Large-scale climatic drivers of bison distribution and abundance in North America since the Last Glacial Maximum

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A B S T R A C T

As the dominant large herbivore in midcontinent North America since the terminal Pleistocene, bison (*Bison* spp.) have been a fundamental component of ecosystems and economies. Despite the importance of bison in late Quaternary North America, large-scale (regional to continental) patterns of bison biogeography are not well understood. Here we integrate archaeological and paleontological bison occurrence data with simulated climate data to better understand long-term drivers of bison distribution and abundance in North America. We used these records to model bison distribution and abundance over the past 20 thousand years at 1-thousand-year intervals. Our results show that late Quaternary changes in the distribution and abundance of bison were influenced by large-scale trends in temperature and precipitation. The distribution of bison since the Bølling–Allerød Interstadial (ca. 14 ka) is primarily explained by seasonal temperature patterns (mean temperature of the coldest quarter is the most important variable for 12 of the 14 1-thousand-year intervals). The modeled climate of bison distributions progressively narrowed since the Last Glacial Maximum (ca. 20 ka) as bison populations retracted from disjunct Pleistocene refugia and congregated in midcontinent rangelands. Through the Pleistocene-Holocene transition, bison experienced rapidly warming summer temperatures that increased faster in midcontinent North America than other regions and the continent as a whole. Model results suggest that Holocene bison abundance was influenced by hydroclimatic shifts that affected the quality and availability of forage. Bison abundances decreased through the dry early and mid-Holocene and increased when moisture availability improved in the late Holocene. We infer that bison have thrived under a broad range of environmental conditions since the Last Glacial Maximum and that the climatic and biogeographic space occupied by bison narrowed in recent millennia.

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1. Introduction

As the largest survivors of the late Pleistocene extinctions in North America (NA), bison (*Bison* spp.) have demonstrated remarkable capacity to persist and thrive despite periods of rapid and severe climatic changes and pressures from shifting predator guilds. From the Pleistocene-Holocene transition to the introduction of Old World livestock ca. 500 years ago, bison were the dominant herbivores throughout mid-latitude NA with population estimates ranging from 30 to 60 million individuals (Flores, 1991;

McHugh, 1979; Seton, 1929; Shaw, 1995). Prior to their near extinction in the early 20th century, the geographic range and density of bison were on par with the world's largest ungulate populations. Despite the historical significance of bison for the evolution of North American ecosystems and Indigenous cultures, there has been little research that examines long-term changes in the distribution and abundance of bison across the continent and the underlying drivers. Additionally, our understanding of large herbivore responses to changing climatic and environmental conditions during the Late Pleistocene and Holocene is limited (Meltzer, 2020).

Previous research examining trends in bison distribution and abundance and the drivers of these trends is mostly restricted to individual sites or subregional studies and/or shorter decadal to millennial time scales (e.g., Byers and Smith, 2007; Cooper, 2008;

Abbreviations

AUC — Area Under the Curve
BA — Bølling−Allerød Interstadial
cal yr — BP Calendar Years Before Present (1950)
CARD — Canadian Archaeological Radiocarbon Database
CCSM3 — Community Climate System Model Version 3
EH — Early Holocene
IQR — Interquartile Range
LGM — Last Glacial Maximum
LH — Late Holocene
MH — Mid-Holocene
MNI — Mean Number of Individuals
NISP — Number of Identifiable Specimens
TraCE-21ka — Transient Climate Evolution Simulation Dataset
YD — Younger Dryas

Lohse et al., 2014; Lupo and Schmitt, 1997; Lyman, 2004; Martin et al., 2017; Scott, 2010; Shapiro et al., 2004). As recent efforts to reintroduce large bison herds in NA accelerate (Martin et al., 2021; Pejchar et al., 2021; Sanderson et al., 2008; Shamon et al., 2022; Steenweg et al., 2016; Torbit and LaRose, 2001; Wilkins et al., 2019), and concerns over the fate of large herbivores increase across the globe, there is a critical need to evaluate bison responses to changing climate. Here we set out to: 1) document changes in the distribution and abundance of North American bison populations since the Last Glacial Maximum (LGM) using archaeological and paleontological datasets of bison occurrences, 2) identify the primary controls on bison distribution and abundance by evaluating changes in these phenomena in relation to modeled and empirical climate data, 3) use a distribution modeling framework to characterize bison responses to shifting environmental gradients during the late Quaternary, and 4) discuss results in the context of current efforts to conserve and restore bison across NA.

1.1. Coevolution of North American herbivores and grasslands and controls on large-herbivore populations

While recent work has advanced our understanding of climate controls on herbivores in contemporary ecosystems (Pachzelt et al., 2015; Payne and Bro-Jørgensen, 2016; Veldhuis et al., 2019), the short duration of the observational record limits our understanding of how herbivores respond to climate change on longer, millennial time scales. In a multi-proxy synthesis of paleoecological records, Strömberg (2011) reports that the first grassy ecosystems in NA appeared in the late Oligocene and early Miocene, followed by the evolution of grassland-adapted fauna in the early to middle Miocene. Open, grass-dominated ecosystems continued to expand through the middle to late Miocene (Janis et al., 2002). The progressive development and evolution of grassland ecosystems was likely driven by long-term regional aridification (Strömberg, 2011). The importance of moisture availability for grassland expansion and persistence is supported by observations of modern grasslands and savannas, where maximum woody cover is primarily constrained by moisture availability, and further reduced by edaphic controls and disturbance from fire, herbivores, and pathogens (Sankaran et al., 2005; Scholtz et al., 2018). The Miocene proliferation of herbivores adapted to open habitats would have introduced novel disturbance processes including the destruction of woody plant species by proboscideans and other large ungulates (Morrison et al., 2016; Rivals et al., 2007) and altered fire regimes (Davies et al., 2015; Donaldson et al., 2018; Starns et al., 2019). Large

mammal species richness peaked during the middle Miocene and subsequently declined (Jardine et al., 2012). As taxonomic richness of large mammals decreased into the Pleistocene, the proportion of taxa adapted to open habitats increased (Janis et al., 2002; Jardine et al., 2012). Concomitantly, the median body mass of artiodactyl and perissodactyl species increased substantially through the late Miocene (Huang et al., 2017). In short, aridification was a primary climatic factor of the expansion of grasslands and subsequent herbivore populations that radiated to fill new open-habitat niches. Bison successfully exploited these open landscapes after crossing the Bering Land Bridge ca. 195-135 ka (Froese et al., 2017).

1.2. Climate-driven stress and large herbivore adaptation

Climatic conditions impact large herbivores via multiple pathways. Because precipitation and temperature govern primary production, and large herbivores have substantial forage and water intake requirements, climate indirectly affects herbivore fitness, production (Coe et al., 1976; Raynor et al., 2020) and diversity (Olff et al., 2002; Veldhuis et al., 2019). Climate also acts as a direct control on individuals and populations by influencing physiological functioning and behavior.

1.2.1. Heat stress

Exposure to temperatures above or below an animal's capacity to thermoregulate can result in thermal stress and, under extreme conditions, mortality (Martin and Barboza, 2020a). In general, large-bodied animals such as bison, are more susceptible to heat stress than their smaller-bodied counterparts. Elevated ambient temperatures limit the capacity of endotherms to dissipate heat, resulting in heat stress (Martin and Barboza, 2020a, 2020b; Speakman and Król, 2010). Larger-bodied animals generally do not dissipate heat in warm conditions as effectively as smaller animals because larger animals have greater volumes per unit of surface area. To mitigate heat stress in the short-term, large herbivores may employ behavioral and physiological strategies including wallowing (Marai and Haeeb, 2010), limiting activity to cooler hours of the day, panting, sweating, seeking thermal cover (McCann et al., 2013), and reducing forage intake (Spiers et al., 2004). Increased frequency of extreme temperatures over millennial timescales can exert pressure on large herbivores to migrate, adapt, or decrease populations in response to thermal stress.

1.2.2. Cold stress

Winter and early spring are the most physiologically stressful seasons for large herbivores at mid- to high latitudes. Harsh conditions including cold temperatures, deep snow, predator pressure, and a lack of high-energy forage coincides seasonally with high energy demands from gestation and lactation. The convergence of these stressors exerts a strong influence on mortality (Gaillard et al., 2000; Horne et al., 2019; Jackson et al., 2021; Singer et al., 1997; Smith and Anderson, 1998). To sustain energy reserves through winter and early spring, large herbivores consume quality forage during warmer months to build energy reserves (Bårdsen and Tveraa, 2012), reduce movement when snow is deep and temperatures are low (Sheppard et al., 2021), and allocate more time to resting and less time to foraging during winter (Beumer et al., 2020).

1.3. Predicting bison response to broad-scale climate changes

Based on known physiological constraints and foraging behavior of bison and other large herbivores, we hypothesize that, (H1) in open habitats, bison abundance will be positively correlated with moisture availability that indirectly influences the abundance and

availability of grassland forage, and (H2) changes in the geographic distribution of bison will respond to long-term changes in temperatures and associated hydrothermal stress.

