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Past and present biomass consumption by herbivores and fire across productivity gradients in North America

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Abstract

Herbivores and fire are important consumers of plant biomass that influence vegetation structure, nutrient cycling, and biodiversity globally. Departures from historic biomass consumption patterns due to wild herbivore losses, livestock proliferation, and altered fire regimes can have critical ecological consequences. We set out to (i) understand how consumer dominance and prevalence responded to spatial and temporal moisture gradients in Holocene North America and (ii) examine how past and present consumer dominance patterns in North America compare to less altered consumer regimes of modern Sub-Saharan Africa. We developed long-term records of bison abundance and biomass burning in Holocene midcontinent North America and compared these records to reconstructions of moisture availability and vegetation structure. We used these reconstructions to characterize bison and fire prevalence across associated moisture and vegetation gradients. We found that bison herbivory dominated biomass consumption in dry settings whereas fire dominated in wetter environments. Historical distributions of herbivory and burning in midcontinent North America resemble those of contemporary Sub-Saharan Africa, suggesting disturbance feedbacks and interactions regulate long-term consumer dynamics. Comparisons of consumer dynamics in contemporary North America with Holocene North America and Sub-Saharan Africa also reveal that fire is functionally absent from regions where it was once common, with profound ecological implications.

1. Introduction

Biomass consumption by herbivores and fire has shaped vegetation structure and composition, and the distribution of terrestrial biomes on Earth for millions of years (Bond and Scott 2010, Charles-Dominique *et al* 2016). From the extinction of most Pleistocene megafauna to the introduction of Old World livestock, bison (*Bison spp.*) were the dominant large herbivore in many of North America's grasslands, woodlands, and savannas (Wendt *et al* 2022). The activities of tens of millions of bison contributed to large-scale biomass consumption and turnover, nutrient redistribution, and direct disturbance of hundreds of millions of hectares (Knapp *et al* 1999, Nickell *et al* 2018). Bison abundance and distribution were influenced by climate, which shaped the quantity, quality, and type of forage as well as interspecific competition and predation dynamics (Wendt *et al* 2022). Fire activity and fire regimes were similarly shaped by variations in climate, fuel type, availability and condition, as well as local edaphic and topographic features (Schoennagel *et al* 2004, Bond and Keeley 2005, Whitlock *et al* 2010). Additionally, after arriving in the Americas over 21k years ago (Bennett *et al* 2021, Pigati *et al* 2023), humans played an important role in modifying the distribution of fire and herbivore 'consumer regimes', by regulating the frequency, timing, and extent of both fire, via intentional burning, and herbivory, via management of wild and domestic herbivores (Nowacki *et al* 2012, Roos *et al* 2018). Beginning with the introduction of cattle by Europeans in the 16th century (Rouse 1977, Delsol *et al* 2023), intensively managed and spatially constrained domestic livestock production systems have largely replaced free roaming herds of large herbivores in North America. Acknowledgement of widespread ecological impacts caused by altered fire patterns and herbivore communities has prompted calls for and motivated initiatives aimed at restoring ancient consumer regimes (Fuhlendorf *et al* 2009, Lorimer *et al* 2015). Yet, the extent to which North American consumer regimes have been altered and the ecological consequences of these transitions remain surprisingly poorly understood, primarily due to the lack of long-term records of domestic and wild herbivore abundance and impacts.

Linking fossil-based reconstructions of past bison abundance with sediment charcoal records of burning provides new opportunities to evaluate past biomass consumption by large herbivores and fire (Wendt *et al* 2022). However, understanding historical and current consumer dynamics in North America is challenging due to recent ecological transformations caused by the removal of large wild herbivore populations, the establishment of modern livestock production systems, fire suppression, and the replacement of native plant assemblages with cropland. In contrast to contemporary North America, Sub-Saharan Africa has retained large, extensive populations of wild herbivores and fire activity is relatively unconstrained by fire suppression. The distribution and drivers of African consumer regimes thus provide a valuable ecological model against which the changes and consequences of anthropogenic ecosystem transformation in North America can be assessed (Gill 2015, Archibald and Hempson 2016). Reconstructing historic consumer prevalence and comparing consumer dynamics with a more intact system is an important step toward revealing the processes that influenced the evolution and persistence of North American ecosystems, and for understanding the implications of human-modified consumer regimes for nutrient cycling, soil development, biodiversity, and ecosystem change.

The relative dominance of fire and herbivores as biomass consumers varies across abiotic and biotic gradients and is influenced by a set of interacting drivers that include climate, vegetation, soil, regional evolutionary histories, consumer interactions, and human activities. While the relative proportion of biomass consumption by herbivores and fire spans a continuum, data suggest there are three general consumer modes that occur in terrestrial ecosystems: herbivore dominance, fire dominance, and co-dominance (Archibald and Hempson 2016, figure 1(C)). These modes reflect general outcomes of competition between herbivores and fire across moisture/vegetation production gradients at large spatiotemporal scales. Climate controls primary production by influencing precipitation, solar radiation, and temperature. While fire and/or herbivory are present in most systems, the relative dominance of either is strongly influenced by moisture availability and related vegetation/fuel characteristics (Whitlock *et al* 2010, Archibald and Hempson 2016, Hempson *et al* 2019). In dry ecosystems, where forage is available, but fire spread is usually limited by discontinuous fuels, herbivores are expected to consume more biomass than fire (Archibald and Hempson 2016; see 'herbivore dominance' in figure 1(C)). Conversely, fire is expected to consume more biomass than herbivores in wetter ecosystems where biomass is abundant but less palatable and/or less accessible to herbivores (Archibald and Hempson 2016, Hempson *et al* 2019; see 'fire dominance' in figure 1(C)). At intermediate moisture levels both fire and herbivores can consume large quantities of vegetation (Archibald and Hempson 2016; see co-dominance in figure 1(C)). These intermediate moisture zones have the greatest potential for synergistic fire-herbivore interactions, exemplified by pyric herbivory (fire-driven grazing) and managed patch-burn grazing (Fuhlendorf and Engle 2004, Archibald *et al* 2005, Allred *et al* 2011), as well as competitive exclusion via positive feedbacks with functionally distinct grass communities (Hempson *et al* 2019). In addition, human activity can dramatically alter biomass consumption patterns resulting in more or less fire or herbivory than expected based on the influence of climate alone (McWethy *et al* 2013, Hempson *et al* 2017). Herbivory and fire are dynamic processes that vary across space and time. As a result, modes of biomass consumption are scale dependent (Whitlock *et al* 2010, Spitz *et al* 2018).

