystem receiving substantially greater rainfall than GRSA or Laikipia. Across all of the grazing intensities illustrated for Serengeti and GRSA (both strata), experimental comparisons with ungrazed grassland showed no evidence that grazing suppressed herbaceous ANPP (this study; McNaughton, 1985). In contrast, grazing enhanced productive sites in Laikipia with high soil nutrients (e.g., >200 g/m^2 ANPP) but suppressed ANPP on nutrient-limited, low-productivity sites (e.g., <200 g/m^2; Augustine & McNaughton, 2006)

intensities depicted in Figure 4 resulted in overcompensation or equal compensation (i.e., no cases of undercompensation; Frank & McNaughton, 1993; Frank et al., 2016; this study). For the studies in Figure 5, all the Serengeti sites showed overcompensation or equal compensation (McNaughton, 1985). In Laikipia, which had the highest grazing intensity of the systems plotted, intense grazing on the productive, nutrient-rich sites resulted in overcompensation, whereas grazing on the less productive, nutrient-poor sites (<200 g/m^2) resulted in undercompensation (Augustine & McNaughton, 2006).

DISCUSSION

Our results provide two important insights concerning the effects of large mammalian herbivores in the Great Sand Dunes ecosystem. First, herbaceous riparian communities exhibited substantial overcompensation in terms of both total herbaceous production and N yield. In the absence of grazing, these communities accumulate senescent plant material, which can lead to increased surface litter and standing material that alters resource availability within microsites, causes self-shading, immobilizes N, and can suppress plant production (Knapp & Seastedt, 1986). Herbaceous riparian areas in the San Luis Valley were highly productive relative to the rest of the ecosystem due to their high water-holding capacity and temporally stable water availability. Grazing prevented accumulation of standing dead material, likely allowing greater light into microsites and increasing nutrient deposition via feces and urine in readily available forms for uptake by herbaceous plants (Singer & Schoenecker, 2003). Second, the slope of the consumption by production line in GRSA was lower or similar to reported slopes for other intensively grazed systems in Yellowstone National Park and savannas of East Africa, which have sustained high ungulate densities for decades to centuries, suggesting grazing levels of elk and bison during the period of our study were not degrading herbaceous community productivity in the vegetation communities we studied.

Our results are mostly consistent with the compensatory continuum hypothesis (Maschinski & Whitham, 1989; McNaughton, 1979), in which plants overcompensate for herbivory in resource-rich environments (herbaceous riparian communities) and not in more resource-poor environments (willow communities), but there were clear inconsistencies. For example, elk-only grazing resulted in overcompensation only in herbaceous riparian communities (resource-rich) in both study years, whereas elk–bison grazing resulted in overcompensation in herbaceous riparian and willow communities (resource-poor) in 2008 (likely due to higher precipitation in 2007–2008 than in 2005–

2006; Appendix S1: Figure S3). Additionally, willow communities exhibited equal compensation in both (elk–bison and elk-only) strata in 2006 and overcompensation in both in 2008, suggesting the wet year in 2008 was locally significant to these patchy willow communities. Further, we observed little differentiation in plant response related to grazing intensity, despite sometimes large differences in offtake, refuting our hypothesis that the addition of a second large ungulate would induce undercompensation by herbaceous plants. In herbaceous riparian sites, growing-season consumption by elk and bison (45% of ANPP) exceeded consumption in sites grazed only by elk (34% of ANPP), yet we documented overcompensation at three of the four sites grazed by elk and bison, and all four of those grazed by elk only. Similarly, in willow communities, consumption by elk and bison (46%) was again significantly greater than by elk only (13%), but plants exhibited equal compensation in both strata in 2006 and overcompensation in both strata in 2008. Notably, soils underlying willow communities differed between the two herbivore strata. We did not measure soil nutrients, but soil types and soil drainage values indicated elk-only willow communities had much higher production potential than elk–bison willow communities. Willow communities experiencing higher grazing intensity in the elk–bison compared with the elk-only strata overcompensated in response to herbivory in 2008 despite having excessively drained soils with lower water tables and less water access for herbaceous plants, particularly during the latter parts of the growing season. We propose precipitation in 2007/2008 was a stronger factor in plant response to herbivory in this system than soil characteristics and grazing intensity, which were seemingly more favorable in elk-only sites. Herbaceous plants in both elk–bison and elk-only willow sites demonstrated strong tolerance to herbivory, also shown by higher N yield in grazed versus ungrazed graminoids (elk–bison) and forbs (elk–only). We considered whether grazing preference by elk and bison may have contributed to herbaceous species composition differences, which influenced vegetation response to grazing (Frank et al., 2016); however, exclosures were established in 2005 and measured in 2006 and 2008. Thus, we did not expect species composition changes to occur within this short time frame. We do note that the species present at our study sites, particularly the abundance of rhizomatous, sod-forming *Carex* species, likely played a role in the capacity for these communities to compensate or overcompensate for grazing effects. Finally, we posit that ecosystem characteristics we did not measure directly may explain variation we found in the degree of overcompensation, such as differing soil nutrient levels and soil microbial activity (Hamilton III & Frank, 2001; Van Der Heijden et al., 2007), preexisting species differences (specific species of graminoids or forbs) between

ungulate strata (see Frank et al., 2016), salinity of soils (Parida & Das, 2005), or other context-dependent characteristics of top-down (herbivore) and bottom-up (nutrient) regulation (Burkepile & Hay, 2006).