2. Methods

2.1. Documenting millennial-scale changes in bison distribution and abundance

Reconstructing long-term trends in bison abundance is limited by the quality and availability of fossil occurrence records, which are temporally discontinuous and can be spatially biased by the distribution of appropriate depositional settings, adequate preservation of identifiable remains, and other taphonomic processes. The rich late Quaternary fossil record in NA, however, provides a unique opportunity to investigate the relationships between climate change, bison range dynamics, and demographic patterns. Past research has employed a variety of metrics to quantify changes in the relative abundance of fossil taxa including the number of identifiable specimens (NISP; e.g., Byers and Smith, 2007; Hill, 2007) and minimum number of individuals (MNI) within an assemblage. In order to examine bison response to environmental and climatic changes, we compared dated occurrences of bison in the fossil record with empirical and modeled paleoclimate data. Instead of relying on traditional abundance estimates from skeletal element counts, we considered individual archaeological and paleontological sites containing bison fossils as evidence for the presence of bison at a given time and place. We infer that large-scale, spatiotemporal changes in bison abundance are reflected in changes in the presence or absence of bison in fossil assemblages within a subregion. We acknowledge the coarse spatiotemporal resolution of the fossil record. Therefore, we evaluate changes in abundance at millennial time scales (between adjacent 1000-year intervals).

2.2. Bison site dataset

We compiled a dataset of *Bison* spp. fossil occurrences in NA (Table S1). Records of direct-dated bones and age-constrained stratigraphic units containing bison were acquired from the Neotoma Paleoecology Database in December 2021 (Goring et al., 2015; Williams et al., 2018). This dataset was supplemented with records accessed from the Canadian Archaeological Radiocarbon Database (CARD; Martindale et al., 2015) in January 2022, and primary source publications. Using the criteria detailed below, only high-quality observations were retained in our analysis. Observations were removed if they were identified as duplicates, non-bison observations, imprecisely dated (radiocarbon date sigma >250 years), stratigraphically dated with overly-broad time periods (e.g., "Pleistocene"), dated outside of the study period (youngest age >20 ka), or dated with material known to be unreliable (e.g., apatite). After removing low-quality observations, the dataset consisted of 2700 observations (Table S1; CARD: n = 1828; Neotoma: n = 731; primary sources: n = 141).

Data processing and analysis were performed with R version 4.1.2 (R Core Team, 2021) in RStudio (RStudio Team, 2018). Radiocarbon (^{14}C) dates reported by original publications were calibrated to calendar years before present (cal yr BP) with the Intcal20 curve (Reimer et al., 2020), using the rcarbon package (Bevan and Crema, 2018). Observations were grouped by median calibrated ages into 20 equal 1000-year intervals spanning 20-0 ka. Observations with dates spanning interval boundaries were classified as present in overlapping intervals.

2.3. Bison abundance

The presence of bison at a dated fossil locality is a necessary precondition for a positive determination from the fossil record. It is reasonable to expect that the abundance of living bison at a given time will be related to the abundance of bison fossils that are subsequently discovered. However, the fossil record does not perfectly represent bison populations in the past because multiple post-depositional processes can influence the frequency of bison observations. Processes contributing to information loss from the fossil record include site destruction from weathering and erosion, poor preservation of fossil materials, gaps in the spatial and temporal focus of research efforts, and taxonomic misidentification.

To correct for the influence of taphonomic bias (i.e., over-representation of younger fossils), the frequency distribution of bison occurrences over time was adjusted with a transformation function following the methods of Surovell et al. (2009). The transformed and untransformed (raw) frequency distributions were then binned into 1000-year intervals, the mean frequency within each interval was calculated, and it was determined whether means increased or decreased relative to the prior interval (Fig. 1). Taphonomic bias will cause a time series of untransformed frequencies to overestimate increases and underestimate decreases in occurrences, whereas a taphonomic correction will adjust observation frequencies such that the probability of site survival decreases over time (Surovell et al., 2009). Because the biases of the untransformed and transformed data are opposed, we interpret directional agreement in the raw and transformed datasets as an indicator of an increase or decrease in bison abundance.

Spatial patterns of relative bison abundance through time were also examined. Time-binned, spatially explicit data on bison occurrences were used to create gridded datasets representing the count of bison sites within each $2.5° \times 2.5°$ grid cell for each 1000-year interval between 20 and 0 ka. Bison sites are defined as localities where bison remains have been positively identified, documented, and dated. Bison site counts were used to derive a second series of gridded datasets that indicate the directionality of change in the number of bison sites between a given time interval and the preceding interval. The resulting raster datasets contained cell values indicating either: 1) increased number of bison sites, 2) decreased number of bison sites, or 3) no change relative to the preceding time interval. Continental-scale trends and spatial patterns in bison abundance were visualized by mapping each gridded dataset at 1000-year intervals (Figs. 2 and 3). This approach indicates the directionality of changes in bison site abundance and does not measure magnitude of change. It is assumed that times and places with high bison populations yield more remains, and therefore, more sites. Conversely, declining populations will yield fewer remains and sites as time progresses. This approach shows the directionality of sub-regional population changes and quantifies the extent of range contractions and expansions.

Our spatial approach also reduces taphonomic bias by comparing the number of bison sites within a given time interval directly to the preceding time interval, instead of relating the number of older sites to a baseline of modern/recent sites that are far more likely to be preserved and discovered (Surovell et al., 2009). This approach is not intended to identify population increases or decreases operating at finer spatiotemporal scales (e.g., population crashes following a harsh winter, or disturbance event, etc.).

2.4. Modeling bison distribution with MaxEnt

2.4.1. Climate data

Climate data for the last 20,000 years were derived from the

Transient Climate Evolution (TraCE-21ka) simulation dataset, run with the Community Climate System Model version 3 (CCSM3) from the US National Center for Atmospheric Research (NCAR). Previous model-proxy comparisons have shown that TraCE-21ka adequately represents key features of late Quaternary climate evolution (He et al., 2013; Liu et al., 2014; Lora et al., 2016; Shakun et al., 2012). Absolute monthly minimum temperature, maximum temperature, and mean precipitation were extracted from the TraCE-21ka climate simulation at 2.5° resolution for the period 20,000-0 yr BP at 80-year intervals taken in 100-year steps with PaleoView software (Fordham et al., 2017). The resulting gridded datasets were averaged to yield 1000-year means. The monthly climate data were used to generate 17 bioclimatic variables that are commonly used predictors in species distribution models (Hijmans et al., 2017). The bioclimatic data were then resampled without interpolation to a 0.25° resolution to increase the number of background points available for model validation. Climate data were masked with ice sheet extent layers based on modeled data from Gowan et al. (2016).

To our knowledge, the TraCE-21ka is the most appropriate climate dataset for the spatial and temporal scale of this study. This simulation has a unique combination of monthly temporal resolution through the past 21,000 years, including abrupt change events such as the Younger Dryas (YD), while also having sufficient spatial resolution to facilitate geographic comparisons with North American bison sites. The TraCE-21ka simulations using the CCSM3 model, however, appear to underrepresent early to mid-Holocene aridity followed by a trend towards wetter conditions across much of NA, outside the southwestern United States, indicated by multiple empirical paleoclimate datasets (Liefert and Shuman, 2020; Shuman and Marsicek, 2016). This discrepancy between the TraCE-21ka simulation and empirical data is common to most paleoclimate model simulations, including up-to-date models with more complete ocean and sea-ice dynamics, atmospheric dust loading, and other relevant processes (e.g., Morrill et al., 2019; Sun et al., 2019). We consider this bias in the discussion and interpretation of results.

2.4.2. Model description

Analysis of the climate drivers of bison distribution was performed with MaxEnt, a software program that employs a machine-learning algorithm to estimate relationships between environmental variables and species occurrences (Elith et al., 2011; Phillips et al., 2006, 2016). MaxEnt uses spatially explicit environmental variables and species occurrence data to predict habitat suitability, which is expressed as predicted probability of occurrence on a scale of 0−1 (lowest to highest).

2.4.3. Variable selection

Initial models used to predict the distribution of bison data included 17 bioclimatic variables. Variable importance rankings were determined by counting how frequently a variable was assigned a given importance ranking (based on percent contribution) across all time intervals. When Pearson correlations between variables exceeded 0.8, the variable with more high rankings across time intervals was retained and the variable with lower rankings was dropped. The resulting 9 bioclimatic variables were selected for subsequent modeling and analysis. Variables used in final model selection are: mean temperature of the coldest quarter, temperature seasonality, mean temperature of the wettest quarter, mean temperature of the warmest quarter, precipitation of the coldest quarter, precipitation seasonality, precipitation of the wettest quarter, precipitation of the warmest quarter, and precipitation of the driest month.

2.4.4. Model evaluation

To evaluate model performance, a random sample of 20% of bison observations was withheld and the remaining 80% of observations were retained for model training. 1000 background points were randomly selected from the climate data for cross-validation of the trained model against the withheld observations. Model performance of each MaxEnt run was evaluated with the area under the curve (AUC) statistic (Table 1). AUC is derived by plotting sensitivity (the proportion of positives that are correctly identified) versus 1 minus specificity (the proportion of negatives that are correctly identified) and quantifying the area under the curve. In other words, AUC is a measure of a model's success in predicting presences and absences. Models with an AUC of 1.0 perfectly differentiate between presences and absences, whereas an AUC of 0.5 indicates that a model performs no better than random chance.

2.4.5. Temporal changes in variable importance

The MaxEnt maximum entropy algorithm quantifies the relative contribution of an environmental predictor variable with a 'percent contribution' score. Percent contribution reflects how much a given variable improves regularized gain (model fit relative to a uniform distribution). To understand how the relative importance of variables changed over time, each predictor variable was assigned a rank corresponding to its percent contribution score (1: highest contribution; 7: lowest contribution) for each time interval. Changes in variable rank over time are interpreted as shifts in the fundamental climatological drivers of bison distribution.