Our overarching hypothesis is, at large spatial (regional to continental) and temporal (centennial to millennial) scales, consumer dominance in temperate North America is primarily driven by the bottom-up effects of moisture availability on primary production, as well as the type, continuity, and structure of vegetation available for herbivores and fire. We predict that biomass consumption was mainly driven by herbivores in open arid and semi-arid environments, while fire dominated biomass consumption in closed mesic and humid environments of Holocene mid-continent North America. Although challenging to directly test, we evaluate this prediction by integrating paleoecological records of climate, vegetation, and fire with paleontological and archaeological records of bison from two regions that span the North American midcontinent moisture gradient (northern grasslands [NG] and grassland-forest transition [GFT]). This approach allows us to assess spatiotemporal changes in biomass consumption by fire and

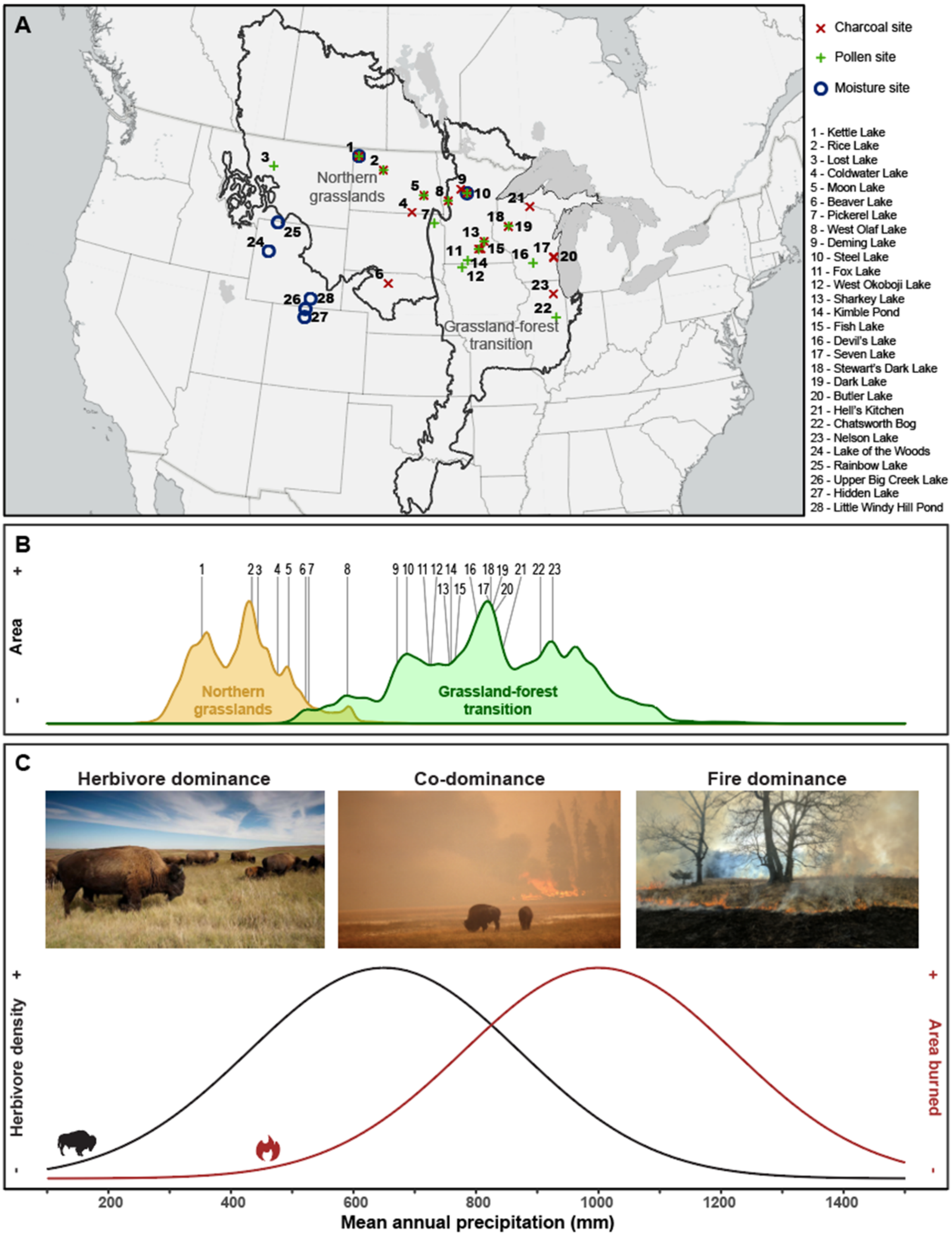

Figure 1. Map of study region and sites, with charcoal, pollen, and moisture records (panel (A)), distribution of study regions and paleoenvironmental sites across the midcontinent moisture gradient in North America (panel (B)), and conceptual diagram of predicted proportion of biomass consumed by herbivores (black line) or fire (red line) across a precipitation gradient (panel (C)). Panel B shows the current density distribution of area at a given moisture value for the northern grasslands (NG; yellow) and the grassland-forest transition (GFT; green), with pollen and charcoal sites labeled. Dominant consumer modes are expected to vary across the moisture gradient (panel (C)). Herbivore density (black line), area burned (red line) curves in panel C represent hypothesized consumer dominance patterns in North America based on empirical data for Sub-Saharan Africa from Archibald and Hempson (2016).

