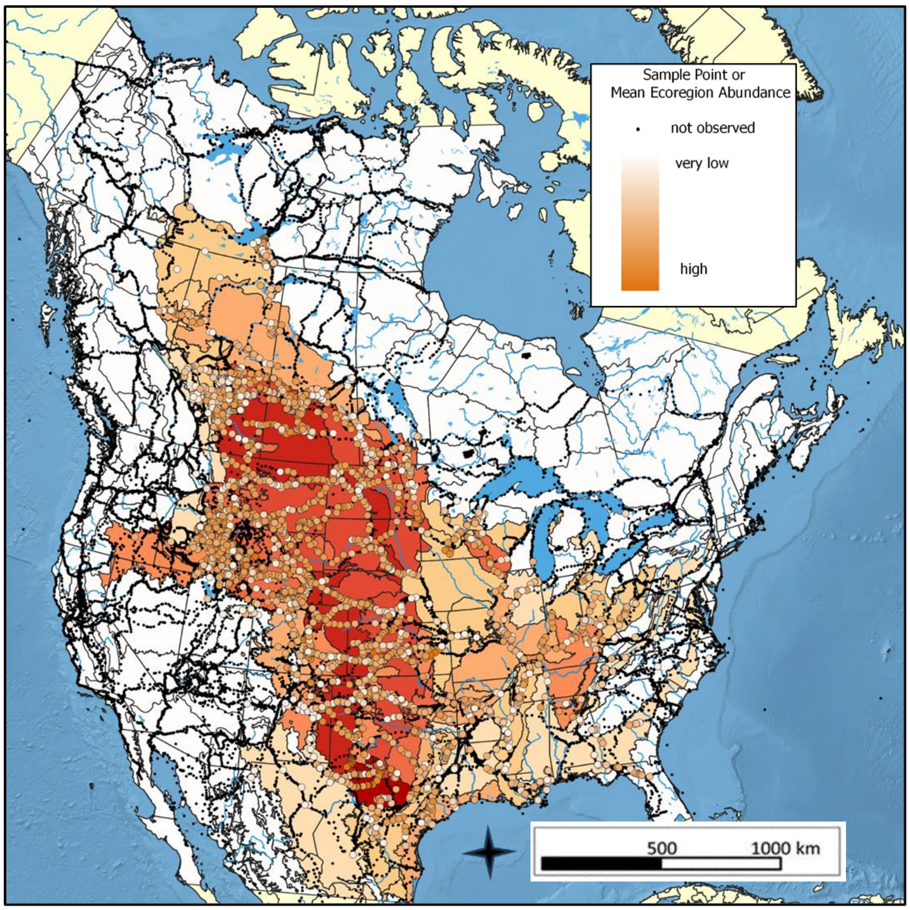
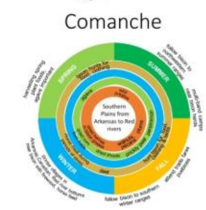
# BUFFALO CONTINENT:
# Historical Distribution and Abundance of the North American Bison











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# SUMMARY

For >15K years since humans entered North America Holocene, they have jointly occupied the continent with "The Buffalo" – an evolving lineage of species of the genus *Bison*, the largest mammal surviving the early Holocene continental extinction event. Eventually *Bison bison*, the subspecies with a distribution centered on the Great Plains, persisted in the presence of people. At the time of European contact, buffalo numbered in the millions, occupying not just the plains, but adjacent areas in the western Cordillera, the northern taiga, and eastern woodlands. Moreover, archaeological and paleontological information indicates that although bison's distribution and abundance has varied over millennium, in general the species has maintained a relatively stable distribution in the center of the continent. Ecologists describe that a combination of biophysical (bottom-up forage production) and cultural (top-down predation) factors determined bison distribution and abundance. At a continental scale a simple bottom-up/top-down interaction fails to describe the feedback mechanisms necessary for bison population regulation and stability. A more complex hypothesis also recognizes the importance of surface water availability in core bison habitat in the center of the Great Plains:

> *Humans, beaver and the buffalo are long-term mutualists. Humans, through fire use and conserving beaver contributed additions to the essentials of bison habitat—forage, water and winter cover. More importantly, by regulating bison populations with predation, humans kept the bison from degrading habitats. In return, the buffalo could provide many humans with nearly everything—food, clothing, shelter and for some cultures, a complete circle of life.*

The evaluation of this hypothesis proceeds by first describing applicable niche construction, optimal foraging, seasonal rounds and foraging, and mutualism theory. This is then used to develop a preliminary conceptual model for bison distribution and abundance influenced by biophysical, cultural and mutualistic factors. The model is evaluated using fire history evidence from ~150 studies across the continent, food resource abundance data from ~30,000 days of first-person journal observations from early European travellers' crossings of ~140 ecoregions, and current ecological data on the effects of bison and other large herbivores in select areas. This data was evaluated with three analyses: 1) spatial evaluation of fire frequency, biophysical variables and resource abundance indices across ecoregions during the European contact period, 2) temporal evaluation of how bison and human abundance varied in select regions during the immediate pre-contact and early contact periods, and 3) utilizing current data to estimate historic bison densities and fire regimes that would maintain the pre-contact condition riparian zones as visible in historic photographs.

At a continental level, a multivariate random forest analysis of biophysical and cultural data showed bison abundance was best predicted by ecoregions with high grassland cover, followed by fire frequency (almost always Indigenous ignitions), deciduous forest cover (providing habitat for humans on the edge of grasslands), alternate resources available to humans (plants, fish, fowl, other sources meat), and human abundance. Bison showed a consistent pattern of expanding into various regions after human depopulation events ~ CE 1200 to 1800. At regional scales, the pattern of bison abundance and distribution varied. Although decreasing grassland cover and increasing human abundance was always correlated with bison population declines and range edges, the alternate resources used by humans varied. In the SW plants (corn resources used by Pueblos)

were the primary alternate resource, in the NW fish (salmon bearing streams), in the NNW a combination of fish and other prey (caribou and moose), in the NNE wild rice, and in the NE and SE a range of domestic and wild plants.

Historical photographs and journal accounts consistently document vigorous riparian zones, aspen communities, and beaver abundance. The mean historic bison resource abundance index for ecoregions was calibrated using modern analogs for stocking densities to develop a range of likely historic bison densities that would maintain these conditions. This method predicts 8 ecoregions in the core of the Great Plains with high bison abundance (> 3 bison/$km^2$), 18 ecoregions with moderate bison abundance (1 to 3 bison/$km^2$), 44 ecoregions with low abundance (< 1 bison/$km^2$), with a further >60 ecoregions with no bison observed. Extrapolating by the area of ecoregions, and periods when bison range expanded for various ecoregions, this method predicts a total continental bison population of approximately 5 to 10M bison at ~ CE 1200, increasing to 12 to 25M bison at ~CE 1700 to 1800 due to Indigenous depopulations followed by increases in bison's distribution and abundance. These estimates are supported by other researchers using other methodologies.

The analysis concludes that a long-term human-bison-beaver mutualistic relationship provides a reasonable explanation for the historical spatial and temporal variation in bison at a continental level, and long-term habitat conditions. Human's primary role in the mutualism was in hunting bison to densities of <1/$km^2$ in most ecoregions and possibly stimulating bison behavioral avoidance of riparian zones and other risky terrain. Low bison densities maintained beaver habitat which in turn provided water for both humans and bison, woodlands important for humans, and herbaceous and woody fuels for fire. Successful restoration of bison requires human predation to maintain habitat for both beaver and bison, and many ecological communities.

**Data Sources:**

-Ecoregions visible online at: https://ecoregions.appspot.com/

-Wildlife and plant resources observed in historical journals currently at: https://lensoftimenorthwest.com/themes/lens-northwest-files/google-earth-map-journal-wildlife-observations/

-After c. 2026, back-up digital databases and a copy of this report will be archived with various global biodiversity data centers (hopefully) and at very least, at the Whyte Museum Archives, Banff, Alberta Clifford A. White fonds: https://www.whyte.org/digitalvault/categories/archives-library

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# ACKNOWLEDGEMENTS

This paper is the fourth in a series of technical reports growing from the realization that although Indigenous peoples and current interdisciplinary researchers know the processes determining long-term distribution and abundance of bison for many individual regions, this had not been synthesized for the continent. Why has this continental analysis been done for many other species, but not bison? This is a puzzling question. The “buffalo” is designated the United States’ national mammal—an iconic species, saved from extinction and then restored in what is becoming one of humankind’s greatest ecological and cultural restoration stories. Perhaps the answer lies in the complex historical interactions of both biophysical and cultural influences. An interdisciplinary approach is required. As I reviewed the literature the breadth of this literature, what was apparent is that the ecological and cultural history of the bison is essentially the Holocene story of the North American continent. Where bison were--and more importantly where they weren’t-- embraces biophysical and cultural interactions from coast to coast to coast for at least the last 10 millennium.

Clearly no one person, and especially me (a mountain guy from a narrow valley), has the mental capacity to tell this story that largely centers on the vast central prairies but extends to the edges of the continent. I am grateful to the scholars and deep thinkers—both Indigenous and newcomers--that have given me some grace in my failure. They provided information, asked questions, and gave stimulation that made continental synthesis necessary and partially possible:

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Figure A-1. Captive buffalo (wood bison ecotype) in the paddock built in 1897 as a tourist attraction near Banff townsite in Banff National Park (Douglas Leighton photograph). In 1998 the paddock was removed, and in 2017 a free-roaming plains bison ecotype herd was restored to the northeast corner of the park in the Canadian Rockies. The density and abundance of both captive and free-roaming bison in the Canadian Rockies may be influenced by long-term patterns of human-bison mutualism. For further description see: https://lensoftimenorthwest.com/galleries/alberta/south-saskatchewan/banff-bow-valley/banff-buffalo-paddock/

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# 1. INTRODUCTION

The genus *Bison* is the largest survivor the 10-12K years BP extinction of a plethora of other species >40kg across North America. For the subsequent >10K years of the Holocene, evolving bison thrived, largely on the continent's Great Plains [1–5]. By the mid-Holocene, the species *Bison bison*, commonly called the buffalo, numbered in the millions and was both an ecological and cultural keystone species [5–8]. Numerous Indigenous peoples were at least partially dependent on bison for food, shelter and clothing [9,10], and this helped define territorial homelands and eco-cultural biomes [11,12]. European contact and expansion into North America after ~1500 CE commenced another crisis for the continental faunal assemblage. Again, the large mammals were susceptible. In the period from ~CE 1750 to ~CE 1880, bison were reduced to fewer than 1000 animals [5] of the plains bison ecotype on the southern plains, and the wood buffalo ecotype in the boreal woodlands[13,14]. Humans' role in the overkilling of bison is well-documented [15], and researchers [2,3] mapped the spatial pattern of extirpation within years of the species' near-demise (Figure 1.1).

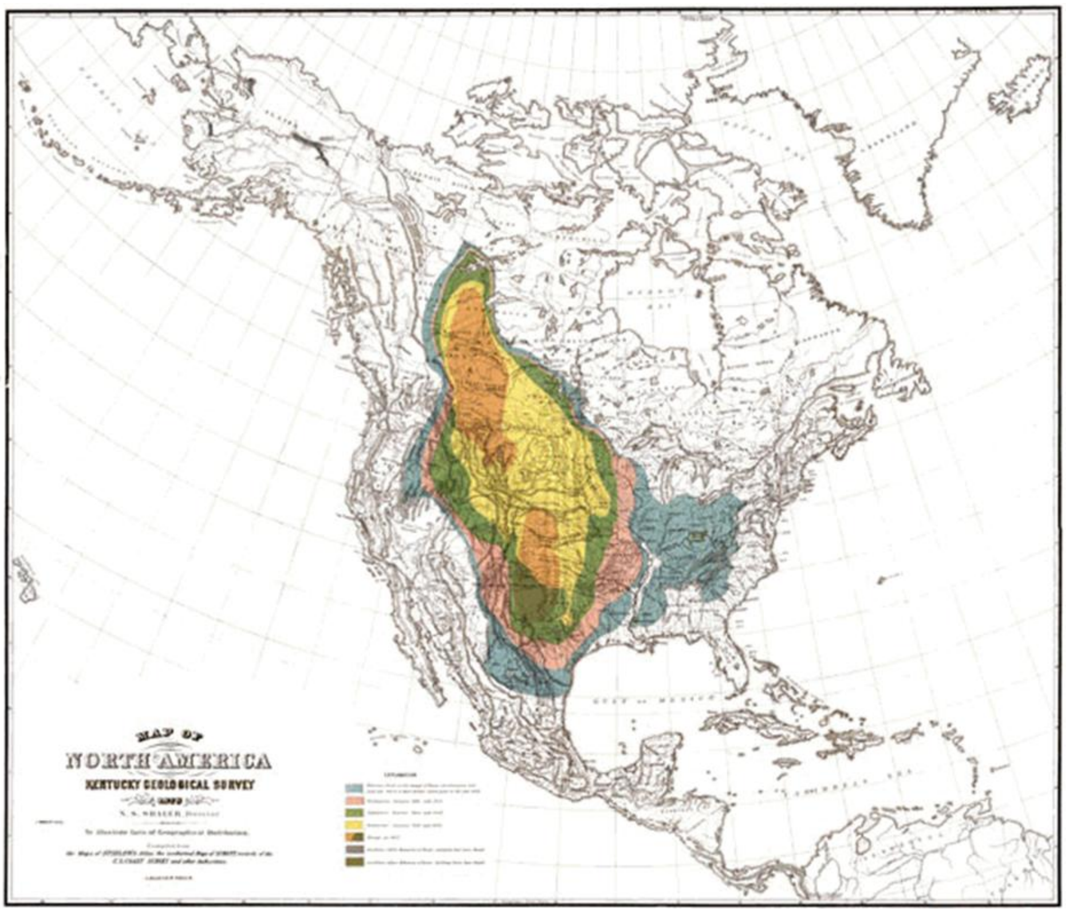



**Figure 1.1.** Range contractions of the American bison during the period from pre-1800 to 1875 as mapped by Joel Allen in 1876 of the Kentucky Geological Survey [2]. The figure shows the edge of the historic bison range before 1800 (blue), the range contraction from 1800 to 1825 (pink), 1825 to 1850 (green), 1850 to 1875 (yellow), and the range in 1875 (orange).

Although the buffalo was North America's largest, numerous, and most iconic herbivore, factors influencing its distribution and abundance remain poorly understood. Indeed, even defining the post-European contact distribution and abundance has long been controversial [16–19]. Researchers recognize that both biophysical and human cultural factors were important [20–22] but integrating the knowledge and investigation techniques of several academic disciplines is daunting. Ecologists and other biophysical scientists focus on quantified studies of climate, terrain, vegetation and effects of non-human predators and competitors [14,23–25]. Indigenous knowledge and the social sciences evaluate human-bison interactions, but often for small regions not determinant of bison distribution or abundance. However, given the visibility of bison observations in the archaeological and historical record, and their importance to both biophysical and cultural understanding, the study of the bison's interactions with humans can yield significant interdisciplinary understanding [6,8,26]. We can summarize hypotheses for bison's historical distribution and abundance under 3 broad hypotheses: bottom-up, top-down, and mutualism.

## 1.1 "Bottom-up" Grassland Productivity Hypothesis

In the earliest serious quantitative estimate of bison's total population, Ernest Thomas Seton [27]:258-260 stratified Joel Allen's [2] North American bison range map (~ 7.77 million km$^2$, Figure 1.1) into 3 broad grass productivity categories with estimates of bison densities based upon a 1900 census of rancher stocking rates of cattle, horses and sheep: 1.29 million km$^2$ of fertile prairies (at ~23 bison/km$^2$); 3.88 million km$^2$ of open plains (at ~10 bison/km$^2$), and 2.59 million km$^2$ of forest habitat (~2 bison/km$^2$) yielding an overall estimate of ~75 million bison for the continent. Subsequent researchers have reduced this total number to ~30 million based upon observations on the density of wild bison herds, and allowances for more variable habitat even on the highest quality ranges, domestic stocking rates that maintain ecosystems, water availability, animal movement, periodic drought, and predation [28,29].

The grassland productivity hypothesis fails to explain historic no or low bison numbers across most of North America. For areas of west of the continental divide, "bottom-up" advocates suggest occasional heavy snowfalls [30], unfavorable grassland phenology [31], or discontinuous habitat [20] are potential productivity explanations for few bison . For tallgrass prairies east of the Mississippi, potentially lower protein content has been suggested as a cause of low historic bison numbers [32].

## 1.2 "Top-down" Human Predation Hypothesis

Human predation has long been recognized an important factor in limiting historic bison distribution and abundance. As Kingston [33] observed:

> *The distribution of the buffalo over the continental area depended on a number of factors. Among these were the normal length of life of the species, and the rate of reproduction; the amount of available food as affected by soil, temperature and rainfall; such major obstacles as mountain chains, dense forests, deep canyons and areas of extreme desert type; predator animals and human enemies. In considering the range of the buffalo the Columbia Basin presents a curious and rather intricate problem and biological distribution in which the hunting by the Indians and physiographic difficulties explain in the most part the scarcity or absence of the buffalo*.

Researchers have refined human predation influences on bison abundance along the route of the 1804-06 Lewis and Clark expedition or as a function of terrain and vegetation along bison movement corridors through the Western Cordillera. In general, bison numbers decline with distance from high density core populations on the grasslands of the Great Plains, increasing human numbers, increasing vegetation cover or with increasing terrain constrictions or snow cover along bison movement routes [33,20,34,35,22]. Moreover, researchers have identified two different strategies for bison to reduce human predation risk [36,37]: 1) by forming large herds and long-distance movement on the plains, or 2) by maintaining low densities and "spacing out" in woodlands. In 2016 Bailey [38] evaluated factors influencing bison's distribution concluding:

> *These observations provide compelling evidence that human predation was a major, perhaps preponderant, factor limiting bison distribution in the Rocky Mountains. While other factors varied geographically and temporally, Native American predation was more persistent, mobile and widespread.*

Most recently Shaw [39] concluded:

> *Humans have affected bison populations for millennia primarily through hunting…Hunting impacted bison demographically, through reductions in numbers or skewing of sex ratios, and indirectly by concentrating bison in areas in which they were relatively safe. Similarly human hunting pressure excluded bison from areas in which they were particularly vulnerable to hunters.*

## 1.3 Issues with Simple "Top-Down vs. Bottom-up" Human-Bison Explanations

Researchers describe for select local study areas that a relatively simple combination of biophysical (bottom-up forage production) and cultural (top-down predation) factors determined numbers and range of the species, with Indigenous hunting primarily determining the edges of the species range.  These explanations can partially explain bison abundance on the plains where they fed by productive grasslands, and bison rarity in forests, mountain valleys and other areas of poor habitat quality habitats where human hunting risk was high. At a continental scale a simple bottom-up/top-down explanation is unsettling.  There are several incongruities. For example, a plausible estimate for bison numbers at European contact is ~30 million. But why not 3 million if humans were such a deadly predator, or perhaps 300 million if they were not? In fact, given the fates of other large mammals at the hands of humans in the early Holocene, why did bison survive at all? Certainly, in the period BCE 5000 to CE 1800 bison were abundant on central grasslands and periodically in Texas, but why did their range not periodically extend to other coastlines of the continent? Feral domestic cattle escaping from European contact extended well into these coastal regions and often thrived. Why core bison habitat on the plains peripherally surrounded on nearly all sides by ecoregions with foraging species relatively intolerant to grazing, and exacting fire regimes?

These questions lead to consideration of four main issues with a simple "bottom-up/top-down" ecological perspective related to the stability of bison distribution/abundance, and habitat over time.

*Indigenous traditional knowledge and population*- Humans significantly influenced the evolution of North America's *Bison bison* [13,5,40,41]. In return, in their >10K years of their interacting with bison on the continent, humans both adapted to and manipulated the species and its habitat, and this is reflected the traditions of many Indigenous groups on the Great Plains [42–48], the western cordillera [49–55], the northern parklands and boreal mixed-wood [8,56–58] , and the eastern tallgrass prairies and savanna [59–61]. This body of knowledge has rarely been integrated into to understanding population-level, long-term human influences on the distribution and abundance of bison. Moreover, in comparison to many continents, human population density and land use have been relatively stable around core bison range on the North American grasslands for most the period since ~ BCE 8K [62,63]. Epp and Dyck [10] describe an interactive predator-prey scenario where a combination of ~24M migratory and ~6M non-migratory bison would have been an important sustainable resource for ~100,000 people—an estimate close to other Indigenous human population estimates for the Great Plains pre-contact period.

*Stable bison distribution and abundance*- Although there is certainly variability in bison's range and numbers in the last 500 years [21,39,64–66], it is also striking how, for the last 5000 years, bison fossil and historical observations occur in the central continental grasslands (Figure 1) with few bison elsewhere [23,67]. For example, California's Central Valley was a massive area of grassland, easily accessible from occupied bison range to the northeast but has little evidence of bison use throughout the Holocene. No bison occurred on the Flathead Prairies of Montana despite being <100 km west of large bison herds on the Missouri River headwaters. Yet a group of four bison calves brought here from the plains in the late 1870s grew to a herd of nearly 5000 in two decades [54,68] . The grasslands are now the site of the National Bison Refuge. Elsewhere along the Western Cordillera, bison thrive in several other restoration efforts outside of historic range [22]. Moving east, ecosystem net primary productivity increases, and expansive grasslands likely occurred east of the Mississippi River and along the Atlantic Seaboard [69,70]. But again, there is no substantial record of historic bison presence [2]. Clearly the processes that held bison populations "in check" in the central part of the continent were persistent and powerful, but at the same time did not "overshoot" and result in extinction. For millennium these influences must have interacted with other phenomena such as climate and cultural change.

*Persistence of habitat*- Paleo-ecological research on the Great Plains and peripheral areas describes a relatively stable flora, fauna, and associated disturbance regimes present and interacting for thousands of years [71–74]. Herbivory and fire were the primary interacting and competing processes influencing species cover and abundance-- with herbivory most significant in the center of the grasslands, and fire more important in peripheral regions [75,76]. Was the herbivory-fire interaction partially result from the relative stability of bison populations described above being influenced by changing climates and cultural regimes? On the shortgrass prairies of the southern and central Great Plains, grasses such as grama and buffalograss with a $C_4$ photosynthetic pathway have dominated since ~BP 5000 [69,77]. These species are grazing tolerant with larger cell-walls and less protein than their $C_3$ counterparts. As bison continued to evolve during the Holocene, on the central plains its body-size declined, partially due this lower forage value and competition for forage in large herds [40,78,79]. In contrast, the north and west edges of the grassland, bison remained generally larger. This region is dominated by plant species and communities with high nutritional value such as $C_3$ pathway grasses (e.g., rough and Idaho fescue, blue-bunch wheatgrass), sedge meadows, trembling aspen, and riparian willows [80–82]. Many of these species have a low tolerance to grazing or browsing from large herbivores, but are adapted to frequent burning to reduce forest cover [83–86]. This pattern fire adaption, high nutritional value but low tolerance to herbivory requires careful modern management of cattle grazing allotments [72,87,88] and for elk and bison on winter ranges in parks and protected areas [89–91]. Similarly, on the eastern edge of bison range, current efforts in restoring oak savanna and tallgrass prairies recognize that fire is an essential process to reduce regional "mesophication" resulting in higher forest cover and less grassland [92,93]. Moreover, researchers recognize that a careful blend of fire and bison herbivory management may be required to restore native tallgrass-oak savanna prairie [94] and grasslands on the eastern periphery of the Great Plains [95].

*Availability of Water*- Many studies of historic bison distribution and abundance assume that water was generally not limiting and focus on grassland production. Although this may apply to many some areas of pastureland today, the situation was vastly different in the past. Historically, across the Great Plains water sources were often distant, ephemeral, dependent on climate and season, and could be a location of high predation risk for bison. Indigenous humans knew where water sources were and were equally dependent on it- for direct survival, for the possibility of prey being nearby, and for riparian vegetation that provided food, shelter, and heat. Modern range managers have an array of tools to create and maintain water sources. Indigenous peoples similarly could also manage water by harnessing the planet's most prolific native dam builder—the beaver [96,97].

These four incongruities, where human patterns of landscape occupation, hunting, burning and water management could have influenced bison's abundance and distribution suggest a potential mutualistic human-bison ecological relationship, possibly mediated by beaver,at a continental scale. Simply put, it would be surprising that in several thousand years of co-existing as predator and prey that humans and bison did not co-evolve positive interactions that stabilized their respective distribution and abundance.

## 1.4 Human-Beaver-Bison Mutualism?

R. Grace Morgan's 1991 doctoral dissertation [98] on the human-beaver-bison relationship braided together old and new thinking. In 2020 the work was deservedly published as the book: "Beaver, Bison, Horse: The Traditional Knowledge and Ecology of the Northern Great Plains" [8]. The writings here are instrumental in bringing into mainstream anthropological and ecological research a deeper perspective that Indigenous knowledge was required to more fully explain bison's distribution, abundance, and habitat. Morgan recognized that native people with homelands on continent's grasslands revered and protected the beaver. Plains groups clearly understood the beaver's role in creating water storage in their arid homelands, whereas peoples based in the forest rapidly enjoined in the European fur-trapping industry. Morgan also studied the relationship between people and annual bison movements [99] , and how spring grassland burning influenced bison foraging patterns [100], again integrating traditional knowledge and bison ecology.

Morgan's linking of ecological, anthropological and traditional knowledge provides a basis for a more complex hypothesis for the resilience of bison's populations for greater than 10K years. We must consider that even in the presence of ongoing hunting from humans, the two species were intertwined in a long-term mutualistic ecological relationship [98,41,48,101]. Bison provided humans with many resources including food, clothing and shelter. In turn, humans, through several processes, influenced bison distribution and abundance: 1) because humans require wood for heat and shelter in winter, they retreated from grassland habitats giving bison a seasonal refuge from predation; 2) bison found refuge from predation in territorial buffer zones between Indigenous water groups of people; 3) through use of fire and bison hunting people maintained high quality bison habitat on the edge of core bison use areas. Bison used these areas during droughts or intense winters; 4) plains cultures valued and protected the beaver due to its role in impounding sources required by both people and bison, and 5) human presence, communal hunting practices (herding, burning), and perhaps even direct transplanting could stimulate bison dispersal from source population areas into adjacent regions with lower bison use.

Mutualism requires regulatory, feedback mechanisms that either benefit, or at least prevent long-term harm to interacting species. For humans, beaver and bison, two potential key regulatory feedback processes are:

- *Variable predation*- Humans require wood for heat and shelter in winter—thus humans retreat from grassland habitats into peripheral woodlands, reducing predation rates as distance increases from woodlands. As bison numbers increase, they disperse from grasslands into peripheral woodlands and experience higher predation rates. Similarly, humans could adjust predation rates on beaver depending on the need to conserve water.
- *Variable habitat management*- Humans could use fire, or predation effects (direct or behavioral) that effect bison density to maintain habitat themselves, bison and beaver. Humans adapt fire timing and intensities to maintain vegetation. High bison densities are beneficial to humans in the short-term but degrade important human habitats (woodlands, riparian zones, valued human foraging species etc.). Similarly, variable beaver densities influence a myriad of habitat conditions near water [97,102] . Human awareness of habitat conditions created by fire, bison, and beaver could provide the feedback that regulated human abundance and behavior.

## 1.5 General Research Approach

Reviews of historical records are one means to describe and quantify human-bison-habitat influences. Beginning in the 1500s, often financed by the demand for beaver and other skins [103–106], European traders and trappers began to enter the interior of the continent, reaching the edges of the bison's massive core range on North America's interior plains. After living with Indigenous peoples on the southern coastal plains of Texas in the period 1528-35 Cabeza de Vaca first recorded the presence of buffalo-- *"Cattle come as far as this. I have seen them three times and eaten of their meat."* [2]:131. More than a century later, after canoeing up the rivers from Hudson's Bay and wintering on the Saskatchewan River, William Henry Kelsey trekked onto the northern Great Plains. Led by Cree and Assiniboine groups he travelled southwards. Although his journal entries are terse, and his locations sometimes a puzzle [107,108], he likely followed a long-used Indigenous trade route to reach the Mandan and Hidatsa villages along the Missouri River valley [109]. While crossing today's southern Manitoba and North Dakota, Kelsey became the first European to describe the bison herds and Indigenous hunting techniques on the northern plains [110]. The writings of these early travellers, and those who followed not only describe expansive herds of bison, but an awe-inspiring ecosystem of grasslands, other herbivores and predators. Most significantly, these writings document Indigenous cultures with annual rounds dependent on bison either seasonally, or nearly totally for meat, hides, and numerous other products. The early journals often describe the intricate traditional knowledge of Indigenous peoples, and the varied hunting, gathering and culturing practices that allowed these cultures to persist through time, often in a very hostile climatic environment out on the Great Plains.

Most importantly for considering Indigenous culturing of landscapes, the journals of early travellers are replete with references to wildland fire. They provide descriptions on the timing and cause of these fires, and in come cases the ecological outcomes. Further, I combine the historical journal records with fire history data available from dendrochronology (tree-ring) studies that provides further basis to evaluate the years of burning, fire frequency and seasonal timing of fires across the continent.

In this technical paper, my main objectives are to: 1) summarize past research on bison abundance and movement patterns, 2) propose a continental-level conceptual model on the interaction between biophysical, cultural and human-bison mutualistic factors influencing bison and beaver distribution and abundance, 3) evaluate the model with spatial and temporal variation of these conditions in the early and mid European contract period with Indigenous patterns of subsistence, traveller's first person journal observations, dendrochronological fire history studies and other evidence, and 4) on the basis of findings make some tentative recommendation for bison conservation and restoration programs.

In doing background research and evaluating and discussing results I was immediately overwhelmed by the amount of historical and current research on North American ecosystems than links humans, bison, and other species (e.g., domestic cattle, other predators). Unlike Seinfeld's problem of telling "a story about nothing", the buffalo continent theme quickly expands into "a story about everything". Thus, in this technical report a purpose is to round-up and cite a great deal of this literature, and trust that reviewers and future researchers will dig out those wily strays that got missed in the sweep.

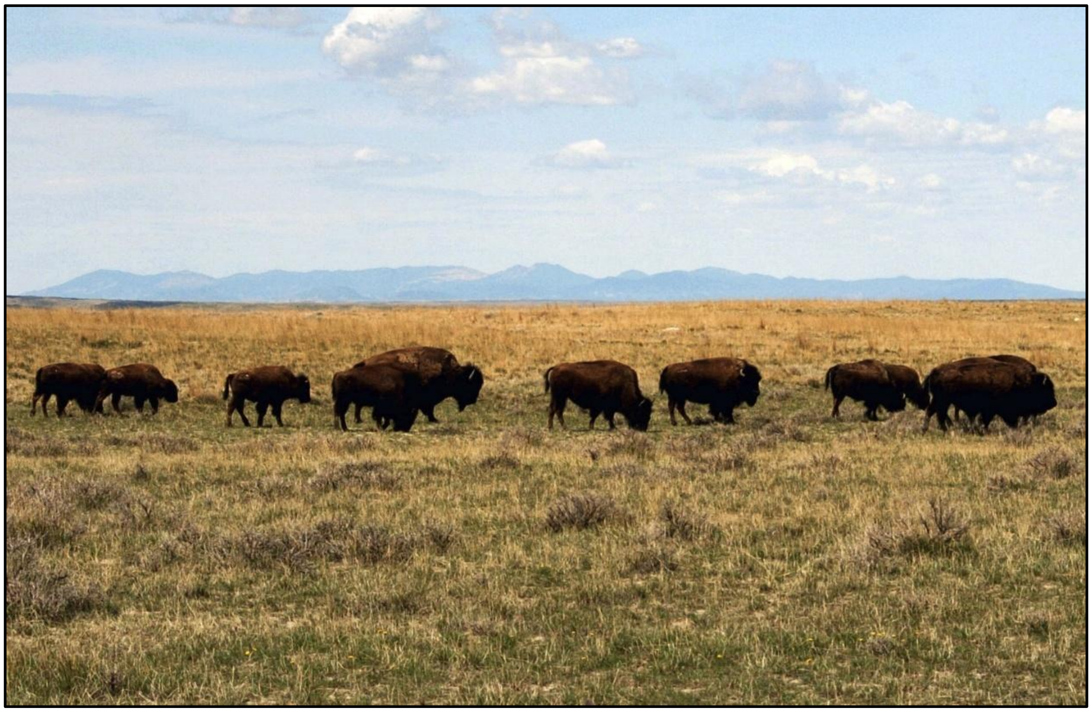


Figure 1.5.1. Bison on the American Prairie Reserve near Malta, Montana (photo credit:Matt Brown/AP).

Figure 1.5.2. Riparian zone with beaver ponds on a Montana stream (photo credit: Montana Fish and Wildlife).

# 2. THEORETICAL CONSIDERATIONS

Several complementary bodies of theory allow conceptualization of general human resource management and use, and potential application to bison. Based on seasonal round analysis (SRA) of traditional knowledge, these run on a gradient from relatively pure, rational evolutionary decision making to careful long-term resource stewardship: optimal foraging theory (OFT) to niche construction theory (NCT) to mutualistic species interaction (MSI). From the continental to ecoregion-scale perspective of this paper, OFT helps explain human activities at the edge of their territories whereas the seasonal round and mutualistic interaction better explain human activities at the center of their territory where they have more control over resource abundance.

## 2.1 Seasonal Round Analysis (SRA)

Botanist and traditional knowledge recorder Nancy Turner [111] describes seasonal rounds as "patterns of seasonal movement and residence … within and across diverse geographic and ecological areas, [which] reflect and embrace the complex systems of knowledge and practice that integrate all the different aspects of peoples' lifeways." Theoretically, the Indigenous seasonal round (Figure 2.1) is, for a given region, a potentially optimal combination of human activities such as communal meetings, trade, territorial defense, hunting, gathering, and resource culturing that maintains sustainability [112]. Long-term stability in food web structure and productivity were achieved by using routine observations of local conditions as feedback to routinely modify these behaviors (e.g., campsites, villages, travel patterns, time of burning, the intensity of hunting), and passing these adaptive behaviors through generations by social learning [111–118].

SRA can be a foundational, transdisciplinary building block for evaluating the distribution and abundance of ecologically and culturally valuable species such as bison [8,98,101,119]. For a given area, these studies often describe and quantify the timing and location human use, the sizes and gender-mix of communal task groups, the mix of resources available, and the territorial security for humans utilizing various areas. Detailed SRA studies provide Indigenous terminology for species, their location, their phenology and movement patterns, and timing of use by humans and the specific food, shelter, or other resources they provide. This spatial and temporal information can then be applied to disciplinary research testing hypotheses on optimal foraging, niche construction, or mutualism.

As Kassam et al. [112] explain "seasonal rounds are an articulation of a community's engagement of the sociocultural with the ecological in their habitat". Thus, beyond being a reasonable theorical framework, there are other benefits to using this approach. First, an SRA approach ethically requires researchers to specifically acknowledge the Indigenous peoples homeland and history in their study area, and depending on the methodology, consult with elders and others with traditional knowledge, and recognize that seasonal round information is the Indigenous Cultural and Intellectual Property (ICIP) of the people, communities and Indigenous knowledge holders who share the data [120]. Second, by consulting with traditional knowledge-keepers' researchers can learn the terminology and memories of these eco-cultural practices. Every year this body of knowledge and language is shrinking as Elders pass [121]. Finally, by considering knowledge of Indigenous seasonal rounds, current and future generations of ecological restorationists can seek to re-apply, or if necessary, even re-learn these techniques on the ground [122,119].


Figure 2.1.1. Examples of seasonal rounds: a. the Coast Salish from 2014 Exhibit "Native People of Vachon Island: Navigating Seas of Change" Vachon-Maury Island Heritage Museum. Poster design and graphics by Sandra Noel; b. Northern Shoshone adapted from image in North American Indian Jewelry and Adornment (by Lois Sherr Dubin); c. Northern Athabasca round gathered from information provided by elders in Minto Alaska: (http://www.anku.uaf.edu/curriculum/Athasbacan/ObservingSnow/fourcorners.html ), and d. the Gooniyandi peoples of Australia: ( https://www.csiro.au/en/research/indigenous-science/Indigenous-knowledge/Calendars/Gooniyandi ).

## 2.2 Optimal Foraging Theory (OFT)

Optimal foraging theory predicts that organisms develop behaviors to harvest resources with maximum efficiency to maintain high genetic fitness [123]. As applied to humans, OFT provides a group of models evaluating resource selection, time allocation, and habitat patch choice. Model evaluation generally requires a goal (e.g., optimize acquisition rate), a currency (e.g., energy spent versus energy acquired), a set of constraints reflecting cultural and environmental conditions, and a range of feasible alternative actions [124]. OFT models rank diet items in terms of their nutritional return in terms of procurement or culturing effort [125]. Researchers generally rate large mammals as the highest-ranked items, followed by smaller mammals, fish, and plant resources [126,127].