2.4.6. Defining bison distribution

The boundaries of the geographic distribution of bison were defined by imposing a threshold to convert predicted probabilities to binary presence/absence data (Fig. 4). The threshold is defined as the predicted probability value where model sensitivity and model specificity are equal. As such, threshold values varied across time intervals. Grid cells with predicted probabilities that exceeded the threshold were classified as presences and cells with values below were classified as absences. To characterize climatic conditions experienced by bison, changes in climate variables throughout the threshold-defined ranges of bison were summarized by medians and 25% and 75% quantiles (interquartile range: IQR). The distribution of climate variables throughout the ice-free landmass of North America were similarly summarized. Climate within the model-defined bison distribution was contrasted with the medians and IQRs of the continental North American climate (Fig. 5). Because IQRs do not span the entire range of each independent variable, it is possible for the IQR of the predicted bison distribution to fall entirely outside of the NA IQR.

Because bison distribution was modeled at the genus level, observations from late Pleistocene and early Holocene intervals included specimens originally ascribed to multiple bison taxa. In our analysis, we consider bison as part of a large, geographically variable meta-population on the basis of genetic and morphological evidence (Heintzman et al., 2016; Martin et al., 2018; Shapiro et al., 2004; Zver et al., 2021). While we do not attempt to define sub-populations and characterize niche variability between them, our results may be useful for identifying ecologically distinct sub-populations for future investigation.

3. Results

3.1. Climate and patterns of bison distribution and abundance

Analysis of the bison fossil record shows that the spatial distribution and density of bison populations have varied considerably since the LGM (Figs. 2 and 3). Millennial-scale changes in the
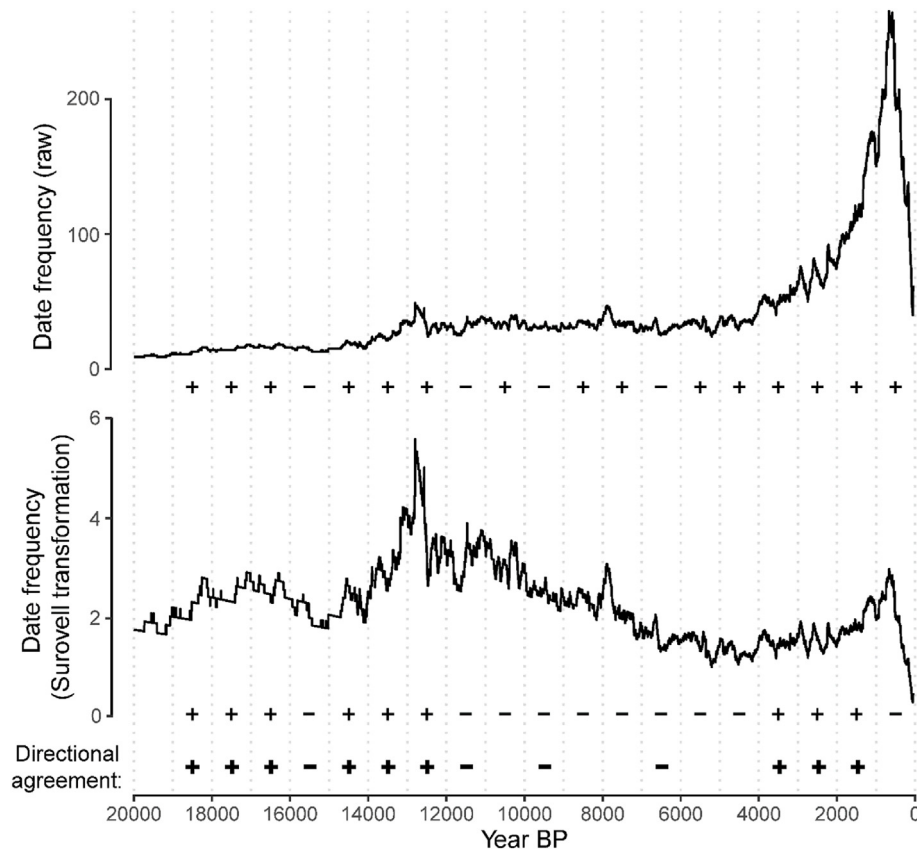
Fig. 1. Raw (top) and transformed (middle, via Surovell et al. method) frequency distributions of bison observations in North America 20-0 ka. Signs indicate whether mean frequencies increased (+) or decreased (−) relative to the prior 1000-year interval (top and middle) and whether there is directional agreement between raw and corrected frequency datasets (bottom).

distribution and abundance of bison were linked to climatic and environmental variability. During the LGM ca. 20-17 ka, the distribution of bison was widely scattered across NA into regional clusters, suggesting subpopulations were isolated into disjunct glacial refugia (Fig. 4). As post-glacial ecosystems developed, some regionally isolated subpopulations migrated and/or became extinct. By the late Holocene, the distribution of bison was largely spatially contiguous throughout the Great Plains and Intermountain West.

Based on the simulated climates of the last 20 ka, bison consistently inhabited places with warmer winters, summers, and wet seasons relative to the overall climate of the ice-free North American landmass. Within the climatic envelope where bison occurrences were most dense, Holocene temperature was slightly less seasonal, and precipitation was slightly more seasonal than the continent-wide climate. The geographic areas inhabited by bison experienced less seasonal variation in precipitation during the Holocene relative to the late Pleistocene due to declining winter precipitation and increasing summer precipitation during the Pleistocene-Holocene transition.

The simulated climatic envelope occupied by bison progressively narrowed since the LGM (Fig. 5). Interquartile ranges contracted for eight of the nine climate variables (mean temperature of the coldest quarter, temperature seasonality, mean temperature of the wettest quarter, mean temperature of the warmest quarter, precipitation of the coldest quarter, precipitation seasonality, precipitation of the wettest quarter, and precipitation of the warmest quarter). For example, the bison distribution IQR for mean temperature of the coldest quarter was 10 °C (16-6 °C) at 20-19 ka, but

it narrowed to 6.5 °C (14.25−7.75 °C) by 1−0 ka. Similarly, the precipitation of the coldest quarter IQR decreased from 8 cm (11-3 cm) to 2 cm (4-2 cm).

Variable importance for defining the distribution of bison varied over time. During the Bølling−Allerød Interstadial (BA) ca. 14.7−12.9 ka, as the range of temperatures encountered across NA increased, the distribution of bison shifted from primarily precipitation-limited to primarily temperature-limited (Fig. 5). Precipitation seasonality was the most important variable between 18 and 16 ka and mean temperature of the coldest quarter ranked first or second in relative importance between 14 and 0 ka. The predicted distributions of bison largely correspond to observed presences across all time intervals. The AUC evaluation metric suggests that the model achieved good differentiation (AUC >0.70) between bison presences and absences across all time intervals, except 20-19 ka (AUC: 0.65), which only had 11 observations (Table 1). Model performance improved with more recent time intervals, partially due to a greater number of more recent bison observations and increasing spatial cohesion of bison sites over time.