herbivores over the past 10k years, and to characterize likely historic consumer regimes in North America (see figure 1). We then compare modern herbivore and fire patterns in Sub-Saharan Africa and North America to determine whether historic North American consumer regimes resemble consumer dynamics in a less altered continent. Contemporary data from Sub-Saharan Africa provide critical context for understanding general fire-herbivore interactions and biomass consumption patterns in other locations and time periods. Finally, we utilize continent-scale data on livestock populations and fire occurrences to identify differences between historic and modern consumer regimes in North America and consider the implications for ecosystem dynamics.

2. Methods

2.1. Reconstructing modes of herbivory and fire

Improved understanding of long-term consumer interactions and impacts requires the integration of long-term records of burning and herbivore abundance. Recent advancements in laboratory and statistical charcoal analyses have improved our understanding of the role of fire in long-term ecological dynamics (Whitlock and Larsen 2001, Higuera *et al* 2009). However, methods for reconstructing herbivore abundance have lagged. As a result, it has been difficult to quantify abundances and subsequent ecological effects of ancient herbivores. We set out to address this problem by leveraging databases and new analytical techniques for radiocarbon dates to reconstruct regional-scale records of bison abundance. All following statistical and geospatial analyses were performed with R software (v. 4.1.3) in RStudio (R Core Team 2022, Posit team 2023). All ages presented in this paper are calibrated with the Intcal20 curve (Reimer *et al* 2020) and are given as calendar years before present (cal yr BP).

2.2. Bison abundance

Holocene reconstructions of regional bison abundance were developed using data and methods from Wendt *et al* (2022). Bison observations are defined as archaeological or paleontological sites containing at least one bison fossil. Bison observations were extracted and classified by study region (NG or GFT). The frequency distributions of bison observations over time were transformed according to the transformation presented in Surovell *et al* (2009) to account for progressive site loss with time. The GFT frequency distribution was multiplied by the ratio of the area of the NG to the area of the GFT (1.31) to account for the area difference.

2.3. Charcoal

Charcoal data were accessed from the Global Paleofire Database (supplementary table 2). Age models were not modified from original database submissions. Charcoal data were converted from concentrations (particles cm^{-3}) to influx values (particles cm^{-2} yr^{-1}) and standardized using methods described in Power *et al* (2010).

2.4. Pollen

Pollen data were retrieved from the Neotoma Paleoecology Database (NPD; supplementary table 3; Williams *et al* 2018). Updated chronologies were used, if available. Classification of arboreal and non-arboreal taxa was based on 'Ecological Group' classification in the NPD. Trees and shrubs were categorized as arboreal pollen (AP) and upland herbs were classified as non-arboreal pollen (NAP). AP:NAP ratios were calculated for each site and averaged to characterize the relative dominance of woody versus herbaceous species and provide information about vegetation structure and fuel characteristics.

2.5. Study regions

Study region definitions were based on ecoregion boundaries from WWF Terrestrial Ecoregions of the World (Olson *et al* 2001, figure 1(A)). The NG region includes Canadian Aspen Forests and Parklands, Northern Mixed Grasslands, Northern Tall Grasslands, Northern Short Grasslands, Montana Valley and Foothill Grasslands, and Nebraska Sand Hills Mixed Grasslands. Small, forest-dominated areas within the geographic boundaries of the broader NG ecoregion were included in the NG. These include Mid-Continental Canadian Forests and South-Central Rockies Forest. The GFT region is defined as Western Great Lakes Forests, Upper Midwest Forest-Savanna Transition, Central Tall Grasslands, and Central Forest-Grasslands Transition.

Although midcontinent North America and Sub-Saharan Africa differ in terms of species composition and certain biophysical conditions (e.g. soils, geology, temperature, seasonality), these regions span similar precipitation gradients and manifest similar biomes including grasslands, woodlands, and dry forests. Midcontinent North America is generally characterized by high temperature seasonality, with freezing winter temperatures (<0 °C), while Sub-Saharan is very climatologically diverse, with warmer annual temperatures and growing season primarily driven by precipitation seasonality. The range of mean annual precipitation (MAP) in the NG (250–600 mm) corresponds to herbivore dominance in Sub-Saharan Africa (figure 1(C)) and MAP in the GFT (350–1150 mm) spans the range from herbivore dominance to fire dominance in Sub-Saharan Africa (figure 1(C)).

2.6. Regional composites

Bison, charcoal, and pollen records were interpolated to 1-year steps, and then binned and summarized at 50-year intervals. Bootstrapped mean estimates and 95% confidence intervals were calculated for each interval (1000 iterations with replacement). Proxy record means and confidence intervals were summarized (figure 2) by fitting local polynomial regressions (loess; window = 2925 yr).