As the earth's top trophic level omnivore, humans have the highest capability to select, exploit, and culture a wide range of species. Moreover, humans also have the greatest capability to preserve and store resources during times of abundance (e.g., dried meat, fish, and plant products), and use them in later times [128]. Both these traits allow people to subsist on relatively low-ranked resources and then "prey-switch" to heavily exploit higher-ranked resources when intermittently available in the core of their territories or to use the preserved resources during travel to more distant areas to exploit these resources. Through specialization in processing some resources (e.g., hides, pemmican, and eulachon grease in northwest America) humans can further extend the exploitation of resources by trade with adjacent indigenous groups. Trade networks between adjacent ecoregions with a different set of resources were a common characteristic of indigenous cultures [129,130] that have evolved into the globalized trade networks of today. As powerful consumers with a range of alternatives, people are therefore strong direct competitors with other predators, omnivores, and herbivores dependent on the same resources, and can even theoretically extirpate a competing consumer obligated to a depleted resource. When two potentially competitive species at the same trophic level are both used by humans (and/or other consumers), OFT predicts that the more numerous or resilient resource species will persist while its competitor's numbers may be strongly depressed—not through direct competition, but through "apparent competition" where humans (and other consumers), supported by a competing species or alternate resources, continue to consume the less resilient species [131,132]. Predator-prey theory predicts the extirpation of the less resilient species if it does not have refugia from this utilization [133], and negative population growth at low density could create a range limit for the species [134]. Theoretically, this type of relationship between humans and alternate, resilient resources (white-tail deer, plants, fish) could have determined the edge of bison's range in North America.

Intertribal buffer zones are potentially important refugia for highly ranked resources (such as bison) exploited by humans [135–138]. Bayham et al. [139] integrate human foraging and group interaction theory to predict outcomes for bison in buffer zones with different scenarios of human cooperation and conflict.

## 2.3 Niche Construction Theory (NCT)

For Indigenous peoples in a central region of North America, Smith [113] describes that long-term sustainability followed a general pattern of:

> *1) a primary reliance for protein on a set of animal species and species groups (deer, fish, migratory waterfowl) that combined both a high biotic potential and relative immunity from over-exploitation; and 2) a coherent and integrated overall strategy of restructuring vegetation communities in ways that enhanced and expanded the habitats of many plant (and some animal) species that were important sources of food and raw materials.*

This may be the general pattern of resource exploitation and enhancement by small-scale human societies across a wide range of ecoregions and eco-cultural biomes in the pre-Anthrome period. NCT posits that species that modify environmental conditions to be more favorable for survival will increase their fitness with evolutionary consequences for themselves and associated species. Classic examples are dam-building by beavers and the domestication of milk cows by humans [140]. Theoretical conditions favoring localized niche construction or resource management by small-scale human societies include [114,141]: a) the resource is not super-abundant across the landscape; b) access to the resource is controlled, usually in a localized area; c) the resource rapidly or easily responds to cultural management; d) the resource has relatively low unit value (minimizing raiding or hoarding): and e) human group size is small stable allowing monitoring and adaptive management. Smith [142] elaborates further that the basic tenet of NCT is that indigenous societies routinely modified their environment to increase the accessibility, abundance, and reliability of plant and animal resources by activities such as altering vegetation by burning, broadcast sowing annuals, transplanting, and in-place encouragement of perennials providing important fruits, shoots, or roots, and landscape-level creation of habitat by burning to increase animal prey. Although humans applied these techniques broadly across North America and elsewhere [143], they are especially well-documented for the Pacific northwest's salmon biome [111] where productive fisheries and vegetation supported dense human populations, long-term villages, and localized niche construction practices described above.

NCT provides perspective on human's ancient and most powerful ecosystem management tool- the use of fire. Indigenous peoples universally lit fires for warmth, cooking, food preservation, hide treatment, signaling, wildlife and plant habitat, herding wildlife, clearing travel routes, warfare, and other uses [144–148]. Although humans ignite fires at chosen times and locations, the further spread of flames is a physical process driven by terrain, fuel, and the vagaries of weather [149]. Under certain conditions, any fire, independent of its ignition source, can spread to vast areas [150]. However, in contrast to lightning ignitions that often require summer convective conditions, human ignitions could occur during cooler and wetter conditions in the fall as soon as grasses senesce, during the winter where there is no snow cover, and during the spring before green-up. Thus, many areas could be burnt early in the annual temperate zone cycle of spring biomass growth and late summer senescence. In the west, this may have started in the fall. In the north and east, anthropogenic burning may have been in the early in spring, or even the winter in the southeast. This burning reduces fuels before drier conditions that occur in summer. A large-area "burn early-burn light-burn often" [146]:52 human ignition pattern could yield several positive outcomes for North American Indigenous cultures: 1) early, partial removal of biomass typically stimulates an earlier "green up" in the following late fall, spring, or early summer periods, stimulating roots and shoot production, and high-quality wildlife habitat, favoring resources all valuable to humans; 2) early partial removal of fuels during moister and cooler conditions protects habitats valuable to humans by reducing the possibility of intense fires in hot and dry periods that would kill many plants and require long recovery times; 3) the timing of burning can be altered to compensate for climatic and weather fluctuations. For example, people would simply burn later in a dry fall, and earlier during a dry spring; 4) light burning typically maintains a diverse range of tree ages and sizes. For example, older trees often persist in moist areas near streams. These trees eventually fall, and their large woody debris provides habitat for numerous organisms, and 5) light burning typically removes some canopy trees, and favors herbaceous plants and shrubs that in turn are more apt to burn during low to moderately dry conditions. This positive feedback loop in which cultural fires create and maintain the herbaceous fine fuels that in turn facilitate future early senescence-period fire use, even during moderate fire danger, is theoretically a key ecological relationship between people, plants, weather, and fire frequency [122,144,146]. For bison, Indigenous burners could have exploited this relationship to create an optimal mix of human and bison habitat on the edge of grasslands [8].

## 2.4 Human-Large Mammal Mutualism

One of the greatest tests for evolutionary theory is to explain potential positive interactions between two species [151]. This is complex for consumers and their preferred resources , and especially complex for humans and their prey [152] . Although optimal foraging theory described above provides a relatively simple framework to predict areas with no bison due to intense hunting by humans with alternate resources, or bison rich areas with few humans, the long co-existence of humans and bison on the continent, niche construction theory, and historical experiments in domestication suggest mutualistic relationships between the two species-- at least some regions. Clearly humans obtain substantial benefits from bison (e.g., food, clothing, shelter), but what and how would they confer long-term benefits to bison? The expectation is from OFT described above is that humans would kill preferred prey such as bison whenever they are encountered, with little consideration for long-term conservation [136,153]. However, researchers from diverse disciplines recognize that the long-term human-bison relationship was clearly more complex [8,41,98,101]. What conditions would theoretically favor local cases of mutualism between humans and a highly preferred prey? Palameta and Brown [154] help set the context here:

> *Human economic decision-making is rarely based on simple payoff maximization. Humans bargain. They anticipate and try to influence each other's behaviour. Strategies based on reputation building, trust, scorekeeping and punishment can flourish under conditions where the short-term costs of cooperation are outweighed by its long-term benefits.*

Thus, in the human case, it is necessary to consider not just passive interactions where species may be influenced by some anthropomorphic activity, but active mutualism where people are managing for joint independence [155]. Mutualism can be theoretically evaluated at several levels of ecological integration, from individuals to biomes.

## 2.4.1 Individual-Local Population Mutualism

Large mammals such as caribou, wolves, or bovids that became highly related to humans have a specific range of physical and behavioural characteristics favoring commensalism, mutualism and eventually domestication [74]. Larson and Fuller [158] and Steklis et al. [159,156] recognize that human-large mammal mutualism is on a spectrum from predation to domestication. These researchers synthesize theories by Charles Darwin [160,161], Jared Diamond [157], Melissa Zeder [162] and others on the variable social and biophysical characteristics that lead to close beneficial interaction. Three processes for development from wild to mutualistic to domestic interaction are proposed: 1) Commensalism pathway where a species is benefitted by conditions created by human activities not specifically targeted to them (e.g. Indigenous camp waste or burning for other reasons); 2) Prey pathway where human hunting techniques (e.g., gentle herding) or habitat enhancement e.g., planting burning) specifically increase a species' abundance in pre-defined areas; and 3) Directed pathways where a prey species are deliberately domesticated. Bovine species domestication likely followed the prey pathway [163].

Diamond [157] further describes traits related to mutualism, and eventually domestication:

- Diet- Herbivores or omnivores predominate through conversion of relatively low-edibility plant products or human wastes to meat or milk. Carnivores are generally too inefficient except for dogs that have other uses beyond food (e.g., searching, and hunting), and are also partially omnivorous.
- Growth rate- Animals must grow quickly, usually becoming edible or mature domesticates within a year. A relatively "fast return on investment" would favor human conservation.
- Problems with breeding- A wide variety of behavioral issues arise when humans try to facilitate or manage animal reproduction.
- Nasty disposition- It may be dangerous to keep animals in close to proxity to humans. This frequently arises with carnivores or large male herbivores and omnivores (e.g. bull bison or bears).
- Tendency to panic- Animals prone to "instant flight" when frightened are difficult to maintain near humans.
- Social structure- Three characteristics favor potential close interaction with humans: 1) living in groups; 2) maintenance of a well-developed dominance strategy, particularly with extended periods of female dominance; 3) herds occupy overlapping home ranges rather than exclusive territories.

Recently, researchers have shown the importance of genetic introgression as a source of adaptive variation and domestication of the Bos genus (containing the cattle and bison species), and propose that the genus evolved as a complex of genetically interconnected species with shared evolutionary trajectories [164].

## 2.4.2 Community-scale Mutualism

A large body of current theory on community mutualism follows from Hairston, Slobotkin and Smith's [165] classic 1960 paper recognizing that "the world is green" -- where long-term "bottom-up" plant productivity and diversity depends on the "top-down" influences where carnivores and omnivores reduce the impacts of herbivores on the plants. In much current research this is often termed "trophic cascades" [166] or "food web" [167] analyses and focusses on biophysical rather than cultural interactions. However, observations arising from considering multi-species predator-herbivore-plant trophic level mutualisms obviously extend to human culturing and harvesting. There are many theoretical interactions and variations linked to the general "world is green" hypothesis. I summarize a select few here with application to humans, large mammals and associated species:

- Mutualism requires regulatory, feedback mechanisms that either benefit, or at least prevent long-term harm to interacting species.
- The basic hypothesis is the three-level trophic cascade model (predators-herbivores-plants) where top-down predation or human management reduces the number of herbivores and hence their consumption, trampling and other impacts on plants. This premise underlies theory on "carrying capacity" [168,169] for large wildlife mammals [133,170], agricultural domestic herbivores on rangelands [88], conservation biology , and other fields of ecological research. Chapman and Byron's [169] literature review describes four main groups of ecological implications of exceeding carrying capacity: 1) a decrease in species biodiversity and richness, 2) a decrease in primary productivity, 3) changes chemical cycling , and 4) an increase in the vulnerability to exotic species invasions.
- Animal-plant interactions in multi-trophic systems are not just driven by abundance, but also by behavior [171]. Spatial behavioral patterns range from long-distance migration and movements such as for wildebeest in the Serengeti [133]:176 or North American bison [6,172] to fine scale, predation sensitive foraging in adjacent vegetation types [86]. Again, animal reaction to long-term human predation, herding etc. may be an important factor in behavior. This can be considered human-animal mutualism to the extent this behavior maintains an ecosystem's long-term states and processes.
- Due to limited resources, plants make trade-offs between functional traits such as resistance to drought, herbivory and disturbance [77,173]. Communities are usually adapted to some level of herbivory or disturbance. Classic examples include increased productivity in grasslands with moderate herbivory [174] or after fire [175]. As above, the degree to which human influence herbivory levels or disturbance can be considered mutualistic to other species in the ecosystem.

### 2.4.3 Population Distribution, Ecoregion, Biome Scale Mutualisms

The long-term range of bison and many other species may approximate a classic "abundant center distribution" model (Sagarin et al. 2006), where a species' numbers are generally highest in the center of the range and declined towards areas of more unfavorable habitat or intense predation condition (Holt and Keitt 2000). For potential human-large mammal mutualism, it is useful to consider that long-term, closely interacting species may have a range of interactions from facilitative to antagonistic across their shared range [176]. At this scale, ecoregions, where groups of species (communities) coexist [80,81] can provide a useful scale of integration to evaluate human and large mammal distribution, abundance, movements and habitat use [133]. Boivin et al.[143] and Ellis et al. [177] extend niche construction theory described above to provide a theoretical framework for human structuring of ecoregions and potential effects on species.

Along this line of theory, in a recent review of mutualism research, Fowler et al. [178] describe that potential effects mutualists could have on their partner's distribution and abundance, stressing range limits or the potential "ecological 'footprint' of mutualism" or as the effects on interacting species' geographic distributions attributable to positive interactions. This footprint arising from two general processes: modification of a partner's niche through environment-dependent fitness effects and, for a subset of mutualisms, dispersal opportunities that lead suitable habitats to be filled. Over space, interaction processes (niche creation, effects on dispersal) may increase or decrease species' densities in some regions. Although mutualism should improve the overall fitness of participants, depending on the location it may *extend*, *contract*, *constrain*, or have *no effect* on range limits for participants. Fowler et al. [178] describe the population dynamics behind the process by recognizing that range limits for any given species can be understood by answering two questions:

> *"(1) What are the environmental conditions in which that species can maintain at least replacement-level population growth ($\lambda \geq 1$)? and (2) Can the species disperse to (and perhaps beyond) these suitable environments? The first question defines the limits of the niche; the second determines the extent to which the niche is "filled", i.e., how much of the environmental space where $\lambda \geq 1$ is occupied. These two elements of a species' distribution roughly correspond to the classic concepts of fundamental and realized niches, which contrast distributional limits without and with, respectively, the influences of species interactions and dispersal limitation…"*

For humans and large mammals, researchers stress negative impacts such as reduced biodiversity and overkill, but human influences at a landscape level with processes such as fire and predation could be important by extending areas where populations where population growth can occur or be maintained over time by habitat enhancement or protection from degradation. For large mammal species, this could include North America bison and woodland caribou [179]. Evaluations of mutualism theory evaluations at this spatial scale remains sparse:

- Geist [180,181] and Haynes [182] recognize the diversity of human and large mammal behavior in early Holocene colonizers of North America. A dispersal phenotype for both humans and animals would be is an epigenetic adaptive form with bold behavior, rapid learning, and large body size. These morphs would be rapid learners, accustomed to travelling long distances across unfamiliar landscapes. They would rapidly seek out rich sources of forage or prey, then move on before completely depleting the resource.
- In large mammal population theory, regulation of a herbivore prey species requires a feedback mechanism where predation rates increase when prey is abundant, but where rates decrease as prey numbers decline [183,184]. Sinclair [185] observes "regulation tends to keep populations near equilibrium". If humans regulated herbivore densities at an equilibrium level that prevented degradation of plant communities, this could be considered mutualistic to the herbivore-prey species themselves and other species in the ecosystem.

Moreover, and most relevant to this study for bison, a species whose core habitat centered on a drought prone biome, researchers rarely consider that humans could influence the amount and distribution of essential resources—forage, cover, and surface water (Figure 2.4.3.1). The general presumption is that in the past these factors were controlled by biophysical and climatic processes beyond human influence [23,76] . Of course, through human use of fire, and potential conservation of a dam-building species, this might a defensible assumption at a continental scale, but not tenable for many regions at a finer scale.

Figure 2.4.3.1. Bison cow/calf herd on the Bare Bison Farm in Madison County, near Des Moines, Iowa. Modern ranching is a form of human-bison mutualism requiring water, security, habitat management (mix of grazing lands and cover), and population regulation that ensures bison do not degrade the habitat's productivity. Could varied forms of these practices occur in the past?
(Photo by Duane Tinkey, https://dsmmagazine.com/2020/08/27/bringing-back-the-bison/ )

# 3. PRELIMINARY BIOPHYSICAL-CULTURAL BISON INTERACTIONS MODEL

## 3.1 Historical Bison Abundance and Movements

Based on studies of other migratory ungulates by Fryxell et al. [186] and other studies, Epp [36] and Epp and Dyck [37] described bison abundance, distribution and movement behavior on a spectrum from migratory in large groups on to the prairies, to non-migratory in smaller groups in woodlands. This range of movement behavior for *Bovidae* has been described for the African wildebeest by Estes [187]:188:

> *The wildebeest's variable social system enables it to alter its distribution pattern to fit a wide range of environmental conditions. Populations can follow any pattern from completely sedentary to migratory and more or less continually nomadic… Sedentary and migratory patterns often coexist within the same populations, and even at the same time and place.*

### 3.1.1 "The Buffalo's Great Heartbeat": High Abundance Migratory Herds on the Prairies

Binnema [6,172] synthesized biophysical and cultural research [26,36,99,188] to describe the general historic pattern of bison and Indigenous people's abundance and annual movements on the northern Great Plains. Cooper [67]:242 used archaeological data to extend this analysis to the central and southern plains for the since CE 500. Figure 3.1.1.1 uses this information to describe potential dispersal dynamics across continental bison range. This pattern follows a general source-sink population movement model with an abundant center distribution [189]. However, as Epp [36] describes, low densities of relatively stationary bison may remain in peripheral areas. On the basis of prehistoric bone isotope data, McKetta [190] also proposes a pattern of non-migratory bison in the Colorado Rocky Mountain region.

Brink [48] describes the closely linked seasonal round of bison and human movements on the Great Plains. In early spring, usually preceded by small groups of bulls, most bison leave winter ranges on the periphery and move towards the center of the grasslands where snowmelt and grass green-up occurs early. Calves are born as the female groups move which may reduce predation by wolves on their dens, bears with young cubs, or humans wary of spring blizzards on the open plains. By early summer large bison herds are on the shortgrass prairie grazing C4 species such as buffalograss that are relatively resistant to early season grazing on ongoing intensive use [191,192] . Small groups of human males have now ventured into the region to scout for enemies in inter-tribal buffers zones [137,139], followed by large groups of families capable of communal hunts and processing the resulting volume of meat and hides. By early summer large mixed herds of bison cows and calves occupy the open plains, with movements depend on recent fires, moisture conditions, forage regrowth, and disturbance by human hunters and other predators [48,99]. Large bison numbers reduce the mortality rate, and the herds can move long distances rapidly to avoid predation risk.

In July and August bulls join the herd for the mating. Herds may be huge. Wallowing occurs frequently possibly due to a combination of high insect activity and aggressive behavior by males [193,194] . If predation risk is low, this may occur on routinely used rutting grounds with soft soils where previous wallows are abundant, often near sources of drinking water that support high metabolic activity [14]. By mid-September, many Indigenous groups moved back towards wooded areas on the periphery of the plains in preparation for fall hunts and cooler weather. Bison generally remain on the open plains throughout the fall and most the winter, but in some years may be forced into the woodlands due to human grassland burning, deep snows, or cold weather [6,172].

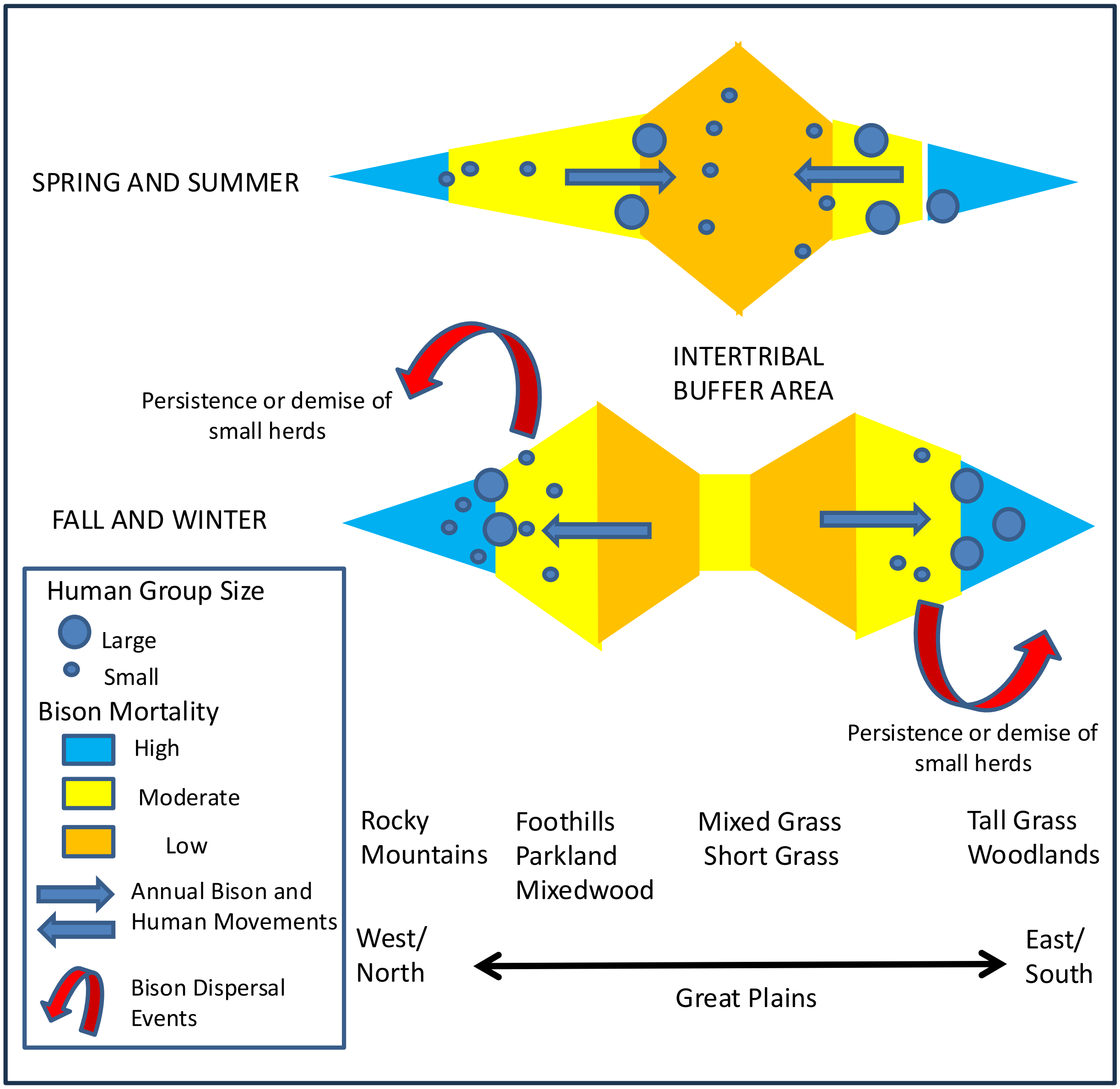



Figure 3.1.1.1: "The Buffalo's Great Heartbeat": A model of seasonal bison abundance/movements and mortality regions, and human abundance/movements (adapted from Binnema [6,172]; Morgan [8,98,99]; Peck [188]; Bamforth [26] ; and others).

### 3.1.2 Low Abundance Bison in Woodlands and Mountains

Historic bison range extends thousands of kilometers northwards (see Figure 1.1) into the foothill and boreal forests of North America [2–5]. Bison are much less abundant in these habitats and have smaller home ranges [195]. The difference between bison behavior on the prairie versus woodlands has long been recognized. William Pink, a Hudson's Bay Company trader wintering with the Cree, likely northeast of Edmonton near Lac La Biche, made some of the first written observations of "wood bison":

> November 13, 1766—"... *Heare I find Beaver very plenty the contrey here being fool of small rivers or cricks and standing waters, the land coavered with woods. Boffalous likewise plenty but very wilde to what the are in the oapen contrey* " (from William Pink's Journal [196]).

Hunting bison in forests required different hunting techniques than for those on grasslands. For example, in 1791 Hudson's Bay Company trader Peter Fidler hunted bison with the Chipewyan's in the forests south of Great Slave Lake, and the next winter he was with the Piegan hunting on the plains west of Calgary. With this knowledge, he remarked:

> December 28, 1792: ... *the Buffalo in the Plains will not run half so far when frightened as those that are found amongst the woods. They will sometimes run & gallop several miles before they even stop the least. Those in the Plains generally stand several shots, particularly if first shot kills, before they run away, Those in the woods seldom more than 1 shot.* (from Fidler's Journal [197]:41)

James Hector made a similar journal observation near Pipestone Pass in today's Banff National Park:

> August 26, 1859: *William told us at night that two years ago he killed a buffalo cow at this place, and that he saw at the time a band of seven,—two bulls, four cows, and a calf. They were of the thick-wood variety, which are larger and blacker, and with more spreading horns, than those of the prairies. They run swiftly through the woods, and, are quite as wary and difficult to hunt as the moose deer* ( [198]:441).

## 3.2 Seasonal Rounds: Humans, Beaver, Bison and Water

Researchers have routinely considered the role of potential Indigenous practices to conserve or enhance bison [15,199]. Morgan [8] recognized the important differences in the cultural values and resource use patterns of Indigenous people associated with large herds of bison grasslands on the plains versus woodland people hunting the more sedentary and less dense bison populations in the mixed-woods, savanna, foothills and parklands surrounding the grasslands. Here I summarize her research on the Indigenous perspectives on the economic and ecological values of beaver.

### 3.2.1 Trapping and Trading Beaver in the Woodlands

The first Europeans reaching the North American continent immediately tapped into a long-standing Indigenous trading systems bringing hides and pelts from the interior to the more populous areas near coastlines and rivers [105,106,129,200–203]. For both their own personal survival and for trade, this fundamental pattern of purchasing hides from Indigenous people repeats in the written accounts of de Vaca (CE 1528-34) along the Gulf of Mexico [204,205] , Cartier

(1534-43) in the Gulf of St. Lawrence [206] , Coronado (1539-42) on the southwest plains [207], de Soto 1540-42 along the Mississippi [208,209], Champlain (1604-16) from Plymouth Bay northwest to Georgian Bay [210], Henry Hudson from Manhattan north to Hudson's Bay [211] , and Radisson and Grosseliers (1652-59) from the Gulf of St Lawrence to Hudson's Bay to the Mississippi headwaters [212]. Beaver was the most treasured pelt—durable, waterproof, and with high trading value in Europe. Indigenous traders rapidly adapted and expanded their networks to maintain a supply of beaver to the Europeans [103–105,213]. The Woodland Cree maintained one of the most expansive beaver-trade networks, bringing thousands of pelts from Indigenous groups as far away as the Mackenzie River in NW Canada over 3000 km by birchbark canoe along a network of rivers and lakes northeast to the English trading posts on Hudson's Bay [106], or southeast to the French posts on the Great Lakes [212]. By the mid-1600s first the French, then the English, and eventually the Americans began to follow these trade routes into the interior the sources, finding First Nations in woodlands— directly trading with woodland peoples like the Cree, Anishinaabe and the Dene who were willing and capable to trap and trade the beaver, and by the early 1800s the beaver was trapped out of vast regions [106]:263-280. Competition for pelts intense between the Hudson's Bay and Northwest companies, and start-up American entrepreneurs [214]. Traders and trappers such as the Jacob Astor began to look towards remaining sources of beaver across the central grasslands of the Great Plains and on to the headwaters of Pacific-flowing streams beyond the mountains [103,215].

For an example of Indigenous peoples integrating the fur trade into their seasonal round, Ridington [216] and Burley et al. [217]:15-20 describe the subsistence pattern of the Dane-Zaa (Sekani Beaver) First Nations on the upper Peace River, a region of grasslands and forest on the northwest edge of bison range (Figures 1.1, 3.2.1.1). Each year, members from each band would return to the trading post in early spring with the furs from the late winter hunt (Figure 3.2.1.1) then move into new territories for a spring beaver hunt. While travelling during the spring, the Indigenous people burned the grasslands and meadows [144,218]. Trader Hugh Faries at Fort St. John records in his journal:

> *Thur., 15$^{th}$ May, 1823: Rained a little in the evening and it happened very apropos as the Indians had set fire to the grass on the hill & it was spreading very rapidly*. [217]:181

These grasslands attracted great numbers of bison and elk in the spring. Alexander Mackenzie came this way decades earlier on his 1793 trip to the Pacific Ocean. While ascending the Peace River he passed through an intertribal buffer zone between the downstream Cree and the Dane-Zaa to the west. Here he observed:

> *Friday, May 10: … This magnificent theatre of nature has all the decorations which the trees and animals of the country can afford it: groves of poplar in every shape vary the scene; and their intervals are enlivened with vast herds of elks and buffaloes; the former choosing the steeps and uplands, and the latter preferring the plains. At this time the buffaloes were attended with their young ones who were frisking about them.*. [219]:222

After their spring trapping season, the Dane-Zaa would aggregate in large groups at traditional campsites, possibly hunting game in freshly burned habitat, then disperse in smaller groups to their individual late summer and fall hunting territories. Some members might return to the fort later in the fall to obtain trade goods (pots, knives, guns, powder, traps), then return to individual family's winter traplines. Apparent from the seasonal round, the Dane-Zaa had a broad suite of alternate resources—they were not totally dependent on either the beaver or buffalo, but as optimal foraging theory would predict, humans would preferentially harvest them if available. Indeed, within the few decades both species were rare in the region.

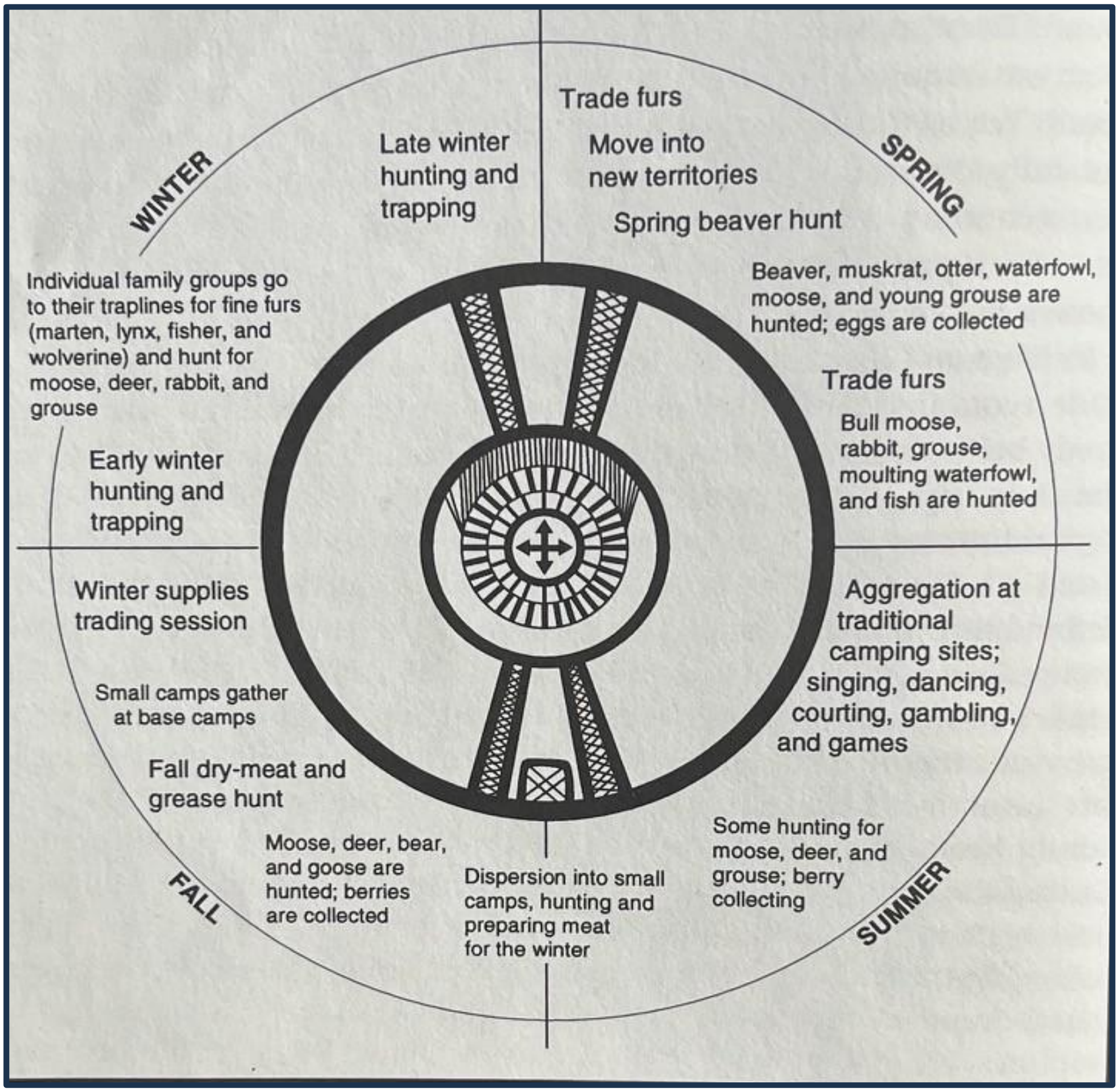



Figure 3.2.1.1: Seasonal round for upper Peace River Beave people in the early historical period (from Ridington [216] and Burley [217]. This seasonal round represents the period shortly after bison were extirpated from the region in the early 1800s, likely due to meat demands from fur trading posts, and relatively abundant alternate prey that sustained Indigenous hunters. The authors note that the central design is sketched from the Dreamer’s Drum held by Charlie Yahey in a photograph by Robin Ridington.

### 3.2.2 Conserving Beaver on the Grasslands

In contrast, Morgan [8]:3-20 and other researchers [220,221] describe that traders found that prairie Indigenous groups had little interest or ability to trap beaver. As early as 1738, French trader La Verendrye learned that nations on the Great Plains were not traditionally beaver hunters [222]:301. In 1808, Alexander Henry the Younger described that in Blackfoot territory "beaver are numerous but they will not hunt them with any spirit" [223]. Similarly Alexander Mackenzie recognized that the Assiniboine and Gros Ventre who visited the posts on the northern plains were not beaver hunters [219,224]. Further south, Jean-Baptiste Truteau traded along the Missouri near the Black Hills in the 1790s, observing that although beaver were common in the region, the Arapaho, Cheyenne, Pawnee and Kiowa had not hunted them in prior times [225]:215-217. It is logical to simply assume that people of the plains did not kill beaver because the meat and hides of the buffalo were more available. However, the aversion to beaver hunting could be a deep cultural taboo due to their role in water and woodland conservation. Ethnologist George Bird Grinnell described the sacred status of the beaver to the Cheyenne:

> *The beaver was reverenced to some extent.... from the fact that beaver built dams to raise waters in streams, and houses to live in. It is said that in very old times were not often killed, and than no Cheyenne woman would dress or even handle a beaver-skin.* [226]:104

On the prairies the beaver meant survival to both humans and the buffalo. Clearly during droughts, the beaver-created ponds and streams hydrated both species. But also, streams and raised water-tables created shrublands and forests, essential winter shelter for both species, and most importantly for humans— a source of wood for heat and cooking. The human respect for the beaver extended to the Comanche of the southern plains, a nation highly antagonistic towards trappers. One of their important group rituals was the "Beaver Ceremony" involving a modelled construction ponds, lodges, and other parts of beaver habitat [227]:175.

## 3.3 Conceptual Model of Biophysical, Cultural and Mutualistic Influences

From the description of the bison and human seasonal cycles described above, we can outline biophysical and cultural factors that could hypothetically influenced bison distribution and abundance. Metcalf et al. [228] and Pilowsky et al. [229] likewise describe a process to evaluate both groups of factors to interpret the long-term biogeography of American and Siberian steppe bison respectively. Figure 3.3.1 conceptualizes these by trophic-level in a food-web model where "bottom-up" factors control vegetation productivity and hence herbivore, predator and omnivore numbers, and ultimately, at the top trophic level, human abundance. In contrast are "top-down" factors where predation and herbivory can alter conditions in lower trophic levels and generally reduce abundance. I briefly discuss existing knowledge on many of these factors below, stratified by the disciplines of biophysical and cultural research, then linking these through hypothetical opportunities for human-bison mutualism.