During most thousand-year intervals, the distribution models show moderate predicted probabilities in Beringia despite the presence of multiple bison sites in the region. This is related to the strong influence of midcontinent bison sites on the model fit. As such, the models best represent the potential range of bison originating from south of the continental ice sheets. This result indicates that there are likely meaningful ecological differences between Beringian and southern bison populations that may explain limited north-to-south dispersal (Heintzman et al., 2016), a
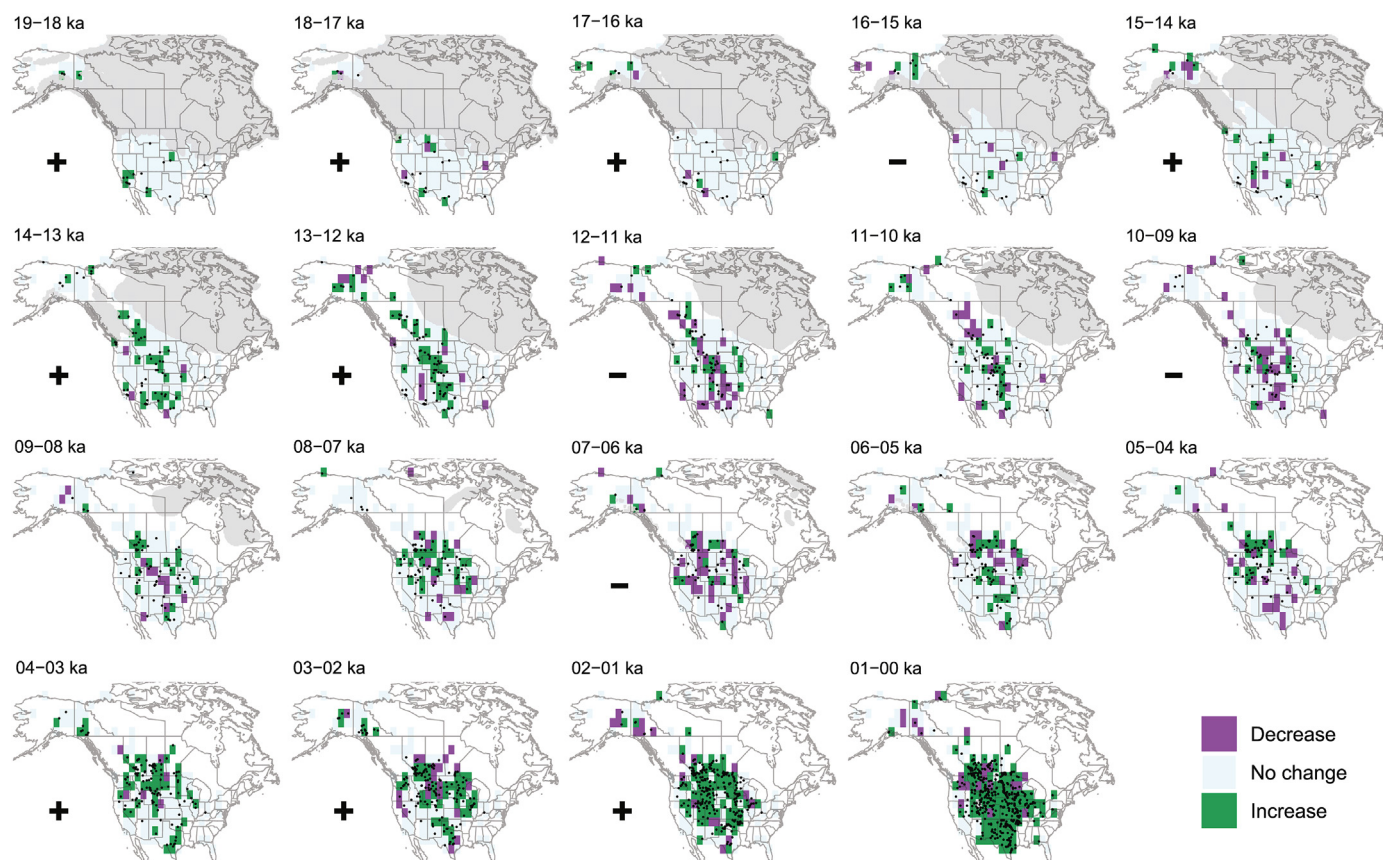
Fig. 2. Relative change in bison abundance based on raw bison site counts. The color of each 2.5° × 2.5° grid cell indicates whether the number of bison sites (black dots) within the cell decreased (purple), did not change (light blue), or increased (green) relative to the preceding 1000-year interval. Ice sheet extent shown in gray (Gowan et al., 2016). Signs indicate directionality of agreement (positive: + or negative: −) between raw and corrected frequency datasets within each 1000-year interval. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)
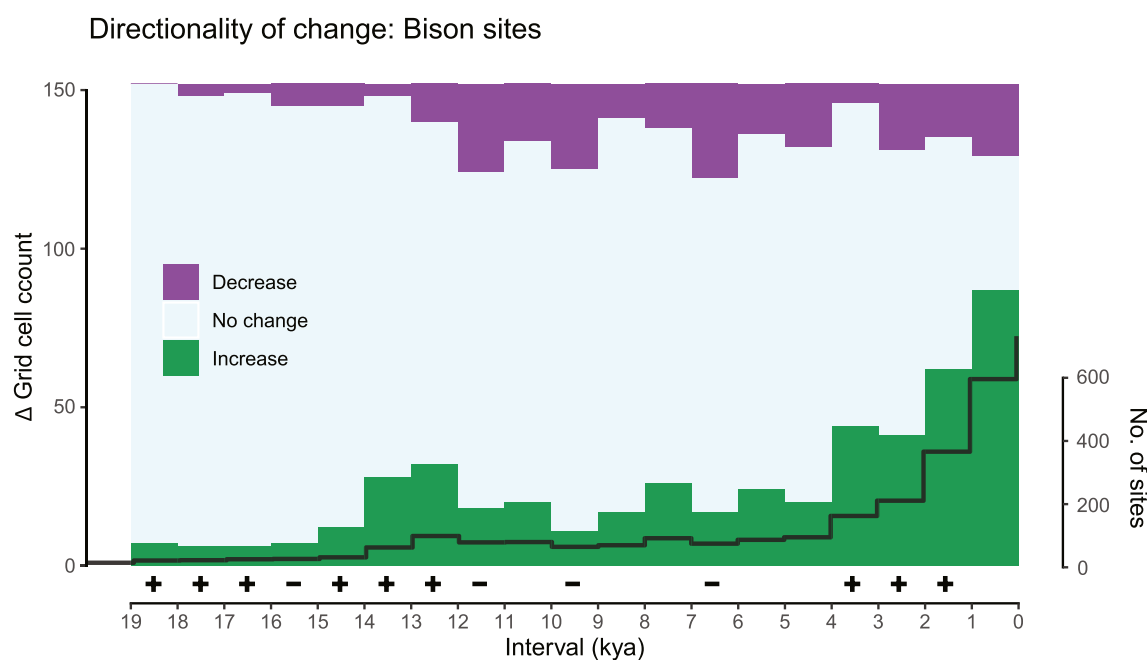
Fig. 3. Directionality of change in raw bison site counts (bars; left axis) and sums of site counts (black line; right axis) over the past 20,000 years. Cell count change reflects whether the number of bison sites within a given spatial grid cell (2.5° × 2.5°) increased (green), did not change (gray), or decreased (purple) with respect to the prior 1000-year interval. Signs indicate directionality of agreement (positive: + or negative:) between raw and corrected frequency datasets within each 1000-year interval. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Summary of area under the curve (AUC), threshold value (sensitivity = specificity), count of observations used for model training, and count of background points for evaluation across all time intervals modeled.

Interval (ka)	AUC	Threshold (sensitivity = specificity)	Observations
20−19	0.65	0.63	11
19−18	0.81	0.47	18
18−17	0.76	0.55	20
17−16	0.76	0.61	24
16−15	0.79	0.57	23
15−14	0.74	0.58	27
14−13	0.73	0.56	58
13−12	0.84	0.54	85
12−11	0.79	0.65	70
11−10	0.80	0.54	73
10−9	0.82	0.59	55
9−8	0.86	0.57	64
8−7	0.87	0.54	78
7−6	0.87	0.54	69
6−5	0.86	0.54	78
5−4	0.91	0.39	93
4−3	0.88	0.47	160
3−2	0.89	0.55	208
2−1	0.88	0.62	360
1−0	0.87	0.63	722

topic warranting further investigation.

3.2. Last Glacial Maximum (LGM): 20.0−14.7 ka

LGM bison localities are few in number but broadly distributed throughout much of ice-free NA. Precipitation seasonality best explains the 18-16 ka distribution of bison (percent contribution: 33−50%). Simulated precipitation seasonality across the bison range during this period exceeded the continental median and it ranks within the top three variables for the other LGM intervals. Between 19 and 14 ka simulated precipitation of the driest month was 0 cm and median precipitation of the warmest quarter ranged between 3 and 5 cm within the bison distribution. During the LGM, bison site turnover patterns were relatively minor and localized (Fig. 2). The absolute number of bison sites increased from 11 at 20-19 ka to 23 at 16-15 ka.

### 3.3. Bølling−Allerød Interstadial (BA): 14.7−12.9 ka

At 14 ka, mean temperature of the coldest quarter became the most important variable and maintained first or second importance rank among variables until present (percent contribution range: 17.0−66.5%). This shift in variable importance does not correspond to a substantial change in simulated mean temperature of the coldest quarter within the bison distribution. During the Bølling−Allerød Interstadial bison expanded northward into the ice-free corridor and additional bison observations appear in the southwestern United States and the western Great Plains. A substantial increase in sites and range extent took place at 14-13 ka. Predicted probabilities are highest in the southwestern United States, Idaho, and eastern Montana. At 14-13 ka, simulated median precipitation of the coldest quarter dropped to 3 cm and remained at or below this level to present.