2.7. Holocene hydroclimatic phases of midcontinent North America

We used a multiproxy approach to describe general moisture trends and phases between 9 and 0.5k yr BP in midcontinent North America. The selected geophysical and geochemical records reflect long-term moisture availability trends with decadal-to millennial-scale variability and centennial- to decadal-resolutions (supplementary figure 2 and supplementary table 1).

The mineral composition of Kettle Lake sediments reflects changes in local water availability. Aragonite is deposited via groundwater flow while other minerals (quartz, calcite, dolomite, and gypsum) are primarily aeolian dust (Grimm *et al* 2011). High percent aragonite at Kettle Lake is interpreted as an indicator of elevated groundwater flows, while low aragonite indicates drought. Sand dune activity in the Nebraska Sand Hills is inferred from compiled luminescence dates (supplementary table 5). Luminescence dates reflect elevated upland dune activity and are interpreted as evidence for drought conditions. Luminescence dates indicate sediment burial, and thus constrain the timing of dune stabilization, meaning the timing of dune activation is less certain.

Declining lake levels in the Rocky Mountains, low groundwater flows at Kettle Lake, persistent dune activity, and high dust influx at Steel Lake indicate broadly dry conditions in midcontinent North America between 9 and 6k yr BP. Moisture availability generally increased between 6 and 4k yr BP, but two periods of low groundwater flows at Kettle Lake indicate some sub-regional variability during this period. Between 4 and 1.5k yr BP, most records suggest generally wet conditions, with few severe droughts, but multiple upland dune activations may reflect periods of sub-regional aridity. While lake levels remained stable or rose between 1.5 and 0.5k yr BP, other records show evidence of multiple severe droughts at lower elevations to the east.

Maximum aridity progressed across a longitudinal gradient, with peak dry conditions occurring earlier in the east and later in the west (Wright *et al* 2004, Nelson and Hu 2008). Dust influx at Steel Lake was greatest at ∼8k yr BP, peak dune activity in the Nebraska Sand Hills occurred between 8.5 and 7.2k yr BP, Kettle Lake experienced repeated episodes of low groundwater flows between 8.2 and 7k yr BP, and Rocky Mountain lakes levels were lowest between 6.5 and 6k yr BP.

2.8. Spatial analyses of modern fire and herbivory

Data on fire and herbivory in North America were collected and processed following methods of Archibald and Hempson (2016) to facilitate intercontinent comparisons. Data on area burned, herbivore density, dry matter consumed, and proportion of dry matter consumed for Sub-Saharan Africa are from Archibald and Hempson (2016).

Fire and herbivory data for modern North America were collected and processed as follows. Precipitation data was extracted from the WorldClim2 gridded 30 s mean monthly precipitation product for North America 1970–2000 (Fick and Hijmans 2017). Monthly precipitation rasters were summed to produce an average annual precipitation dataset. Monthly area burned and dry matter consumed by fire for 1997–2015 were extracted from Global Fire Emissions Data (GFEDv4; Giglio *et al* 2013). This is a satellite-based product that includes but does not differentiate anthropogenic and natural wildfires and prescribed burns. Annual totals and medians for area burned and dry matter (biomass) consumed were then calculated.

All variables related to livestock consumption (dry matter consumed, livestock mass density) were derived from census-based livestock population data which include high-density feedlots, intensive pasture-based systems, and extensive rangeland-based systems. Spatial livestock population data were extracted from the Gridded Livestock of the World 3 (GLW 3) dasymetric products for cattle, goats, horses, sheep (Gilbert *et al* 2018). GLW livestock population estimates were based on the most recent census result (all conducted in 2003 or later in North America). Biomass for each species was calculated by multiplying population by average mass estimates (supplementary table 4). Total herbivore biomass was calculated as the sum of all species biomass. Dry matter consumed by herbivores was calculated as a function of population, body weight, and net energy concentration of diet following standard IPCC methods outlined in Archibald and Hempson (2016).

Predicted proportion of dry matter consumed by herbivores versus fire in North America (figure 4(C)) was modeled by fitting a generalized additive model to the data for the proportion of dry matter consumed by herbivores in Sub-Saharan Africa (supplementary figure 3(B)) and projecting to North America with the WorldClim2 precipitation data.

Wild herbivore populations of North America were not included in modern calculations because accurate continent-scale datasets are not available. We assume that biomass consumption by wild herbivores in North America is negligible compared to that of domestic herbivores. Globally, the biomass of all wild mammals is 1–2 orders of magnitude less than that of livestock (Bar-On *et al* 2018). We suspect this difference is even greater in North America, where there is substantial investment in high-density livestock production.

3. Results and discussion

Paleoenvironmental reconstructions of regional hydroclimate, biomass burning, and bison abundance in midcontinent North America reveal how moisture availability once governed consumer dominance patterns at regional to continental scales. Over the past 10k years, the NG had more bison, less burning, and more open vegetation structure than the wetter GFT. These observations correspond with consumer dominance patterns in Sub-Saharan Africa, suggesting a level of generality among the biophysical constraints