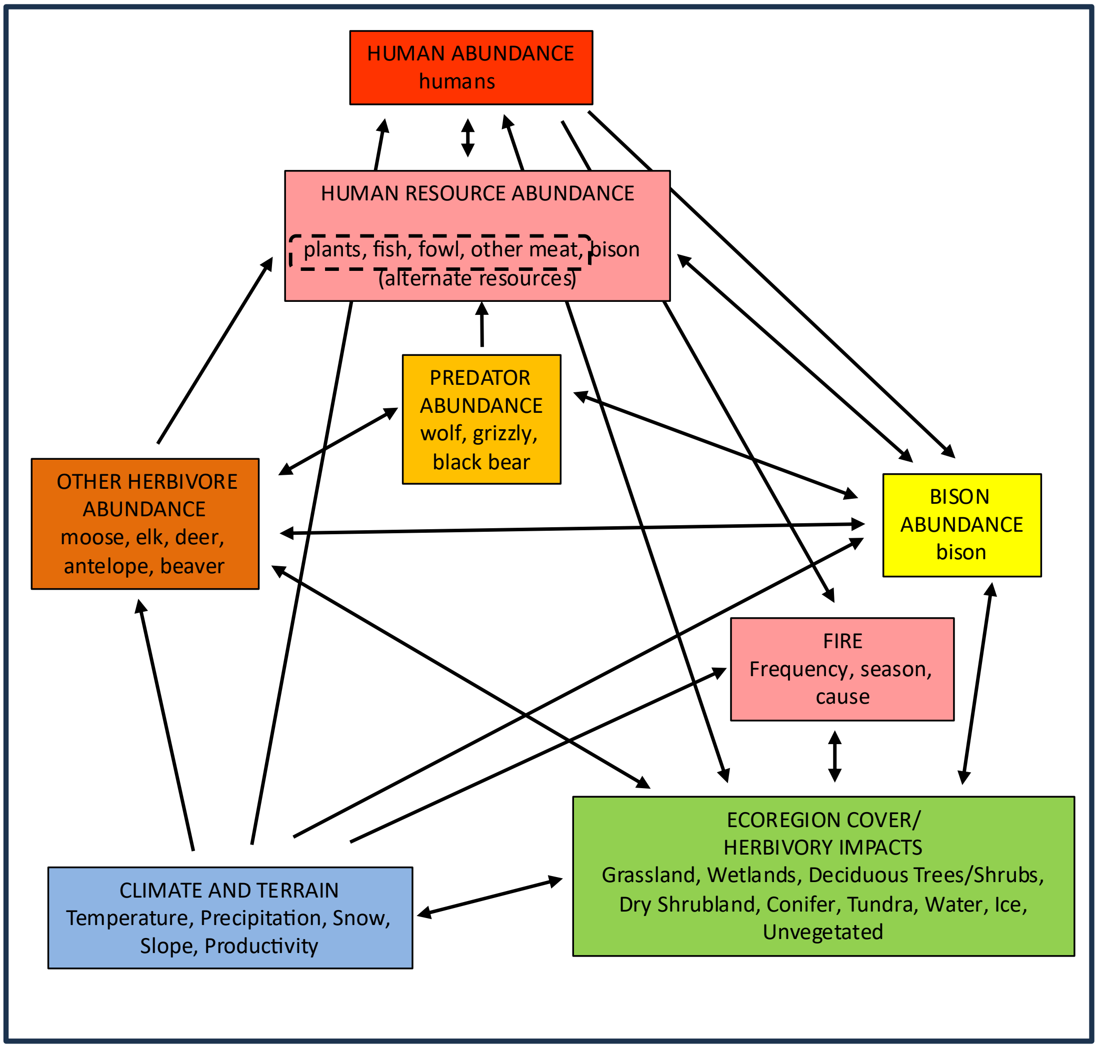



Figure 3.3.1: Preliminary model for bison abundance synthesized from literature with potentially important covariates from biophysical mapping and interpretation (in caps) or historical journal observations (no caps)

## 3.3.1 Biophysical Influences

Grassland cover, and the climate and terrain drivers that create grasslands (Figure 3.3.1) are recognized as primary “bottom-up” determinants of bison distribution and abundance [23,71,78]. Timing of bison use for various grassland types and phenology are also described [99,230]. There is a synergy between large herbivores and grasslands where grazing removes excess biomass and litter, and the herbivores excrement and urine in turn returns easily nutrient to the soil [174,231], [232]:319. On the North American grasslands, forage quantity increases from west to east and north to south with local areas in high production on the northwest plains and Black Hills [26,233]. Researchers propose increases in bison size and numbers in areas or time periods with greater precipitation and grassland productivity [23,78]. Conversely, studies document reduced bison abundance with lower cover of grasslands, and increasing cover of forests, rugged terrain and deep snow [20,22]. Competition from other herbivores with bison could occur (Figure 3) but except for horses in the mid-historic period [234,235] this is rarely considered an important factor. Likewise, "top-down" predation from wolves or bears may limit abundance in ecoregions with low-density bison populations such as in the boreal mixed wood [236–238], and may have reduced the survivorship of bison calves on the Great Plains [239].

Variations in climate and weather conditions may have greatly altered bison distribution [64,21,23]. Drought could reduce grass productivity forcing bison movements. Drought could facilitate expansive wildfires with short-term removal of food and cover, followed by increases in grassland productivity [175,240].

### 3.3.2 Cultural Influences

Humans are the continent's long-term top carnivore and omnivore and have altered ecosystems through predation [136,138,241] , plant use [111,242], or culturing practices such as use of fire [122,147,218,243,244], managing fisheries and aquatic resources [245], or planting crops [246]. Human abundance is related to "bottom-up" factors such climate, terrain, and ecoregion cover (Figure 3.2.1), and most directly by availability of food resources such as plants, fish, and meat [11,12]. The effects of pre and early contact human populations on bison abundance is variable. Human density was low across most the Great Plains and as described above, often ephemeral due to climatic conditions. Here, human predation may have only marginally decreased bison abundance. In contrast, on the periphery of the plains, plant domestication began as early as 5000 years BP [247], and led to major increases in human numbers [63]. Near oceans, rivers and lakes the availability fish and other marine/aquatic resources could provide food for high numbers of Indigenous people [248,249]. Potential human predation rates on bison could be high in these areas due to 1) the high number of humans fed by alternate resources, and 2) the demand for bison products such as hides and fat not provided plant or fish resources. This demand stimulated bison hunting and trade routes that extended well into the Great Plains from adjacent areas of high population [129].

### 3.3.3 Human-Beaver-Bison Mutualism

*Background*

From this review, there is reasonable interdisciplinary evidence to consider human-bison mutualism at a continental scale over long time period. Regional research from several North American regions includes for Great Plains, northeast [3,250], southeast [2,18,66], southwest [2,26], and northwest [3,4,20,38,137,138,251] supports this hypothesis. However, there remains a need to integrate these regional perspectives into a holistic model for the continent. Using a continental scale a pre-contact to mid-contact period (~1300 CE to ~1850 CE) allows consideration of several spatial and temporal variation tests applied to the ecosystem trophic framework (Figure 3.1.2).

However, as described in the Introduction, at a continental scale the simple "bottom-up/top-down" interaction described above fails to describe the feedback mechanisms necessary for bison population regulation and stability. Bison were the largest mammal to survive the Holocene arrival of humans in North America, and persisted, in increasing abundance, for thousands of years thereafter [41,5,23]. Several researchers suggest a more intricate human-bison relationship. Morgan [98,8] evaluated Indigenous traditions that preserved beaver, riparian zones and water sources on the northern prairies. Flores [252]:124-128 describes the processes where both humans and bison thrived during periods of cool climate on the southern grasslands. Morrissey [61]:52-58 further elaborates on human-bison interactions leading to southeastward expansion of bison range across the Mississippi River. A more complex hypothesis for the resilience of bison in the presence of ongoing hunting from humans suggests would be that the two species maintained a mutualistic ecological relationship. There are several potential processes for human-bison mutualism that could cumulatively maintains bison's long-term persistence at a continental scale:

- For >10K years, bison provided Indigenous people with important resources including food, clothing and shelter [2,7,41,253]. The traditional knowledge base of bison-human interaction is immense with numerous references to respect and ceremonial practices of bison harvesting [254], and the seasonal rounds, numerous species used, and resource management techniques of Indigenous peoples in bison habitat [9,255–257].
- Morgan ([8], Section 3.2.2 above) describes that plains cultures valued and protected the beaver due to its role in impounding water sources required by both people and bison.
- Humans require wood for heat, shelter, and cooking. In winter people moved from grasslands into woodlands giving bison a seasonal refuge from predation [6,36] .
- Indigenous peoples often maintain territorial buffer zones between hostile groups. Bison found refuge from predation in these areas [137,139].
- Through use of fire, people increased the area of bison habitat by expanding grasslands into adjacent woodlands [8,98,258] and increasing the productivity of existing grasslands by removing litter and providing nutrients with the resulting ash [175,240].
- There are numerous observations of direct domestication when Indigenous peoples captured and raised calves [2]. As a classic example, in the 1870s Pend d'Orielle hunters brought four buffalo calves from the plains across the mountains to the prairies of the Flathead Indian Reservation west of the Rockies— an expansive grassland not previously used by bison. By 1906 the Flathead herd expanded to thousands, providing seed herds for later conservation efforts [68,259].
- Communal hunting practices (e.g., herding and burning) could stimulate bison dispersal from source population areas into adjacent regions with lower bison use [36].
- Through hunting, or bison's avoidance of hunters, people reduced bison density on many areas of high-quality habitat and thus protected these habitats from overgrazing. However, these could be periodically utilized by bison under varied circumstances that enhanced either bison or human population survival, or both. For example, the generally lightly grazed fescue grasslands along the north and western edges of the range [87,260] were more heavily used during by bison during deep snow winters or when the plains to the east and south were burned [6,22]. Similarly, upper elevation wheatgrass habitat in the Middle Rockies (today's Montana and Wyoming) were also usually lightly grazed [136,261,262], but can periodically support high numbers of bison [263] in valleys that facilitated Indigenous hunting.
- The above humans-bison-grasslands-fire-woodlands interactions suggest a potential long-term, mutualistic relationship. Humans possibly regulated bison populations at a continental scale in abundance and distribution patterns that maintained the habitat

quality of grasslands. The mechanisms are as follows: 1) Due to lack of wood and other resources, human populations were low on the central plains. As a result of low predation bison populations were high and generally increased in the center of grasslands; 2) grass species here (e.g. grama and buffalograss) were generally herbivory and drought resistant but fluctuated greatly in cover with moisture availability; 3) Human burning maintained meadows and savannas on the edge of grasslands. Due to low rates of herbivory, these areas were often dominated by high nutrition species (e.g. fescue and wheatgrass) with high productivity, but low herbivory resistance-- they could sustain bison for brief periods; 4) When bison numbers increased on the edge of grasslands, human numbers and burning increased. 5) Human predation then forced bison to retreat from these areas towards the central plains, and increased anthropogenic burning removed woodlands forcing humans to retreat towards the forest: 6) The retreat of bison from these areas allowed recovery of high quality forage, but herbivory susceptible native species such as rough fescue, wheatgrasses, and a mix of tall grass prairie grasses and forbs that provide habitat for a future periodic bison use.

- This human-bison regulation hypothesis would be a mutualistic, long-term relationship where human predation maintains bison numbers in an equilibrium range that does not degrade important forage species (especially herbivory sensitive grasses) on the edge of heavily used range, but could be strongly influential in central, high bison-use grasslands.

The overall hypothesis then is as follows:

> *Humans, beaver and the buffalo are long-term mutualists. Humans, through fire use and conserving beaver contributed additions to the essentials of bison habitat—forage, water and winter cover. More importantly, by regulating bison populations with predation, humans kept bison from degrading habitats. In return, the buffalo could provide many humans with nearly everything—food, clothing, shelter and for some cultures, a complete circle of life.*

### *Summary of key mutualism processes*

Bison provided humans with many resources including food, clothing and shelter. In turn, humans were the keystone species that maintained bison in numbers that did not degrade ecosystems. Key interactions between humans, fire, climate, and the alternate resources used by humans created this mutualism. Mutualism requires regulatory, feedback mechanisms that either benefit, or at least prevent long-term harm to interacting species. For humans and bison, two potential key regulatory feedback processes are evident:

- Variable predation- Humans require wood for heat and shelter in winter—thus humans retreat from grassland habitats into peripheral woodlands, reducing predation rates as distance increases from woodlands. As bison numbers increase, they disperse from grasslands into peripheral woodlands and experience higher predation rates.

- Variable habitat management- Humans could use fire, or predation effects (direct or behavioural) that effect bison density to maintain habitat both for themselves and bison. Humans adapt fire timing and intensities to maintain vegetation. High bison densities are beneficial to humans in the short-term but degrade important human habitats (woodlands, riparian zones, valued human foraging species etc.). Human awareness of habitat conditions provides feedback that regulate human abundance and effects.

## 3.4 Evaluating the Model

The ecosystem states and processes shown in Figure 3.1.2, and the predicted source, sink and mutualism zones can be partially evaluated through three "natural experiments" [264] occurring during the immediate pre-contact and historical periods across the North American continent.

### 3.4.1 Spatial Variation

Measures of mutualism remain difficult to quantify or compare between different sets of species [265]. If the above biophysical, cultural and mutualistic processes occurred historically, using Fowler et al.'s [178] "ecological footprint" framework (Section 2.4.3 above) these could be evident on the landscape in three broad zones:

*Source bison population zone*- high bison population areas where a combination of abundant grasslands, low human abundance, and lack of alternate resources to support humans.

*Sink bison population zone*- areas of no or very low bison abundance where abundant humans and many alternate resources to support humans result in very high predation rates on bison.

*Human-bison mutualism zone*- a region on the periphery of source populations where variable human predation and burning rates provides favourable habitat for both bison and humans. Within this zone, mutualism processes might be evident at three scales: but regulates bison to numbers low enough to maintain high habitat quality. Within this broad zone, mutualisms might occur at three scales:

1) Individual//local bison population scale herding or domestication by humans,
2) Community scale interactions by humans and bison including top-down (predation, herbivory) and bottom-up (productivity) interactions that may support assemblage of species and communities co-existing in ecoregions (Table 5.1.1) or
3) Biome or large population scale regulation and stability. This could be provided by two key regulatory mechanisms with feedback: 1) variable human predation on bison, and 2) variable habitat management dependent on fire use and herbivore density.

### 3.4.2 Temporal Variation

Numerous human depopulation periods occurred across the continent during the pre-contact to mid-contact period [21,266] and this was followed in the mid-contact period (>1750 CE) by increasing Indigenous and European densities and predation [2]. Bison population/distribution should thus increase during the early period to a potential maximum [39]. The general hypothesis can be evaluated by temporal analysis of biophysical and cultural variables from across the continent. Regions with human depopulation adjacent to bison populations should show increases in bison numbers due to reduced predation; Regions with stable human populations adjacent to bison populations should show no change; and by the mid to late contact phase, bison distribution and resistance to extirpation should approximate Allen's [2] map (Figure 1.1.1).

## 3.4.3 Range Condition, Trend, and Historic Bison Abundance

The general theories of human niche construction with fire use, and Morgan's specific theory linking humans, bison, and beaver discussed above imply unique habitat conditions. At least in some areas these require fuel to burn, and beaver habitat to conserve. Range and wildlife managers and researchers clearly document that recent historic (e.g., after ~CE 1850) high domestic stock and wildlife densities levels reduced grassland productivity (e.g., [72,73,267] and degraded riparian zones (e.g., [268–271]). These herbivore-impacted grasslands and shrublands in turn altered long-term interactions between fire and herbivory where lower herbivory favored more fire, and visa versa [272] — a process termed "pyric herbivory" [273]. This implies that in long-term ecosystems, herbivory effects were less due to lower numbers and perhaps different behavior of native species such as bison, elk, and deer. Evidence of this pattern could be available from historic versus current accounts of herbivore density, habitat conditions, and then-now historic photographs.

Figure 3.4.3.1. Bison and calves in Elk Island National Park, Beaver Hills Biosphere Reserve in the Aspen Parklands Ecoregion. Historical human-bison interactions in the Aspen Parklands Ecoregion may have been strong including Indigenous burning to maintain grasslands, and relatively high rates of bison predation that reduced herbivory and trampling impacts on riparian zones and beaver [274]
(Photo: https://biospherecanada.ca/biosphere/beaver-hills/ ).

# 4. METHODS

## 4.1 Data Collection

The analysis required specific observations of bison locations and abundance, human cultural practices, the abundance of other predator and prey species present in historic landscapes combined with biophysical covariates related to climate, terrain, and land cover (Table 4.1.1). These were then grouped North American ecoregions mapped and described by Wiken et al. [80] and Dinerstein et al.[81].

### 4.1.1 Human, Wildlife and Resource Abundance

Historic bison, and select other herbivores, predators and herbivores occurrence and abundance were indexed using the first-person daily wildlife observations obtained from the journals of European mariners, fur traders, trappers, and government mappers for the period generally prior to historical range contraction (Figure 1.1): CE 1510-1750 in east and southern United States, CE 1691–1860 in southern Canada and the northern United States, and CE 1770–1928 in northern Canada and eastern Alaska. The study area encompassed the historic bison distribution in North America (Figure 2) extended out to the nearest ocean (Pacific, Arctic, Hudson Bay, Atlantic, Gulf of Mexico). This period of European contact and colonization of North America had massive repercussions for Indigenous peoples including mortality, societal disruption and changes in territories and lifeways [63,275]. Data from both individual journal entries to the compiled results must interpreted with this perspective.

Methods followed Kay's procedures for tallying observations from the Lewis and Clark journals [30]. For wildlife species, three measures quantify the observations of journalists. The first is the animals seen, where a value of 1 was assigned if journalists reported an old sign, 2 if the sign was fresh, and 3 if they sighted the animal. The second index is animals killed, where either the exact number killed was recorded, or where "some" or "a few" was recorded as 3, "several" as 7, and "many" as 10. The third measure is the herd or group size. When journalists report sighting large numbers of a species, a value of 10 was assigned, and 5 was assigned for moderate amounts. The animals seen and killed, and the herd/group size were then added together to obtain a measure of abundance. Observations made by journalists at long-term camps or trading posts may be tallied by specified periods of 4 to 30 days with the total kill numbers for the period divided by the number of days. For quantifying human abundance, if an old sign was observed, this was assigned a 1, a fresh sign a 2, and if the journalists sighted people a 3 was assigned, or 10 if the human group size was greater than ten. Further, the quality of the journal observation was rated as "ND" or no data for the day/period, or low, moderate, or high depending on the level of detail. The location was plotted as the nightly campsite, and again from low to high quality depending on the journalist's description of the location. In several instances, trading post or multiple-day camp data was utilized. Here, the total kill was divided by number of person-days estimated to obtain it.

Table 4.1.1: Definition, computation, and source of variables used as predictors or in discussion of ecoregion historical human and bison abundance. Variables with lower case are from this study, capitalized from other sources.

| Variable Group | Variable Name | Description | Source |
|---|---|---|---|
| Humans | Humans | average abundance index from journal accounts | [109], this study |
| Human | alternate foods | sum of plants, fish, fowl, other meat abundance indices | this study |
| Resource | plants | average abundance index from journal accounts | [109], this study |
| Abundance | fish | average abundance index from journal accounts | [109], this study |
| | fowl | average abundance index from journal accounts | [109], this study |
| | altmeat (other meat) | sum of black bear, moose, elk, deer, antelope abundance indices, not including bison | this study |
| | altres (alternate resources) | sum of all food resources for humans except bison (alternate meat, fish, fowl, and plants) | this study |
| Predator | wolf | average abundance index from journal accounts | [109], this study |
| Abundance | grizzly | average abundance index from journal accounts | [109], this study |
| | blkbear (black bear) | average abundance index from journal accounts | [109], this study |
| Bison | Bison | average abundance index from journal accounts | [109], this study |
| Other | Moose | average abundance index from journal accounts | [109], this study |
| Herbivore | Elk | average abundance index from journal accounts | [109], this study |
| Abundance | Deer | average abundance index from journal accounts | [109], this study |
| | Antelope | average abundance index from journal accounts | [109], this study |
| Wildland | fire | historic mean fire interval/fire cycle (years) | [276], this study |
| Fire | Cause | cause of fires from journal accounts | [109], this study |
| | Season | time of year fires occur | [179,276],this study |
| Historical | Grass (Grassland) | % cover of shortgrass, mixedgrass, tallgrass, fescue grasslands, palouse prairies, other graminoid fields | [80,81,71,70], this study |
| Ecoregion | Wet (Wetland) | % cover of muskeg, peatlands, bayous, marshes, riparian zones, | [80,81], this study |
| Vegetation | Decid (Deciduous) | % cover of deciduous forests and shrublands: willow, aspen, birch, oak, maple, hickory and other hardwoods | [80,81], this study |
| Cover | Dry Shrub (Dry Shrublands) | % cover of shrublands of pinyon-juniper, eastern red juniper, mesquite, creosote, cactus | [80,81], this study |
| | Conifer | % cover conifer forests: subalpine, boreal, coastal, white pine, longleaf pine, | [80,81], this study |
| | Tundra | % cover alpine or arctic tundra | [80,81], this study |
| | Water | % cover of fresh or saltwater within ecoregion | [80,81], this study |
| | Ice | % cover of glacial ice within ecoregion | [80,81], this study |
| | Unvegetated (NoVeg) | % bare rock or soil within ecoregion | [80,81], this study |
| Climate and | Tav (Temperature) | Average annual temperature (degrees C) | [277] |
| Terrain | Precip (Precipitation) | Average annual precipitation (mm) | [277] |
| | Snow | Average snow depth water equivalent (mm) | [278] |
| | Slope_mean | Average ecoregion slope angle 1 km resolution (degrees) | [279] |
| | NPP (Productivity) | Average net primary productivity (g/m2/year | [277] |

To evaluate spatial or temporal trends in species, or groups of species abundance based on historic journal observations, I calculate mean daily abundance indices for the North American ecoregions [31,32] mapped for our study area. The ecoregion scale is useful for delineating terrestrial biodiversity patterns for global land-use planning and conservation across taxa [33] and has recently been used in studies of large mammal restoration [34]. Where ecoregion boundaries extend beyond the study area, the mean abundance index includes observations from across the ecoregion. For all multivariate analyses, I excluded observations where the wildlife or location data quality was rated as no data. For mapping several ecoregions with less than 10 observations are combined with nearby adjacent ecoregions. The complete database for these observations is the North America Historical Journal Database [109] and is available for download in spreadsheet and Google Earth format.

### 4.1.2 Historic Wildland Fire Regime

A region's fire regime is defined by fire frequency, timing, intensity, and severity [149]. No detailed continental-scale spatial mapping of North American fire frequency yet exists. For this study regional fire history studies for Canada (e.g., [122,280,281]) and the United States (e.g., [75,282–288]) were synthesized with a database of additional site specific studies [276]. I selected for research that evaluated both cultural period and site characteristics. This allows evaluating causal mechanisms in fire frequency by independently known past anthropogenic events and seasonal rounds (Section 2.1), and local/regional biophysical differences such as elevation, temperature, precipitation and topography [289] . Where fire frequency patterns trends transcend study area biophysical or cultural variation, broader climatic or cultural change processes can be surmised [75,290].

In most cases, fire history studies used dendrochronology to determine either the time-since-fire (in high-severity regimes) or fire intervals (in low-severity regimes). From this information, either the fire cycle (years required to burn an area equivalent to the study area), or the mean fire interval (years) can be estimated. In landscapes with periodic random fire occurrence that is consistent over time and space, these estimates of fire frequency will be equivalent [291,292]. In cool and moist areas, researchers used soil charcoal evidence from sediment cores (e.g., [293,294]) to evaluate fire frequency. For studies reviewed that describe fire cycles or intervals over multiple time periods, the earliest period was assumed to provide the best estimate of long-term conditions before alterations caused by more recent cultural and land use changes. Historic fire frequency (years) was then stratified by weather zones [75,122,295], and ecoregion estimates quantified on this basis. A key assumption here is historically ignition was not a significant limiting factor— most important is weather, terrain and fuels as integrated within ecoregions. Even in regions where lightning was limited, human density and travel patterns during the fire season, and human use of fire ensure a source of ignition given suitable weather and fuels [147,296,297].

The period during the year when fires occur is an important component of fire regimes [298,299]. Most the fire history studies reviewed for this study [276] describe the season of historic fires from the position of fire-scars in dendrochronological analyses, usually classified into the categories of dormant, early-earlywood, earlywood and latewood (e.g.,[283]). Earlywood generally refers to the spring season, latewood to summer, and dormant to the fall, winter, and/or spring depending on the weather patterns and current fire activity pattens within the region. The North American Historical Journal Database [109] lists further information on fire seasonality and cause. Observations of wildland fires in the database were classified by date (spring, summer, fall, and winter seasons) and cause (unknown, unknown human, signal, accident, hunt, war, plant habitat, humans-other, or lightning).

### 4.1.3 Ecoregion Vegetation Cover, Climate, and Terrain

Ecoregions are characterized by unique combinations of historic vegetation cover, climate and terrain [80,81]. Farr and White [22] quantified biophysical factors influencing historic bison distribution and abundance in northwest North America where landcover remains relatively unchanged [81]. The important factors affecting bison distribution included, in order: grassland cover, coldest month temperature, mean annual radiance (indicator of productivity), tree cover ruggedness, and snow cover. For this study, the following variables were estimated for ecoregions (Table 4.1.1.1):

- Vegetation cover- Quantifying historical vegetation cover is problematic. No ecoregion-scale continental scale map yet exists. This study simply uses 9 broad classes ( adding up to 100% based upon ecoregion baseline vegetation descriptions [80–82], visual estimations from Google Earth, United States' LANDFIRE's Biophysical Settings mapping and database [300] and Canada's ecozone status and trends analyses [301,302] . Given its importance for bison, estimating historical grassland cover is particularly important. For the southeast, Hanberry and Noss [258] modelled potential historical grasslands based upon wind patterns and soil mapping.
- Climate and Productivity- Costanza et al. [277] and the provide ecoregion-level estimates for mean annual temperature, precipitation, and productivity. Additional climate data related to cultural ecoregions was available from anthropology databases [116,118,303]. Brown and Bratten [278] map mean annual snow depths for North America based upon 1946-1995 data.
- Slope- In this study terrain ruggedness is captured through mean slope angle with ecoregions as extracted from Natural Earth's  [279] database at a 1 km resolution.

## 4.2 Preliminary Analyses

The conceptual model for factors influencing bison distribution and abundance (Figure 3.1.2) can be evaluated with the data assembled in Table 4.1.1.1 at both continental and regional scales. As described above (Section 3.5), the continental-scale of historic journal observations provides a basis for two "natural experiments" [264]:

- Spatial analysis- Numerous varied, but replicated landscapes (e.g., ecoregions) to evaluate the importance of various biophysical and cultural factors.
- Temporal analysis- A relatively long period (~300 years) to evaluate bison population change in several regions because of changing human abundance.
- The analyses described here are <u>preliminary,</u> with open data available for future more detailed research. Current analyses are constrained by the coarse, ecoregion scale of many datasets for the continent, and assumptions for the relevance of current historic vegetation and climate covariates to historic conditions [22].

### 4.2.1 Continental Spatial Analysis

At the continental-scale, covariate data (Table 4.1.1.1) is available for >100 ecoregions. I used random forest (RF) statistical process [304] for preliminary analysis. The RF process is machine learning technique used many analyses. RF is computationally rapid for both model training and evaluation, is robust to outliers, can evaluate complex nonlinear associations, is relatively insensitive to class sample size imbalance, and produces competitive performance for high dimensional data. It has also been shown to handle challenges arising from small sample sizes. The "Variable Selection Using Random Forests" (VSURF) package [305] selected the covariates from Figure 3.1.2 that were most predictive of bison abundance in ecoregions. This routine randomly shuffles a variable of interest across observations and defines importance as the increase in prediction error. I discarded variables with low importance, or were likely driven by bison abundance, not visa-versa. The model retained has the least variables having prediction less than the minimum prediction error plus one standard deviation. This was then fitted to a regression tree to obtain an interpretable model [304].

I then used a Welch Two Sample t-test to evaluate the importance of select important predictors on human and bison abundance in ecoregions. The general hypotheses here are:

- The predictor separates bison from humans, thus reducing predation and increasing bison abundance; or
- The predictor enhances both bison and human abundance (mutualism).

### 4.2.2. Continental Temporal Analysis

Historical bison observations occur in 6 broad regions where Indigenous populations declined substantially during the immediate pre-contact or early contact periods. I evaluated human effects on bison abundance and distribution by summarizing, for each region, pre versus post human decline on bison abundance. For several regions, the abundance of bison prior to human depopulation was estimated through archaeological data. Historical journal observations then provided data on the remaining regions for the pre and post periods. I predicted that human depopulation would increase observed bison numbers in each region.

### 4.2.3 Regional Analyses

I use a framework of the North American ecoregions within ecological-cultural biomes [11,12,306] that extend across broad areas of North America. Six broad belt transects of ecoregions are ordinated from high to low bison abundance areas. Bar graph profiles for each ecoregion are made for groups of variables: 1) biophysical factors, 2) abundance of herbivores, and 3) abundance of predators. Then, for 3 broad areas of North America (west, north, east) and the 6 transect across them I review research from the fields of archaeology, ethnology, anthropology and traditional knowledge to describe the seasonal rounds of indigenous peoples whose homelands occur within the transects. I then describe human resource use patterns that, interacting with biophysical factors, could limit bison abundance or movement as distance from source to sink areas along the transect, and identify ecoregions where potential human-bison mutualistic processes occur at three scales: individuals and local populations, communities, and local and ecosystem/biomes.

For regional transects I also provide descriptions of "modern analogs" for areas where we have specific quantified information on domestic stock and wildlife abundance, herbivory effects, fire frequency and management techniques. Where these selected areas manage bison, this is, in a sense, a modern version of human-bison mutualism.

# 5. CONTINENTAL ANALYSIS: RESULTS AND DISCUSSION

In this report I briefly describe results for continental and regional analyses and immediately follow with a discussion section due to an immense literature on bison and human ecology that is often specific to various scales and regions.

## 5.1 Data Summary

### 5.1.1 Historical Journal Observations

Of the 29,777 observations mapped and recorded in the historical journal database 21,026 include descriptions of wildlife, humans, other resources (e.g., plants, fish etc.), or wildland fire. Of the 137 ecoregions in the study area, 117 had greater than 5 observations (Table 5.1.1.1) and were used for analysis. Ecoregions with <5 observations were combined to adjacent areas with similar land cover and terrain for analysis and mapping.

Journalists described 466 occurrences of wildland fire. Bison were reported 3,398 times, mostly as sightings (86.1%), but other evidence of their presence was also recorded (13.9%) based on traditional ecological knowledge acquired from guides or other Indigenous people, feces, tracks, or wallows. Humans were reported as seen or encountered in 8858 journal observations, and in another 1173 records, evidence of humans was observed without encountering people. Evidence or visual sightings of wolves or grizzly bears were less frequently reported, in 373 and 430 journal observations, respectively. Black bear sign or sightings numbered 613. Beaver sign or sightings numbered 1719, but observer records vary in detail depending on their travel objective (e.g., mappers versus trappers).

### 5.1.2 Fire History Studies Reviewed

The continental fire history database [276] currently contains ~185 studies, favouring research that evaluates both biophysical and cultural covariates as potential influences of fire frequency. Table 5.1.1 lists number of studies by ecoregion. Given that detailed research usually requires tree species that can be scarred by fire (e.g. ponderosa pine, western larch, lodgepole pine) studies are more common in ecoregions with these species. As observed in other reviews. most studies occur in ecoregions with large areas of wilderness or parks where wildland fire may be used for management or is not suppressed [122,282,283,287,307,308].

Table 5.1.1.1: Ecoregions and characteristic native species [80,81], number of days or periods recorded in historical journal database, and number fire history studies reviewed. Where journal observations n<5, ecoregions are mapped or merged with adjacent regions as described.

| Biome | Ecoregion Code and Name | Native vegetation and wildlife | n J_Obs | n fire studies |
|---|---|---|---|---|
| Great | 3.3.2 Hay and Slave River Lowlands | aspen, poplar, spruce, jack pine, whitefish, geese, bison, moose, caribou | 640 | 2 |
| Plains | 5.4.1 Boreal Uplands/ Peace Lowlands | mixed conifer-deciduous, moose, white-tailed deer, black bear, wolf, bison | 832 | 6 |
| | 5.4.2 Clear Hills/ Western Alberta Upland | conifer and deciduous forest, moose, deer, elk, caribou, black bear, wolf | 284 | 1 |
| | 5.4.3 Boreal Lowland/ Interlake Plain | spruce, balsam fir, jack pine, white-tail deer, moose, black bear | 276 | 0 |
| | 6.2.6 Cypress Upland (merged with 9.2.1) | wheatgrass, fescue, aspen, lodgepole pine, deer, elk, bison | 5 | 1 |
| | 6.2.10 Middle Rockies | douglas-fir, lodgepole pine, aspen, sagebrush, fescue, wheatgrass, Sandberg bluegrass, deer, elk, sheep, goat, bison | 1591 | 10 |
| | 8.2.3 Central Corn Belt Plains | bluestem, Indiangrass prairies, oak, hickory, white-tailed deer, coyote, bison | 93 | 0 |
| | 8.3.8 East Central Texas Plains | oak savanna, cedar, little bluestem, purpletop, bison, white-tail deer, javelina | 145 | 1 |
| | 9.2.1 Aspen Parkland/Glaciated Plains | aspen and oak groves, rough fescue grasslands, waterfowl, deer, bison, moose | 913 | 1 |
| | 9.2.2 Lake Manitoba/ Agassiz Plain | aspen parkland boreal forest transition, waterfowl, white-tail deer, fox, coyote | 157 | 0 |
| | 9.2.3 Western Corn Belt Plains | tallgrass prairie (bluestem, Indiangrass), small oak woods, deer, bison, geese | 308 | 1 |
| | 9.2.4 Central Irregular Plains | grassland/forest mosaic: bluestem/oak, w-t deer, bison, geese, quail, pheasant | 131 | 0 |
| | 9.3.1 Northwestern Glaciated Plains | grama and wheat grass, white-tail deer, pronghorn, bison, wolf | 574 | 0 |
| | 9.3.3 Northwestern Great Plains | grama, wheat and needle grass, sagebrush, pronghorn, bison, deer | 714 | 0 |
| | 9.3.4 Nebraska Sand Hills (mapped as 9.4.1) | bluestem, sandreed, grama grasses, bison pronghorn, bison, wolf | 0 | 0 |
| | 9.4.1 High Plains | grama, buffalo, wheat grass, bison, pronghorn, wolf | 512 | 0 |
| | 9.4.2 Central Great Plains | bluestem, grama, buffalo grasses, bison, pronghorn, wolf | 656 | 1 |
| | 9.4.3 Southwestern Tablelands | shortgrass (grama, dropseed), juniper, oaks, bison, wolf, mule deer, pronghorn | 649 | 0 |
| | 9.4.4 Flint Hills | edge of tallgrass prairie (bluestem/switchgrass), bison, elk, w-t deer, coyote | 70 | 2 |
| | 9.4.5 Cross Timbers | bluestem grassland, hickory, greenbriar woodland, w-t deer, wild turkey, bobcat | 105 | 3 |
| | 9.4.6 Edwards Plateau | juniper-oak-mesquite savanna, w-t deer, javelina, bobcat,periodically bison | 106 | 0 |
| | 9.4.7 Texas Blackland Prairies | tallgrass prairie of bluestem, asters, bison, pronghorn wolves | 91 | 0 |
| | 9.5.1 Western Gulf Coastal Plain | tallgrass prairie in north, mesquite, oak, xerophytic shrub in south, deer, ocelot | 163 | 0 |
| | 9.6.1 Southern Texas Plains/Hills | lowlands: grassland/mesquite savanna, xerophytic oak hills, deer, javelina | 269 | 0 |
| | 10.1.4 Wyoming Basin | arid grassland (, sagebrush, mule deer, pronghorn | 724 | 0 |
| SW Basins/ | 6.2.13 Wasatch and Uinta Mountains | sagebrush, pinyon-juniper, aspen, conifers, black bear, elk, cougar, bobcat | 110 | 0 |
| Deserts/ | 6.2.14 Southern Rockies | sagebrush, mahogany, pinyon-juniper, aspen, conifers, elk, mule deer, sheep | 323 | 0 |
| Mexico | 10.1.5 Central Basin and Range | sagebrush, saltbrush-greasewood, pinyon-juniper, mule deer, pronghorn, sheep | 549 | 1 |
| | 10.1.6 Colorado Plateaus | blackbrush, saltbush, pinyon-juniper, mahogany-oak shrub, mule deer, pronghorn | 462 | 0 |
| | 10.1.7 Arizona/New Mexico Plateau | saltbrush, greasewood, gramas, pinyon-juniper, mule deer, pronghorn, cougar | 837 | 3 |
| | 10.2.1 Mojave Basin and Range | creasote, palo-verde, cactus, sagebrush, pinyon-juniper, sheep, pronghorn, coyote | 277 | 1 |
| | 10.2.2 Sonoran Desert | palo-verde-cactus shrub, cresosote, ocotillo, sheep, mule-deer, coyote, javelina | 411 | 0 |
| | 10.2.3 Baja Californian Desert | agave, cirio, cactus, pitaya, pronghorn, bighorn sheep, desert fox, sea lion | 34 | 0 |