3.4. Younger Dryas (YD): 12.9−11.7 ka

While portions of the North American ice-free land mass experienced a reversion to seasonally colder temperatures, simulated temperature changes within the reconstructed bison distribution varied by season. The simulated median mean temperature of the warmest quarter dropped from 33 °C to 31 °C, while the median mean temperature of the coldest quarter remained unchanged at 7 °C. At 13-12 ka, the modeled bison distribution spanned from northern Alberta to Mexico. Observations increased throughout a corridor that corresponds to the leeward side of the Rocky Mountains from Alaska to the Gulf of Mexico.
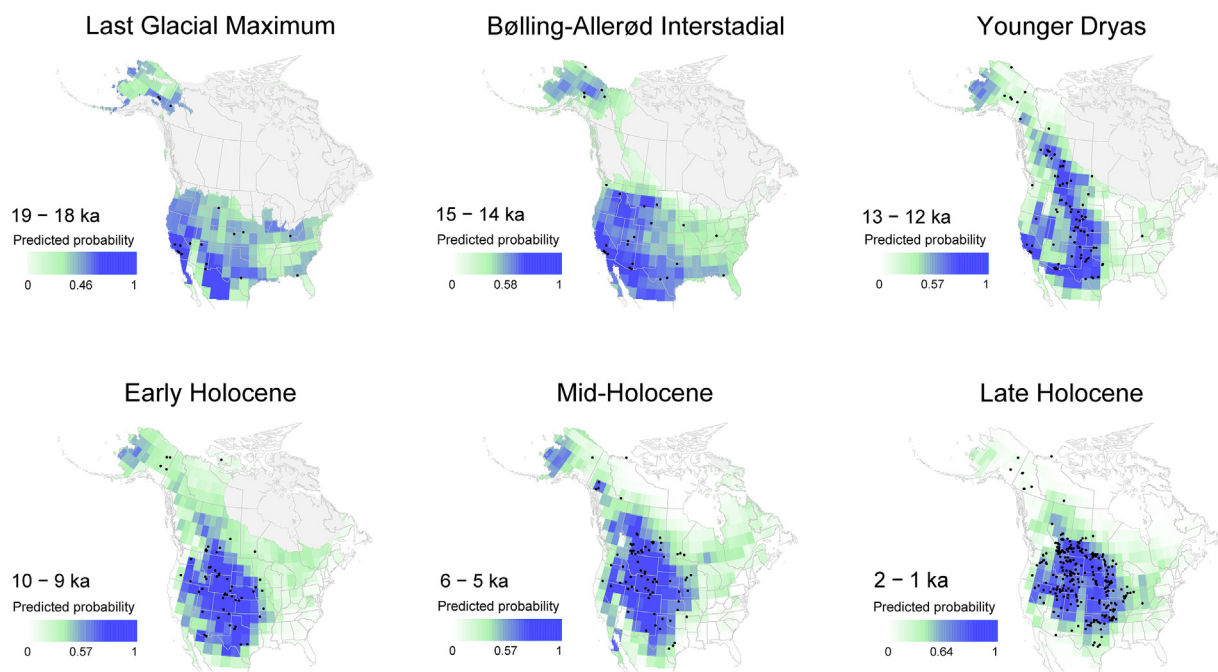
Fig. 4. Geographic representation of modeled bison distributions at key intervals between 20 and 0 ka. The middle number on each scale identifies the interval-specific predicted probability threshold for defining bison presences (blue) and absences (green and white). Observations (bison sites) shown as points (black). Ice sheet extent shown in gray (Gowan et al., 2016). All maps are available in the supplementary material. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)
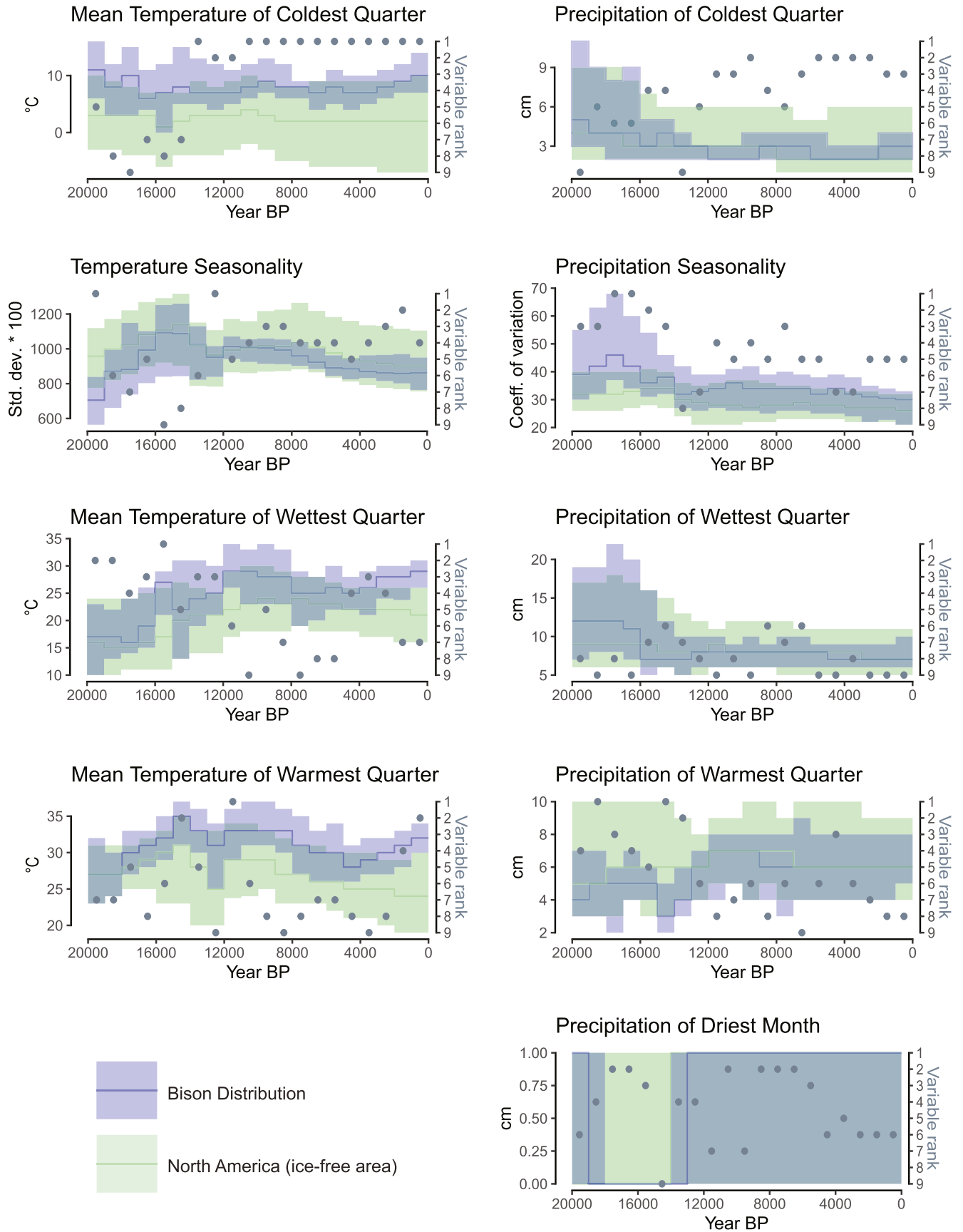
Fig. 5. Simulated evolution of climate conditions and variable rank for each 1000-year interval since 20 ka. The distributions of climate variables within the model-defined distribution of bison (blue) and North America minus ice-covered areas (green) are summarized with the median (line) and 1st and 3rd quartiles (IQR; shading). Variable rank (gray dots) reflects the ranking of the percent contribution score relative to the other climate variables (right axis) within a given interval. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.5. Early Holocene (EH): 11.7−8.0 ka

During the early Holocene, the predicted bison distribution area grew despite declining local abundances. Based on the TraCE-21ka simulation, early Holocene bison experienced warm summers and dry winters throughout their range. During this period, bison occurrences increased in west and central NA (Figs. 2 and 4). Increases primarily occurred within the Rocky Mountains and Great Plains regions. Widespread decreases in bison sites occurred at 12-11 ka and 10-9 ka, especially at the geographic perimeter of the bison distribution in southern, coastal, and low-elevation regions. Many sites in California, Nevada, Arizona, New Mexico, Utah, and Colorado cease recording bison presences during the early Holocene. A retraction of bison from the southwest during the early Holocene is also evident in the distribution models which predict the presence of bison in most of the southwest (excluding the Lower Colorado River Valley) until 9-8 ka, when bison became absent from the contemporary Mojave and Sonoran Deserts.

3.6. Mid-Holocene (MH): 8.0−4.0 ka

During the mid-Holocene, the predicted range of bison extended from northern British Columbia and Alberta to southern Texas and from the southern California coast to Iowa. This large mid-Holocene bison range coincides with low site counts (69 sites at 7-6 ka). These records suggest that continental population densities in the mid-Holocene were generally low relative to other time periods. Precipitation of the driest month is the second ranking variable between 9 and 6 ka (percent contribution: 18−20%) and precipitation of the coldest quarter ranks second in importance between 6 and 4 ka (percent contribution: 18−21%). Mid-Holocene bison distribution patterns are dynamic in the southern plains. At 5-4 ka, individual observations and the modeled bison distribution recede from Texas and significant portions of previously occupied areas of New Mexico, Oklahoma, Kansas and Missouri.

3.7. Late Holocene (LH): 4.0−0.0 ka

Raw numbers of bison occurrences increased in the late Holocene more than any other period since the LGM. The number of bison sites rose dramatically from 160 to 722 between 4 and 0 ka (Table 1). Site increases between 4 and 1 ka likely reflect rising bison abundances, because the increases are detected after controlling for taphonomic effects on occurrences (Fig. 1). The predicted distribution area also reached its greatest extent at 4-3 ka (Fig. S1). The predicted distribution of bison became more confined as the late Holocene progressed, but this change appears to be primarily driven by the increase of sites in the core of the distribution rather than site losses at the margins. Simulated temperatures in areas inhabited by bison rose throughout the late Holocene. The simulated median mean temperature of the coldest quarter in the bison distribution steadily increased and reached Holocene highs of 10 °C at 1-0 ka.

4. Discussion

Our analysis of archaeological and paleontological bison assemblages reveals dynamic changes in bison distribution and abundance, and highlights linkages between these changes and environmental variability. Results suggest that late Quaternary changes in the distribution and abundance of bison were directly influenced by effects of large-scale climate and by biophysical and environmental changes (e.g., ice sheet recession, biome shifts including the expansion and contraction of grasslands, and changes in growing season length). Our results provide support for our hypotheses that: (H1) bison abundance in open habitats is positively correlated with moisture availability, and (H2) temperature changes and associated hydrothermal stress act as important controls on bison distribution.

### 4.1. Key intervals of change for bison populations

4.1.1. Pleistocene-Holocene transition

From the LGM to the beginning of the Holocene, the distribution of bison became increasingly widespread as populations dispersed from glacial refugia and expanded onto deglaciated lands. The Pleistocene-Holocene transition was a period of rapid climate change and dramatic ecological reorganization involving mass extinctions and drastic geographic range shifts. Despite the critical role that bison played as the most abundant large herbivore in NA since the LGM, changes in the abundance and distribution of bison and underlying climatic and environmental drivers are not well understood. Prior analyses of radiocarbon-dated bison fossils indicated that long-term bison abundance was relatively stable at the continental scale (McDonald, 1981; Scott, 2010). However, spatial patterns of bison occurrences reveal changes in abundance that reflect regional range shifts and extirpations. The first widespread decline in bison abundance occurred during the first millennium of the Holocene (12-11 ka) when site losses are recorded throughout bison's entire distribution. Bison site turnover and regional distribution shifts indicate that bison were retreating from southern and southwestern NA and shifting to higher latitudes, especially to Alberta, Montana, and Wyoming. This elevated site turnover follows a genetic bottleneck observed ca. 15-13 ka (Heintzman et al., 2016). Between 16 ka and 8 ka the mean latitude of bison site observations increased from 43.9 °N to 46.7 °N and the mean elevation increased from 772 m to 1049 m (Fig. 6). This shift to higher latitudes and elevations coincides with the flattening of the latitudinal temperature gradient, rising summer insolation, recession of the Cordilleran and Laurentide Ice Sheets, and the expansion of grasslands across recently deglaciated landscapes (Grimm et al., 2011; Power et al., 2011; Williams et al., 2004).