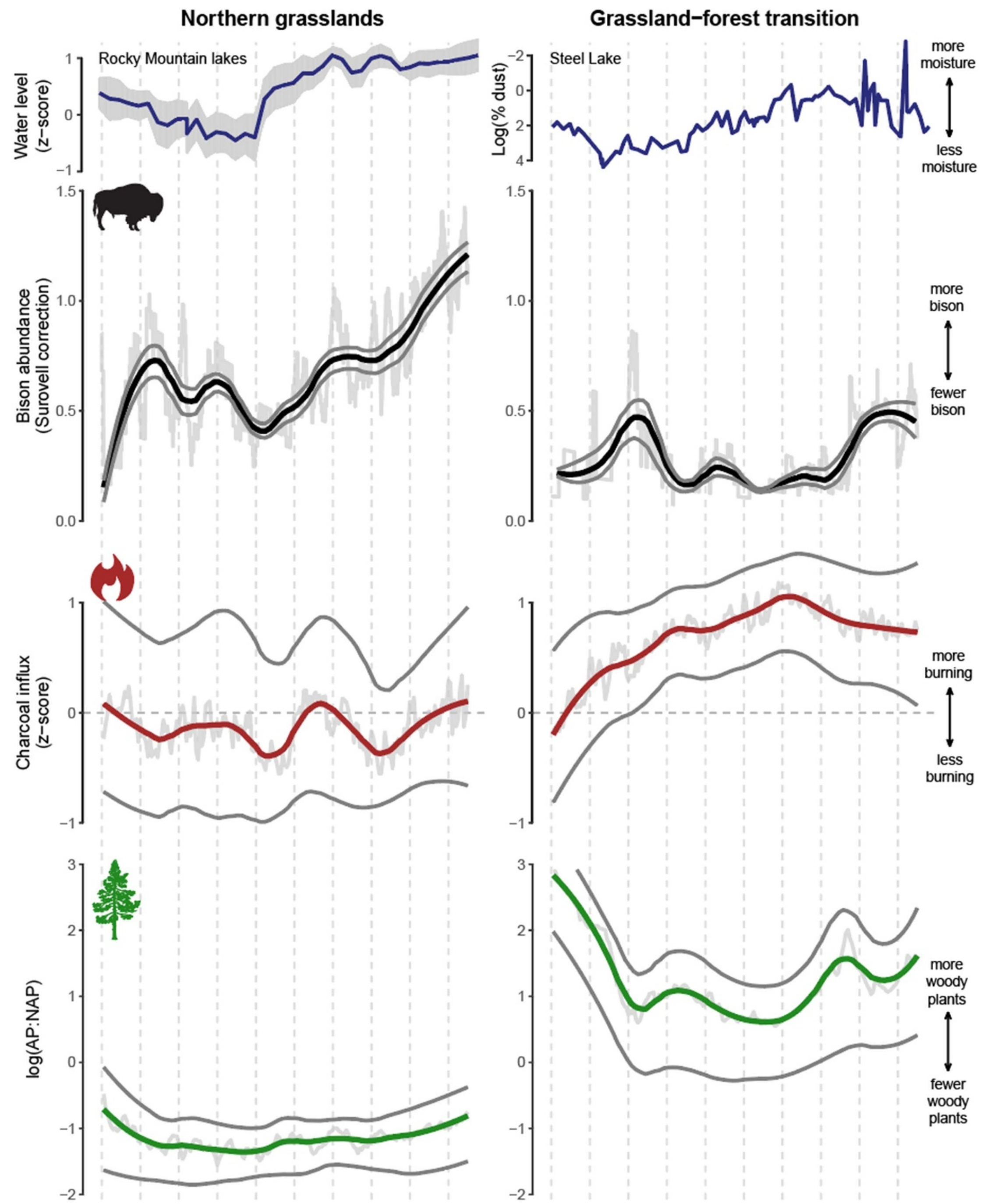

Figure 2. Regional comparison of reconstructed bison abundance (black line), biomass burning (red line), and woody plant dominance (green line) between 10 and 0.5k cal yr BP in the northern grasslands and grassland-forest transition regions. Bootstrapped means (thick colored lines), 95% confidence intervals (dark gray lines), and unsmoothed composite means (light gray lines) are shown. Units for mean charcoal influx are particles cm^{-2} yr^{-1}. AP:NAP is the ratio of arboreal pollen to non-arboreal pollen; higher values reflect greater arboreal pollen abundance.

that shape consumer regimes on different continents. Yet current biomass consumption patterns in North America indicate that human activities have greatly expanded herbivore dominance and essentially eliminated the functional role of fire even in historically fire-dominated systems. This human-mediated shift in broad scale consumer dominance has important implications for biodiversity, nutrient cycling, carbon storage, and habitat structure.

Multiple hydroclimate records indicate that the period between 9 and 6k yr BP was the driest phase of the Holocene in midcontinent North America (figure 2, supplementary table 1 and supplementary figure 2). In the NG, woody plants were relatively sparse, biomass burning generally remained below the Holocene average, and bison populations were progressively declining (figure 2). To the east, the GFT experienced a substantial reduction in woody plant biomass between 10 and 8k yr BP. This transition to a more open landscape corresponds with rising biomass burning and rising bison populations. A peak in GFT bison abundance just after 8k yr BP coincides with a low point in woody plant dominance.

Moisture availability began to increase between 6 and 4k yr BP (supplementary figure 2). The timing of the inflection point and the rate of change vary by region and record. Rocky Mountain lake levels began to rise rapidly at 6k yr BP. Two notable droughts are evident at Kettle Lake at ∼5.4k yr BP and ∼4.5k yr BP but limited dune activity in the Nebraska Sand Hills and dust deposition at Steel Lake suggest that the impacts of these droughts may have been geographically limited. The shift toward wetter conditions during the mid-Holocene corresponds with rising bison abundance and biomass burning in the NG. During this interval, NG biomass burning shifted from a record low at ∼5.6k yr BP to a high at ∼4.5 yr BP. Bison abundance followed a similar pattern with a low at ∼6k yr BP followed by a peak at ∼4k yr BP. GFT bison abundance briefly peaked at ∼5.6k yr BP and then dropped to Holocene lows at ∼4.5k yr BP, whereas GFT burning remained elevated and rose to Holocene highs by 4k yr BP.