| | | | | |
|---|---|---|---|---|
| | 10.2.4 Chihuahuan Desert | desert grassland (grama, muhley), shrubland (creasote, tarbush), sheep, pronghorn | 633 | 2 |
| | 12.1.1 Madrean Archipelago | grasslands (grama, sideoats), mesquite, yucca, shrub oak, pines, mule deer, cougar | 143 | 8 |
| | 12.1.2 SW Piedmonts and Plains | grasses, desert shrub, pine-oak-mixed forest, black bear, badger, mule deer, pronghorn | 57 | 0 |
| | 13.1.1 Arizona/New Mexico Mountains | chapparral, pinyon-juniper, oaks, conifers on mountains, sheep, mule-deer, cougar | 180 | 0 |
| | 13.2.1 Sierra Madre Occidental | temperate pine, oak, mixed forest, small grasslands, w-t deer, coyote, mtn lion, | 15 | 1 |
| | 13.3.1 Sierra Madre Oriental (mapped as 13.2.1) | tropical deciduous and conifer forests, 6 felines, w-t deer, peccary, black bear | 0 | 0 |
| | 14.1.1 Gulf Tropical Coastal Plain (mapped as 14.3.1) | mangroves, tropical thornscrub, thorn forest, deciduous forest, w-t deer, coyote, boar | 0 | 0 |
| | 14.3.1 Sinaloa Coastal Plain | mangroves, tropical thornscrub, opossum, jackrabbit, waterfowl, marine species | 26 | 0 |
| | 14.3.2 Sinaloa and Sonora Hills | tropical deciduous forest, jaguar, w-t deer, | 36 | 0 |
| 3California | 6.2.12 Sierra Nevada | diverse conifer forests, ponderosa pine to sequoias, black bear, deer, sheep, cougar | 67 | 6 |
| | 11.1.1 California Coast | chapparral, sage, oak woodlands, mule deer, gray fox, cougar, turkey | 513 | 3 |
| | 11.1.2 Central California Valley | bunchgrasses, riparian oak, willow, sycamore, pronghorn, elk, mule deer, coyote | 457 | 0 |
| | 11.1.3 Baja & South California | chapparral, oak woods, mixed conifer, b-t deer, coyote, bobcat, cougar | 30 | 1 |
| 4NW Coast | 6.1.1 Interior Highlands/Klondike Plateau | tundra, dwarf shrubs, spruce, caribou, Dall sheep, moose, caribou | 67 | 0 |
| | 6.1.2 Alaska Range (mapped as 6.1.1) | journal obs mapped as 6.1.1, tundra, dwarf shrubs, ice, sheep, caribou | 0 | 0 |
| | 6.1.3 Copper Plateau (mapped as 6.1.1 | journal obs mapped as 6.1.1, tundra, dwarf shrubs, ice, sheep, caribou | 0 | 0 |
| | 6.1.4 Wrangell and St. Elias Mountains (mapped as 6.1.1) | journal obs mapped as 6.1.1, tundra, dwarf shrubs, ice, sheep, caribou | 0 | 0 |
| | 6.1.5 Watson Highlands | tundra, birch-willow shrublands, spruce, moose, caribou, Dall sheep | 447 | 0 |
| | 6.1.6 Yukon-Stikine Highlands/Boreal Mtns | tundra, birch-willow, spruce-fir, moose, caribou, stone sheep, grizzly | 174 | 0 |
| | 6.2.1 Skeena-Omineca-Rocky Mountains | aspen, lodgepole pine, spruce, salmon, moose, caribou, bear | 301 | 0 |
| | 6.2.2 Chilcotin Ranges and Fraser Plateau | bunchgrasses, aspen, pine, spruce, salmon, deer, sheep | 64 | 2 |
| | 6.2.3 Columbia Mountains/Northern Rockies | white pine, hemlock, cedar, fir, salmon, bear, caribou, elk, moose, goat | 611 | 5 |
| | 6.2.4 Canadian Rockies | aspen, lodgepole pine, spruce, deer, elk, sheep, goat, bison (eastside) | 512 | 14 |
| | 6.2.5 North Cascades (mapped as 6.2.5) | douglas-fir, hemlock, cedar, salmon, deer, elk | 0 | 0 |
| | 6.2.7 Cascades | douglas-fir, hemlock, cedar, salmon, deer, elk | 81 | 1 |
| | 6.2.8 Eastern Cascades Slopes and Foothills | sagebrush, ponderosa pine, salmon, deer, black bear | 82 | 2 |
| | 6.2.9 Blue Mountains | wheatgrass, sagebrush, ponderosa pine, salmon, deer, elk | 219 | 2 |
| | 6.2.11 Klamath Mountains | firs (douglas, white, oaks, pines (Jeffrey, ponderosa), salmon, deer, elk | 96 | 4 |
| | 6.2.15 Idaho Batholith | firs (grand, douglas), pines (ponderosa, white), salmon, deer, black bear | 201 | 1 |
| | 7.1.4 Pacific Coastal Mountains | tundra, hemlock (mtn, western), sitka spruce, otter, salmon, goat, bear | 32 | 0 |
| | 7.1.5 Coastal Hemlock-Sitka Spruce Forest | hemlock, red cedar, sitka spruce, Douglas fir, salmon, otter, shellfish, elk | 277 | 4 |
| | 7.1.6 Pacific and Nass Ranges | hemlock, red cedar, douglas fir, salmon, eulachon, herring, deer | 121 | 0 |
| | 7.1.7 Strait of Georgia/Puget Lowland | camas, oak, douglas fir, salmon, herring, black-tailed deer, elk, black bear | 180 | 3 |
| | 7.1.8 Coast Range | sitka spruce, redwood, douglas fir, salmon, deer, elk | 244 | 2 |
| | 7.1.9 Willamette Valley | oak savanna, douglas fir, salmon, black-tail deer | 152 | 0 |
| | 10.1.1 Thompson-Okanogan Plateau | grasslands, douglas-fir, lodgepole pine, salmon, deer, bighorn sheep | 80 | 4 |

| | | | | |
|---|---|---|---|---|
| | 10.1.2 Columbia Plateau | grasslands, sagebrush, salmon, mule-deer, pronghorn | 465 | 1 |
| | 10.1.3 Northern Basin and Range | grasslands, sagebrush, mule deer, pronghorn, coyotes | 355 | 0 |
| | 10.1.8 Snake River Plain | dry grassland, sagebrush, salmon, mule deer, bison, bighorn sheep | 898 | 0 |
| 5Subarctic- | 2.1.5 Foxe Uplands | discontinuous tundra, sedges, caribou, muskox, polar bears, seals | 33 | 0 |
| Arctic | 2.1.9 Banks Island / Amundsen Lowlands | moss, mixed low herbs, shrubs, caribou, muskox, polar bears, seals | 43 | 0 |
| | 2.2.1 Arctic Coastal Plain | shrubby tundra, caribou, arctic fox, wolf, brown bear, | 49 | 0 |
| | 2.2.2 Arctic Foothills | shrubby tundra, sedge tussocks, caribou, musk ox, wolf, brown bear | 48 | 0 |
| | 2.3.1 Brooks Range/Richardson Mountains | tundra, open woodlands, caribou, moose, Dall’s sheep, caribou, grizzly | 16 | 1 |
| | 2.4.1 Amundsen Plains | rock, shrub tundra, stunted spruce, caribou, musk ox, moose, grizzly bear | 485 | 0 |
| | 2.4.2 Aberdeen Plains | shrub tundra, whales, geese, caribou, moose, lynx, wolf, grizzly bear | 148 | 1 |
| | 2.4.4 Queen Maud Gulf /Chantrey Lowlands | shrub tundra, geese, caribou, musk ox, grizzly bear, walrus, seal, whales | 82 | 0 |
| | 3.1.1 Interior Forested Lowlands and Uplands | spruce, tamarack, tundra, salmon, caribou, moose, bears, wolf | 74 | 1 |
| | 3.1.2 Interior Bottomlands (mapped as 3.1.2) | wetlands, spruce, aspen, birch, salmon, geese, moose, bear, lynx | 0 | 1 |
| | 3.1.3 Yukon Flats | open spruce, birch, moss-lichen, moose, caribou, Dall’s sheep, grizzly bear | 45 | 1 |
| | 3.2.1 Ogilvie Mountains | tundra, open spruce, barren talus, caribou, moose, sheep, grizzly, wolf | 36 | 1 |
| | 3.2.2 Mackenzie and Selwyn Mountains | tundra, open spruce-tamarack, caribou, moose, grizzly-black bear, wolf | 108 | 2 |
| | 3.2.3 Peel River and Nahanni Plateaus | open spruce-tamarack, trout, caribou, moose, grizzly-black bear, wolf | 66 | 1 |
| | 3.3.1 Great Bear Plains | tundra-forest transition, caribou, black bear, arctic fox, wolf | 267 | 2 |
| | 3.4.1 Kazan River and Selwyn Lake Uplands | tundra-forest transition, caribou, moose, grizzly and black bear, wolf | 307 | 1 |
| | 3.4.2 La Grande Hills/Quebec Central Plateau (mapped as 5.1.3) | open coniferous forest transitional to tundra, caribou, wolverine, hare, fox | 0 | 0 |
| | 3.4.5 Coppermine River / Tazin Lake Uplands | tundra-forest transition, caribou, moose, grizzly and black bear, wolf | 469 | 2 |
| | 4.1.1 Coastal Hudson Bay Lowland (mapped as 4.1.2) | wetlands, cottongrass, black spruce, shrub birch, caribou, moose, lynx, geese | 0 | 0 |
| | 4.1.2 Hudson Bay and James Bay Lowlands | wetlands, cottongrass, black spruce, shrub birch, caribou, moose, lynx, geese | 100 | 0 |
| | 5.1.1 Athabasca Plain/ Churchill River Upland | boreal forest, black spruce, jack pine, caribou, moose, black bear | 297 | 0 |
| | 5.1.2 Lake Nipigon and Lac Seul Upland | conifer forest, some poplar, fens, bogs, wolf, lynx, moose, black bear, caribou | 146 | 1 |
| | 5.1.3 Central Laurentians/Mecatina Plateau | black spruce, balsam fir, birch, jackpine, caribou, moose, | 85 | 2 |
| | 5.1.5 Hayes River Upland and Big Trout Lake | boreal forest, black spruce, jack pine, moose, caribou, lynx, black bear | 77 | 1 |
| | 5.1.6 Abitibi Plains/Riviere Rupert Plateau | mixed conifer-deciduous forest, moose, black bear, lynx, hare, caribou | 41 | 2 |
| 6Northeast | 5.2.1 Northern Lakes and Forests | conifer (pines), hardwood forest (birch, maple), moose, bear, deer | 439 | 10 |
| Woodlands | 5.2.2 Northern Minnesota Wetlands | mixed conifer/bog forest with boreal vegetation, wt deer, black bear, wolf | 40 | 0 |
| | 5.2.3 Algonquin/Southern Laurentians | mixed forest spruce/fir/tamarack, moose, black bear, lynx, hare, deer | 112 | 5 |
| | 5.3.1 North Appalachians/Atlantic Highlands | mixed hardwood/spruce-fir forest, moose, black bear wt deer, red fox | 55 | 3 |
| | 5.3.3 North Central Appalachians (mapped as 5.3.1) | hardwood forest: maple, beech, birch, black bear, wt deer, bobcat, coyote | 0 | 0 |
| | 8.1.1 Eastern Great Lakes-Hudson Lowlands | mixed conifer-deciduous forest, deer, black bear, moose, coyote, wolf | 541 | 3 |
| | 8.1.2 Lake Erie Lowland | mixed and deciduous forest (maple, oak), wt deer | 104 | 0 |
| | 8.1.3 Northern Allegheny Plateau (mapped as 5.3.1) | oak hickory forests, northern hardwoods, black bear, w-t deer, fox, geese | 0 | 1 |

| | | | | |
|---|---|---|---|---|
| | 8.1.4 North Central Hardwood Forests | oak savanna, oak-hickory forest, bison, elk, wolf, wt deer, coyote, grey fox | 178 | 0 |
| | 8.1.5 Driftless Area | mosiac tallgrass prairies, oak and maple forests, w-t deer, coyote, grey fox, turkey | 101 | 0 |
| | 8.1.6 Michigan/Indiana Drift Plains | oak-hickory forest, swamps, beech, oak, hickory, w-t deer, coyote, fox, fisheries | 54 | 0 |
| | 8.1.7 Northeastern Coastal Zone | oak and oak-pine forests, w-t deer, black bear, bobcat, coyote, beaver | 123 | 1 |
| | 8.1.8 Acadian Plains and Hills | maple, beech, birch , pines (white, red, jack), moose, black bear, w-t deer | 125 | 2 |
| | 8.1.9 Maritime Lowlands | closed mixed forest red spruce, fir, mpale, hemlock, pine, moose, bear, wt deer | 0 | 1 |
| | 8.1.10 Erie Drift Plain | beech-maple, oak-hickory forests, elm-ash swamps, w-t deer, red fox, woodchuck | 67 | 0 |
| | 8.2.1 Southeastern Wisconsin Till Plains | transition hardwood, oak savanna, tall grass prairies, w-t deer, red fox, coyote, turkey | 99 | 0 |
| | 8.2.2 Huron/Erie Lake Plains | elm-ash swamp, beech forest, oak savanna, w-t deer, racoon, woodchuck | 74 | 0 |
| | 8.2.4 Eastern Corn Belt Plains | beech forests, elm-ash swamps, white-tail deer, coyote, fox, cottontail rabbit | 77 | 0 |
| | 8.3.1 Northern Piedmont | oak, hickory, ash, poplar forest, cedar on disturbed lands, w-t deer, gray fox, cottontail | 24 | 0 |
| | 8.3.2 Interior River Valleys and Hills | oak-hickory forest, small prairies, black bear, w-t deer, bobcat, gray fox | 273 | 0 |
| | 8.4.1 Ridge and Valley | oak forest in N, oak-hickory-pine forest in S, w-t deer, black bear, bobcat, red fox | 244 | 2 |
| | 8.4.2 Central Appalachians | chestnut-maple-oak forest, black bear, w-t deer, fox, bobcat, grouse | 132 | 0 |
| | 8.4.3 Western Allegheny Plateau | oak-hickory-maple forest, w-t deer, gray fox, woodchuck, turkey | 222 | 1 |
| | 8.5.4 Atlantic Coastal Pine Barrens | pitch pine, scarlet/black oak, cedar swamps, dune woodlands, w-t deer, fox, rabbit | 85 | 2 |
| 7Southeast Woodlands | 8.3.3 Interior Plateau | oak-hickory forest, bluestem prairie, cedar glades, black bear, w-t deer, bobcat, fox | 161 | 4 |
| | 8.3.4 Piedmont | oak-hickory-pine forest, w-t deer, black bear, bobcat, fox | 312 | 1 |
| | 8.3.5 Southeastern Plains | longleaf pine, oak-hickory-pine, cypress, w-t deer, black bear, bobcat, gray fox | 495 | 0 |
| | 8.3.6 Mississippi Valley Loess Plains | oak-hickory-pine forest, oak-hickory on hills, w-t deer, black bear, bobcat, gray fox | 31 | 0 |
| | 8.3.7 South Central Plains | longleaf pine savannas, flooplain oak, sweetgum, cypress, w-t deer, coyote, beaver | 413 | 1 |
| | 8.4.4 Blue Ridge | broadleaf temperate forest: oaks, cove hardwoods, pine, black bear, w-t deer, bobcat | 80 | 0 |
| | 8.4.5 Ozark Highlands (mapped as 8.4.7) | oak-hickory-pine forest, some bluestem savannas, w-t deer, coyote, bobcat, turkey | 0 | 2 |
| | 8.4.6 Boston Mountains (mapped as 8.4.7) | oak-hickory forests, pine-red cedar in lowlands, black bear, w-t deer, turkey | 0 | 1 |
| | 8.4.7 Arkansas Valley | oak savanna, oak-hickory forest, bison, elk, wolf, wt deer, coyote, grey fox, rabbit | 241 | 1 |
| | 8.4.8 Ouachita Mountains (mapped as 8.4.7) | oak-hickory-pine forest, w-t deer, black bear, coyote, bobcat, gray fox | 0 | 0 |
| | 8.4.9 Southwestern Appalachians (mapped as 8.4.4) | uplands: mixed oak, shortleaf pine, ravines: hardwoods, w-t deer, black bear, bobcat | 0 | 2 |
| | 8.5.1 Middle Atlantic Coastal Plain | longleaf pine in S, oak-hickory-pine in S, oak on barrier islands, black bear, w-t deer | 157 | 0 |
| | 8.5.2 Mississippi Alluvial Plain | bottomland deciduous forest, swamplands water hickory, cypress, deer, black bear | 573 | 0 |
| | 8.5.3 Southern Coastal Plain | longleaf pine savannas, wetlands: cypress, water tupelo, black bear, w-t deer | 296 | 0 |
| | 15.4.1 Southern Florida Coastal Plain (mapped as 8.5.3) | mapped as 8.5.3, sawgrass marshes, tree islands: slash pine, gumbo limbo, alligator | 0 | 0 |

## 5.2 Wildland Fire

### 5.2.1 Fire Ignition Cause and Seasonality

The historical journal database includes 466 observations (Table 5.2.1.1) of either ongoing or recent fires that had spread or would likely spread beyond a campfire size. On average, across ecoregions, journalists recorded these fires on ~1.5% of days. The Great Plains and California had the highest frequency of observed fires. Apart from the subarctic and arctic regions that burned mostly in spring and summer, and very rarely in the winter, the journalists observed fires in other biomes burned in all seasons, and the season of burning as observed in historical journals corroborates the position of fire scars in dendrochronology studies. Most fires occurring in the dormant seasons (fall, winter, spring) when tree-ring growth is not occurring. In California and the Northwest Plateau fires occurred mostly fires in the late summer and fall. The Southeast had a pronounced winter burning season. The Great Plains grasslands appear to have started burning in the late summer, with similar numbers of observed fires occurring through the fall and winter. In spring fewer numbers of fires were observed, but for the northern mixed-wood on the plains, the preponderance of tree-ring scars in the earlywood and dormant season (Table 5.2.1.1) suggests that large areas may have burned during this period.

Averaged across all biomes, the proportion of causes are as follows: unclassified (25%), unknown by but likely started by humans (14%), signaling (30%), accidental fire escape (8%), hunting (10%), warfare (5%), habitat improvement (4%), other human purposes such as insect reduction or tree-felling (2%), and lightning (<1%).

### 5.2.2 Fire Frequency

The fire ignition pattern, and the resulting spread of fire as influenced by weather, fuels, and terrain over time creates landscape level fire frequency. Reviewed fire history studies [276] estimate fire frequency from stand age, fire scars or lakebed pollen/carbon studies. Most North American ecoregions do not have area-specific fire history studies (Table 5.1.1). However, assuming fire ignition is relatively abundant in most areas (Tables 5.2.1.1. 5.2.1.2.), fire frequency ranges can be approximated by grouping ecoregions into zones with similar fire weather patterns. Within ecoregions, cool-moist areas (riparian zones, higher elevation, north slopes) will be at the upper end of fire frequency ranges, warm-dry areas at the lower end of the frequency range.

Figure 5.2.2.1 maps historic fire frequency classes for the North American ecoregions. A massive area of central North America had relatively short fire intervals (<15 years) running NNW from the Gulf of Mexico across southern woodland ecoregions, then into the tallgrass, shortgrass prairies, then 10-30 years across the central plains into fescue grasslands, and oak savanna and aspen parklands surrounding the plains, and 20-80 years in the mixed-wood and boreal forests on the northern plains. Similarly, swaths of high fire frequency banded the western and eastern coasts, and up the St. Lawrence River into the Great Lakes region. Another band of high frequency extended up a rain shadow behind the Coast Ranges on the Columbia and Fraser Plateaus in the central Western Cordillera. The southwest basin and ranges, plateaus, and deserts generally had longer fire frequencies due to lack of surface fuels.

Table 5.2.1.1. Summary of journal observations of fires by percent of days/periods of observation and season, and location of fire-scars in dendrochronology studies.

| Biome | Journal Days | Burn Obs | % days | 1Fall | 2Winter | 3Spring | 4Summer | Period of burning from fire-scars |
|---|---|---|---|---|---|---|---|---|
| 1.Great Plains | 10008 | 192 | 1.92 | 49 (26%) | 49 (26%) | 25 (13%) | 69 (36%) | N: dormant>earlywood>latewood S: dormant=latewood>earlywood |
| 2.Southwest-Great Basin | 4093 | 54 | 1.32 | 14 (26%) | 9 (17%) | 12 (22%) | 19 (35%) | early-earlywood>dormant |
| 3.California | 1067 | 20 | 1.87 | 10 (50%) | 1 (5%) | 1 5%) | 8 (40%) | dormant>latewood |
| 4.Northwest Coast-Plateau | 5659 | 93 | 1.64 | 35 (38%) | 2 (2%) | 13 (14%) | 43 (46%) | dormant>latewood>earlywood |
| 5.Subarctic-Arctic | 3022 | 40 | 1.32 | 0 (0%) | 1 (3%) | 6 (15%) | 33 (83%) | ND |
| 6.Northeast Woodlands | 3169 | 30 | .95 | 7 (23%) | 8 (27%) | 7 (23%) | 8 (27%) | dormant>latewood=earlywood |
| 7.Southeast Woodlands | 2759 | 37 | 1.34 | 4 (11%) | 20 (54%) | 6 (16%) | 7 (19%) | >90% dormant |
| **Grand Total** | **29777** | **466** | **1.56** | **118** | **89** | **70** | **187** | |

Table 5.2.1.2 Summary of fire cause by biome

| Biome | Cause | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **1unknown** | **2human unknown** | **3signal** | **4accident** | **5hunt** | **6War** | **7plant habitat** | **8humans other** | **9lightning** | **Grand Total** |
| 1.Great Plains Prairie/Mixedwood | 63 | 30 | 47 | 18 | 21 | 8 | 3 | 1 | 1 | 192 |
| 2.Southwest-Great Basin | 1 | 5 | 38 | 5 | | 4 | | 1 | | 54 |
| 3.California | 6 | 6 | 2 | | 3 | 2 | | 1 | | 20 |
| 4.Northwest Coast-Plateau | 33 | 8 | 14 | 13 | 9 | 6 | 5 | 4 | 1 | 93 |
| 5.Subarctic-Arctic | 2 | 4 | 26 | 1 | 3 | | | 4 | | 40 |
| 6.Northeast Woodlands | 4 | 5 | 7 | 1 | 4 | 2 | 7 | | | 30 |
| 7.Southeast Woodlands | 6 | 6 | 8 | 1 | 6 | 3 | 5 | | 2 | 37 |
| (blank) | | | | | | | | | | |
| **Grand Total** | **115 (25%)** | **64 (14%)** | **142 (30%)** | **39 (8%)** | **46 (10%)** | **25 (5%)** | **20 (4%)** | **11 (2%)** | **4 (1%)** | **466** |

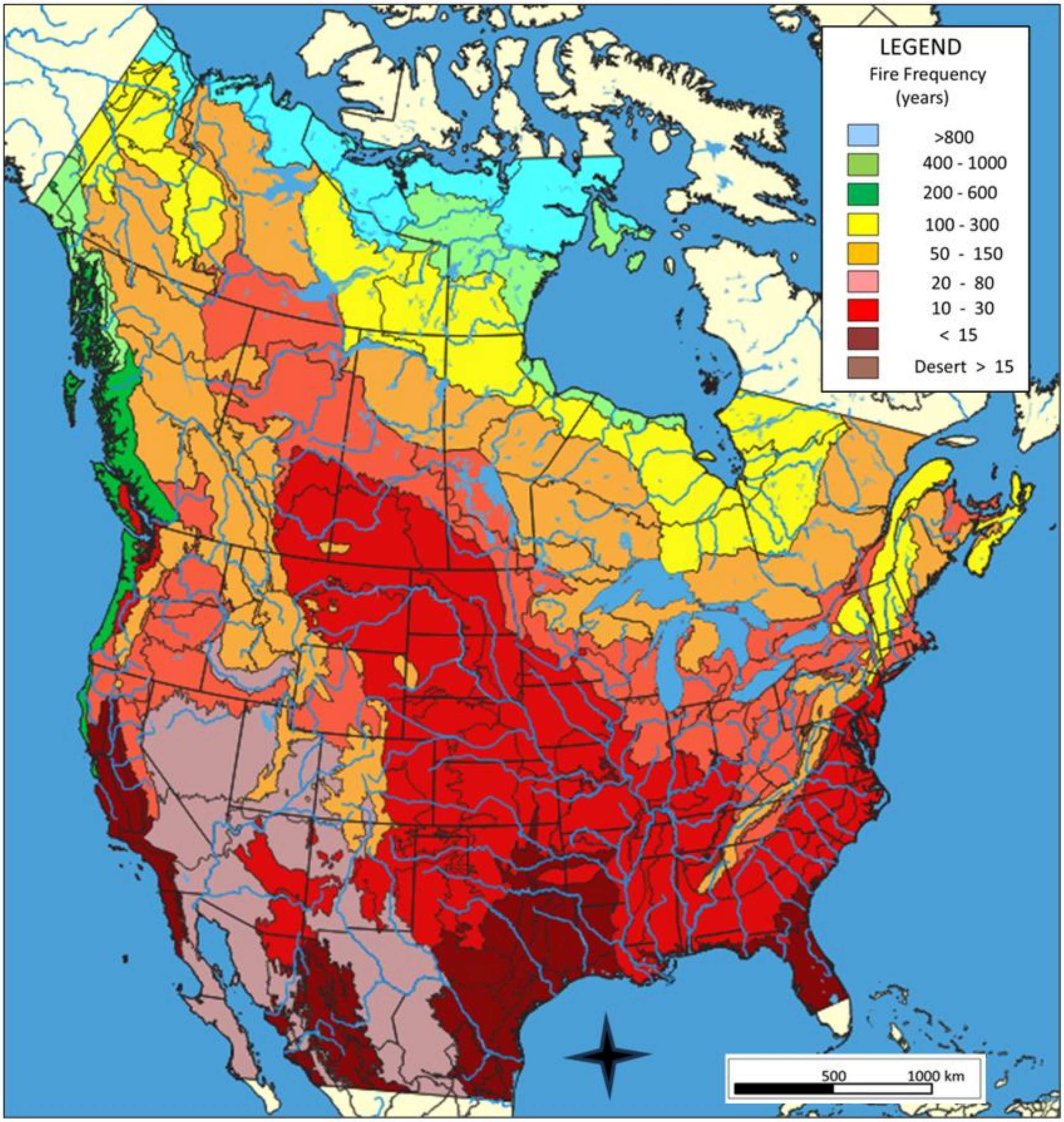



Figure 5.2.2.1. North American historic fire frequency for ecoregions derived from ~200 fire history studies [276].

### 5.2.3 Discussion: Fire Regimes, Humans and Bison

Journal observations show that during the historic period human ignitions overwhelmed lightning ignitions—a pattern observed most previous research [309,147,297,288]. The importance of Indigenous fires is described for a wide range of North American landscapes in, or on the periphery of bison range [243,244], and specific regions including Great Plains grasslands [310–314] , boreal mixed-wood [218,315], Rocky Mountains and foothills [288,316–318], relatively dry western coastal mountains and lowlands [288,319,320], northeastern conifers and hardwoods [321], and southeastern mixed-woods and conifers and grasslands [321]. On the edge of the Great Plains fires likely competed with herbivory as a primary agents of biomass consumption [76]. The historical journal observations for season of burning (Table 5.2.1.1) concur with dendrochronological [276] and anthropological-historical studies [243,244,298,322] that show that in most regions most of the burning occurs in shoulder seasons (fall, winter, spring). The exception is the subarctic boreal where large areas burn mainly in the summer.

Anthropogenic fire was so common that many early European journalists were unaware that lightning could cause fires [323]. Given the many fires lit throughout the year by a region's residents for many varied purposes (Table 5.2.1.2), only a few, by intent or accident, spread to large areas. However, the timing of their spread— often early in a drying period, and their location—near human travel routes and occupation areas either precluded lightning ignition or obscured evidence of its occurrence [297,122]. This corresponds with the oft-observed anthropogenic pattern of firing vegetation: "burn early, burn light, burn often"[324]:52. Burning starts as early as possible in the annual cycle of herbaceous growth (described in Section 3.1) when light-burning is possible as soon as plant growth cures in late summer and fall, continues into winter and spring when conditions are favorable, and may be subsidized by some lightning fires that occur mainly in summer.

Historically, the transition zone from grasslands to forest at the edges of the Great Plains was important habitat for bison, humans, and numerous other species [8,61,71,314]. This ecotone was at the upper range of the 10-30 years fire frequency class (Figure 5.2.2.1). This frequency of burning maintained some grasslands, was long enough to allow persistence of deciduous trees but was too short for the survival of conifers. On the east and north-east of the plains, this mixed deciduous-grass zone was an oak savanna interspersed with larger grasslands [70,258] ; on the north and northwest it was aspen parkland (Section 6). Oak species have many adaptions to frequent fire including thick bark, sprouting after top-kill, recovery from stem scarring, and rapid seeding by acorns in fire-bared soils [283]. Similarly, poplar species such as aspen have widespread underground root-clones that rapidly send up shoots after fire kills above ground stems[8,71,325]. Aspen seedlings, like oaks, rapidly recolonize bare soils after burning or erosion. Moreover, both groups of species, once "greened-up" with their characteristic lush, moist herbaceous understories restrict fire spread in early and mid-summer but are flammable in the dormant season. This variation in flammability in deciduous forests favors human fire use [175].

## 5.3 The Beaver

### 5.3.1 Historical Journal Beaver Observations

Beaver sightings or sign occurs 1718 times in the journal database (Table 5.3.1.1). The records have strong observer bias. In general, beaver was not an important source of traveller sustenance, so is not reported as meticulously as ungulates, fish, or fowl. The early Spanish travellers were searching for corn stores or gold and had little interest in beaver. In contrast, British, French and American trappers, traders and travellers were aware of the economic value of beaver, and more frequently commented on their occurrence. The trading post journals provide daily and period tallies for beaver taken in their region. The most aggressive tallying of beaver abundance in the field occurred when the Hudson's Bay Company and their associated Indigenous partners were purposely trapping out western watersheds in the 1820s to 1840s. The journals of Peter Ogden and John Work provide daily tallies of beaver taken in the Snake, upper Missouri, and other western watersheds.

Table 5.3.1.1. Summary of journal observations (Obs) of beaver sightings or sign by biome.

| Biome | Journal Days | Beaver Obs | % Obs |
|---|---|---|---|
| 1.Great Plains | 10008 | 507 | 5.1 |
| 2.Southwest-Great Basin | 4093 | 135 | 3.3 |
| 3.California | 1067 | 129 | 12.1 |
| 4.Northwest Coast-Plateau | 5659 | 636 | 11.2 |
| 5.Subarctic-Arctic | 3022 | 133 | 4.4 |
| 6.Northeast Woodlands | 3169 | 166 | 5.2 |
| 7.Southeast Woodlands | 2759 | 12 | .4 |
| **Grand Total** | **29777** | **1718** | **5.7** |

### 5.3.2 Preliminary Discussion: Beaver Abundance

The best that can be concluded from Table 5.3.1.1 is that based upon first person journal observations the beaver was generally well distributed across the continent, and possibly abundant in Californian and Northwest-Plateau biomes, and had possibly low abundance in the southeast woodlands and southwest deserts and the Great Basin. Researchers are investigating models of beaver habitat quality and abundance across broad regions with current land uses (e.g.,[326–329]). Relatively consistent influencing factors include vegetation cover (deciduous, conifer, herbaceous), stream gradient, roads, land use (logging, agriculture), diameter of woody material near stream. Given the current land use focus, Indigenous land practices for beaver that might benefit humans and bison (as reviewed by Morgan [8,98], Section 3.2 above) are often are not applicable in these studies. However, numerous studies in many ecoregions describe negative effects of high current bovid stocking levels on riparian and beaver habitat (e.g., [102,269,272,330]). Research for specific areas is discussed in Section 6 below. A great deal more research is required to better understand the long-term interactions between humans, beaver, and bison's distribution and abundance.

# 5.4 Bison Continental Spatial Pattern

## 5.4.1 Historic Abundance of Bison

The mean bison abundance bison for ecoregions derived from journal observations (Figure 5.4.1.1) approximates the historic distribution (Figure 1.1) mapped by Allen [2] with highest bison abundance on the grasslands of the Great Plains. From here, bison extended northwards up the plains into the aspen parkland, and then into mixed woods of aspen and conifers to the Mackenzie River's exit from Great Bear Lake. Again, in this northern region, bison was constrained to the boreal plains' areas, and did not extend into the Western Cordillera to the west, or the Canadian Shield to the east. To the south, bison range had, by the CE 1500s recently extended to the Gulf of Mexico (see Section 5.5 below). To the east, bison were at this time still generally west of the Mississippi River, but over the early historic period extended their range east to the Appalachians. In the west bison were rarely observed in the Rocky Mountains ecoregions and only extended west of the mountains in the central portion of the range where they crossed South Pass on to the headwaters of the Snake River.

## 5.4.2 Results: "Random Forest" (RF) Statistical Analysis

A total of 117 ecoregions had robust data for analysis, providing mean values for 24 covariates (Figure 5.4.2.1) for evaluation of the preliminary model of processes influencing bison distribution and abundance. Of these covariates, <10 had variable importance variables >5 for predicting bison abundance in the first pass of the random forest analysis (Figure 5.4.2.3a). Grass cover was by far the most important predictor, followed by wolf abundance, fire frequency, deciduous forest cover, fish resource abundance, grizzly abundance, human abundance, and plant abundance.

To simplify the next RF iteration, I summed the four variables that quantify alternate resources available for humans instead of bison (fish, plants, other meat, and fowl) to create the single predictor "Alternate Resources". These all had relatively similar importance in the first iteration. I then discarded both wolf and grizzly bear abundance because their abundance was positively associated with high bison numbers in the center of the range, not negatively associated with lower numbers elsewhere—indicating that bison influenced their numbers, not visa-versa. I retained average temperature and snow because previous research indicated their potential importance [22]. This RF analysis reduced set of variables (Figure 5.4.2.3b) again showed the importance of grass cover (Grass), followed closely by fire frequency (Fire), deciduous forest cover (Decid), alternate resources (altres: sum of of fish, plants, other meat, and fowl), human abundance (humans), followed with lower importance by average temperature (Tav) and snow depth (Snow).

The full RF regression tree built with these variables accounted for ~48% of the variance of bison abundance. To interpret the relationship between the selected variables and bison, I focus on the first 5 splits (Figure 5.4.2.4), where the most frequently selected model partitions bison abundance into 9 groups, ranging from a group of 46 ecoregions have very low or no abundance, to a group of 5 ecoregions with high bison abundance. Grass cover is the predictor at 3 decision nodes, human abundance at 2 nodes, and alternate resource abundance, deciduous forest cover, and average temperature important at one node each.