4.1.2. Younger Dryas

The long-term effects of Younger Dryas climate change on the distribution and abundance of bison were minor relative to the consequences of warming and drying trends that occurred through the Pleistocene-Holocene transition. Bison abundance generally increased throughout NA ca. 13-12 ka (Fig. 1) and bison observations increased substantially throughout portions of the western Great Plains and Rocky Mountains from Alaska to Texas (Fig. 2). The most notable YD distribution losses occurred along the Pacific Coast of northern California, Oregon, and Washington and in portions of the Intermountain West in Arizona, Utah, and Idaho (Fig. 4, Fig. S1). Bison do not appear to have experienced a sustained, dramatic decline during the generally cooler YD. The median mean summer temperature in the bison distribution decreased by 2 °C, but model results show cooling temperatures explain only a small portion of changes in bison distribution at this time, suggesting climatic changes associated with the YD do not appear to have driven widespread bison declines.

Paleobiologists have remarked that it is not especially surprising that "Ice Age" bison survived a reversion to purportedly colder conditions during the YD (e.g., Fiedel and Haynes, 2004). However, paleoclimatic evidence suggests climatic conditions during the YD were spatially variable (Fastovich et al., 2020; Meltzer and Holliday, 2010). For example, multi-proxy temperature reconstructions reveal stable or warming temperature trends throughout the southeast United States (Fastovich et al., 2020) and northward
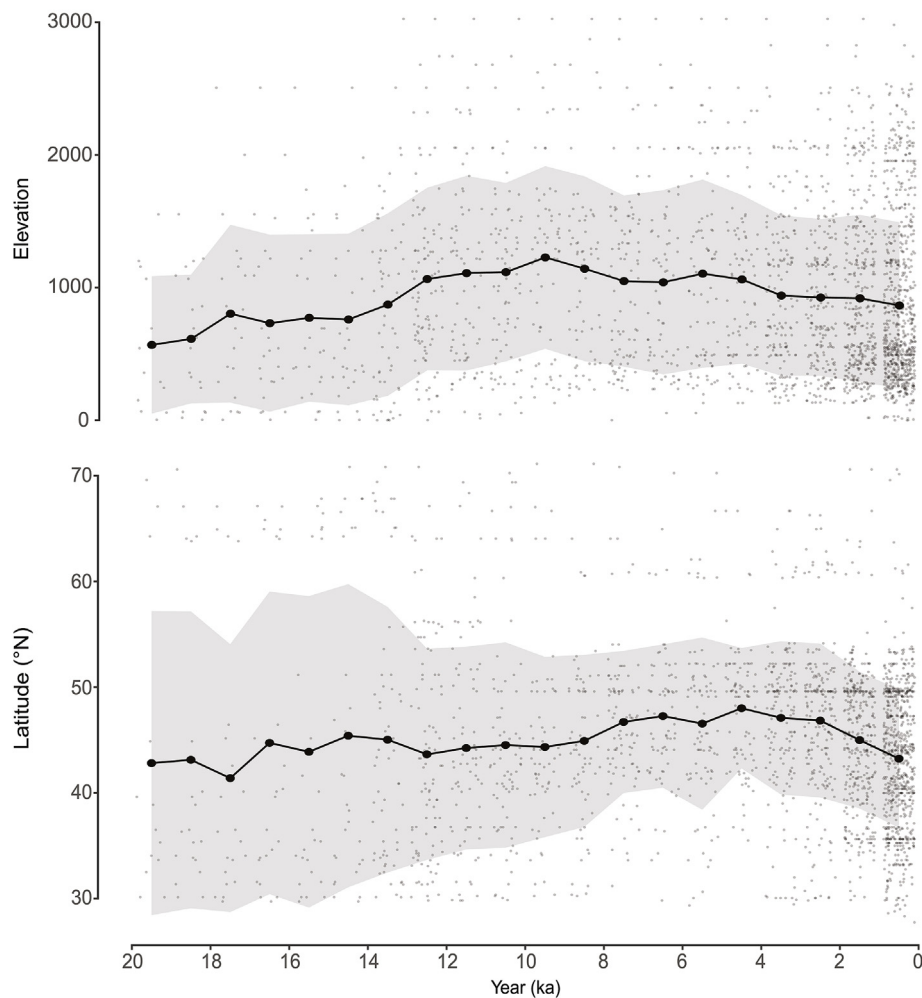
Fig. 6. Elevation (top) and latitude (bottom) of bison observations (small dots) across 1000-year intervals between 20 and 0 ka. Summarized by mean (large black dots) and standard deviation (gray shading).

advection of the warm southerly air masses combined with high summer insolation produced elevated summer temperatures in the continental interior (Shuman et al., 2002). Additionally, results from multiple climate simulations (including TraCE-21ka) show temperatures were warmer during the YD than the preceding Bølling-Allerød Interstadial in interior NA (Renssen, 2020). Our results provide little evidence that bison experienced stress from declining temperatures during the YD, possibly because their geographic range was largely isolated from dramatic temperature drops that affected other regions. These findings have important implications for understanding organism response to current warming.

While bison persisted, other North American megafauna experienced extinctions between 14 and 11.5 ka (Broughton and Weitzel, 2018; Stewart et al., 2021; Widga et al., 2017). Indeed, in the late Pleistocene, several important changes took place: 1) multiple abrupt climate changes of different types impacted different portions of the continent (Fastovich et al., 2020; Meltzer and Holliday, 2010), 2) many animal species went extinct (Meltzer, 2020), and 3) Clovis hunters expanded across the continent which suggests changes in human use of ecosystems (Waters, 2019). The relationships among these changes are still unclear, but

they mark a shift in the ecological context in which bison persisted for the remainder of the Pleistocene and Holocene. Consequently, the transient increase in bison abundance at this time (Fig. 1) could represent a release of bison from competition with other large grazers (e.g., horses, camels, mammoths, etc.) or a similar change in ecological dynamics after the extinction of other large herbivores.

4.1.3. Early and mid-Holocene

Through the early to mid-Holocene, bison experienced a series of regional declines in abundance, especially at range margins, resulting in the consolidation of bison presence toward the continental interior. The most substantial abundance declines took place 12-11 ka, 10-9 ka, and 7-6 ka (Fig. 1). Following the YD, continental climatic conditions were generally warm and dry (Fig. 5). Orbital changes that led to increasing summer insolation and recession of the Laurentide Ice Sheet resulted in increasingly warm and arid conditions throughout portions of the bison distribution as evidenced by dune and loess activity in the Great Plains (Forman et al., 2008; Halfen and Johnson, 2013; Miao et al., 2007), increasingly open landscapes at grassland-forest ecotones in the Northern Rocky Mountains (Alt et al., 2018), grassland expansion at the eastern prairie peninsula (Nelson et al., 2006), and the continued

recession of Great Basin pluvial lakes (Lyle et al., 2012; Reheis et al., 2014). Surface water was relatively scarce throughout the northern Great Plains. Many lakes in the region were significantly drawn down or completely desiccated (Donovan and Grimm, 2007; Filby et al., 2002; Schweger and Hickman, 1989; Smith et al., 2002). The timing of drying events varied by location (Liefert and Shuman, 2020), but by the mid-Holocene, bison had retracted from the southern, eastern, and western margins of their range (Fig. 4) towards higher latitudes and elevations (Fig. 6), which were presumably wetter and cooler. The number of sites recording bison during this interval increases in Rocky Mountains and portions of the Great Plains and decreases in southern and coastal NA. Early Holocene trends in bison skull morphology are indicative of a transition from "hook-and-roll" to "clash-and-release" dominance behavior (Widga, 2013). This behavioral shift possibly resulted from growing herd sizes and increasingly hierarchical social dominance hierarchies (Widga, 2013).

4.1.4. Late Holocene

Through the late Holocene, bison abundances increased but bison distributions became more spatially confined to central NA. Over the course of the Holocene, changes in local to regional bison observations correspond closely with the timing and distribution of moisture availability. Rising lake levels coincide with increased bison observations throughout the Great Plains and Intermountain West between 4 and 1 ka (Fig. 2; Liefert and Shuman, 2020; Shuman and Serravezza, 2017). Bison abundances increase when winter precipitation increases during the late Holocene ca. 2-1 ka (Fig. 5). A trend towards wetter conditions during the late Holocene would have resulted in reduced drought stress, more forage production, and improved water availability. The southward distribution shift between 4 and 0 ka may indicate that bison expanded south as northern latitudes experienced greater snowfall and drought eased in the south.

These results support the idea that late Holocene bison populations operated in a strong source-sink dynamic whereby bison source populations existed in the Great Plains and Intermountain West. We expect that hunting pressure would have exerted top-down pressure on bison abundance where climate conditions and habitat were marginal for bison. Although bison can persist in closed habitats, forest-dwelling populations were less numerous than those inhabiting open grasslands. Isotope and dental wear analysis suggest that during the late Holocene, forest-dwelling bison of the Ohio River Valley primarily consumed browse and occupied valley bottoms year-round (Widga, 2006). These behaviors may point to predator-avoidance strategies that have been observed in modern bison (Fortin et al., 2009; Widga, 2006). During the late Holocene, increasing Indigenous populations likely caused increased hunting pressure on bison, especially along the margins of the core bison distribution (Chaput et al., 2015; Chaput and Gajewski, 2016).