Hydroclimate proxies indicate that the period between 4 and 0.5k yr BP was generally wet but punctuated by multiple severe droughts (supplementary figure 2). Woody plant dominance in the NG rose continuously between 3 and 0.5k yr BP. NG biomass burning dropped to match early Holocene levels at ∼3k yr BP, rose to the Holocene average by ∼2k yr BP, and was elevated between 1.5 and 0.5k yr BP. NG bison abundance was elevated but stable 4–3k yr BP and then rapidly expanded to a Holocene maximum 1.5–0.5k yr BP. In the GFT, woody plants expanded from ∼4k yr BP to ∼1.5 yr BP. GFT biomass burning declined from a peak at 4k yr BP to its Holocene mean by 0.5 yr BP. Declining woody plant dominance beginning at ∼2.5 yr BP is mirrored by increasing bison abundance. GFT bison abundance remained elevated to 0.5 yr BP.

The observed shifts in consumer dominance through the Holocene (figure 3(E)) correspond with modern patterns of consumer turnover in Sub-Saharan Africa (Archibald and Hempson 2016, figure 1(C), figures 3(B) and (D)), suggesting that biophysical constraints shape consumer regimes in similar ways on different continents. As in Sub-Saharan Africa, large herbivores dominated biomass consumption in dry, open environments and fire dominated in wetter, more wooded environments (figures 2 and 3(E)). As moisture availability in the drier NG increased after 6k yr BP, bison abundance increased while fire activity remained relatively modest. Additionally, results from the GFT suggest that the region expressed a fire-dominated consumer regime when moisture availability was greatest between 4 and 3k yr BP. The following drop in moisture availability led to a transition towards herbivore/fire co-dominance as biomass burning declined and bison expanded 3–2k yr BP. These trends are consistent with Africa-based predictions (i) that as a dry systems become wetter, herbivore density will approach maximum potential, while potential biomass burning will increase modestly and (ii) wetter systems will shift from fire dominance toward consumer co-dominance as they dry. Temporal variation in fire and bison prevalence in relation to changing moisture availability broadly conform to expected grass palatability-flammability trade-offs established in African ecosystems (Archibald *et al* 2019).

Regional differences in vegetation structure and fuel type complicate interpretation of regional charcoal influx composites. Higher charcoal influx in the GFT may result from an increase in dominance of woody vegetation, which can result in greater charcoal production and preservation relative to finer, low-lignin grassland fuels (Yang *et al* 2007, Feurdean 2021). In this case, higher charcoal influx may reflect an increase in woody biomass and not necessarily an increase in fire frequency. However, it is unlikely that wood-fueled fires consumed less overall biomass than bison because GFT ecosystems burned regularly, and bison were relatively scarce.

Relatively high bison abundance and low fire prevalence in the Holocene NG suggests that the region predominantly functioned within an herbivore-dominated consumer regime. NG bison abundance trends broadly track changes in moisture availability, suggesting that forage quality is not limiting in this region, and accordingly, that moisture-driven variation in forage availability is directly linked to bison population trends. In contrast, bison abundance is lower in the wetter, more closed GFT. This may indicate that forage quality, which decreases as grasses become taller in wetter areas (Hempson *et al* 2019), places a greater constraint on bison populations than forage availability does in that region. A high biomass and spatially continuous grass layer is, however, ideal fuel for spreading fire (Simpson *et al* 2022).

The proxy measures we assess here are necessarily coarse, making it difficult to reveal the complex contingencies that would characterize a co-dominance consumer regime. Fire and bison were present in both regions throughout the last 10k years, and it is likely that both would have experienced periods when fire and herbivory were co-dominant consumers at varying scales. One such instance occurred in the