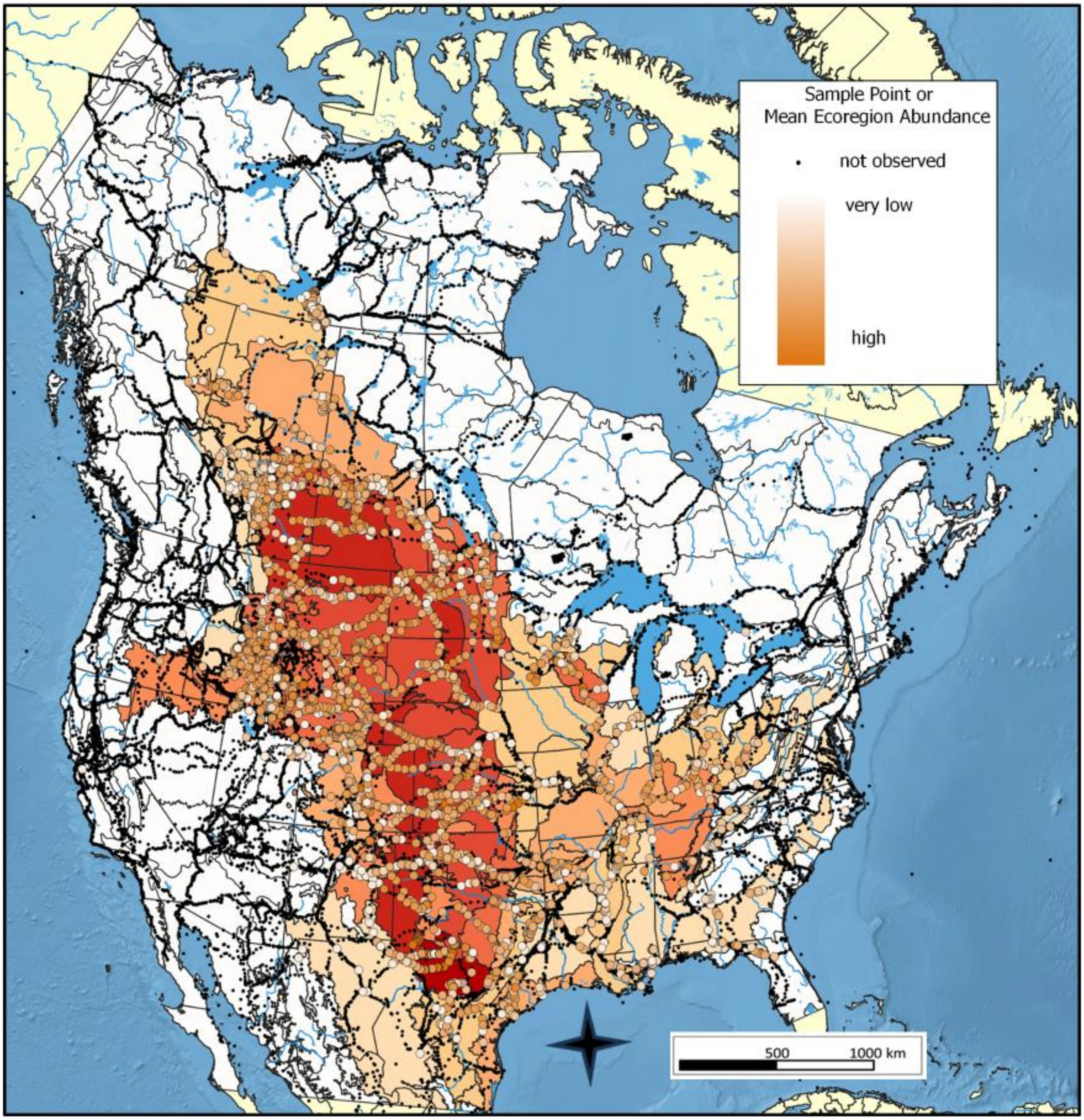
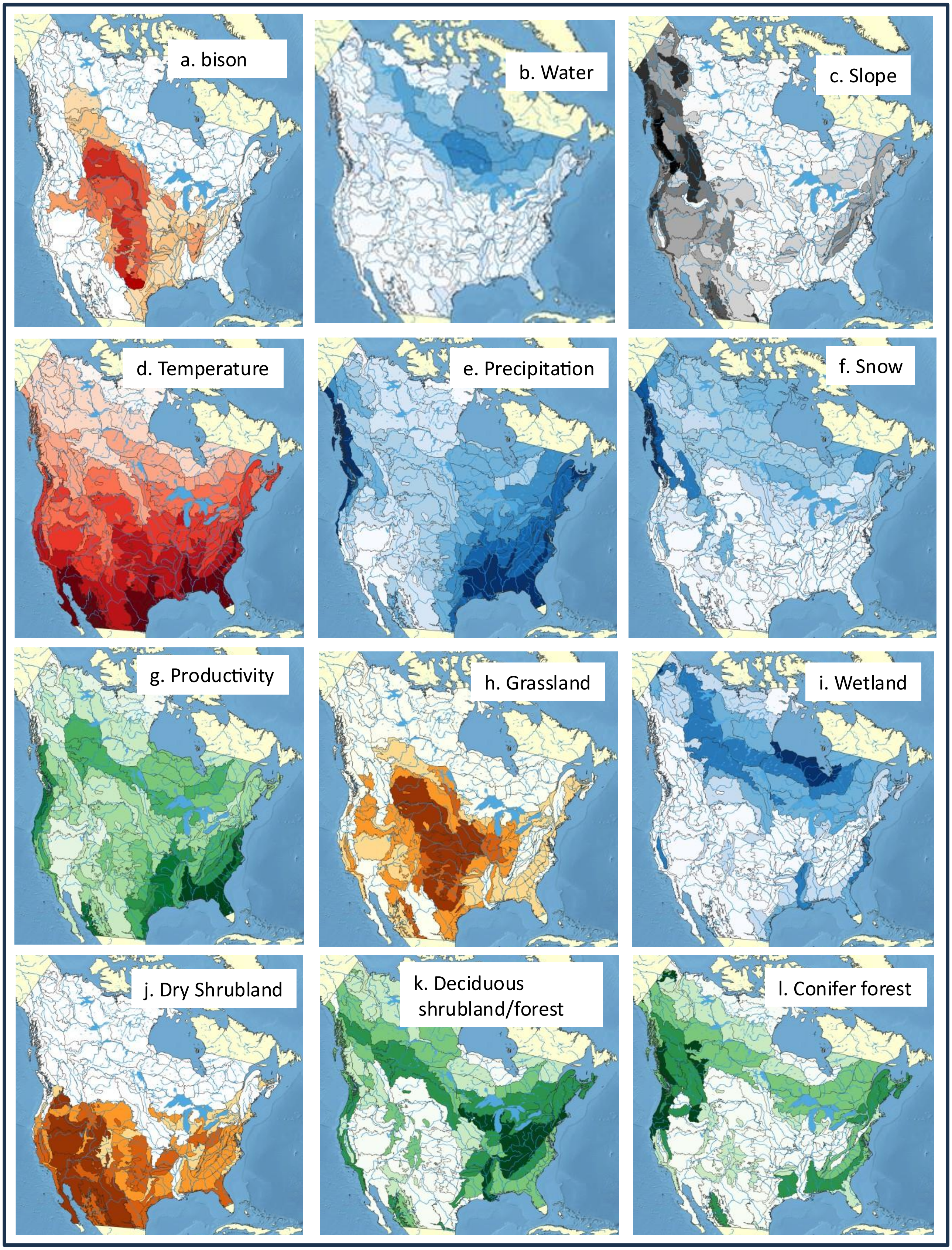



Fig 5.4.1.1: Bison point and mean ecoregion abundance from ~30,000 daily or multi-day historical journal observations (~1538 CE to ~1870 CE).


a. bison
b. Water
c. Slope
d. Temperature
e. Precipitation
f. Snow
g. Productivity
h. Grassland
i. Wetland
j. Dry Shrubland
k. Deciduous shrubland/forest
l. Conifer forest

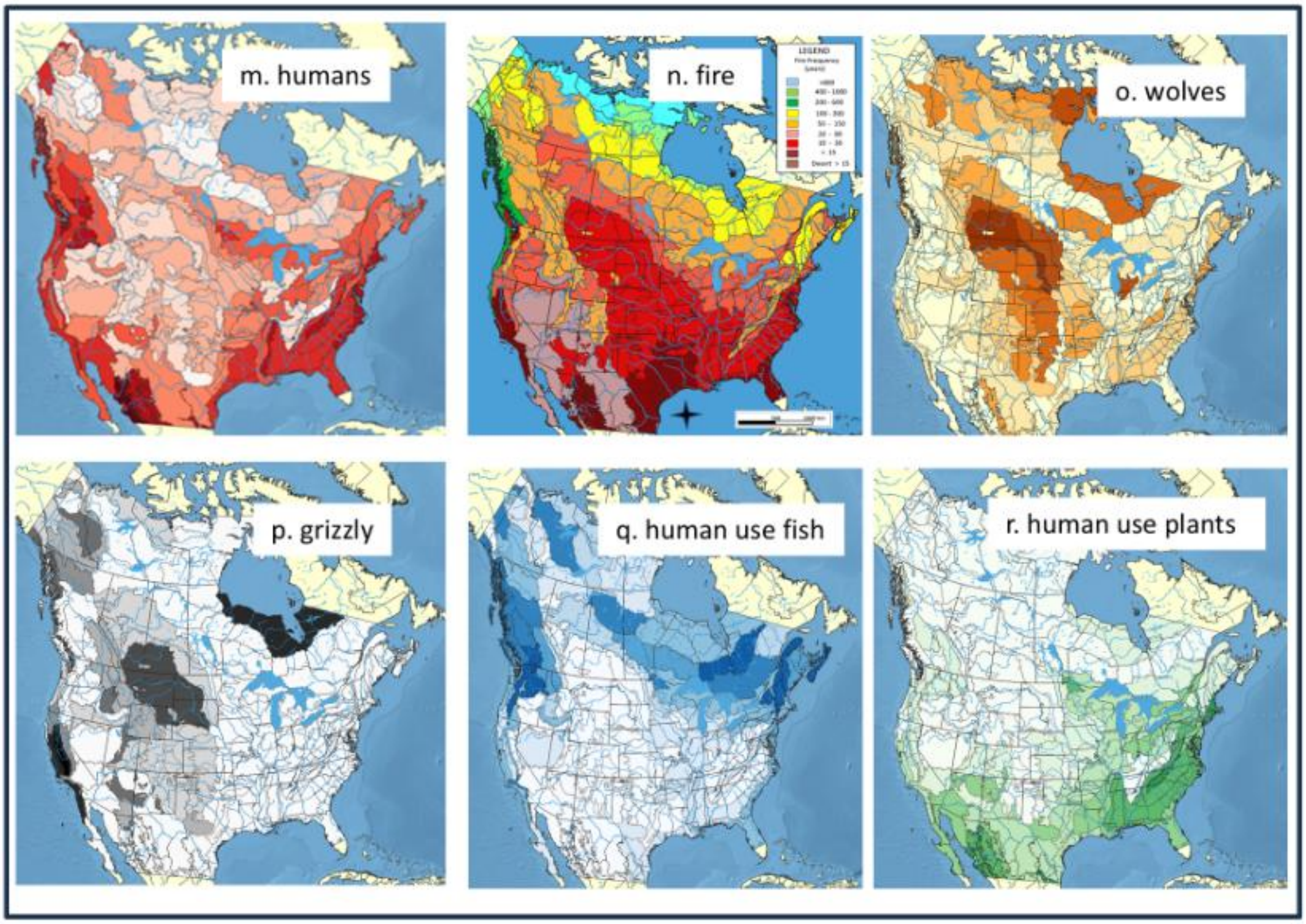



Figure 5.4.2.1. Ecoregion biophysical and cultural characteristics. Covariates in lower case from historical journals (this study). Covariates with capitals from other studies. See Table 4.1.1 for variable descriptions.

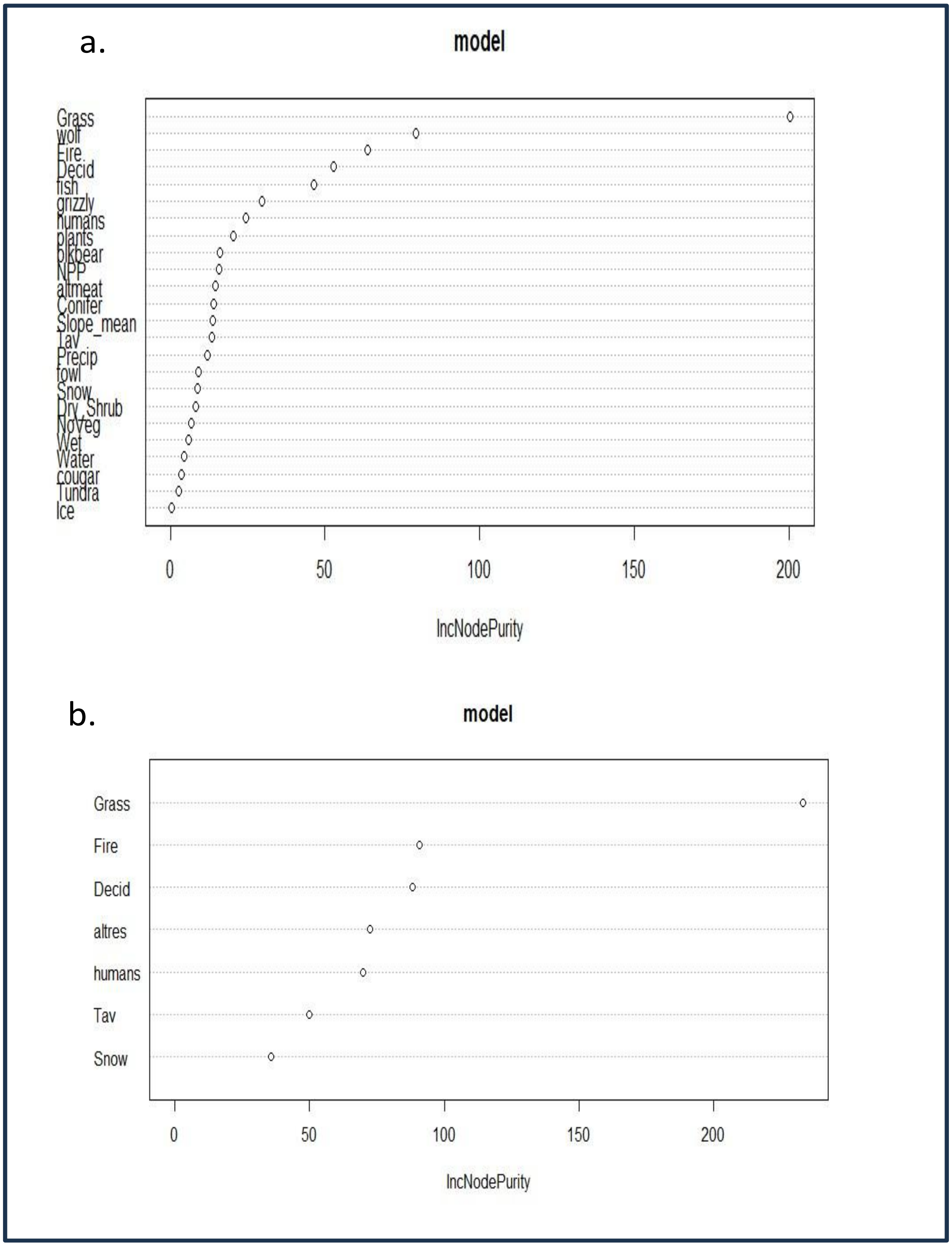



Figure 5.4.2.2. Random forest analysis of importance of covariates predicting the ecoregion mean bison abundance index for: a. all covariates and b. the seven best predictor covariates. See text for further explanation. Covariates in lower case from historical journals (this study). Covariates with capitals from other studies. See Table 4.1.1 for variable descriptions.

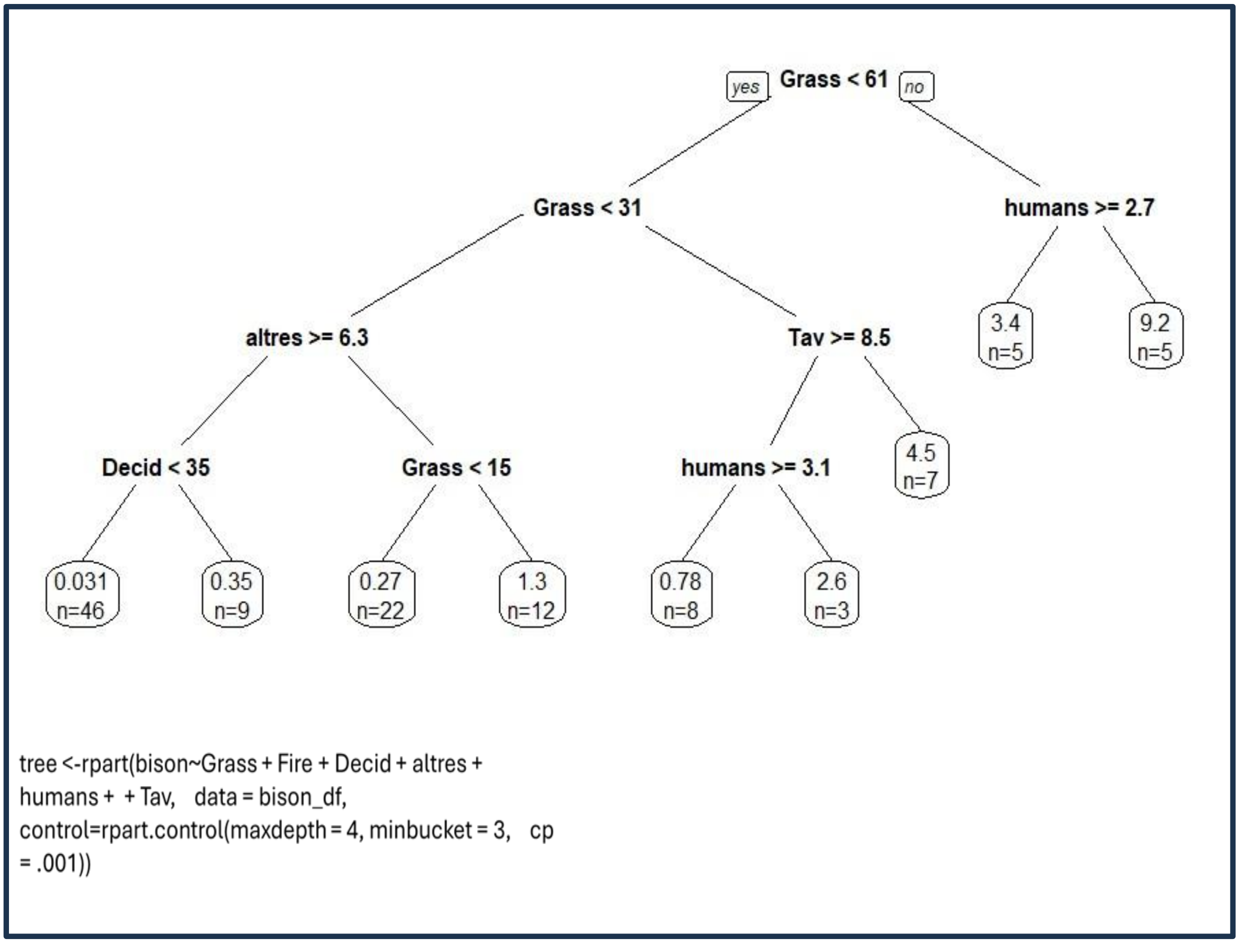



Figure 5.4.2.3. A random forest decision tree for the mean ecoregion bison abundance index showing a 9-groups run, the covariates making splits, the mean abundance for each group, the number of ecoregions in each group, and selected random forest algorithm parameters. In this random forest grouping result, a total of 46 North American ecoregions historically had no or very low bison numbers (group mean bison abundance index < 0.031), 39 ecoregions had low to moderate densities (abundance index of 0.27 to 0.78), and 32 ecoregions had moderate to high abundance (mean group abundance index 1.3 to 9.2).

Further evaluation on the importance of these variables is shown with Welch Two Sample t-tests. Grass cover significantly differentiates between human and bison abundance (Figure 5.4.2.5a). Bison are abundant in ecoregions with high cover of grass, humans are not (p<.005). Although both species abundances overlap in high fire frequency regions (Figure 5.4.2.5b), bison are more common in the most flammable areas of <20 years (p<.05). In contrast to grasslands, deciduous cover (Figure 5.4.2.5c) has similar abundances of both bison and humans (p= 0.169), but humans are more relatively more common here than in grasslands in comparison to bison. Ecoregions with higher abundance of alternate resources for humans (plants, fish, fowl, other meats) have high human abundance (Figure 5.4.2.5d), and bison numbers in these regions are significantly lower (p<.005).

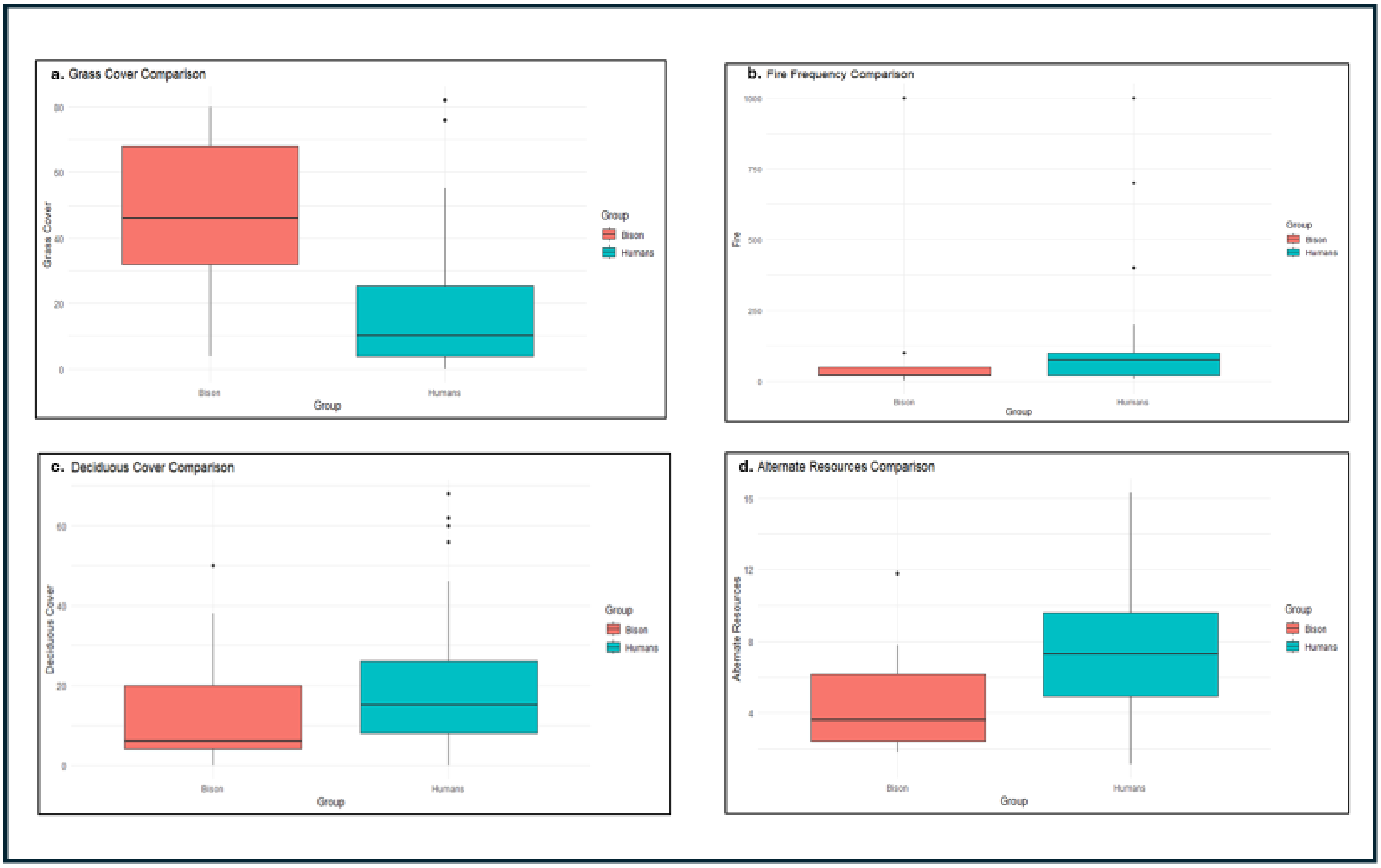



Figure 5.4.2.4. Bison and human abundance as a function of mean ecoregion grass cover (a), fire frequency, years (b), deciduous forest cover (c), and alternate resources (meat beside bison, fish, fowl, and plants) available to humans (d). Welch two group T-test for the alternative hypothesis indicates that the true difference in means between Bison and Humans groupings is not equal to 0 significant at $p < .05$ for grass cover, fire frequency and alternate resources.

## 5.4.3 Discussion: Factors Influencing Continental Bison Abundance

The abundance and distribution pattern of bison centered on the Great Plains has been relatively stable over the past 5k years [23]. Although their range and numbers did fluctuate [39], bison herds neither disappeared from the plains nor expanded across the continent. At European contact, bison occupied the center of the continent (Figures 1.1, 5.4.1.1) and may have numbered ~30 million [29]. Given potential rates of population growth exceeding 10% [5,22], and many ecoregions with at least some grassland habitats, why did the modern bison species not periodically spread to most the continental coasts in past times?

Ecoregion grass cover is the overwhelming best predictor of bison abundance. This is logical. All studies concur that bison's long-term niche is centered on the grasslands of the Great Plains [2,4,5,23]. Here, bison subsist on herbaceous forage, but humans have low numbers (Figures 5.4.2.2m, 5.3.2.5a) due to rigorous climatic conditions (especially in winter), lack of wood, and bison herd movement beyond the range of hunting groups [8,172,331]. Both humans and bison are most abundant in the frequently burned ecoregions of the continent (Figure 5.4.2.4b), but the shortest fire intervals (<30 years) in central and southern the Great Plains (Figure 5.2.1.1) remove woodlands important for human subsistence.

At the continental scale, a belt of ecoregions with moderate cover deciduous and shrublands rings the grasslands of the Great Plains (Figure 5.4.2.2k). These regions are used by both bison and humans (Figure 5.4.2.4c). Here bison were fewer than found on the prairies, but the grazers still found small grasslands or savannas, important during extreme winter or drought conditions [61,71,99,331], However, predation risk was high due to more humans utilizing not just bison, but alternate resources such as plants, fish, fowl, and other meats (Figure 5.4.2.4d). Moreover, the meadows provided driveways for human herding and hunting, and the trees themselves the fences for the killing-pounds [4,41]. The relative abundance of grassland versus forest and shrubland was determined by fire frequency and herbivory [71,94,332,333] (Figures 3.1.2, 5.2.1.1), and this in turn was determined by interactions between Indigenous ignitions and season of burn (Tables 5.2.1.1, 5.2.1.2). Too little fire, or too cool of burns expanded tree cover and favored humans over bison. Too frequent or hot fires favored broad grasslands-- good for bison, but suboptimal for humans in some seasons.

The analysis presented above is preliminary and limited by coarse-scale biophysical and cultural covariates estimated at an ecoregion level. Following up on previous work evaluating historical records for northwest region of bison range [22], Farr and White (in progress) are using similar methods and sequential equation models to evaluate biophysical and cultural factors influencing bison distribution and abundance across the whole of bison range [334].

## 5.5 Bison Continental Temporal Fluctuations

If humans had an important role in bison's abundance and distribution, Indigenous demographic declines after CE 1150 that are associated with climate change, European contact, and other factors [21,266,266,275,335] be should hypothetically have resulted in expansions in bison abundance and distribution.

### 5.5.1 Results: Bison and Human Population Changes over Time

Six groups of ecoregions (Figure 5.5.1.1) likely had major human population declines after CE 1150. Table 5.5.1.1 summarizes bison population estimates, with a regional description, periods of human depopulation, bison population estimates from archaeological, anthropological, traditional knowledge and historical sources. In most areas, human population decline adjacent to core bison habitat was associated with bison range expansions, with the major exceptions being the Colorado Plateau, and the interior cordillera Columbia and Fraser Plateaus.

### 5.5.2 Discussion: Human/Bison Population Variations after CE 1150

Human population declines occurred in many North American regions in the last 1000 years [11,336,337]. Indigenous die-offs could be partially tied to epidemics resulting from arrival of the Norse on the northwest Atlantic coast as early as CE 1021 [338], and by ships from other European countries reaching the Americas after Columbus in CE 1492 [339,340] . Early population declines (CE 1000-1500) in the mid-continent were prevalent in agricultural societies, possibly related to climatic events, wars that disrupted sustenance tasks and killed many people, and societal movements [266,341]. Figure 5.5.1.1 shows the general process that might result in bison range expansions associated with human depopulation. First, as described more fully in Section 3.1.1, bison's annual cycle of concentrating on the central plains for the spring and summer birthing and breeding season, followed by return to peripheral areas in fall and winter (Figure 5.5.1.1a) could lead to the periodic dispersal events [35]. Secondly, habitat connectivity to these peripheral areas would influence frequency, distance and magnitude of dispersal events [342,343]. Figure 5.5.1.1b is a simple model of connectivity based upon distance and corridor width based on western range edge movements [35]. Thirdly, an Indigenous population collapse should also favor bison range expansions. Figure 5.5.1.1c illustrates potential areas where human depopulation occurred after ~CE 1150 based upon archaeological and historical information [21,266,344,345]. Figure 5.5.1.1d shows areas where a combination of these factors could have led to bison range expansion, as described in Table 5.5.1.1 and discussed below.

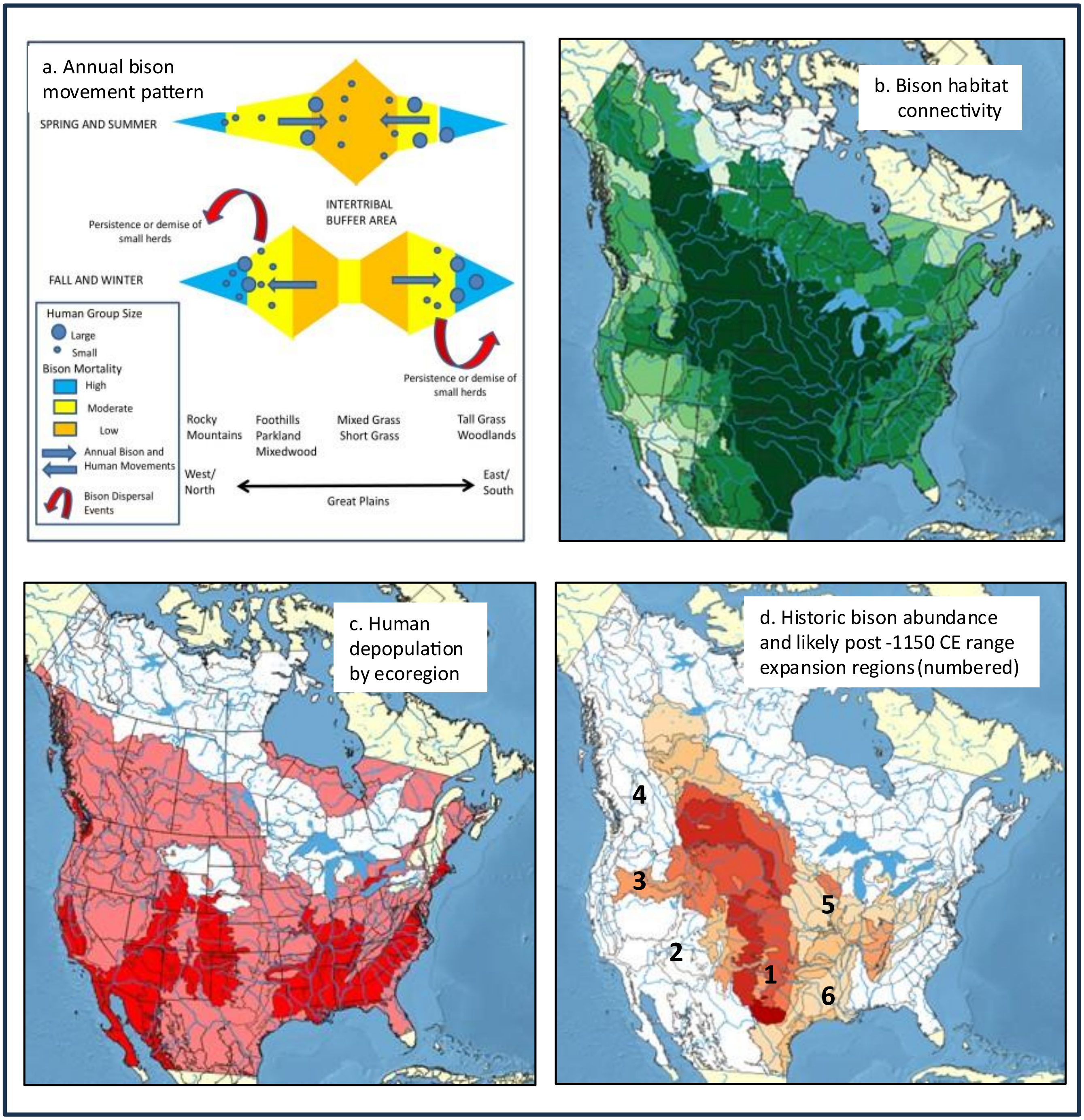



Figure 5.5.1.1: Potential factors influencing bison population changes over time: a. Annual central plains population movement patterns; b. Bison habitat connectivity to central plains; c. Regions with human depopulation post CE 1150; and d. regions adjacent to core bison population with potential for bison range expansion, described by number Table 5.4.1.1 and text.

Table 5.5.1.1. Temporal bison population change by region.

| Region | Human depopulation region and period (years CE) | Bison Population Estimate | | | Remarks [References] |
|---|---|---|---|---|---|
| | | Late prehistory | Early contact | Mid-contact | |
| 1.Southern plains of Colorado, Oklahoma, New Mexico and Texas | Colorado plains/foothills (CE ~1250 — ~1450) | No-very low | Low | Moderate-High | Climatic cooling, drought etc. reduces human numbers and agriculture in region [21,266,346,347], bison advance southward from Central Plains into Texas and to Gulf Mexico by 1540 [64,348,205,349] |
| 2.Colorado Plateau | Chaco Canyon, western Pueblos (CE ~1150 — ~1500) | No-very low | No-very low | No-very low | Population decline from multiple causes [266,337,350], bison advance westwards possibly impeded by hunting and trading by Rio Grande pueblos [349,351–353] |
| 3.Wyoming Basin and west slope of Middle Rocky Mountains | Shoshone territorial retreat to south and west (CE ~1740 — ~1790) | No-very low | Low | Moderate | Smallpox epidemics in ~1735 and ~1780 [344,345] , Shoshone population decline [51], low bison numbers 1300-1800, but then move westwards into inter-mountain valleys after ~1800 [38,354,355] |
| 4.Columbia and Fraser Interior Plateaus | Interior Indigenous peoples along/near salmon streams (CE ~1790 — ~1860) | No-very low | No- very low | No- Very low | Numerous epidemics during period [344,356] but bison advance northwest from south Idaho or westwards from plains possibly limited by terrain and snow [4,20,35] |
| 5.Upper and middle Mississippi/ southern Great Lakes | Cahokia decline and collapse (CE ~1150 — ~1300) | Very low | Moderate | Moderate | Human population decline from multiple causes [266,337,357,358], bison expansion from west first time in many centuries [250,61,359] |
| 6.Lower Mississippi-East Gulf Coast and Piedmont | Southeast decline after de Soto/de Luna expeditions (CE~1570 — ~1750) | No-very low | No-very low | Low-Moderate | Indigenous peoples decline from epidemics and other causes [360,361], bison not observed in region by early European expeditions, but occur by CE 1670 [18,66,337,362] |

Each of the six regions in appears to have relatively unique reasons for why bison range expansion either occurred or did not occur post-1250 CE.

### *1. Southern Plains*

For most the last 5 millennium bison were rare or did not occur on the southern plains [64]. Possibly bison's southern expansion was hindered by poor forage [348] or hunting by dense populations of humans [201,205]. At ~CE 1000, peoples associated with the Caddoans to the east were numerous along the Arkansas River [346], and there was small permanent farms of Indigenous hunter-gatherers/horticulturalists on the river's headwaters in the Apishapa region [347], and elsewhere on the central and southern plains [67]:289. The Platte, Arkansas and Canadian rivers would also be major activity corridors for both for bison [67]:222-225, and Native Americans travelling westwards from the Mississippi lowland settlements [363] and people coming over the Rockies from the west. For example, during historic times there are accounts of Native American camps numbering in the hundreds of tipis bordering these rivers [364–366]. After ~ CE 1250-1300, human activity in the region declines substantially [346,347], possibly due to a series of intense droughts across the southwest and central plains [21,266]. During the period bison distribution and abundance expand southwards [64,348]. Cooper's [67]:211 regional analysis by time period of archaeological sites with human-procured bison bone assemblages shows the pattern of range expansion (Figure 5.5.2.1).

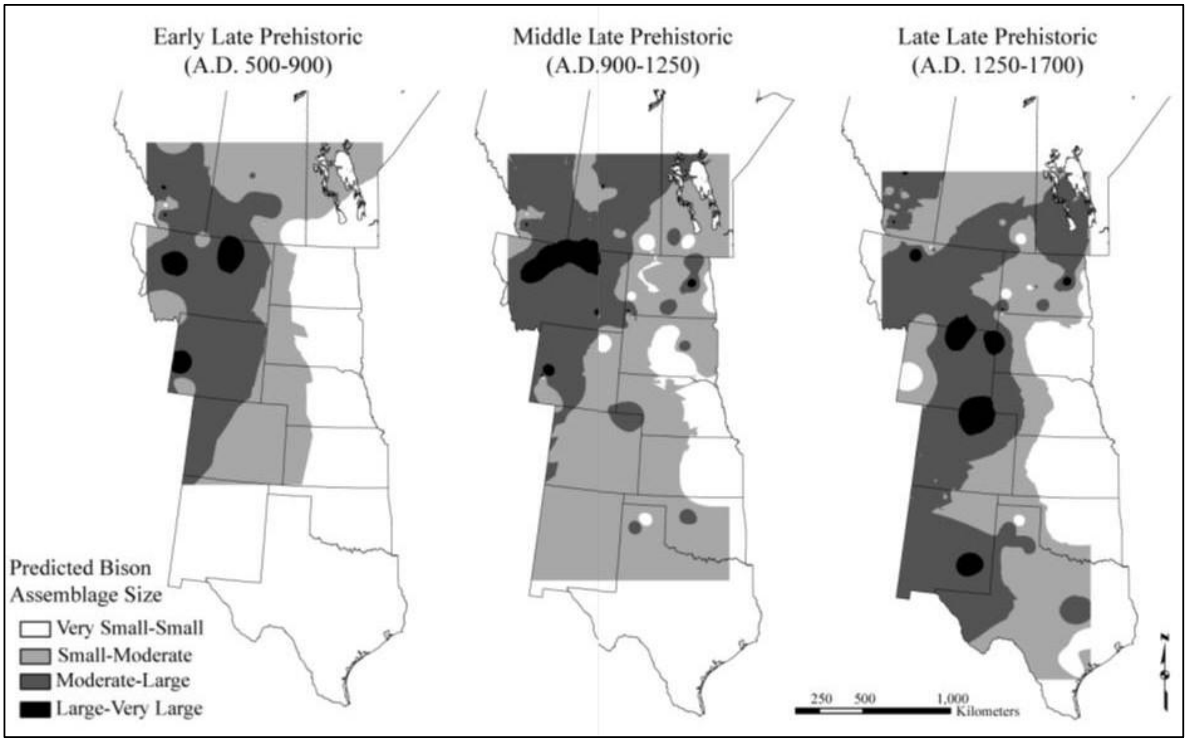



Figure 5.5.2.1. Patterns of bison population density on the Great Plains and adjacent areas as inferred from predicted bone assemblage for archaeological sites for 3 time periods from A.D. 500 to A.D. 1700 (from Cooper [67]:211).