4.2. Regional bison abundance and distribution patterns

4.2.1. Northward migration into the ice-free corridor

Bison distributions were disjunct before the opening of the ice-free corridor between the Laurentide and Cordilleran Ice Sheets. Bison expanded northward into the ice-free corridor by approximately 13.5 ka. The recession of the continental ice sheets and opening of the ice-free corridor facilitated the northward migration of the southern bison and subsequent genetic admixture of the Beringian and southern populations (Heintzman et al., 2016). Phylogenetic evidence demonstrates that bison migrating into the ice-free corridor primarily originated from south of the ice sheets, as there was little southward gene flow from Beringian populations

(Heintzman et al., 2016). In our study, distribution expansions associated with ice sheet recession are contiguous with the mid-continent bison distribution. The expanding midcontinent bison distribution reached its northern limit south of the Yukon. This northern limit is corroborated by evidence from mitochondrial DNA (Heintzman et al., 2016). Predicted probabilities of bison presence in the ice-free corridor are greatest between 13 and 12 ka, which agrees with the timing of gene flow between midcontinent and Beringian populations and inferred habitability of the corridor.

4.2.2. Bison persistence in the Intermountain West

The historical abundance and ecological role of large herds of herbivores in the Intermountain West has been a topic of interest among scientific and management communities for decades (Mack and Thompson, 1982; Perryman et al., 2021). According to Mack and Thompson (1982), the historical scarcity of large herbivores, and subsequent lack of evolutionary adaptation by grasses to grazing, has contributed to the apparent fragility of Great Basin ecosystems to domestic grazing. The results presented here demonstrate that while the late Quaternary distribution and abundance of bison did indeed fluctuate in response to changes in temperature and precipitation, bison herds were never completely absent from the Intermountain West during the last 20 thousand years. At millennial timescales, the climate-predicted distribution of bison consistently included most of the Intermountain West region. In agreement with previous studies, our results demonstrate that since the LGM, climate conditions throughout most of the region were suitable for bison. Declining bison observations in the Great Basin and southwestern United States between 14 and 8 ka correspond to a major shift in regional hydroclimate. During this period, an intensifying moisture deficit, caused by rising summer insolation and northward migration of prevailing storm tracks, resulted in the widespread recession of intermountain pluvial lakes (Adams and Rhodes, 2019; Ibarra et al., 2014; Lyle et al., 2012; Reheis et al., 2014; Santi et al., 2019) and the expansion of semi-arid vegetation throughout the Intermountain West (Mensing et al., 2004; Nowak et al., 1994, 2017). Simultaneously, dominant open conifer woodland communities in southern New Mexico, Arizona, Nevada, and California were replaced by desert taxa (Thompson and Anderson, 2000). Bison became largely absent from much of the current extent of southwestern deserts by 8 ka, but they persisted in portions of the Great Basin and Colorado Plateau (Martin et al., 2017), and archaeological evidence points to bison reestablishment in the modern Chihuahuan Desert of northern Mexico and southern Texas, New Mexico, and Arizona ca. 2-0 ka (List et al., 2007).

Multiple sites record bison presences during periods when low abundances or absences have been previously inferred for the Great Basin. In fact, late Pleistocene bison site densities and predicted probabilities for the Great Basin are comparable to those of the Great Plains. The fossil record demonstrates that bison herds persisted during the late Quaternary throughout portions of the Great Basin (Grayson, 2006), Columbia Plateau (Chatters et al., 1995; Lyman, 2004; Lyman and Livingston, 1983), and Snake River Plain (Plew and Sundell, 2000). Grayson (2006) explored the distribution and abundance of bison in the Great Basin with a finer temporal resolution than our study and found that bison were most abundant in the northern and eastern portions of the Great Basin during the late Holocene. Similarly, several studies have demonstrated low artiodactyl abundances at Great Basin sites during the early and mid-Holocene and increasing abundances beginning approximately 4 ka (Byers and Broughton, 2004; Durrant, 1970; Schmitt and Madsen, 2005). In a survey of dated bison specimens in eastern Washington, Lyman (2004) suggested that bison may have been completely extirpated from the region around 8 ka and scarce

between 6 and 2.5 ka. However, extirpation seems unlikely since several bison fossils in eastern Washington date to this period. Additionally, in a review of the archaeological record of the Snake River Plain, Plew and Sundell (2000) demonstrated that bison herds were present and utilized by hunters throughout the Holocene. This evidence runs counter to claims that the Intermountain West historically lacked herds of large herbivores (e.g., Mack and Thompson, 1982).

4.2.3. Bison in midcontinent North America

Increasing bison observations and range expansions in central United States and south-central Canada coincide with well-documented eastward expansion of prairie assemblages at the grassland-forest ecotone beginning ca. 10 ka (McAndrews, 1966; Nelson et al., 2006; Williams et al., 2009; Wright et al., 1963). The fossil record documents the presence of resident bison herds that occupied habitats with varying degrees of openness across the grassland-forest gradient (Hill et al., 2014; Widga, 2014). Rapidly declining forest cover during the early Holocene is attributed to drying of the continental interior and associated fire-vegetation feedbacks (Williams et al., 2009). The persistence of grasslands in the prairie peninsula region after 6 ka, despite wetter conditions, highlights the role of disturbances such as fire in maintaining grassland systems (Anderson, 2006). While horning and rubbing can damage and kill a fraction of woody plants (Coppedge and Shaw, 1997), it is unlikely that these behaviors alone can prevent forest expansion.

A handful of additional records provide more detailed information on long-term local to regional trends in herbivore abundance and impacts in the North American continental interior (Fig. 7). Byers and Smith (2007) reconstructed Holocene trends in bison abundance from archaeological surveys of Wyoming Basin oil and gas fields. They quantified changes in large artiodactyl (bison and elk) fossil abundance in relation to the fossils of medium sized artiodactyls (deer, sheep, and pronghorn). The abundance of large artiodactyls was found to be positively correlated with moisture availability (Byers and Smith, 2007). Large artiodactyl abundance throughout the Wyoming Basin began to rise ca. 7 ka and reached a maximum at ca. 0.5 ka. Additionally, the Kettle Lake sedimentary record of *Selaginella densa*-type spores (a spikemoss) has been hypothesized to represent the impacts of herbivore populations on local vegetation in the paleoenvironmental record (Grimm et al., 2011). Today, *Selaginella densa* occurs throughout much of the northern Great Plains. In modern livestock grazing systems within the region, *S. densa* has responded positively to light grazing (Smoliak, 1965) and rotational grazing (Hubbard, 1951; Smoliak, 1960), but it can be reduced by high-intensity trampling (Coupland, 1950). A step-wise increase in *S. densa* at Kettle Lake ca. 0.9 ka corresponds to the initiation of a warm, dry episode (Shuman and Marsicek, 2016). Despite a return to cooler and wetter conditions regionally by 0.35 ka (Shuman and Marsicek, 2016), *S. densa* remained elevated, suggesting abundant bison (and other un-gulates) may have facilitated the persistence of *S. densa* at Kettle Lake in spite of changing climatic conditions. *S. densa* then rose dramatically with the introduction of domestic livestock at 0.1 ka. The herbivore population changes shown by these independent records corroborate the coarse scale temporal patterns in our bison abundance dataset (Fig. 7).

### 4.3. Bison adaptation: Evolution of the bison climate "niche"

Since the Bølling−Allerød Interstadial, the modeled long-term distribution of bison was primarily controlled by the mean temperature of the coldest quarter (Fig. 5). The simulated median mean temperature of the wettest quarter and mean temperature of the

warmest quarter within the bison distribution sharply diverged from the median continental temperatures ca. 18-17 ka (Fig. 5). From this point onward, bison continuously experienced temperatures exceeding the continental median. Hence, as temperatures rose, bison distributions shifted to higher latitudes and elevations (Fig. 6). These trends suggest that thermal stress applied considerable selective pressure, resulting in shifts in the distribution of late Quaternary bison populations.

Bison body mass has declined substantially since the LGM (Hill et al., 2008; Lyman, 2004; Martin et al., 2018). The most rapid body size loss occurred during the Pleistocene-Holocene transition when body size dropped by 26% over 3000 years (Martin et al., 2018). Researchers have debated the potential causes of this remarkable diminution. Proposed drivers have included human predation, forage quality and availability, predator avoidance, and thermal regulation. Together, sex, mean decadal temperature, and drought explain over 95% of decadal variance in body size of bison at Wind Cave National Park, South Dakota (Martin and Barboza, 2020b). Additionally, bison body size was found to be negatively correlated with global temperature anomalies derived from the GISP2 $\delta^{18}O$ ice core record at millennial timescales (Martin et al., 2018). The negative relationship between temperature and body size indicates that long-term diminution may be an evolutionary response to selective pressure exerted by rising temperatures throughout the late Pleistocene and early Holocene. The Heat Dissipation Limit (HDL) theory posits that the maximum energy expenditure of endothermic animals is limited by their ability to dissipate heat and avoid hyperthermia (Martin and Barboza, 2020a; Speakman and Król, 2010). HDL theory thus predicts that when animals are limited by their capacity to dissipate heat, large-bodied individuals will be disadvantaged relative to smaller individuals, which possess a higher surface-to-volume ratio. Hence, warming temperatures, especially at the Pleistocene-Holocene transition, may have selected for smaller-bodied bison. We note that rapid bison diminution between 16 and 8 ka (Hill et al., 2008; Martin et al., 2018) coincides with the highest simulated summer temperatures within the bison distribution (Fig. 5).