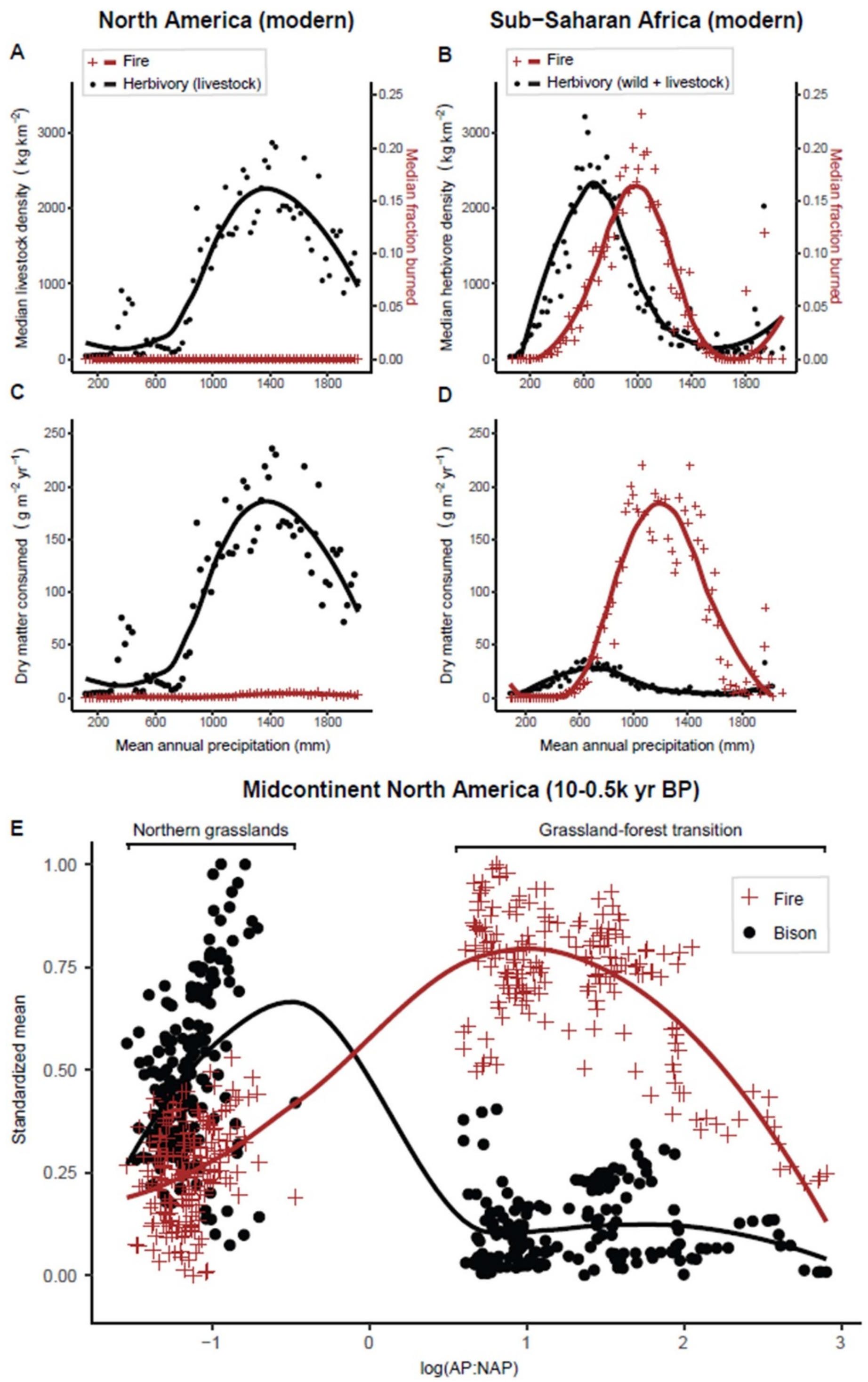

Figure 3. Fire and herbivory dynamics across moisture gradients in modern North America (left column), modern Sub-Saharan Africa (right column), and Holocene midcontinent North America (bottom panel). For modern data, points represent median values within each 25 mm mean annual precipitation band. Panels (A) and (B) compare herbivore biomass to area burned, and panels (C) and (D) compare dry matter consumed. Panel E shows regional consumer dominance in Holocene midcontinent North America, points represent the mean of bison abundance or charcoal influx at a given level of woody plant dominance (arboreal pollen:non-arboreal pollen) for every 50 year interval between 10 000 and 250 cal yr BP. Bison abundance and charcoal influx were standardized at the population level. Lines are based on loess regressions through the points. Data for Sub-Saharan Africa are from Archibald and Hempson (2016).

NG at 2–0.5k yr BP, when both fire and bison prevalence increased during a relatively mesic period. One interpretation for this is that conditions may have been wet enough to promote high availability of moderately palatable grasses, providing forage for bison and continuous fuels for fires. Pyric

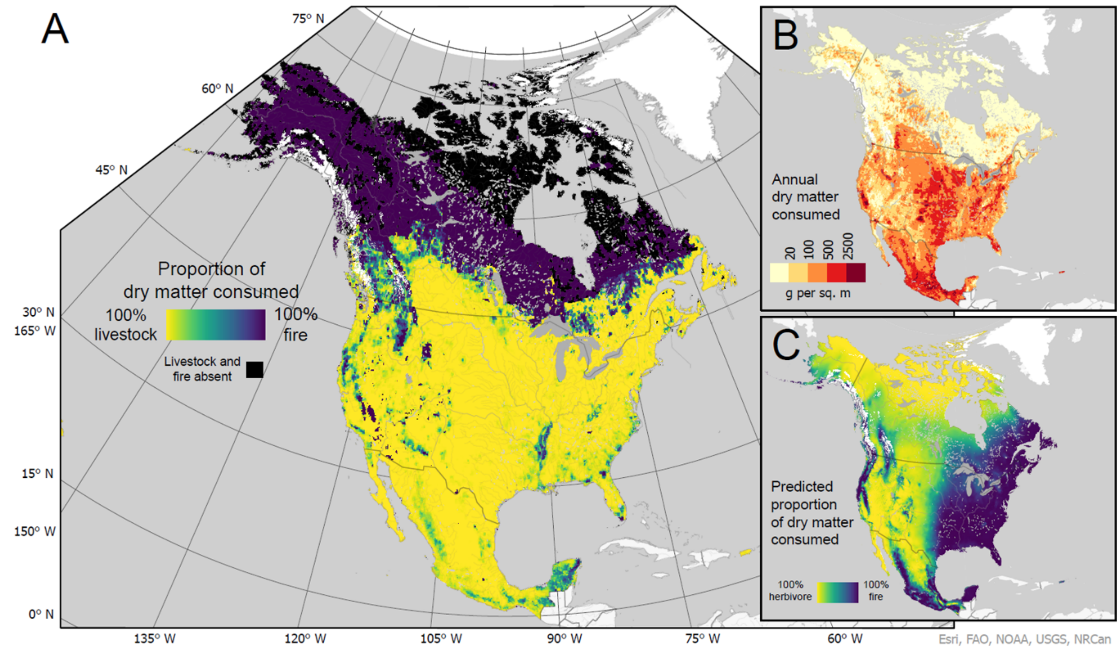

Figure 4. Maps of relative proportion biomass consumed by herbivores and fire in contemporary North America (panel (A)); annual total dry matter consumed by both livestock and fire in contemporary NA (panel (B)); and predicted relative proportion of dry matter consumed by herbivores and fire (panel (C)) are based on the observed precipitation-consumer dominance relationship for Sub-Saharan Africa (Archibald and Hempson 2016, supplementary figure 3 (B)).

herbivory, with the potential to produce patches of high-quality forage, may have further bolstered bison populations. Archaeological evidence suggests that bison affinity for recently burned patches was exploited by Indigenous hunters in the NG (Roos *et al* 2018).