Determination of causal factors for variable bison abundance and range shifts on the southern plains after CE 1200 remains inconclusive. Generally, researchers do not refer to the extreme periods of drought or cultural change, and assume a "carrying capacity model" where that forage and hence bison abundance increased due to generally cooler and moister conditions [64,26,349]. Cooper [67]:304 favors this forage model but recognizes that social conditions pre-CE 900 and post CE 1500 could have influenced Indigenous people's bison procurement. Assuming that climate change was a primary driver, Lohse et al. [348] describe that central Texas proxy climate records are often contradictory and difficult or impossible to reconcile. They conclude that bison were consistently associated with cool climates, although each of these events differs in terms of effective moisture and degree of coldness. An alternate explanation is that humans, largely dependent on aquatic and plant resources, could, in the period of favorable climate prior to ~CE 1000 increased to high densities (e.g., >10 persons/100 $km^2$ ) across much of Texas [118,367] and may have also had localized high densities in agricultural areas such as the headwater's of the Arkansas River in southern Colorado [346,347] . Humans at these densities would depress preferred prey such as bison, and possibly other ungulates to low numbers [205]. If human predation was important, the general collapse of human cultures and trade networks ~CE 1200-1400 across North America's south central and western areas [21,266,357,368] could have reduced human densities from the Arkansas River southwards, and thus allowed bison numbers to increase and allow large herds to eventually expand southwards across the plains and into central and southern Texas.

Whatever the cause, the spread of bison into the southern plains greatly changed human lifeways. Mixed agricultural-foraging economies shifted towards hunting as Lipan Apache followed the bison southwards and some existing peoples adapted their lifestyles to procure this increasingly abundant new resource [21,369].

### *2. Colorado Plateau*

North America's most carefully researched Indigenous depopulations is the ancient Puebloans on the southern Colorado Plateau [21]. Numerous, well-preserved archaeological sites with cross-referenced dating of annual rings for trees used for dwelling construction facilitate opportunities fine-scale spatial and temporal analysis [370]. From CE 1250 to 1500 a widely distributed and dense network of hundreds of farming villages and pueblos across the region dramatically declined less than<50 pueblos [368,371], and Coronado's entrada recorded that almost all of these lay along or near the Rio Grande River [207]. At least two mega-droughts causing maize-crop failures likely triggered the demographic decline [266,372] followed by collapse of trade-networks, warfare and human movement to new settlements [201,350].

As described in Section 6.1.2 below, archaeological and historical records show that bison were rare on the Colorado Plateau, but they occurred nearby in the southern Rocky Mountains to the northeast [52,373], and after CE 1200 on the Southern Plains to the to the east (Figure 5.4.1.1). Why did the human population decline not result in an expansion of these nearby bison into the region? Only moderate areas of grassland habitat (Figure 5.3.2.2h) may be a partial reason, but by the mid-1700s the Navajo were herding thousands of sheep on the plateau, wild cattle became common in southern regions near the Mexico border by the 1800s, and today there are thousands of cattle in east Texas and New Mexico. A more plausible explanation is that long-distance trade routes for exchanging bison products (hides and meat) obtained from east had developed prior to CE 1200, and even with population decline and resettlement, the pueblos along the Rio Grande continued to maintain this trade network [201,349,374,375], and intense hunting on the plains and in the mountains thus blocked bison colonization further to the west (see Section 6.1.2).

### *3. Wyoming Basin, South Pass and western slopes region*

Over the past 10k years, bison evolution and abundance west of the Rocky Mountains was likely influenced by connectivity to the larger herds on Great Plains [35,376]. The main ecological corridor was likely Wyoming Basin, across South Pass, then into the Great Basin and upper Snake and Columbia River basins. Table 5.4.2.1 synthesizes bison abundance over time from archaeological sites in various regions along the corridor. No obvious spatial or temporal pattern exists in this data, possibly due to low resolution and different methodologies. However, as Lyman [376] describes, the simultaneous diminution of bison in the northwest with those on the plains is potentially evidence of connectivity. In the last ~500 years two of most significant cultural events on the northwestern plains were the expansion northwestwards of Numic-speaking ancestors out of the Great Basin, then through the Rocky Mountains, and shortly thereafter, their adoption of the horse for transportation [51]. These people eventually became the Paiute, Shoshone, Ute and Comanche. By CE 1700 advance groups had likely reached the bison-rich Great Plains, and in the northeast the Shoshone were pushing the Absaroka and Kiowa eastwards down the Yellowstone River and groups of the Blackfoot confederacy northwards across the Missouri into the Saskatchewan watershed [6]. The Numic expansion's impact on bison in and west of the Rocky Mountains is uncertain, but Table 5.5.2.1 indicates that possibly bison abundance declined in the archaeological record after 500 years BP. Similarly, the historic record shows few bison west of the continental divide on the headwaters of the Snake River prior to CE 1810 (Table 5.5.1.1, more details in Section 6.2.3 below). Moreover, there is a strong and ancient traditional knowledge information of Shoshone and other Indigenous peoples needing to travel east across the Rocky Mountains to the Great Plains to obtain bison [50,51].

The first smallpox epidemic reached the eastern plains peoples CE ~1737, likely transmitted through Indigenous and European trade routes from the western Great Lakes [345]. It is possible the Shoshone and other peoples on the western plains were not effected, but the next smallpox epidemic in 1780-82 devastated Indigenous cultures across the west [6,51,344,345]. The Shoshone retreated southwestwards to a core homeland on the headwaters of the Wind and Snake rivers [51]. The earliest European expeditions near and west of the continental divide prior to 1810 report few bison, however by the 1820s and 30s bison were moderately abundant within and west of the Rocky Mountains on the large, middle elevation grasslands on the upper reaches of the Yellowstone, Missouri, Snake, and Bear rivers, and bison observations occur as far west as eastern Oregon (Figure 5.4.1.1).

### *4. Columbia and Fraser Interior Plateaus*

Indigenous populations along the northwest coast and into the Western Cordillera were relatively dense due to rich fisheries and vegetation resources [11,377,378]. Human numbers began to decline possibly as early as the 1740s, but certainly with the massive mortality of the 1780s smallpox epidemic [344,356]. Depopulation continued across the region through the early to mid-1800s due to introduced diseases (smallpox, malaria, measles etc.), and the increased displacement, competition, and disruption of trade routes by fur traders, settlers and miners, and other societal impacts associated with global contact [344,356,379] . The interior plateaus along the Columbia and Fraser rivers, and other dry regions within the northwestern Cordillera contain expansive grasslands (Figure 5.4.2.2h). During the Holocene, bison did not utilize these areas apart from the extreme southern region of the Columbia Plateau (south Washington/Oregon and southwestern Idaho) where infrequent archaeological (Table 5.5.2.1) and historical (Figure 5.4.1.1) observations occur. As noted above, these bison were probably linked to plains herds by an ecological corridor running northwest from Wyoming. In contrast, in the northern Rockies, although bison remained abundant on the eastern foothills through the 1700s and 1800s, their range did not expand into the Cordillera here despite falling regional human numbers.

Table 5.5.2.1. Relative *Bison* genus species' abundance since 10K BP approximated by 500-year periods for the middle Rocky Mountains and areas further west into eastern Washington and Oregon from select studies ( [376,380–388], compiled in White [35]). Relative abundance is rated as very low (VL), Moderate (M), High (H), and Very High (VH) within studies.

| | Bison Abundance by Time Period (k years BP) | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Location and Reference** | 10 | | 9 | | 8 | | 7 | | 6 | | 5 | | 4 | | 3 | | 2 | | 1 | | 0 |
| Wyoming Basin (Lubinski 2000) | H | H | H | H | H | VL | VL | VL | VL | VL | L | L | M | H | H | L | L | H | H | H | VL |
| Great Basin (Janetski 1997) | | | | | | | | | | | | | | | | | | H | M | | |
| NE Great Basin (Lupo and Schmidt 1997) | | | | | | | | | | | | | | | | | VL | L | H | H | M |
| Northern Utah (Lupo 1996) | | | | | | | | | | | | | | | | | | | | M | L |
| Salt Lake (Lupo and Schmidt 1997) | | | | | | | | | | | | | | | | | VL | L | M | H | L |
| E Great Basin (Grayson 2000, 2006) | | | | | | | | | | | | | | | | L | L | L | M | M | |
| W Great Basin (Grayson 2000, 2006) | | | | | | | | | | | | | | | | VL | VL | VL | L | L | |
| Snake R. Plain (Plew and Sundell 2000) | VL | VL | VL | L | L | L | L | M | M | M | M | L | L | L | L | H | H | H | H | H | |
| Oregon Basin and Range (Stutte 2004) | VL | VL | VL | M | M | M | M | VL | VL | VL | VL | VL | VL | VL | VL | L | L | L | L | H | H |
| Oregon Blue Mtns (Stutte 2004) | VL | VL | VL | VL | VL | VL | VL | VL | VL | VL | VL | VL | VL | VL | VL | VL | VL | VL | VL | L | L |
| Oregon Columbia Plateau (Stutte 2004) | VL | VL | VL | VL | VL | VL | VL | VL | VL | VL | VL | VL | VL | VL | M | M | M | M | M | VL | VL |
| Columbia Plateau (Chatters et al 1995) | L | L | L | L | L | L | L | VL | VL | VL | VL | VL | M | M | M | H | H | H | H | H | VL |
| Columbia Platea (Schroedl 1973) | | | | | | | | | | | | | | | | | H | H | M | M | M |
| Eastern Washington (Lyman 2004) | M | M | M | M | M | VL | VL | VL | L | L | L | L | L | L | L | M | M | M | M | L | VL |

The failure of bison to expand its range westwards can be attributed to several factors, well-recognized in the historical and ecological literature, where even declining numbers of Indigenous hunters could be important:

- Bison entering Cordilleran valleys were often in narrow terrain traps where even a few human hunters could easily locate and kill them [233,389,390].
- Trading and travel networks developed between Cordilleran peoples from the west dependent on salmon fisheries and plant resources, and bison-dependent peoples on the foothills and plains to the east [197,391], or in many areas, west slope peoples even expanded their territories onto plains and seasonally hunted here [54,392–395] . Although the frequency of Indigenous travel decreased on these networks after ~CE 1700, encounters with humans in the mountain passes could still result in high mortality.
- Cordilleran steep terrain, dense forest cover, and deep snow (Figure 5.4.2.2c,f,l) are all biophysical factors that limit historical bison abundance [22,71], and mountain valley corridors that narrow to under 1 km in width appear to be particularly restrain westward movements [35], and again, even a few Indigenous hunters could have been important here in killing dispersing bison.

### *5. Upper/middle Mississippi and southern Great Lakes*

Bison on the northeast Great Plains had good landscape connectivity to the east and may have advanced eastwards due to human depopulation (Table 5.5.1.1, Figure 5.5.1.1d). Archaeological bison evidence is infrequent during the mid-late Holocene in the southern Great Lakes region [250]. Morrissey [61]:52-58 describes a potential pattern and processes of human and bison population changes in the tallgrass prairie/forest ecotone on the northeast edge of the plains during the pre-contact to contact period. Under this scenario, the Neo-Atlantic Episode or Medieval Warm Period (CE 850-1250) was favorable for both abundant humans raising maize agriculture along the Mississippi River and tributaries, and to the west, growth of bison populations on the Great Plains. Possibly small herds of bison periodically spread eastward, but large herds avoided the eastern prairies. This pattern changed dramatically with the beginning of the Little Ice Age. Climatic cooling and extreme droughts led to the agricultural declines, and the collapse of the metropolis of Cahokia, and many other cultural regions[21,266,357]. Morrissey further discusses that drought had three possible effects on bison: 1) on the Great Plains reduced forage production forced large herds eastwards to more mesic tallgrass prairies and oak savanna, 2) reduced precipitation possibly reduced productivity but increased palatability of tallgrass communities, and 3) fire frequency possibly increased in the region further creating high quality bison habitat. Under this hypothesis these biophysical processes led to expansion of bison eastwards towards the Great Lakes, Ohio River, and further south onto the plains of modern-day Kentucky where they were moderately abundant in the 1700s [61]:52-58.

Alternate theories stress cultural causes where that the widespread agricultural declines tied to drought led to generally less people along the eastern edge of the prairies, thus less hunting of bison and less trade of its meat and hides, and with less mortality, bison numbers grew and expanded eastwards [66]. Moreover, intensive warfare between remaining communities, and particularly due to the westward advance of the Iroquois and epidemic diseases [396,397], led to lightly used buffer zones between peoples where bison could thrive, and possibly more widespread fire due to warfare and abandonment of agriculture. Likely both biophysical and cultural causes contributed to increases in northeastern bison numbers, with the species occurring as far east as eastern Pennsylvania in the early 1700s [2,398].

### *6. Lower Mississippi and Southeast Piedmont*

The movement of bison into the southeast (Figure 5.5.1.1d, Table 5.5.1.1) has the best historical documentation of the CE ~1200-1800 range expansions [2,66] and is more completely described in Section 6.4.3 below. For most the Holocene, there is archaeological evidence of bison on the south east edge of the prairies, with infrequent occurrences further eastwards into the northern Ozarks Highlands [362]. The pre-CE 1600 accounts of de Vaca [204,205], de Soto [208,209], de Luna [399] and others have no observations of bison along the Mississippi Valley, or further east towards the Atlantic Coast. Instead, these travellers encountered abundant Indigenous peoples fed by maize, fruit orchards, fish, some deer, and other resources (Figure 5.3.2.2). By CE 1700 human numbers had declined dramatically across the region (Figure 5.4.1.1c). Researchers attribute this to epidemics, warfare, decline of agriculture, slave-taking, and other societal upheavals related to European contact [360,66,400,361]. The first recorded sightings/sign of bison in the southern Mississippi valley in the North American Historical Journal Observations Database are those of Joliette and Marquette in 1673 [401], and thereafter observations occur periodically across the south until CE 1741 [109].

There is an interdisciplinary consensus that that human depopulation was the primary factor in bison's southeast range expansion [66,362,39]. The southeast had strong terrain and habitat connectivity to bison herds to the west (Figure 5.5.1.1b), and the remaining population centers on the Mississippi may have been broadly spaced due to warfare creating broad intertribal zones.

Bison expansion eastward may have initially been favored by expansive grasslands created by previous Indigenous use of fire the abandonment of croplands.

*The Corn, Canoes and Captives Hypothesis for Pre-CE 1200 Bison Distribution and Abundance*

In the millennium prior to ~CE 1200 southern bison distribution appears to have been constrained between two broad Indigenous empires and their associated trade networks: on the southeast was the were Middle Mississippi cultures with Cahokia and other trade centers. On the southwest was Chaco Canyon, the Hohokam, and immediately to the south the populous Mesoamerican cultures [402]. Could the demand for bison products from these cultures have created the frontier for the buffalo? Certainly, like for many other of the world's past empires, there would be a strong demand for leather products and dried meat. For example, in her classic study of Meccan culture, Crone [403,404] explains the importance of their leather trade to the Roman army. In North American, the economic issues were the weight of the product, the distance of trade routes, and no large domestic beasts of burden (e.g. camels, horses) to move the freight. Three solutions for this are evident for the prehistoric and historic bison trade:

- Corn- Abundant, concentrated and storable human energy would be necessary efficiently access and move the mass of many hides or abundant dried meat. Cultures near the SW edge of bison range began raising corn ~BCE 2000 and by CE 1000 it was supporting increasing number of people on the on the middle and upper Mississippi [402,405].
- Watercraft- Early journalists comment on the well-developed Indigenous technology for hide boats, birch bark canoes, and dugouts [201]. A combination of these craft could move bison products down the Platte, Arkansas, Canadian and Red River of the South into the Mississippi River. Depending on the sources and cost of labor, large dugouts (>15m long) used on the Mississippi [406] could even move heavy products upstream on the Mississippi into the southern Great Lakes and other areas in need leather.
- Captives and other cheap labor- Processing and moving hides, leather and other animal products is labor intensive [407]. In *Pemmican Empire*, Colpitts [408] provides estimates for the number hunters, hide and meat processors (mostly women), and "coeur de bois" (boatmen) with their energetic requirements in corn and pemmican rations, and other factors such as watercraft construction that made the beaver trade viable across thousands of kilometers of the Canadian waterway trade network. Similarly, researchers have provide estimates for the number of people and provisioning requirements for Chaco Canyon's annual operations [409] . Fleets of porters and dogs would have been important across the dry southwest in the pre-horse period [410].

Considering this evidence, a case can be made that complex Indigenous cultures could have certainly reduced bison abundance and distribution across the south prior to a series of societal collapses after ~CE 1200 [201].

### *Synthesis of Post-CE 1200 Bison Range Changes*

The continental spatial analysis reveals that although bison were abundant in the grasslands on the center of the continent, the increasing abundance of humans in peripheral woodland areas likely limited bison abundance and distribution. If it was the case that for several thousand years bison distribution and abundance was heavily influenced by Indigenous harvest and trade, a reasonable prediction is that the massive human depopulation across many regions post-CE 1000 [336] should resulted in bison range expansion. For most regions, the results described above concur with Shaw's [39] conclusion that "drastic reductions in indigenous human populations allowed bison populations to expand." Moreover, given the magnitude of the human die-off, the resulting historical bison distribution as mapped by Allen [2] in Figure 1.1 and herein (Figure 5.5.1.1) had reached a continental extent that had likely not occurred since the human adoption of agriculture several millennia ago, if even then. Indeed, for the America's Koch et al. [336] conclude that:

> *The Great Dying of the Indigenous Peoples of the Americas led to the abandonment of enough cleared land in the Americas that the resulting terrestrial carbon uptake had a detectable impact on both atmospheric $CO_2$ and global surface air temperatures in the two centuries prior to the Industrial Revolution.*

Total or partial human abandonment of this much land likely opened vast areas of bison habitat not available for many previous centuries due to human occupation and hunting patterns. Bison expanded onto the Southern Plains to the Gulf of Mexico, across the central Rocky Mountains to the western headwaters of the Snake River, the northeast across the Mississippi beyond the Great Lakes into the Appalachians, and across the southeast nearly to the Atlantic Ocean (Table 5.4.1.1).

However, bison population expansion was not ubiquitous around the edge of the range. Although buffalo herds did expand southward into Texas, their expansion westwards through the Southern Rocky Mountains onto the Colorado Plateau and further west remained blocked by abundant people, agriculture, and potentially meat and hide trade routes of the Pueblos along the Rio Grande River into the southwest [201,349]. On the northwest the rugged terrain, forests, narrow valleys, and abundant people supported by salmon fisheries blocked bison expansion through the northern Rocky Mountains [35].

## 5.6 Summary Continental-Scale Analyses

The analysis of historic bison distribution and abundance at a continental scale (Section 5.4 above) describes the characteristics of North American ecoregions [80,81] that best predict high bison densities. These include "bottom-up" biophysical influences such as grass and deciduous shrub/tree cover [71], "top-down" influences as quantified by human and other predator abundance [251], and availability of alternate food resources for these predators [124,142] ). The random forest regression tree (Figure 5.3.2.4) shows the differentiation of 20 ecoregions had favorable conditions for moderate to high historic bison densities. The analysis also differentiates another 46 ecoregions with low grass and deciduous cover that predicts very low or no bison density. However, the analysis provides little information on the unique characteristics of 51 ecoregions with low to moderate ecoregions that might have a mutualistic human-bison relationship. Further, the random forest analysis has no spatial context-- all regions are pooled in the analysis-- whereas ecoregions with high bison density are generally grouped together (e.g. source population areas) and sink regions with no to low bison that are distant from the sources. They may have favorable habitat for bison but are not populated due to distance from source areas and intervening characteristics. Ecoregions with a potential human-bison mutualistic relationship should, according to the predictions in Section 3.4 lie adjacent to population regions.

Figure 5.6.1. Paul Kane, “The Buffalo Pound”, c. 1846-49 (Art Gallery of Ontario, Toronto). Kane’s image from the Aspen Parkland Ecoregion (9.2.1, Table 5.1.1.1) captures the important relationship between grass and forest cover as determinants of human and bison abundance at a continental and more local scales. Humans depended on woodlands for heat and shelter and used forests as cover for hunting bison and wood structures for pounding bison. Humans created the mix of woodlands and grass through fire use. Bison depended on woodlands for shelter during extreme periods of winter weather. Kane’s image likely overestimates conifer cover. The parkland ecoregion was dominated by interspersed grasslands and aspen groves adapted to frequent fires Indigenously ignited when vegetation was cured in the early spring or late fall. Further, bison pounding here was most frequent in winter, not summer as shown here.

# 6. REGIONAL PATTERNS: RESULTS AND DISCUSSION

*"Happy families are all alike; every unhappy family is unhappy in its own way."*
Tolstoy, Anna Karenina [411]

## 6.1 Background and Regional Evaluation Subjects of Interest

The continental analysis of ecoregions provides support for three main processes influencing bison numbers: bottom-up grassland productivity favoring high bison numbers (20 ecoregions), top-down human predation resulting in no or very low bison numbers (46 ecoregions), and another group of areas with low to moderate bison numbers that could have bison-human mutualism relationships (51 ecoregions). In this section, I utilize graphical profiles of ecoregion resource abundance and vegetation cover along transects (Figure 6.1.1) from abundant source bison populations to adjacent sink regions with no or low bison numbers. I provide further information on cultural or biophysical evidence that may explain the transition from source to sink population areas. I will focus especially on cultural studies of region and resource use could result in bison numbers reaching to the millions can rapidly relatively short distances become extremely low, or non-existent, or situations that would influence range expansion or contractions. The North American Historical Journal Wildlife Observation database currently contains >29,000 entries. I recommend that readers download both the Google Earth map and the Excel database for reference. Red and orange bubbles are signs or sightings of the buffalo. Table 5.1.1 indicates total number of observations bison abundance by ecoregion. Section 5 above describes factors influencing continental bison distribution and abundance and post- ~1000 CE range expansions. Here I provide further information on subareas of the continent.

Three broad fields of interest are be evaluated with the ecoregion resource abundance transects:

### 6.1.1 Source-sink-mutualism zones

The primary interest here is akin to Tolstoy's analogy for families. Applied to bison, abundant source populations on the Great Plains were "happy" and robust, driven by an alike set of important variables – high grass cover, level terrain, low snow cover, low human abundance. But the transition from source to a fragile "unhappy' sink population could be unique in each region—say one or more of a combination of factors such as increasing human density, an abundant alternate resource for these people, unfavorable terrain such as steep slopes, narrow valleys or low deep snow. The causal factors in this transition might be difficult to detect when all ecoregions are statistically pooled at a continental scale, but apparent when individual regions are evaluated.

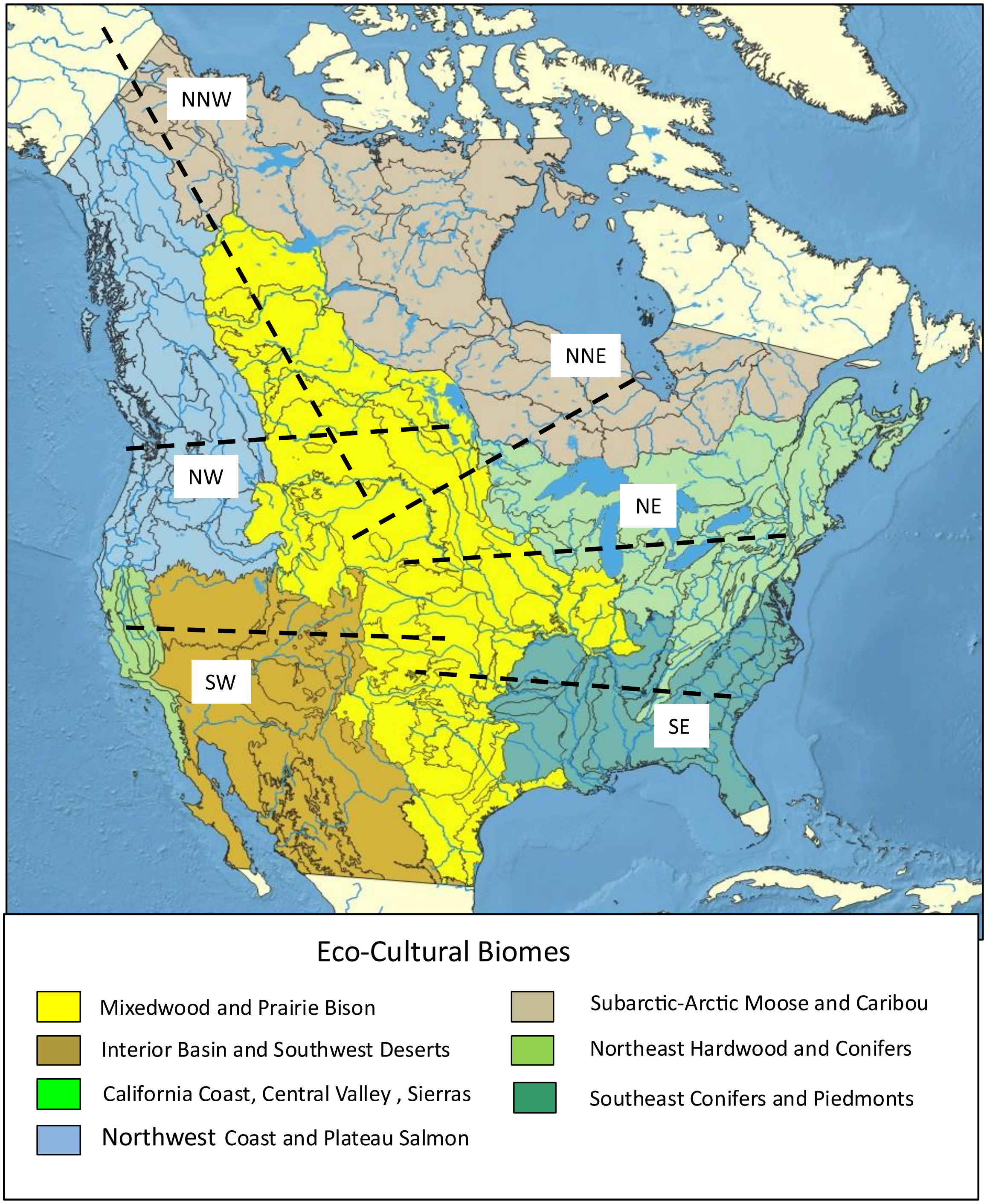



Figure 6.1.1. Resource availability transects from biomes with abundant bison to adjacent biomes with few or no bison.

### 6.1.2 Potential mutualistic interactions

A second focus for transect analysis were the potential processes in their region that could yield human-bison ecological mutualisms. These were evaluated at three levels of integration (see Section 2.4 above):

- Individual/local population scale herding or domestication of bison by humans, or conservation of beaver.
- Community scale interactions by humans and bison including top-down (predation, herbivory) and bottom-up (productivity) interactions that may support assemblage of species and communities co-existing in ecoregions (Table 5.1.1).
- Biome or large population scale regulation and stability. This could be provided by two key regulatory mechanisms with feedback: 1) variable human predation on bison, and 2) variable levels of human habitat management dependent on fire use and control of bison herbivory impacts.

### 6.1.3 Modern analogs- current range management and stocking levels

A third, and most important source of evidence is to compare the historic situation described above to current range and wildlife management practices for ecoregions. Grassland and range ecologists have refined guidelines for managing the density and distribution of herbivores and disturbance processes with the objectives of maintaining native species and plant communities [73,74,87,88,175,240,412] —essentially prescriptions for maintaining a modern human-herbivore mutualism. Given the similarity between cattle and bison, this provides further revelation on current versus historic ecological and cultural conditions. For comparison, a metric I frequently refer to here is an animal unit (AUs) where 1 AU is a 1000 lb domestic cow with calf, .6 is elk, and .4 is sheep. Estimated range capacity or production is often standardized here as AUM/km$^2$ for a specified period where an AUM is the forage necessary to support an animal unit month (~350 kg of dry biomass). The actual or estimated use of ranges is given by specific species or AU number/km$^2$ for specified period (annually if not given). Further site specific information on long-term herbivory is also available from historic photographs showing abundance of palatable shrubs and forest cover [413–417].

# 6.2 The West

## 6.2.1 West Overview

Figure 6.2.1 shows western ecoregions [418] overlaid by the southwest and northwest transect locations. The ecoregions can be grouped into four broad eco-cultural biomes (Figure 6.2.1.1): 1) the ecologically rich California along the southern Pacific coast, 2) the dry deserts and shrublands of the Southwest Plateau and Great Basin, 3) the wet and mountainous Coast and Plateau Salmon, and 4) the Prairie Bison that extends from the Gulf of Mexico, northwards across the Great Plains, and into the aspen parkland along the Saskatchewan River [11,12].

Numerous Indigenous groups have occupied the western North America (Figure 6.2.1.2) for at least the last 15K years. Figure 6.2.1.3 illustrates examples of seasonal rounds for the Umatilla [419], Piikani [101,420], Pueblo [374,375,421], and Comanche [47,366,422]. These people were well-adapted to local ecosystem conditions with high human densities along the coasts and rivers with abundant fish, or near streams with irrigation potential for agriculture (Figure 6.2.4). In addition to crop irrigation (e.g. corn, beans, melons), studies routinely describe people enhancing their resource base through use of fire for grassland and shrubland maintenance, transplanting and managing fisheries, marine aquaculture through construction of shell beds and many other activities. During the historic period considered here (~CE1530 CE to ~CE 1900 in the north), high densities of bison occupied the western plains, but numbers declined sharply in the Rocky Mountains except for a major intrusion of bison through South Pass and other corridors of the middle Rockies into the upper Snake River basin (Figure 6.2.4a). Otherwise, the mountains sharply reduced bison numbers likely due to people using the rugged terrain for communal hunts [233,389], and less expansive grasslands for forage and predator avoidance [22,23,71].

Long-term pre-contact knowledge of many western ecoregions is often exceptional due to due to high density sites, dry areas with good archeological preservation and detailed zoo-archaeological analyses [370]. In the last millennia, two major bison dispersals appear to have occurred in the west: 1) at about ~1200 CE bison expanded southwards from the Arkansas River area across the southern plains into Texas [64,65,67], and by the CE 1670 to the Gulf of Mexico [204], and 2) at about ~1810 CE bison numbers appear to have increased substantially in the intermountain valleys on the west side of the continental divide from Salt Lake north through modern Idaho to the Missouri River headwaters in Montana [354]. These, and previous dispersals in the west likely long counterbalanced by human hunting. As William Hornaday [3] wrote in 1889:

> *It is probable that had the bison remained unmolested by man and uninfluenced by him he would have crossed the Sierra Nevada and the Coast Range and taken his abode in the fertile valleys of the Pacific Slope.*

The potential combinations of biophysical and cultural conditions driving this dynamic distribution and abundance of bison are described below.


Figure 6.2.1.1: Western  ecoregions [80,81]  overlaid by center lines for southwest and northwest transect locations.

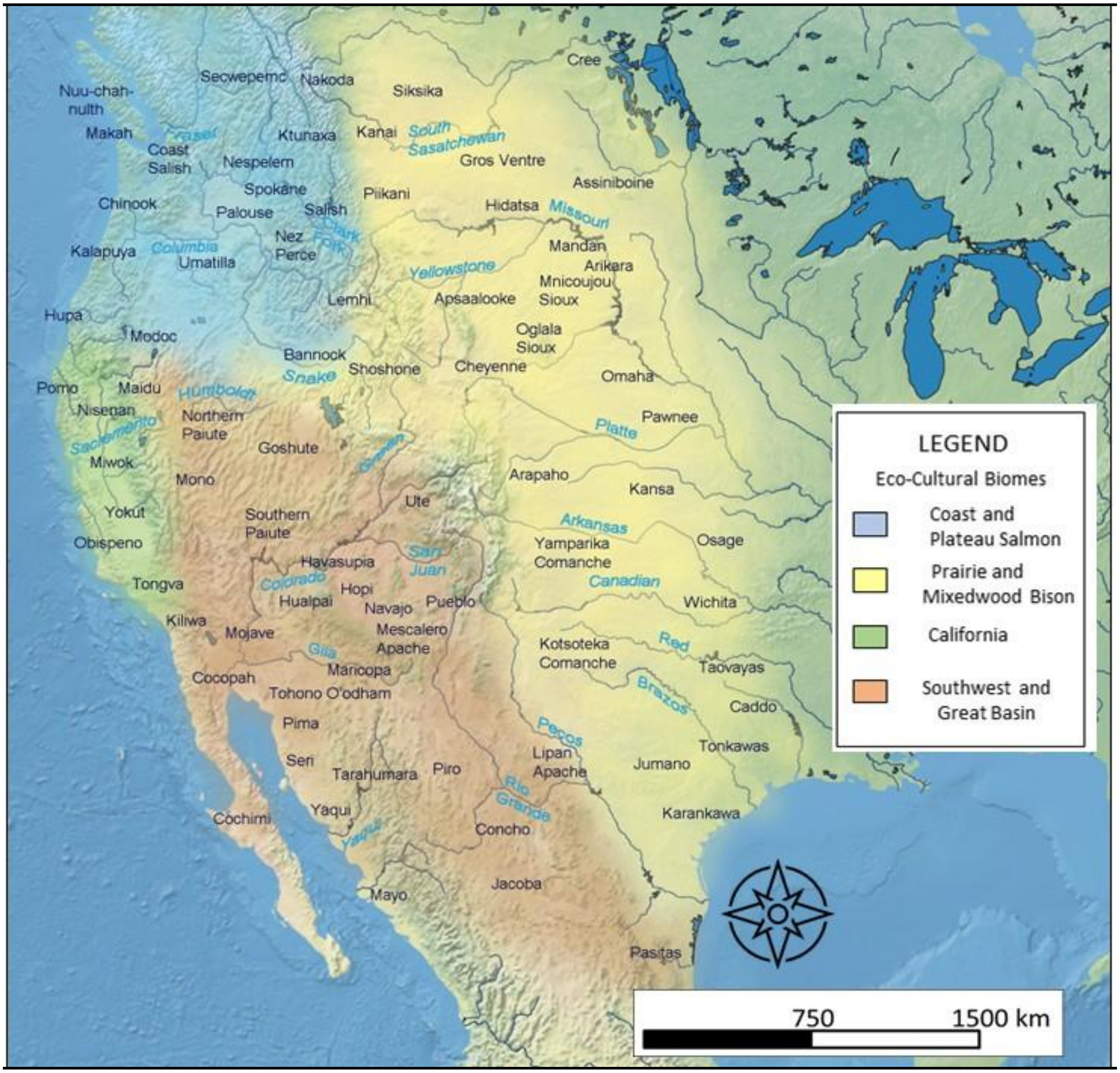



Figure 6.2.1.2: Main eco-cultural biomes for the western area and the general location of homelands for select Indigenous groups for the historic and/or current period.

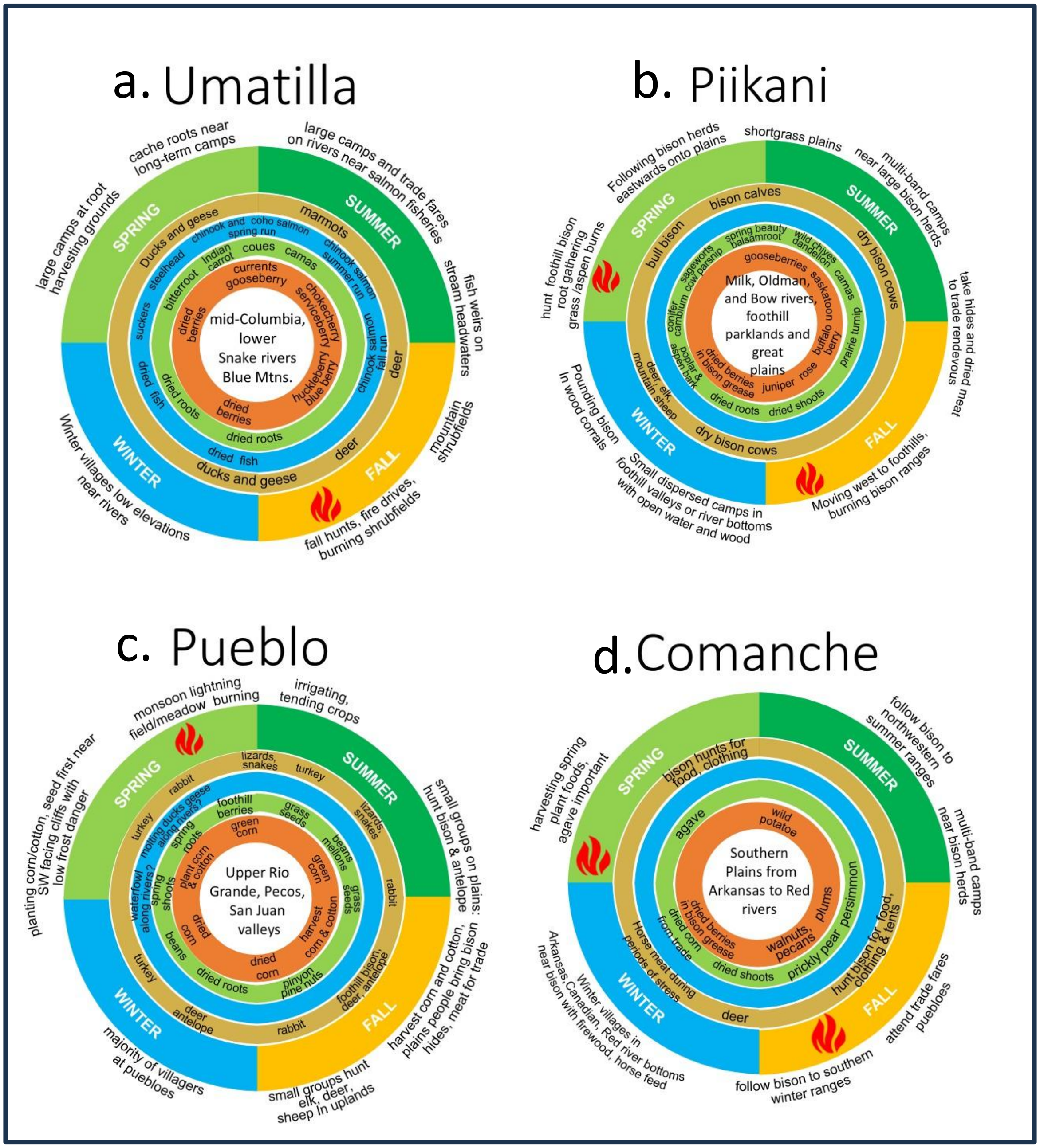



Figure 6.2.1.3: Seasonal rounds of resources used for 4 Indigenous groups or regions: a. Sahaptin on the mid-Columbia and lower Snake River [423], b. Piikani in the Rocky Mountain foothills and northwestern Great Plains [48,53,420,424], c. Pueblo on the Rio Grande and Colorado Plateau [421,425,426] , and d. Comanche on the southern Great Plains [47,366,422,427].