Millennial-scale changes in bison abundance and distribution were also strongly influenced by hydroclimate dynamics. Elevated summer insolation drove pervasive drought conditions in midcontinent North America during the early to mid-Holocene (Shuman and Marsicek, 2016; Williams et al., 2010). The full severity of Holocene aridity in NA is not well captured by most climate models, including both the CCSM3 TraCE-21ka simulations used here (e.g., Befus et al., 2020) and updated generations of CMIP (Climate Model Intercomparison Project) mid-Holocene simulations (e.g., Morrill et al., 2019). Despite this bias in climate model output, patterns in bison occurrence frequencies (Figs. 1−3) parallel those in both time series (Shuman and Marsicek, 2016) and maps of NA hydroclimate (Liefert and Shuman, 2020). Between 12 and 6 ka, bison experienced multiple waves of abundance declines throughout much of their geographic distribution as reconstructed continental aridity intensified (Figs. 1−3). Subsequently, increasing moisture availability throughout midcontinent North America after 5 ka coincided with rising bison abundances throughout in the Great Plains and Intermountain West (Fig. 2). The observed relationship between hydroclimatic conditions favorable for increased abundance and availability of forage and growing bison populations aligns with archaeological records that show an increased investment into the pursuit and procurement of bison and trade of bison products by Indigenous populations in the late Holocene (Cooper, 2008; Roos et al., 2018; Zedeño et al., 2014). Sizable bison populations persisted until intensive harvest of bison in the 19th century led to steep declines. Historical documents describe vast herds throughout the continental interior in the 18th and 19th centuries.
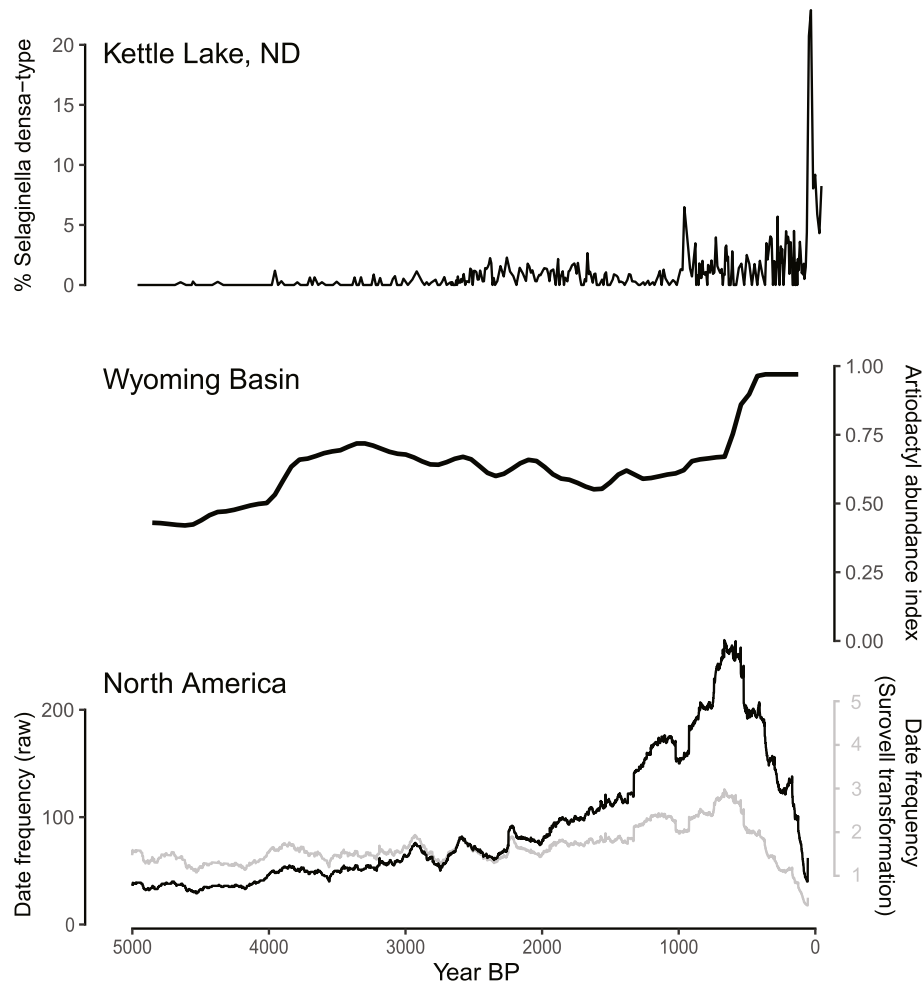
Fig. 7. Comparison of independent records of large herbivore abundance 5-0 ka. The abundance of *S. densa*-type spores (top) is expressed as a percentage relative to the terrestrial pollen sum of a given pollen subsample from Kettle Lake, ND (Grimm et al., 2011). The large artiodactyl index (center) represents the abundance of large artiodactyl fossils (elk or bison size) versus medium artiodactyls (deer, sheep, or pronghorn size) across archaeological surveys of Wyoming Basin oil & gas fields (Byers and Smith, 2007). Frequency of dated strata with bison fossils and directly dated fossils (bottom) from archaeological and paleontological studies throughout North America with raw (black) and transformed frequencies (gray).

Scholarly estimates place Great Plains bison at ca. 30 million animals during this period (Flores, 1991; Isenberg, 2001; Lott and Greene, 2002).

From our distribution maps, modeled climate envelopes, and prior knowledge of past regional biome shifts, we conclude that bison populations persisted throughout a broad geographic range of NA since the LGM, and that the highest bison abundances were found in open temperate rangelands. Although historical distributions of biomes throughout most of western North America are poorly constrained, bison distribution shifts correspond to documented expansions and contractions of grassland and shrubland biomes, including, for example, the northward expansion of open rangelands into the previously glaciated ice-free corridor at 13-12 ka (bison range expansion), the aridification of the southwest through the early to mid-Holocene (bison range contraction), and the retreat of arboreal taxa at the forest-prairie ecotone along the northern and eastern margins of the Great Plains beginning at ca. 10 ka (bison range expansion). Additionally, hydroclimatic conditions appear to act as a strong control on bison abundance in open rangelands. While bison can incorporate woody vegetation into their diet and even subsist on browse, grassy habitats support the greatest bison populations and potential population growth. Perhaps the most striking evidence of bison abundance responding to climate-driven changes in forage production is found in the widespread increases in bison abundance throughout the rangelands of the Great Plains and Intermountain West during the relatively wet late Holocene. This underscores the important influence of climate and climate-vegetation feedbacks on bison distributions at large spatiotemporal scales.

5. Conclusions

Over the past 20 thousand years, bison experienced dramatic environmental changes that shaped their distribution, morphology, behavior, and population dynamics. During the early deglacial period, bison were geographically widespread, yet fragmented into regional glacial refugia. Though large populations of most North American megafauna did not persist beyond the YD, bison survived and exhibited remarkable stability. As temperatures warmed and precipitation declined at the Pleistocene-Holocene transition, bison abundances declined in southern and low-lying regions, and populations shifted northward and upslope. With easing drought conditions in the late Holocene, increased forage production supported increasing bison populations throughout the continental interior. Late Holocene bison populations continued to increase until just recently, when 19th century market hunting led to the

near extinction of bison from North America (Isenberg, 2001).

Our distribution modeling approach demonstrates that bison continuously inhabited significant portions of the Great Plains and Intermountain West since the LGM. Bison populations advanced and contracted in response to climate warming and cooling and changes in hydroclimatic conditions that influenced the quality and availability of forage. Our results highlight the remarkable adaptability of bison to a wide range of climatic and ecosystem conditions and support the premise that modern bison are unique in some ways from their Pleistocene ancestors. The climate envelope occupied by Pleistocene bison was different from the climate experienced by anatomically modern bison during the late Holocene.

Understanding the causes of past extinctions will require accurate reconstructions of the environmental conditions experienced by individual species. Our approach can be applied to other species of Pleistocene megafauna to characterize pre-extinction climate envelopes to understand the species-specific environmental conditions experienced before and during extinction.

A number of tribal entities are leading efforts to restore bison to North American landscapes to reinvigorate important cultural lifeways linked to bison. Results from this research provide important context for these efforts by identifying climatic conditions that pose opportunities and challenges for bison reintroduction. Today, bison face risks from constrained mobility, geographic isolation of herds, habitat loss, artificial selection for nonadaptive traits, inbreeding depression, reduced fitness from cattle introgression, competition with other herbivores, and other sources (Halbert and Derr, 2007; Hedrick, 2009; Martin et al., 2021). These risk factors may reduce bison capacity to adapt to rapid environmental changes in the future. Because the current distribution of bison has been greatly reduced from its historic extent and is highly influenced by human interventions, conservation planning for the establishment of new protected areas or identification of at-risk populations can leverage distribution models trained on bison occurrences in archaeological and paleontological records.

Author contributions

John Wendt: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Software, Visualization, Writing − original draft, and Writing − review & editing. Dave McWethy: Conceptualization, Funding acquisition, Project administration, Supervision, Writing − original draft, and Writing − review & editing. Chris Widga: Conceptualization, Data curation, and Writing − review & editing. Bryan Shuman: Conceptualization and Writing − review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2022.107472.

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