Modern consumer regimes in North America have been greatly modified from the past (figures 3(A) and (C)). The lack of any discernable peak in fire prevalence across the moisture gradient suggests that fires have been strongly suppressed in large parts of the continent. Indeed, mapping relative biomass consumption by livestock and fire shows that fire dominance is now largely restricted to sparsely inhabited boreal and mountain forests and rural areas with fire cultures (figure 4(A)). The widespread lack of fire is likely a consequence of deliberate fire suppression policies as well as extensive land use change and landscape fragmentation that have altered fuel loads and fuel connectivity (Hessburg and Agee 2003, Hessburg *et al* 2019).

While anthropogenic influences have greatly distorted consumer regime distributions in contemporary North America, it is nonetheless intriguing that livestock biomass currently peaks at a much higher rainfall level than observed in Sub-Saharan Africa (1400 vs. 700 mm MAP; figures 3(A) and (B)). This may indicate that the specific environmental drivers of palatability and flammability differ somewhat between North American and African ecosystems. Between 500 and 700 mm MAP, herbivore densities in North America are strikingly low compared to the same range in Sub-Saharan Africa, as these regions are instead primarily used for intensive crop production systems (Massey *et al* 2018). Crop agriculture may have displaced livestock production to wetter regions, where advanced animal husbandry practices such as land clearing, pasture fertilization, supplementary feed and water provision, and veterinary services help support animal densities that may far exceed those possible under natural environmental conditions. However, the herbivore density peak at higher precipitation may alternatively be due to ecological differences between temperate North American and tropical African ecosystems. Forage quantity-quality tradeoffs are linked to productivity and are underpinned by the need for grasses to grow taller to compete for light as productivity increases (Nelson and Moser 1994, Lane *et al* 2000). While productivity is largely determined by rainfall in tropical African ecosystems, temperature plays a much greater role in determining plant growing season duration and hence productivity in temperate North American ecosystems (Churkina and Running 1998). As such, while total annual precipitation may appear adequate to produce a tall, unpalatable grass sward, a shorter, cooler growing season may limit this growth potential and thus enhance palatability, thereby shifting peak herbivore dominance up the precipitation gradient.

The precipitation-consumer dominance relationship for Sub-Saharan Africa can serve as a simplistic null model for biomass consumption patterns in pre-colonial North America (figure 4(C)). This univariate model does not account for non-precipitation drivers of plant palatability and flammability including growing season length, temperature, and seasonality. Precipitation is likely a poor predictor of consumer dominance in high-latitude systems (e.g. boreal forests) with low potential evapotranspiration, low temperatures, and short growing seasons. In such low-energy settings (Veldhuis *et al* 2019), large herbivores may struggle to balance thermoregulatory and food requirements, while fuel continuity and density are sufficient to promote rare, intense, and large fires during hot and dry summer conditions (Archibald *et al* 2013). Therefore, the Africa-based precipitation-only model likely overpredicts herbivore dominance in cold regions. Despite these limitations, this null model is somewhat validated by observed similarities between the consumer distributions in contemporary Sub-Saharan Africa and Holocene midcontinent North America. This model can facilitate further hypothesis generation and testing to identify influential constraints on consumer dominance for other North American regions and climates. Mapping hypothesized paleo-consumer dominance is an important step toward understanding the geographic distribution, relative dominance, and potential interactions of consumers that have long influenced ecosystem structure and biodiversity.

The dramatic distortion of North American consumer regimes by humans in the recent past likely holds major ecological consequences for the affected ecosystems. Among these are critical threats to biodiversity, as both fire and herbivores have structured niches and exerted considerable selective pressures on plant and animal assemblages across the globe (Bond 2005, Bond and Keeley 2005, Lehmann *et al* 2014, Staver *et al* 2021). Removing one or both of these consumers potentiates biome transitions, particularly towards closed canopy ecosystems where environmental conditions allow (Holdo *et al* 2009, Fogarty *et al* 2020). Herbivores and fire both influence a wide variety of ecological processes and functions, ranging from nutrient dispersal (Wolf *et al* 2013, Pellegrini *et al* 2018) and carbon storage (Kashian *et al* 2006, Schmitz *et al* 2023) to habitat structuring (Fuhlendorf and Engle 2004, Staver *et al* 2011) and biodiversity maintenance (Hartnett *et al* 1996, Ratajczak *et al* 2022). Rewilding for ecological restoration has gained considerable interest over the last 30 years. While rewilding initiatives promise to address some of the ecological dynamics missing from ecosystems, evidence from the past suggests that restoring natural fire regimes to North American landscapes is likely as important, and perhaps more readily achievable.

Data availability statement

Charcoal data are accessible through the Global Paleofire Database (www.paleofire.org). Bison observation data are available in the supplementary information of Wendt *et al* (2022). Pollen data are available through the Neotoma Paleoecology Database (www.neotomadb.org).

All other data that support the findings of this study are included within the article (and any supplementary files).

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Author contributions

J A F W and D B M designed research; J A F W, D B M, G P H, E N J B, and S D F performed research; J A F W analyzed data; and J A F W, D B M, G P H, E N J B, and S D F wrote the paper.

Conflict of interest

The authors declare no competing interest.

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