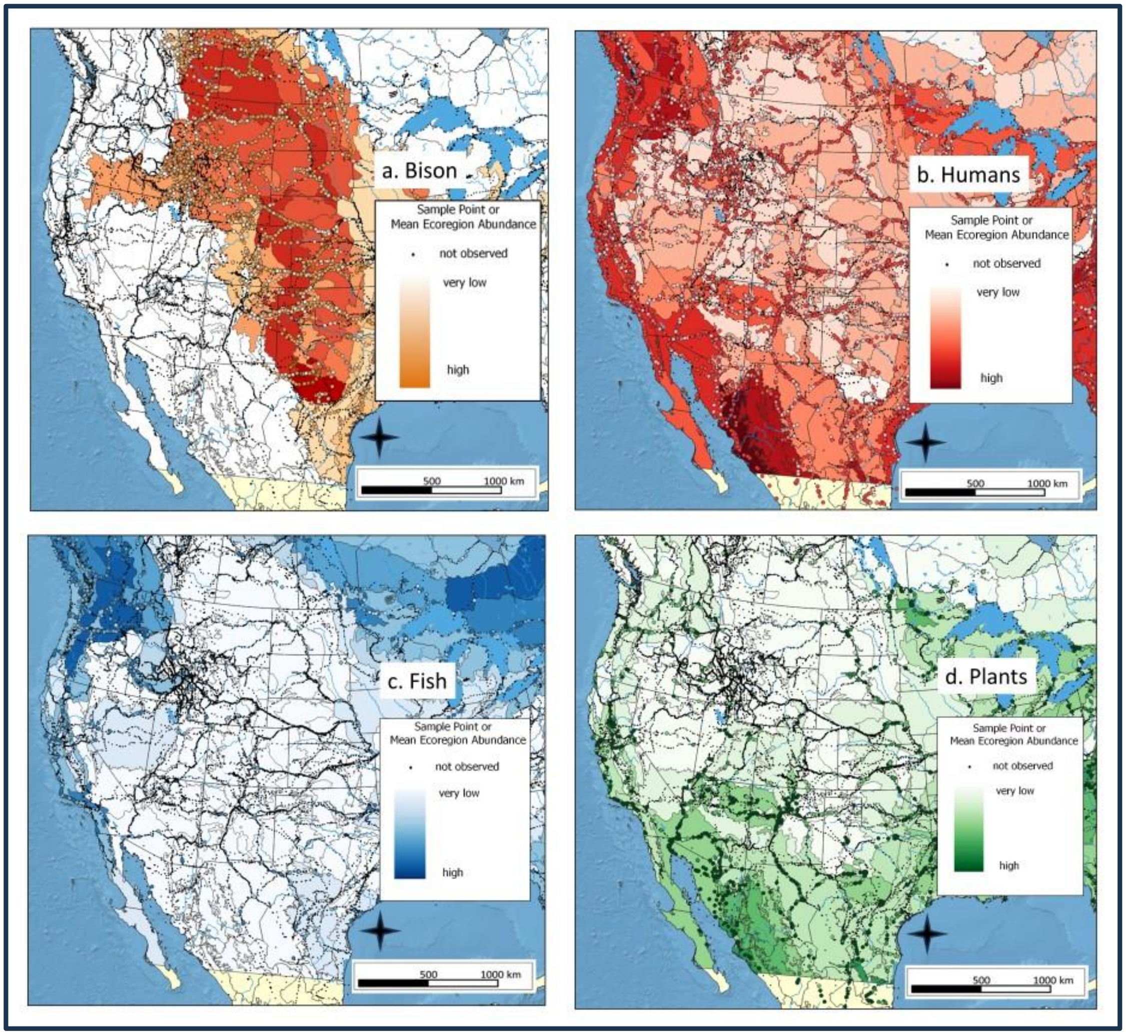



Figure 6.2.1.4. Average daily abundance indices for a. bison, b. humans, c. fish, and d. plants observed in historic journals for the western area of bison range.

## 6.2.2 Southwest (SW) Transect

The SW transect (Figure 6.2.1.1) runs westward from the source bison population on the grasslands of southern Great Plains near the Texas panhandle across the southern Rocky Mountains, then into the dry ecoregions of the southern deserts, Colorado Plateau and Interior Basin, and finally over the Sierra Nevada into California. Average ecoregion species abundance indices are mapped (Figure 6.2.1.4) and graphed (Figure 6.2.2.1). As early as CE 1540s, European travellers were well-aware of the socio-economic system delineating SW bison distribution and abundance. Castaneda, chronicler of the Coronado expedition explained that from the pueblos, hunters went eastward each spring to “follow the cows, hunting them and tanning their skins to take to the settlements in the winter to sell, since they go there to pass the winter”[207]. Apparently numerous people supported by agriculture along the Rio Grande, Pecos, and other rivers made bison colonization here unlikely, but to the east where human numbers were lower, and plant abundance was lower, bison were common [351,428].

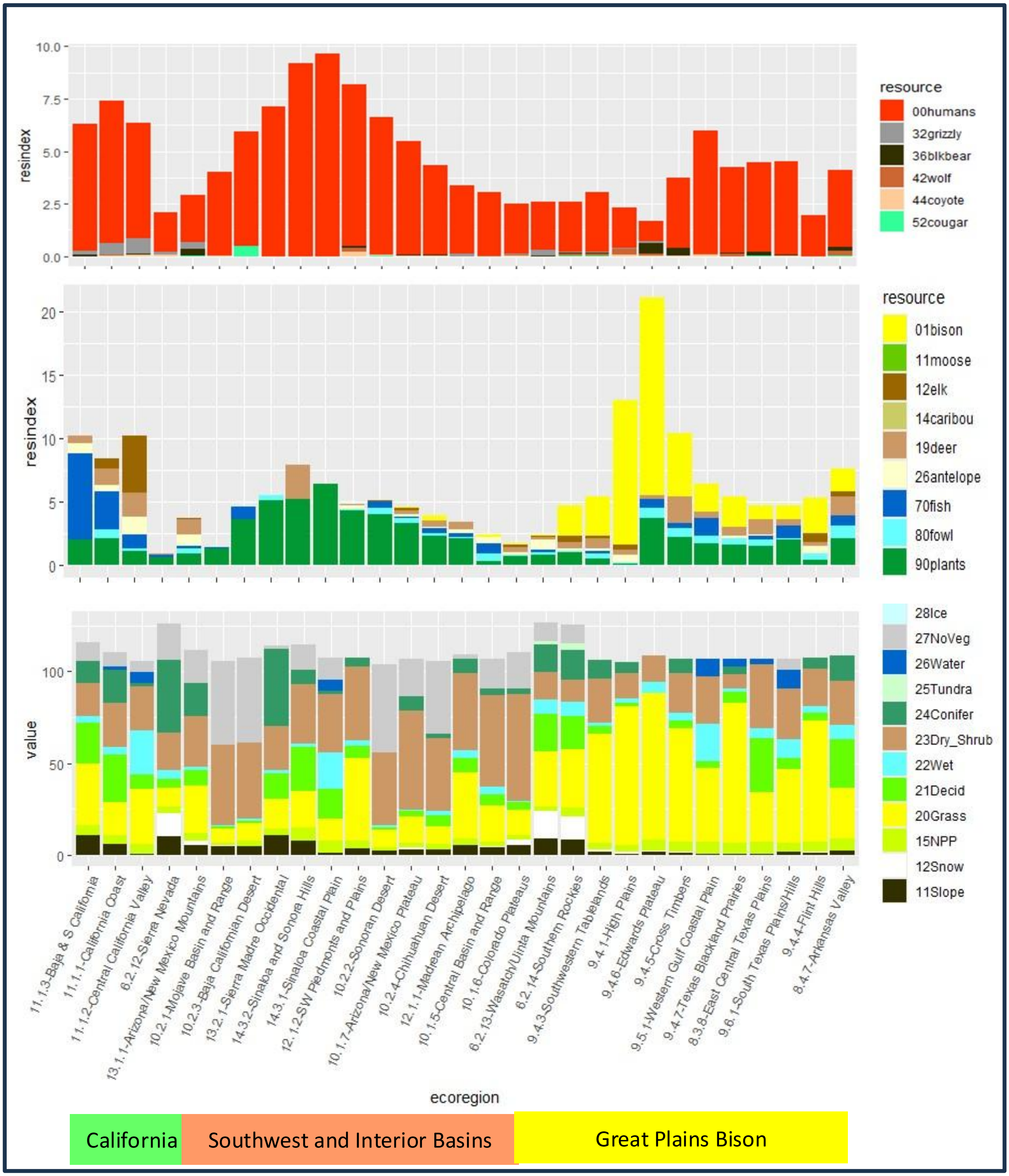



Figure 6.2.2.1. Southwest transect average ecoregion biophysical values and resource abundance indices. See Table 4.1 for variable descriptions.

### *SW high abundance region*

Historically, bison were numerous on the Southern Plains [234,366]. Three ecoregions have highest abundance indices in the journal database [109], from east to west: 9.4.5 Cross Timbers, 9.4.6 Edwards Plateau, and 9.4.1. High Plains. These were unique in the southwest with relatively high grass cover and low human presence (Figure 6.2.2.1). The numbers of bison on the southern plains in the prehistorical period has been highly variable. Dillehay [64] evaluated faunal lists from 160 archaeological and paleontological sites in the Southern Plains and described long-term periods of presence and absence of the genus Bison in the region. Two absence periods are from about ~BCE 6000-5000 to ~BCE 2500 and ~CE 500 to ~CE 1200-1300. He observed that these long-term changes seem to indicate a combination of fluctuating bison population densities and range shifts. Lohse et al. [65] used a XAD-purified AMS radiocarbon method to date 62 bison specimens from different contexts on the very southern extent of the Great Plains in the central Texas area, including the uplifted Edwards Plateau and extending to the Coastal Plain. Bison were present during the periods ~BCE 4455 to ~BCE 4315, ~BCE 1795 to ~BCE 1630, ~BCE 1200 to ~BCE 650, and the final period beginning in the Late Prehistoric period starting ~CE 1300. The last period of abundance extends to later historical accounts of bison moving southwards in Texas. De Vaca [429] describes that in 1528 bison were within a few days travel of the Gulf of Mexico coast and that other wildlife was rare near the ocean [205]. In 1685 La Salle’s colony near Victoria, Texas hunted bison herds right on the coast [430]. Shaw and Lee [431] provide more detailed analysis of the relative abundance of bison, elk and pronghorn in these ecoregions during the late historic period CE 1806-1857.

Determination of causal factors for long-term variable bison abundance and range shifts on the southern plains remains elusive [234]. A period of high bison density and diminution 6-8K years BCE may be related the development of $C_4$ grasses, and intense competition for forage [79,432]. Assuming that climate change was a primary driver, Lohse et al. [65] describe that central Texas proxy climate records are often contradictory and difficult or impossible to reconcile. They conclude that bison were consistently associated with cool climates, although each of these events differs in terms of effective moisture and degree of coldness. A contributing factor may be that humans, largely dependent on aquatic and plant resources, could over time have increased to high densities (e.g., >10 persons/100 $km^2$ ) across much of Texas [367,433] and may have had localized high densities in agricultural areas such as the headwater’s of the Arkansas River in southern Colorado [346,347]. Humans at these densities would depress preferred prey such as bison, and possibly other ungulates to low numbers [116,205]. If human predation was important, the general collapse of human cultures and trade networks ~CE 1200 to ~CE 1400 across North America’s south central and western areas [266,357,368] could have reduced human densities from the Arkansas River southwards, and thus allowed bison numbers to increase and allow large herds to eventually expand southwards across the plains and into central and southern Texas [201]. Moreover, at the time of historical contact, there was possibly a buffer zone between the long-term Toyah (Jumano) peoples both farming and hunting on southern edge of bison range [349,434] and mobile Athabaskan peoples specialized in bison hunting migrating from the north [255,435]. If so, this buffer zone could have been an area abundant bison [137,139].

### *SW migration and dispersal patterns*

Beyond the major north to south dispersal prior to CE 1500, knowledge of southern bison movement patterns is limited. Hart [436] describes a relatively random pattern based upon forage conditions. Speth and Rautman [437] review early Spanish journals and zooarchaeological data, and suggest that bison may have not occurred along the Pecos River between the months of July to December, but may have been present during other times of the year. This suggests that one scenario is that bison in some years would in the early winter move south on the relatively snow-free Edwards Plateau, or even further south. Based upon extensive travels in Texas and northeast Mexico from 1826 to 1834, French naturalist Jean Louis Berlandier [438]:355 reports:

> *Towards the end of autumn, and at the beginning of winter, principally in November and December, the bison advance as far as the environs of Bexar. Before such a large number of them had been killed, they used to cross the banks of the Rio Grande, and the chronicles of bygone days days tell us that they visited Nuevo Leon at that period.*

If so, in spring and summer some of these bison would return north and westward to moister, and higher quality forage to north on the divide between the Arkansas and Canadian rivers, and west in the foothills of the southern Rocky Mountains, passing through the Pecos River valley. A pulse of bison could then enter into the valleys of the Southern Rockies as they followed snowmelt and the phenology of forage green-up with high forage productivity with increasing elevation [439,440]. As Allen [2] described, in late spring and early summer, the southern Plains herds frequently came together and "in great measure, abandoned the plains of Texas in summer for those further north, revisiting them again in winter".

### *SW low to moderate abundance region*

Moving west from the central plains is a narrow zone with only two ecoregions with low to moderate historic bison abundance: 9.4.3 Southwestern Tablelands and 6.2.14 Southern Rockies. Bison's steep decline in numbers here can be attributed to rugged terrain and deep snows at high elevations, and intrusions of high densities of agricultural peoples at lower elevations such as the Puebloans in ecoregion 10.1.7 Arizona/New Mexico Plateau that extends up the Rio Grande. After bison's colonization of this zone after ~CE 1300, a series of Indigenous peoples heavily hunted them here and on the adjacent plains —first the Jumanos and Toyobe, then the Apache, and finally the Ute and the Comanche [26,255,349,366]. Bison meat and hides were important for both survival on the plains, but also for trade to the Puebloans and other agricultural peoples for corn and captives at trading fairs held at Abiquiu, Taos, Pecos, Santa Fe and other villages [366,441]. The earliest Spanish expeditions from the south-- first de Niza in 1539 then Coronado in 1540 [207,442]--came north along an important Indigenous trading route running from Mexico to the Zuni. They routinely describe the high quality of the bison hides encountered. Coronado's did not find riches in gold, but he eventually sent his army eastwards to find the fabled bison on the plains.

An interesting hypothesis for persistence of moderate bison numbers in the Southern Rockies is that Indigenous peoples had long herded them here for hunting and trade [201]. Cooper's [67] analysis of archaeological evidence shows a relatively consistently high bison presence on the plains of western and northern Colorado on the headwaters of the Platte River (Figure 5.4.1.2), and

McKetta [190] found that this prehistoric bison abundance extends southwards just west of the mountains. Perhaps, Indigenous peoples— the Fremont [443] and then the Ute and Arapaho [444,52], used communal herding techniques to move bison in the narrow terrain to valleys and passes leading to large "parks" or grasslands running south towards the Rio Grande valley: first North Park on the North Platte headwaters, then Middle Park on the headwaters of Colorado River, and South Park on the headwaters of the Arkansas and South Platte, and finally the San Luis valley at the head of the Rio Grande. Once behind the front range of the Southern Rockies, these bison could be killed in terrain traps [373,389,445], or driven further south and west. Both Farnham in 1839 [446] and Fremont in 1844 [447] describe Indigenous-driven bison movements and hunting in this corridor. From its southern end in the San Luis valley, bison meat and hides could then be transported to trade fairs in the Pueblo villages further south [441,442].

*SW edge range and beyond*

As described Section 5.5, bison were likely rare on the southern plains prior to CE 1350 and would likely not have approached the southwest area from the east. However, bison numbers increased rapidly after this time, and the species was relatively abundant across much of Texas and eastern New Mexico by the time of first European observations by de Vaca and Coronado [109] in the 1530s and 40s. Interestingly, for the next 300 years bison did not expand their range westward into the southwest region (Figure 6.2.1.4a). The furthest southwest bison were generally observed was the lower Rio Grande. Further north the edge of the range appears to be the Pecos River, and these animals were heavily hunted by both plains people near this river, and hunters travelling west from the Pueblos on the upper Rio Grande [375]. To the northwest in the Colorado River basin, the furthest bison ranged during the historic period were in the Uintah Basin and near Great Salt Lake [109]. Further west in the Central Valley of California, wildlife numbers (particularly elk and grizzly bears) sharply increased in the early 1800s after human depopulation (Figure 6.2.2.1). However, this region was too distant from nearest bison then found near Salt Lake (Figure 6.2.1.4a) for colonization to occur.

How far did bison range to the west during the pre-CE 1500 period prior to European contact? The early historic conditions moving west, first the rugged Rocky Mountains, then across the dry southwest with low grassland cover, few sources of water, and high densities of people dependent on plants or fish (Figure 6.2.1.4, Figure 6.2.1.5) suggest that bison's range edge was not different, especially given bison were rare on the plains to the east prior to ~CE 1400 (see above). Detailed zoo-archaeological data from hundreds of pre-contact sites across the southwest [370] find exceedingly little evidence of *Bison bison* south and west of the Rio Grande, on the Colorado Plateau and west to the California coast [16,19]. One unique area is the Plains of San Augustin, New Mexico where bison periodically occurred during the late Holocene [448]. Here, like the Rocky Mountain interior parks described above, Indigenous people could have herded bison from the east then, using the surrounding mountainous terrain contained or even ranched them here for sustained periods—or as Frison [233] describes "storage on the hoof". However, researchers generally conclude that high densities of people in the SW sharply depressed populations of most large mammals due to intense hunting for meat and hides. In addition to the very low abundance of bison remains, archaeologists describe the rarity of elk, deer and other mid-size mammals in most southwest areas, and particularly near areas with dense human populations [449–453]. The relative abundance of artiodactyls in faunal bone assemblages is typically described by the "artiodactyl index", or the ratio of artiodactyls to artiodactyls plus lagomorphs [449]. Southwest areas with high prehistoric human densities have low values of the index (.4-.7), whereas more remote areas, and particularly those next to mountains or forested habitats have higher indices (.5-.6) generally indicating that a higher abundance of deer, sheep and other larger species were hunted, and less use of small mammals [452].

### *SW Mutualistic interactions*

The general pattern of historic SW human-bison interaction was that human hunting kept moderate to high densities of bison well out on the plains. In the far SW, this was usually east of the Pecos River. This patten of human use and bison abundance preserved high quality forage further west for periodic use during extreme winters or drought on the prairies and maintained grass and literature forage for frequent burning that reduced forest or shrub cover.

*Domestication*- As described above "wild bison" may have not found there way into the far southwest, but could meso-American agricultural peoples have experimented with bison domestication, and brought seed stock of immature animals south from herds to the north? Habitat for cattle, and hence bison occurs across the southwest and into Mexico. Moreover, hide trade network described above shows that Mesoamerican peoples were clearly aware of bison and its value. Hernán Cortés and his conquistadors found a found a garden full of exotic animals and plants when they entered the Aztec capital of Tenochtitlan in 1519, and although bison are not detected in this species melange [454,455], these cultures clearly had the ability to capture and move many species long distances. Given that bison were likely near the lower Rio Grande at this time, young animals could have been brought down the east coast by boat to stock "Montezuma's Zoo" or easily herded to pastures across the Rio Grande. Like today's ranches, maintaining domestic bison is as much a question of governance, ownership, selective breeding and fencing as habitat quality. Again, Berlandier [438];357 describes for bison:

> *There has been success in taming a large number, which have easily become attached to man when they have been captured within a few days after being calved. The friars of Saint Francis have reported that in Zacatecas, in the seventeenth century, two bison were harnessed to a two-wheeled cart and were suited to all work which could be expected of them.*

Periodically these bison would escape captivity. Thus assertions that *Bison* occurred historically in some locations of northeast Mexico well south and west of the Rio Grande or in southwestern New Mexico and Arizona [17,19] are likely. However, due to abundant humans often supported by agriculture, bison (and later the first uses of domestic cattle) were likely ephemeral and strongly linked to local cultural and terrain factors. For example, in 1776 Father Garces found the Havasupai were already tending cattle in their homeland canyons near the Colorado River [456]. Did they experiment with bison domestication even earlier in time?

*Herding and dispersal in the Southern Rockies*- The series of "parks" – north, central and south—in behind the front range of the Colorado Rockies provided habitat and a potential movement corridor for long-term bison along the Platte River southwards into the Southern Rocky Mountains [52]. As described above, White [201] summarizes evidence that the Fremont and later the Utes could have used this corridor to move bison towards traditional hide and captive trading networks (Figure 6.2.2.2) with the populous southern cultures such as the Hohokam and peoples along the Gulf of California [441,457]. Although valleys lining the mountain parks corridor through modern-day Colorado and New Mexico provide excellent terrain to contain and kill herded bison, it's likely that buffalo did escape and formed small, ephemeral herds in the southern Rockies periodically replenished by dispersal or human herding from the east. The prehistoric bison [448] on the San Augustin Plains may also be  example of this human-bison interaction.

*Beaver conservation*- The Comanche were one of the Indigenous peoples most hostile to trappers or traders operating in their territories  [8,366]. An important ritual of the Comanche was the "Beaver Ceremony" involving a modelled construction ponds, lodges, and  other parts of beaver habitat [227]:175. For the arid basins further west, Clemmer [458] makes the case that along the Humboldt River the first British trappers made super-abundant harvests because Indigenous people had previously recognized that:

> .... *it was beaver that constituted the linchpin resource that provided meat, clothing, and ecological stability to drainages in Western Shoshone territory in southern Idaho and northeastern Nevada*.

*Community interactions*- The above analysis suggests the questions: "How far and how many bison could bison spread westward in the absence of human predation?" and further "What was the impact of historic herbivory levels on native plant communities?"  To consider this, we have the recorded results of Indigenous depopulation in the 1500s to 1700s, white settlement, and the and the abundance of feral and managed domestic stock expanding across the southwest. Simply put, the populations of domestic herbivores exploded by CE 1900 [459] . As Wooten [460] recorded in 1906 for the Territory of Mexico, after 1880 cattle numbers increased nearly 8 times from <150,000 to almost 1 million, sheep numbers rose from 2 to 4.5 million, and horse populations reached ~50,000. In the dry southwest this wave of intense grazing combined with drought caused great impacts on native perennial grasses including black grama and needlegrass. The removal of herbaceous plant biomass, combined with increasing fire prevention and suppression to protect fences and settlements, sharply reduced fire frequency across the southwest region [371] . Ongoing longer fire-free periods favored spread of woody species including mesquite and juniper [461]-- a positive feedback loop that further reduced the abundance of herbaceous species and thus decreased frequent low intensity fires, and further increased woody vegetation cover. The results of this modern change suggest that the long-term human-created regime of light herbivory and frequent fires could well have maintained southwest plant communities very favorable for periodic bison foraging, but at the same time kept bison numbers low enough to reduce herbivory impacts.

*Population and biome-scale regulation*- Both archaeologists and historians provide details of how Indigenous hunters and traders maintained a flexible edge to bison range often >50km distant from the Rio Grande and Pecos River pueblos [352,374,375].  During times of bison abundance, bison mortality was likely higher near the villages, and when bison numbers were lower, hunting mortality decreased when bison were more distant. This feedback helped stabilize bison numbers and ultimately maintained ecological communities and Indigenous cultures. The potential time depth and eco-cultural force of this human-bison interaction can be contemplated in while touring the massive prehistoric stone structures in Chaco Canyon, New Mexico (Figure 6.2.2.2a). The obvious questions visitors and researchers all asks is: “Who paid to build all of this?.... and why here?” [409,462–464] One theory is that Chaco was a seasonal trade center [201] -- the canyon lay on a “least cost” route for the hide transport and trade industry of the day (CE ~500 to CE 1130) between the supply of bison on the plains on the upper Arkansas and Platte Rivers to the nearest major market for hides—the great Hohokam cultures farming the irrigated fields near modern day Pheonix [368,465,466]. At Chaco, hunter gathers from the plains would exchange their wares—buffalo hides and captives—with products with goods brought by traders from the southwest (copper bells, turquoise, shells). These annual trade fairs were much larger social conventions, but similar in purpose to those Europeans participated in a few centuries later at the Zuni villages (Figure 6.2.2.2.b), Abiquiu, and Santa Fe [366,441,442].

During the early to middle historic period, the main bison populations on the plains east of the Southern Rocky Mountains were likely human-regulated in distribution and abundance, but still thrived by ranging in the large buffer zone between the Numic peoples with winter camps and territories to the west (Shoshone, Ute, Comanche) and the Cheyenne, Arapaho, Pawnee, and eventually the Sioux who seasonally entered the plains from the east [55,235,467,468]. By the mid-1700s, the Comanche husbanded the large herds on the central southern plains by restricting the travel and hunting by other Indigenous groups and European traders [234,366].

As described above, there is reasonable evidence that long-term Indigenous land use created highly favorable habitat along the periphery of bison range, and that human bison hunting and trading networks were also adaptive and flexible to conditions near the range edge. Is their any historical evidence that these bison response to these variable conditions created broader-scale mutualistic conditions across the region? Yes—first, as would be predicted, there is archaeological evidence during periods of extreme drought bison may have found refuge in the western mountains while on the dryer plains to the east they were rare [190]. These bison persisted on the high-quality habitat created by Indigenous hunters and burners and were important to mountain cultures such as the Fremont and Utes [55,381]. Secondly, as described above, high quality habitat found on the southern plains ~CE 1200, and again partially maintained by human burning and hunting, was rapidly, and successfully colonized by bison from the north [348,348].

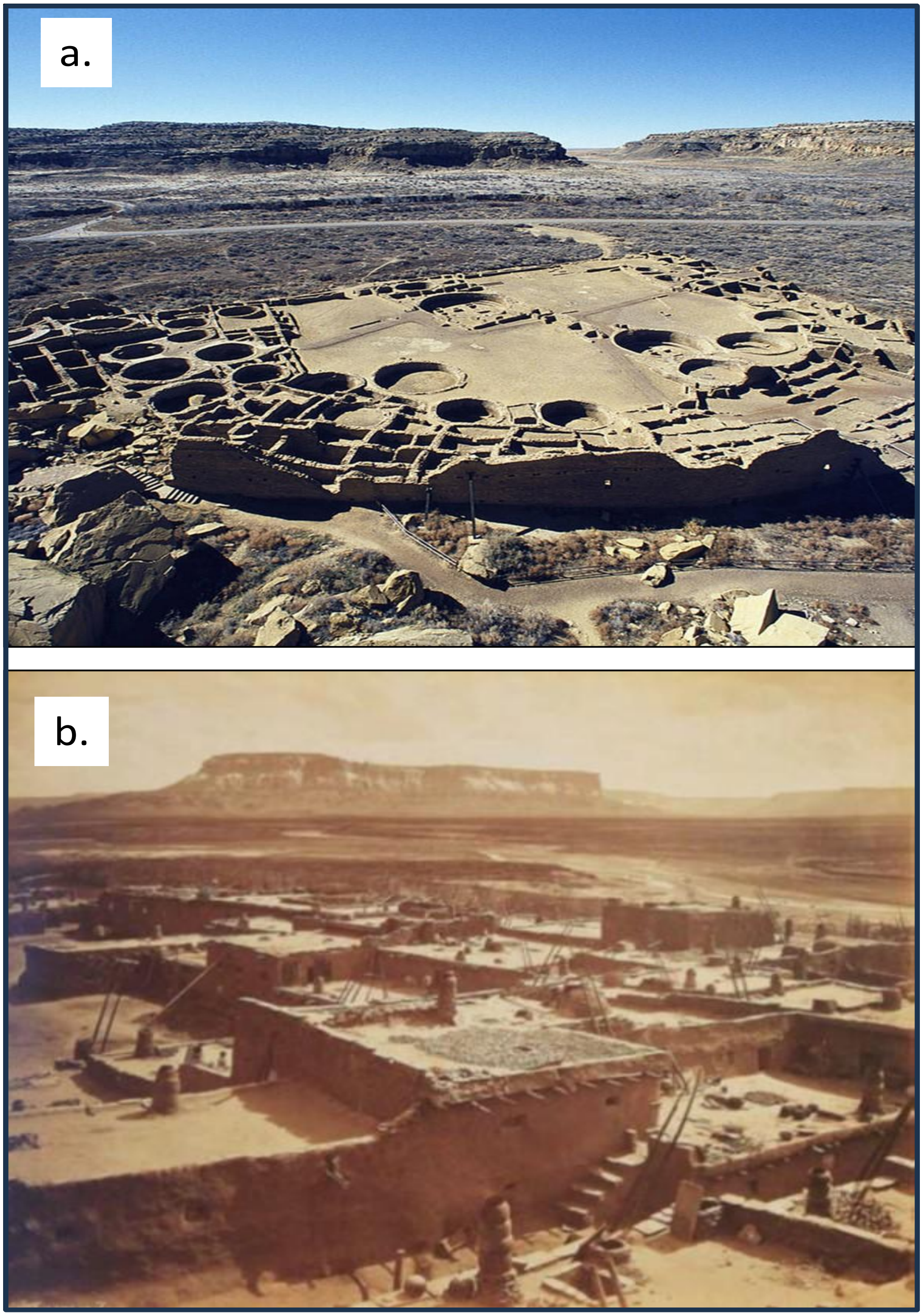



Figure 6.2.2.2: a. Pueblo Bonito archaeological site in Chaco Canyon National Historic Park (USNPS photo), and b. one of the Zuni villages in c. 1875 ((John K. Hillers, USGS photograph). During the prehistoric and historic periods both these trading centers lay on travel routes between the Great Plains and southwest farming centers. Coronado, following a hide trade route northeastward from Culiacán on the Mexican coast looking for the legendary cities of “Cibolla”, arrived at the Zuni villages on July 7, 1540 [201,207].

### *SW modern analogs*

The southwest is the birthplace of modern North American range science-- the research discipline of understanding and sustaining species, ecological communities, and productivity on largely native landscapes [267,469]. Much of research has been done in areas with historically low bison density or at the edge of the range where human-bison mutualisms may have functioned. Research often centers on cattle, a reasonable analog for bison. Recently, the long-term ecological role of beaver (Figure 6.2.2.3) is also gaining attention [470]. How has this science been applied to manage current cattle and bison herds, and what can this tell us about potential long-term mutualisms between humans and bison?


Figure 6.2.2.3: Satellite view of riparian zone protection exclosure and beaver restoration experiment on Ocate Creek in the 9.4.3 Southwest Tablelands ecoregion northeast of Albuquerque, New Mexico (see map Figure 6.2.1.1). This area had moderate bison densities during the historic period and if bison were wary human hunters, herbivory and trampling impacts in riparian zones may have been less than modern cattle impacts.

*General arid southwest range management*- The serious damage done to biodiversity by historic high stocking levels of cattle and sheep is well-recognized [72]. For example, for the southwest desert ecoregions in New Mexico, the 1890s pioneer stocking levels of >15 AU/km$^2$ (an AU, animal equivalent, approximates a female domestic cow with a calf) were reduced on research ranges to ~6 AU/ km$^2$ by the 1910s, and again by 1916 to <1AU/ km$^2$ in attempts to restore degraded grasslands [267,471] . Removal of herbage even in normal precipitation years reduces fire frequency, increases shrub cover, and thus reduces range capacity over time. Today, range managers recognize that in serious drought years arid lands of the southwest have almost no capability to sustain large grazers without human-supplied water and forage. Under these conditions, historic human-bison mutualisms would also be complex. Stressed bison would be easily herded, killed, or contained near water. Continued bison abundance might depend on local cultural factors such as conservation of beaver and bison hunting intensity.

*Janos Biological Reserve, Mexico (JBR)-* List et al. [17] describe the history of small herds of bison ranging the Mexico-US borderlands of Chihuahua and New Mexico for several decades. The JBR was designated in 2009, a unique region of private and public farmlands and native grasslands transitioning to woodland at higher elevations [472] . In 2009, 23 bison were reintroduced within a 15 km$^2$ privately owned paddock with artificial watering on native semi-arid grassland, with the herd growing at >20% /year thereafter (current density > 2.5 AU/km$^2$). Studies are ongoing on wallowing and grazing effects [473].

*Vermejo Ranch, NM bison and elk*- The foothills grassland-forest interface of the Southern Rockies ecoregion (6.2.14) was a potential human-bison mutualism zone. As with other SW regions, the area was super-populated with cattle and sheep by the later 1890s where historically elk and deer densities were very low (Figure 6.2.5). Grasslands and riparian zones did not recover from this intense herbivory. Today, on the Vermejo Ranch in New Mexico, bison are managed at <1/km$^2$ on summer range, and <1.5/ km$^2$ on winter pastures. However bison concentrate on remaining limited areas with forage productivity [474] . Modern predator control and hunting regulations maintain the Vermejo Ranch's elk at year-round overall densities of ~3/km$^2$ or ~2 AUs/ km$^2$ with much higher numbers on winter ranges-- densities that limit recovery of many palatable grasses, forbs and shrub species elsewhere in the Rocky Mountains [90,475]. Watkins et al. [476] surmise that poor forage quantity and quality may be limiting elk birth rates. Elsewhere in the New Mexico's southern Rockies beaver are relatively rare due to historic and current high stocking densities of cattle. In many areas streams are incised and it is uncertain whether reducing herbivory would encourage beaver restoration [477]. Historically, lower wildlife densities, likely maintained by humans, and no domestic stock could have created high quality habitat for bison herds that periodically took refuge in the mountain foothills from Great Plains droughts and winter snows and beaver that maintained stream flows.

*Rio Moro National Wildlife Refuge, New Mexico*- RMNWR is a unique, jointly managed reserve. The Pojaque Pueblo maintains herd of ~60 bison in a paddock of 3.7 km$^2$ (~13.5/km$^2$) along the river [478]. Similar to other areas of New Mexico (see above), the reserve has a long history of stock grazing that impacted riparian zones, and researchers are evaluating potential for beaver restoration [479].

*San Luis Valley (SLV)*- Historically, the broad valley on the headwaters of the Rio Grande (in ecoregion 10.1.7-Arizona New Mexico Plateau, Figure 6.2.2) was possibly a human-bison mutualism zone at the western edge of the range. Bison would periodically venture or been driven by humans < 10 km from the Great Plains into diverse and relatively high-quality habitat (see Section above). The current SLV bison herd is managed at approximately 1,500 bison on 194 km$^2$ or 7.7 bison/km$^2$. These numbers indicate a population substantially higher than historic densities with potential to degrade or limit recovery of the habitat. Schoenecker et al. [480] studied the distribution and abundance of bison also concluding that bison may be above carrying capacity. If so, modern management does not mimic potential conditions of human-bison mutualism on a peripheral range that created high quality forage and cover.

*North Rim-House Rock Herd, Kaibab Plateau (NRHR)-* An introduced herd on the north rim of the Grand Canyon provides the challenge of managing bison where they were extremely rare in the past, and where they have the potential to damage to ill-adapted natural and cultural resources. All large ungulates were rare in the on the Arizona and New Mexico Plateau (ecoregion 10.1.7) prior to European settlement (Figure 6.2.2.1), but in the latter 1800s and early 1900s thousands of sheep and cattle, then deer and elk used the plateau altering plant communities and hydrologic processes [481,482]. Domestic stock and other ungulate densities are now much lower, NRHR bison numbers has increased, and now in 2016 numbered about 450, ranging across public lands on the Kaibab Plateau, and increasingly using Grand Canyon National Park [483,484]. Given the history of herbivory impacts on the Kaibab, interagency managers have goals to maintain the NRHR at a relatively low density of 80 to 200 bison over 870 km$^2$ (0.1 to 0.2/km$^2$). Whether these population objectives, in combination with numbers of other ungulates will reduce vegetation impacts is unclear. Currently, no beaver activity is currently visible on the plateau in satellite images. Riparian willow cover is extremely low. Aspen regeneration appears most prolific in recent burn areas at upper elevations [485].