Herbaceous riparian communities represent a key resource for ungulate grazers in this landscape (sensu Illius & O'Connor, 1999), as they are limited in extent but extremely productive (~400–800 g/m^2 annually). This level of productivity is sustained by subsurface water inputs from the surrounding sand dunes and is substantially enhanced by ungulate grazing in terms of both total biomass production and N yield. The magnitude of this response is likely to vary across the landscape depending on rainfall patchiness, hydrology, streamflow, and other environmental variables, and was greater with lower grazing pressure (i.e., elk-only strata) than with the higher grazing intensity of elk and bison. Previous work also suggests that chronic, year-round grazing by nonmigratory herbivores (e.g., Augustine & McNaughton, 2006; Knapp et al., 2012) may lead to smaller compensatory responses compared with systems experiencing seasonally pulsed grazing by migratory herbivores (e.g., Frank et al., 2002; McNaughton, 1985). Our findings show that even for plant communities grazed throughout the growing season, ungulate grazing can enhance aboveground net primary productivity of herbaceous communities in portions of the landscape where soil resources are least limiting to plant growth (this study; Augustine & McNaughton, 2006), but that the magnitude of enhancement will depend on grazing intensity. A corollary is that long-term monitoring should not just focus on resource-rich patches where grazing is focused, such as herbaceous riparian communities, but also focus on low-productivity sites where soil moisture and nutrient limitation could render the community more susceptible to increasing levels of grazing (such as meadow, greasewood [*Sarcobatus vermiculatus*], and rabbitbrush communities).

Analyses of ruminant energetic constraints predict they will typically select swards of intermediate biomass (Wilmshurst et al., 1999, 2000). This should result in a curvilinear relationship between ANPP and ungulate consumption if a majority of high-ANPP grassland remains ungrazed early in the growing season, and therefore develops into high biomass/low digestibility swards as the season progresses. Such a pattern was observed in Yellowstone grasslands in the early 2000s, when elk and bison populations were relatively low, and the most productive grass patches in the landscape experienced low grazing intensity, although low grazing intensity of those patches was proximally explained by the vigilance of elk at some of their study sites (Frank et al., 2016). Similarly, in mesic grasslands where forage growth rates can outpace ungulate consumption in a majority of the landscape early in the growing season (e.g., unburned

tallgrass prairie or mesic tropical savannas), ungulates may track patches of intermediate productivity such that low- and high-productivity patches experience minimal grazing, or fire–grazer interactions are necessary to facilitate the use of the most productive areas (Fuhlendorf et al., 2009). In contrast, when ungulates were sufficiently abundant in Yellowstone to continually graze productive swards, the relationship became linear even in the presence of wolves and without fire interactions (Frank et al., 2016; see Figures 4 and 5). Furthermore, where ANPP covaries with soil nutrients and forage quality both at small spatial scales (e.g., hectares; Augustine et al., 2003) and across broad precipitation and nutrient gradients (e.g., 10s to 100s of kilometers; McNaughton, 1985), we see linear relationships between ANPP and ungulate consumption. Our findings for GRSA show that this also occurs in an arid grazing ecosystem where productive patches created by subsurface flow attract ungulates and sustain high levels of grazing throughout the growing season. Unlike Yellowstone, where a reduction in ungulate populations and the presence of wolves led to a nonlinear grazing pattern in the 2000s (Frank et al., 2016), the relationship remained linear in GRSA with lower ungulate abundance (i.e., the elk-only strata) and no wolves because of the patchy distribution of highly productive herbaceous resources. A similar dynamic was reported in Laikipia in which patchy distribution of soil nutrients created resource-rich, highly productive herbaceous patches that experienced sustained, intense grazing, leading to a linear relationship between production and consumption across the landscape (Augustine et al., 2003). Notably, in both Laikipia and GRSA, the intensity of grazing documented in these patches did not lead to undercompensation (this study; Augustine & McNaughton, 2006). These findings highlight the need to carefully consider the relative distribution of ANPP across grazed landscapes, and the underlying resource-based drivers of variation in ANPP (i.e., patchiness of resources such as soil nutrients, soil moisture, and precipitation) in order to better understand the sustainability of grazing ecosystems.

CONCLUSIONS

Consumption by ungulates at a given site in Great Sand Dunes National Park was a positive linear function of herbaceous production similar to reported patterns from other temperate and tropical grazing ecosystems. The slope of this relationship was affected by the analytical method used to calculate ANPP and consumption rates. But regardless of the method, it was lower or similar to reported slopes for other intensively grazed systems, such as those in Yellowstone National Park and savannas of East Africa. These ecosystems have sustained high

ungulate densities for decades to centuries. Given that the vegetation communities we studied exhibited equal or overcompensation in terms of total herbaceous ANPP in both years (with ~average rainfall), elk and bison population levels and consumption rates at the time of our study did not impose grazing intensities that degraded herbaceous community productivity. However, if drought conditions persist and rainfall conditions decline, vegetation monitoring would be prudent.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data (Schoenecker & Zeigenfuss, 2022) are available from ScienceBase: https://doi.org/10.5066/P9961IKS.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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