*Henry Mountains (HM)* – Mapped as an outlier to the Wasatch Uintah Mountains (Ecoregion 6.2.13), this isolated mountain range west of the Colorado River also likely had very low ungulate densities (Figure 6.2.1.4a). Early journalists (e.g., members of the Powell expedition) routinely encountered Indigenous people but no bison in the area [109]. In 1941 and 1942 a total of 23 bison from Yellowstone were introduced to the plains north of the mountains. Eventually the herd moved southwards. Today the HM herd is managed at ~400 animals over 1250 km$^2$ (~0.32 bison/km$^2$) and is unique for a conservation herd by long-term sharing the range with cattle [486].

## 6.2.3 Northwest (NW) Transect

The NW transect (Figure 6.2.1) runs westward from ecoregions with high abundance on the Missouri River, over the northern and middle Rocky Mountains into the dry interior plateaus (ecoregions 10.1.1, 10.1.2) on the headwaters of the salmon-rich Snake, Columbia and Fraser rivers, then over the Coast Range to the rain forests of Pacific Ocean near the mouth of the Columbia River. Average ecoregion resource abundance indices are mapped (Figure 6.2.1.4) and graphed (Figure 6.2.3.1).

The northwest is an exceptional region to evaluate of long-term, interacting biophysical and cultural factors on large mammal distribution. Here is a large scale experiment in the landscape connectivity or "wildlife corridors" that animals might use to move between high habitat quality areas, metapopulations, or source and sink population [487,342,343]. In the case of historic and prehistoric bison, abundant bison existed on the Great Plains and were connected through the valleys of the Western Cordillera (Rocky Mountain and Idaho Batholith) to potential area of high habitat quality of the interior west (10.1.1 Thompson-Okanogan, 10.1.2 Columbia, 10.1.3 Northern Basin and Range). Although many "least cost pathways" link these regions, and could be potentially used by bison, the historical data provided here allows ecologists evaluate which corridors were most important in the past and the climatic, vegetation, terrain, and Indigenous use conditions along each [35]. Moreover, a bison dispersal event over the Rocky Mountains from the plains likely occurred early in the historic period (~CE 1810) allowing evaluation of unique conditions that may have stimulated this movement.

### *NW high abundance region*

Historical northwest bison abundance indices (Figure 6.2.3.1) are high in three central ecoregions on the northwestern Great Plains with highest grass cover and lowest forest cover (9.4.2 Central Great Plains, 9.3.1 Northwestern Glaciated Plains, and 9.3.3 Northwest Great Plains). Binnema [6] describes that during the historic period, most this region between the Yellowstone and South Saskatchewan rivers lay in an inter-tribal buffer zone between the northern coalition of the Piikani, Kanai, Siksika, Gros Ventre, Tsuitina Assiniboine and Plains Cree, and the southern coalition of the K'tunaxa, Flathead, Shoshone, and Crow (Figure 6.2.2). As the elder Saukamee recounted during David Thompson's 1793 winter with the Piikani [488], this warfare zone was traversed by small raiding parties, and avoided by large, multi-family communal hunting villages. Kay [137] analysed daily wildlife observations by Lewis and Clark expedition in 1805 and 1806 on the Missouri and Yellowstone rivers [489] showing that wildlife abundance was greatest between Indigenous groups at war, and declined, beginning with large species such bison and elk as the Corps of Discovery travelled closer to villages.

Further south, bison abundance is also high historically and in the pre-contact period [67] on the headwaters of the Platte River south of the Black Hills. Again, as described by the journals of La Verandrye [490], this was a buffer zone between the Crow (Apsaalooke) and the Shoshone in the mid-1700s [51], and later warfare further intensified as the Arapaho, Cheyenne and Sioux advanced towards the Rockies from the east [467,234,468].

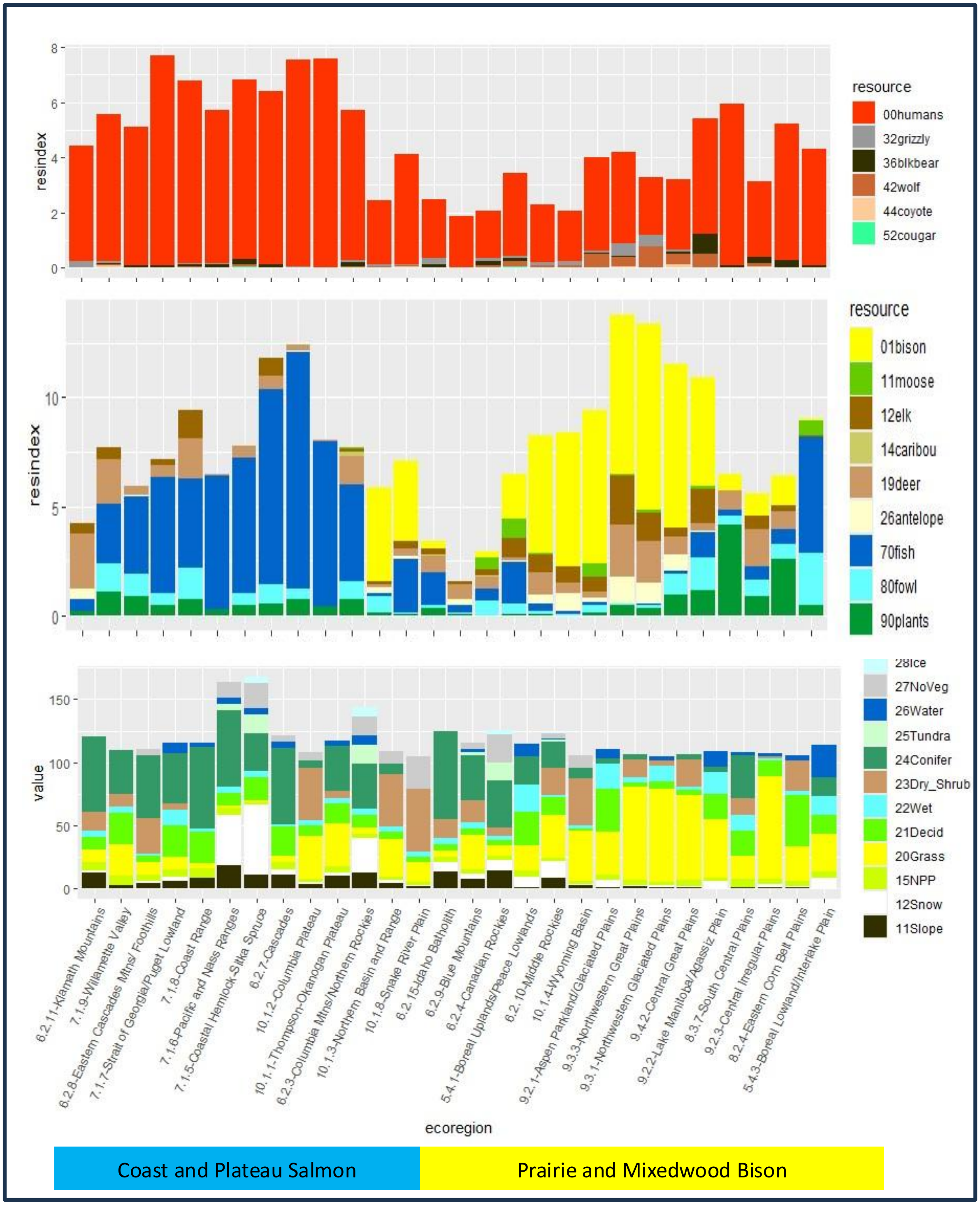



Figure 6.2.3.1. Northwest transect average ecoregion biophysical values and resource abundance indices. See Table 4.1 for variable descriptions.

### *NW migration and dispersal patterns*

Several researchers use fur-trade era accounts and traditional knowledge to describe the inter-linked pattern between bison and humans on the north-western plains [390,6,172,48,36,99,188]. The general pattern (Figure 3.1.1.1) was for bison to aggregate in large herds early each spring in the shortgrass prairie in the middle of the plains. These grasslands are the first to green-up and become productive. As the weather moderated later in spring, groups of human hunters would begin to move out onto the plains, often following stream courses to hunt the bison herds over the summer. In late summer and fall, grass condition was better in the fescue grasslands and parklands on western edge of the plains [6,260] and bison would move this direction, often preceded or followed by people moving towards the wooded valleys in the Rocky Mountain foothills for the winter [6,48,188,390,491]. Once bison neared the western edge of the plains, Indigenous peoples might drive bison further west towards winter villages. For example, during his 1792-93 winter with the Piikanni, Hudson's Bay Company trader Peter Fidler [492] observed groups of young men venturing many kilometers out onto the prairie to surround and carefully move bison west up the Highwood River. Further, he saw the Piikani burning the plains-- possibly to hold bison herds on the forage remaining closer to the foothills.

The high quality forage and cultural herding that drew bison westwards into the foothills in fall and winter possibly facilitated periodic dispersals through ranges of the Rocky Mountains into the intermountain valleys and headwaters of the Missouri River, and Snake and Bear rivers west of the continental divide—areas occupied by bison during the Holocene either periodically or at low densities [382,384,383,22,493]. Bison dispersal though the mountains was likely through wide valleys or passes with high grass cover, and low forest cover, such as through the South Pass, later crossed by the Oregon Trail [35,355]. There is some evidence this corridor was crossed by many bison at ~CE 1812 (Figure 6.2.3.2). The accounts of four expeditions prior to the time report relatively low bison numbers on the headwaters of the Snake and Missouri: Lewis and Clark in 1805-06 [137,489], Thomas James in 1810 [494] , William Hunt in 1811 [355,495], and Robert Stuart in 1811 [355]. In contrast, after ~1812 bison were moderately abundant for three subsequent decades (Figure 6.2.3.2b). During his 1843 trip, Fremont [354] observed that the occurrence of numerous bison west of the continental divide appeared to be a recent event:

> *In the region west of the Rocky mountains, we never meet with any of the ancient vestiges which, throughout all the country lying upon their eastern waters, are found in the great highways, continuous for hundreds of miles, always several inches, and sometimes several feet in depth, which the buffalo have made in crossing from one river to another, or in traversing the mountain ranges. The Snake Indians, more particularly those low down upon Lewis's fork, have always been very grateful to the American trappers, for the great kindness (as they frequently expressed it) which they did to them, in driving the buffalo so low down the Columbia River.*

Several biophysical and cultural factors could have driven this potential bison dispersal event:

- At ~CE 1800 the upper Platte River was a buffer zone between the Sioux expansion across plains and the eastern Shoshone's territory that had recently receded to the west [51]. This could have resulted in large numbers of bison occupying the upper North Platte and Sweetwater rivers;

- The phenology of annual grass productivity in the Rockies would have attracted bison upwards in elevation later in the summer towards the Wind River Range and South Pass [201,230];
- A large early season snowfall such as described by Colonel Dodge that in 1844-45 that trapped thousands of bison in the Laramie River valley [2]:544 could then have blocked bison from migrating back to the east: and
- Once west of South Pass, bison would have either moved down in elevation to avoid deep snows or been driven further westward by the Shoshone (or later by fur trappers) downstream on the Bear and Snake rivers.

Whatever combination of processes drove past dispersal events, the gradual diminution of bison's body mass during the Holocene on the west side of the continental divide followed a general pattern to the Great Plains, suggesting their origin was from relatively regular dispersals through corridors from the heartland of the bison habitat to the east [496], but with local variations [497]. For the next three decades after the potential ~1800 CE dispersal event bison thrived on the grasslands in the broad intermontane valleys of an inter-tribal buffer zone between Shoshone, Flathead and other nations on the southwest, and the Blackfoot confederacy to the northeast [6,393,498]. However, at higher elevations terrain, vegetation cover, and winter snow conditions favored high rates of Indigenous predation that likely created low bison densities in rugged the mountainous terrain [53,390,499].

### *NW low to moderate abundance region*

The potential bison dispersal event of bison South Pass and potentially other corridors to the north (Bozeman Pass, Old North Trail foothills corridor) near the Wind River Range created a broad area of low to moderate bison density on the rolling grasslands and shrublands in the lower elevations of four ecoregions: 10.1.4 Wyoming Basin, 6.2.10 Middle Rocky Mountains, and the eastern areas of 10.1.3 Northern Basin and Range and 10.1.8 Snake River Plain (Figure 6.2.3.1). In winter, these bison were constrained to low elevations by deep snow. During the historic period intense hunting by Indigenous peoples (Shoshone, Bannock and Flathead), and fur traders and trappers both from the east and the west resulted in rapid population decline. With the probability of further bison dispersals from the east declining, bison had nearly disappeared west of the Rocky Mountains by the early 1840s [2].

Moving up in elevation, bison abundance was very low in the narrow valleys and upper elevations of the rugged Rocky Mountains (ecoregions 6.2.4, 6.2.10, Figure 6.2.3.1). From the Clark Fork River for over 1000 km north to the Peace River the historic journalists only infrequently record bison sightings within the Rocky Mountains [35,500], and in only 3 sightings west of the continental divide in this region: in 1806 by the Lewis and Clark expedition on the Blackfoot River [489], in 1808 by David Thompson on the Blaeberry River [391], and in 1830 by John Work, just north of the Clark Fork [501]. The rugged mountains surrounding the Yellowstone plateau similarly constrained bison use with very few historic observations directly within today's park [498,136,261].

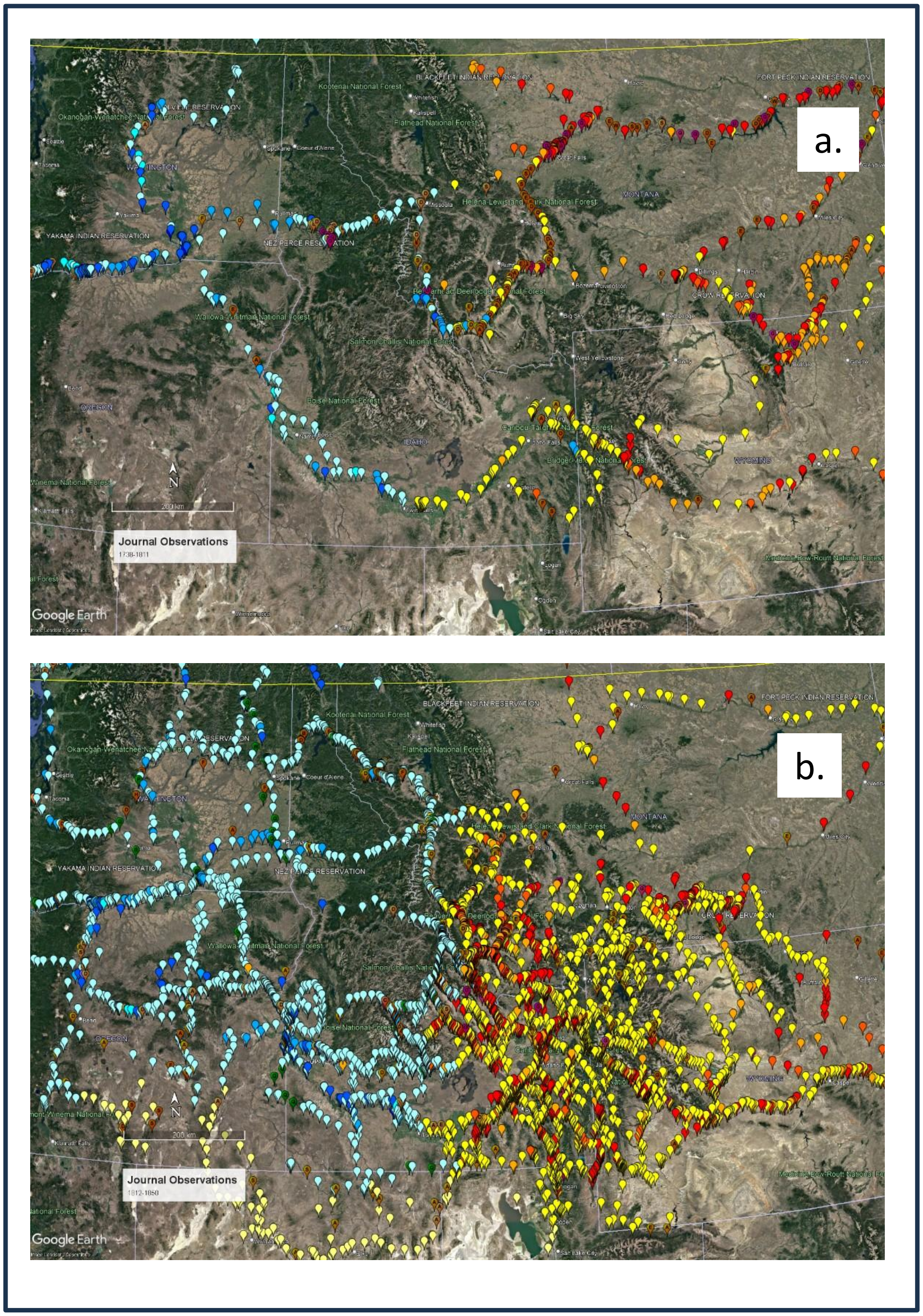



Figure 6.2.3.2. Historic journal bison observations (red and orange markers) for the Middle Rockies and adjacent ecoregions for the period a. CE 1738-1811 and b. CE 1812-1860. Yellow indicates potential bison range but no bison observed, blue shades indicate northwest flowing rivers in salmon/plateau biomes. See Journal Observations database for other codings and individual traveller routes and data [109].

Several factors interacted in or near rugged mountains help explain low bison density:

- Limited areas of grassland and steep terrain (Figure 6.2.3.1) limited bison herd size. Thus encounters with communal hunters had high mortality rates;
- Deep winter snow (Figure 6.2.3.1) further constrained bison to limited areas where they could be detected and hunted.
- Numerous terrain features and traps that facilitated communal hunting [502,233,389,390,48] including: narrow valleys, canyons, poor visibility, low cliffs, stands of trees to build pounds, snowdrifts that remained into summer, meadows and ridges to form driveways towards cliffs or terrain constrictions.

The effectiveness that Indigenous people used these features is well described in the historic accounts for the region. In 1793 Fidler watched the Piikani bringing small herds of bison in off the plains towards the mountains and running them over a steep creek bank into a pound where they were killed [492]. In December 1823, James Clyman participated in a hunt with the Crow, using the narrow valley of the Wind River to constrain and kill many bison [503] . Again on the Wind River, Reynolds [504] described how in the fall of 1859 the Crow had contained a large herd of bison in a narrow valley for their winter food supply. Further from traditional knowledge, there are accounts of the Flathead crossing the mountains to herd bison up the Sun River where they were killed in a canyon in the Front Ranges [54], and the Crow herding 200-300 bison up Buffalo Creek in the Absaroka Mountains where killing occurred against a cliff [261].

#### *NW edge of range and beyond*

From traditional Indigenous hunters to modern ecologists and historians, people have found the northwest's edge of bison wanderings and habitat use an enigma. Why did bison occupy the Great Plains in the millions, yet were rarely found on the rich Palouse Prairie of Washington? How could bison permeate the woodlands and snows to occupy vast areas of the boreal forest north of the Great Plains, yet were usually not found on extensive valley bottom grasslands only a short distance into the mountains to the west of the Rocky Mountains at the headwaters Columbia and Fraser rivers? In 1932 Kingston [33]:164 observed that this northwest edge of bison's range "presents a curious and rather intricate problem of biological distribution in which hunting by the Indians and physiographic difficulties explain for the most part the scarcity or absence of the buffalo.''

Researchers have evaluated four main sets of factors to explain low bison abundance and the range edge in the northwest: 1) human predation [33,34,4,241,138,505,38], 2) poor quality of forage [31] , 3) climatic factors including winter severity and/or drought [30,506,507], and 4) A combination of human predation, forage quality, and migration obstacles [20,22,35,508]. Farr and White's [22] analysis of the bison's northwest distribution from high density populations on the plains westward to low density areas found that a combination of biophysical and cultural factors episodically created the fluctuating northwestern edge of the range. As described above, summer drought and annual phenology may drawn bison herds to the edge of the plains, and into intertribal buffer zones between plains and intermountain peoples, early winter snows may have trapped in valleys near or west of the continental divide, and heavy predation by Indigenous peoples here likely limited growth of these herds [6,22,48,393].

Ultimately, at bison's northwest range edge, it was likely abundant humans, fed by sustainable salmon fisheries, plant harvesting and aquaculture [245,248,509,510] that made it difficult for bison to persist, even in optimal grassland habitats in ecoregions along the Snake, Columbia and Fraser rivers (Figure 6.2.3.1). Not only did these cultures have high population densities, but they had a strong demand for animal fats for nutrition, and hides used for clothing, shelter, binding and many other purposes [511,419,509,512]. Intense human hunting in this region, had, for most the Holocene, likely not just blocked widespread bison colonization, but also limited the range moose and elk [136,505]. Further, a network of Indigenous trade routes from the interior plateaus led eastwards to obtain meat and hides including the "Trail to the Buffalo" up the Columbia and Clarks Fork rivers to the headwaters of the Missouri and Yellowstone [393,395] and up the Snake River towards the South Pass region

Roe [4]:259 described how this cultural process would create bison's range edge in the northwest:

> *"Even before the advance of the white men into the Rocky Mountain territory, the westward advance of the buffalo must have been much impeded by the 'economic pressure' of the Indian tribes beyond the actual buffalo range. For many Indians journeyed through the passes to procure bison meat and hides, either by hostile forays or by trade. This is attested by the earliest (European) observers and by many others and was* ***clearly a long-established process****." (my* emphasis).

### *NW mutualistic interactions*

The proposed general regional pattern of human-bison mutualism was that human hunting kept moderate to high numbers of bison well out on the plains. This maintained high quality forage such as blue-bunch wheatgrass or rough fescue in the foothills that could be used by bison periodically during droughts or severe winters on the plains. During years when bison did reach the foothills, human hunting pressure stimulated bison movement by early spring either eastward, or for the few bison that persisted in the mountains, early migration upwards in elevation from valley-bottom grasslands. High remaining grassland biomass and litter (>70% in most years) fuelled routine burning that reduced shrub and conifer cover, but stimulated aspen and willow regeneration.

*Herding, holding and domestication*- The northwest's archaeological and historical record provides abundant evidence of humans herding bison towards the foothills or in mountains valleys (e.g., [389,492]). At times these may have been held for a month or two before harvesting—what Frison [233] calls "storage on the hoof", but these contained herds were usually rapidly by late winter, and the Indigenous seasonal round took people to more abundant or alternate resources either out on the plains, or back into the mountains (e.g. the Piikani seasonal round, Figure 6.2.3). A unique case of late-contact semi-domestication was Salish herding of several calves across the Rockies from the Missouri plains to develop a large herd on the Flathead River prairies [54]. Possibly in the past under unique societal conditions, Indigenous peoples maintained, for a time, other herds in mountain valleys with good containment.


Figure 6.2.3.3: a. Chief Washakie's Shoshone camp in the foothills of the Wind River Range near South Pass on September 3, 1870, and b: in 2010. South Pass was a major corridor for bison and movements across the Rocky Mountains. Indigenous burning and hunting maintained open forests and low rates of herbivory that had low impact on riparian zones. This camp lay along a riparian zone impacted by Shoshone horses and today is an irrigated field lightly stocked in summer with cattle and horses. Photos: William Henry Jackson, Utah State Historical Society (USHS-970.8-14638) and in 2010 (CW-2010-09-26-454).

*Beaver conservation*- Hudson's Bay Company traders routinely commented that Indigenous groups on the northwestern Great Plains including the Piikani, Kanai, and Siksika were reluctant to trap beaver, and in some cases even prohibited it [8]:4. Alexander Henry the Younger [223] recorded that for the foothills and prairie regions on the upper Saskatchewan River:

> *Beaver are numerous but they* (the Blackfoot confederacy nations) *will not hunt them with any spirit, so that their principal product is dried provisions, buffalo robes, wolves, foxes and other meadow skins, and furs of little value.*

As described above, the Shoshone peoples that advanced northwestwards into the Rocky Mountains and plains in the 1700s may have also recognized the importance of beaver for riparian zone and fisheries conservation. The first European fur trappers on headwaters of streams running to the Pacific and Atlantic found made found abundant beaver in what appeared to be a previously lightly harvested areas [269,379]. At the time of park establishment in 1874 and through the 1940s Yellowstone had abundant beaver colonies that served as the study sites for Ernest Thomas Seton's early research on the species [27].

*Community-scale interactions*- Historically, Indigenous and other predators in the northwest preferably hunted bison, elk, and other herbivores, often to very low densities west of the mountains [136,138,241]-- this reduced impacts on susceptible native species such as bluebunch wheatgrass, Sandberg bluegrass, and big sagebrush on dry grasslands, rough and Idaho fescue, Columbia needlegrass and mountain big sagebrush on mesic grasslands [89,91]; and willow and aspen on moister sites and riparian zones [136,271,475,513]. Seasonal rounds such as described for the Sahaptins (Figure 6.2.3) maintained riparian vegetation provided habitat for beaver, waterfowl, and numerous salmonid species which in turn supported humans. [330,514].

Indigenous management of fire and herbivores interact [272]. Low herbage utilization by herbivores provided fuel for frequent Indigenous and lightning-ignited fires that removed conifers such as pinyon pine and juniper, created mosaics in sagebrush-perennial grass communities, and maintained important Indigenous foods [147,515]. The use of fire by Indigenous peoples of the northwest is well-documented [111,282,288,322,516] . In mid-elevation forests, the Tsimshian and the Sahaptin burned shrub fields to maintain berry production (Figure 6.2.3). Burning typically occurred in the fall, when grasses and shrubs were cured [419,517] before moving to winter villages. Other plant communities maintained by routine fall burning included camas fields, bunchgrass prairies, gary oak savanna, and beargrass patches [288,319,320,518]. In summary, Indigenous management of low herbivore numbers and routine burning along the western edges of bison range created unique vegetation communities that would benefit the people themselves, and for low densities of bison that periodically dispersed westwards from the plains.

*Population and biome-scale regulation* – Bison on the northwest plains had to make an annual trade-off between the mortality risk of winter severity in the center of the plains or human-harvest if they ventured too close to Indigenous camps in the Rocky Mountain foothills or wooded river valleys (Figure 3.1.1.1) [48,172,188,331,390]. In early spring the bison would move back eastwards towards the shortgrass prairie, followed by (from south to north) by groups of Shoshone across South Pass (Figure 6.2.3.3) into the Wyoming Basin [51], the Crow along the Yellowstone [519], consolidated groups of Flathead, Kootenai and other western groups on the upper Missouri [393], the Piegan on the Sun, Milk and Oldman [43,48,256,424,491], and Piikani and Siksika on the Bow and Red Deer [520]. The degree of hunting mortality this influx of human hunters onto the plains would inflict upon the bison would depend on herd size and movements, and buffer zones between other nations, but over time this interaction between humans and bison appears to have kept the northwest bison population viable and in with balance with grassland productivity.

In contrast to modern conditions, bison periodically dispersing from the Great Plains into the western Cordillera likely encountered high quality habitat conditions, and under some conditions could persist at low densities. Numerous movement corridors provided bison access from the plains westwards [22,35]. Lyman [376] recognized a potential human influence on bison using these corridors:

> *If bison immigrated to eastern Washington from southwestern Montana and western Wyoming, and passed through southern Idaho, then the increased incidence of (anthropogenic?) fires over the past 2000 or so $^{14}C$ yr may have enhanced forage quality along that route and thus allowed larger numbers of bison to immigrate.*

### *NW modern analogs*

The demise of native wildlife, and introduction of cattle and sheep greatly disrupted NW ecosystems, and particularly those west of the continental divide that in the past had relatively low numbers of ungulates, thus likely low adaptions to herbivory [85,272,521]. Range science and rangeland management and restoration techniques are now well-described (eg:, [72,412,522]). Several case histories have application to interpreting historic NW bison distribution and abundance:

*High Plains Research Center (HPRC)*- Long-term (25-year) studies evaluated stocking rate and grazing system on northern mixed grass prairie near Cheyenne, WY. [523,524], with stocking rates for the growing season of lightest (8 AU/km$^2$) to moderate (13.3 AU/km$^2$) to heavy (17.8/AU km$^2$). Short-term, higher stocking rotational grazing treatments (possibly mimicking bison movements did yield small gains (6%) in cattle weights compare to season-long grazing. However, the study demonstrated major long-terms reductions in grassland productivity (16-34%) with moderate and heavier treatments compared to light stocking. With heavier grazing warm season grasses (blue grama) and forbs increased, cool season grasses (western wheatgrass, needle and thread) declined. No treatments with very light stocking (e.g. <2AU/km$^2$) with fire use (which may better represent “natural” conditions) are reported yet for this region. Satellite images appear to show abundant beaver activity in fenced areas along Crow Creek near HPRC.

*American Prairie Reserve (APR)* - Historically, northwest source population bison herds ranged across the northern plains (ecoregions 9.3.1 and 9.3.3, Figure 6.2.4). The APR Foundation on the Missouri River ~50-80 km east of the Rockies is gradually assembling deeded lands and grazing leases that could eventually partially emulate source bison population conditions [525,526]. As of December 2024, the APR’s area was ~2140 km$^2$, with >90% seasonally stocked (June to October) with ~9000 cattle. The region remains predominantly a native sagebrush steppe community of blue grama (*Boutulua gracilis*), needlegrass (*Stipa* spp.), crested wheatgrass (*Agropyron cristatum*), silver sagebrush (*Artemsia cana*), and Wyoming big sagebrush (*Artemisia tripartita*). Research projects are ongoing to evaluate bison rotational grazing and carrying capacity. In one project, bison numbering 147 and 215 in 2010 and 2011 respectively were stocked in a ~36 km$^2$ pasture (~5/km$^2$) from May 1 to October 31 with 15 water reservoirs with habitat use compared to cattle in nearby pastures. Both bison and cattle favored riparian zones and areas near water, but bison moved faster, and further from water, and caused less riparian zone impacts [527]. Cattle selected for high biomass whereas bison selected for intermediate biomass [528].

*Yellowstone National Park (YNP)* - In the early 1800s, numerous bison used the grasslands of the intermountain valleys surrounding the high plateau along the continental divide at the headwaters of the Yellowstone and Snake rivers, attracting both Indigenous peoples and fur hunters (Figure 6.2.3.3). However, early travellers observed few bison at higher elevations in what is today's YNP. Likely Indigenous people used a combination of the narrow valleys and deeper snows on the plateau to successfully hunt bison, as evidenced by numerous archaeological features such as driveways and jumps [499] and historical records of Indigenous hunts [35,109,261]. However, a small herd of bison survived in the park, and after various phases of management now numbers >4000—the largest free-roaming herd on the continent [262,529]. Grizzly bears, wolves, and humans hunt some bison, but none of these predators substantially reduce numbers [530]. Bison numbers are generally regulated by annual forage ability and snow depth and some out-of-park dispersal with an estimated carrying capacity of 2500-5000 (~5/$km^2$ on winter range) [263,531]. The observed count in 2018 was 4500 (.405 bison/$km^2$ across the total 9400 $km^2$ range), with winter and early spring density estimates of 2-3/$km^2$ on the northern range to 6-8/$km^2$ on the central range [263,529]. High bison densities, combined with a previous history of high elk numbers has effected many native species (Figure 6.2.3.3) including native wheatgrasses, fescue, sagebrush [89,91]; and riparian willow and trembling aspen [136,251,268,271,475,513,532]. Beaver, once common in the park is now relatively rare because of aspen and willows demise [330,514]. Modern YNP grasslands are now up to 30% less productive than historic conditions and are increasingly dominated by Eurasian species [532]. Kauffman et al. [268] describe that the many exotics such as Kentucky bluegrass that now dominate riparian zones have better adaptions to continuous grazing pressure than the native bunchgrasses. Yellowstone's grasslands once had a ~30-year fire frequency [414,533]. The Parks Service rarely does prescribed burns in YNP, but fire behavior would be altered in many locations due to reduced herbaceous biomass and altered grassland and shrubland communities [251,534].

Historically, Yellowstone's native species, and their associated communities and ecological processes facilitated summer use from bison that wintered on the plains moving upwards in summer and low densities of year-round bison-- both finding some refuge from predation from humans more commonly found at lower elevations. Consider that a small, surviving resident herd on the plateau was the source for the modern population [529], and this type of refuge-effect likely occurred in other Holocene population fluctuations of bison and the northwest edge of their range. How important were the now lost productive grasslands, rich riparian zones, dense aspen thickets and more open forests of past times (Figure 6.2.3.4) for bison in this refuge? Current-day YNP bison annually migrate >30 km between winter and to summer ranges [230], with dispersal triggered at densities as low as ~0.5/$km^2$ [263]. While migrations of this distance were reasonably secure on the open plains, or in modern day Yellowstone with few Indigenous hunters, bison historically moving long distances in Yellowstone's narrow valleys and grasslands would be at high risk from native hunters [22,35,261,499] . Low movement distance in high quality habitat was likely important for low densities of bison historically seeking refuge from predation on the Yellowstone plateau.

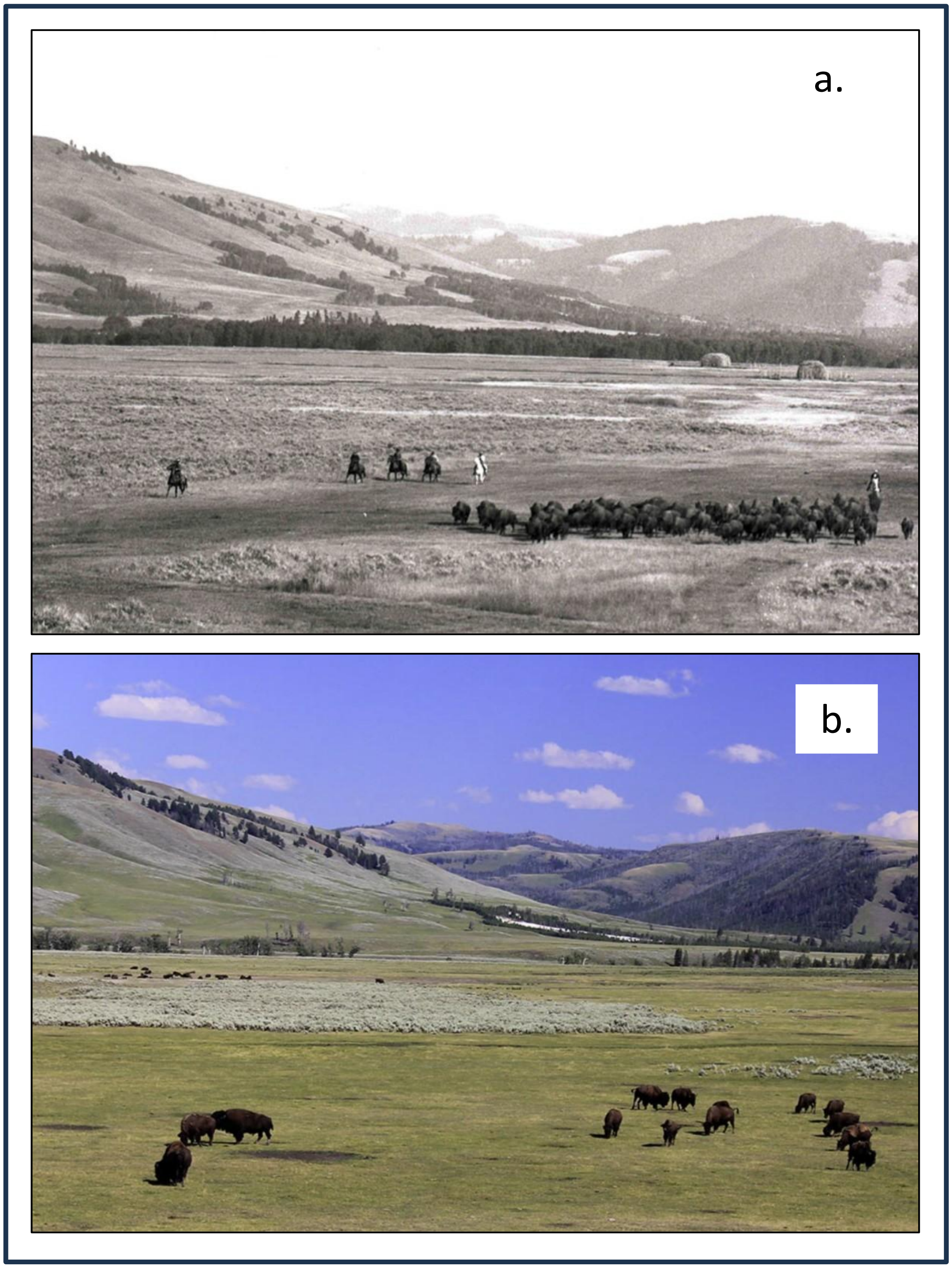



Figure 6.2.3.4. Lamar valley bison c. 1924 (Yellowstone National Park Archives NPS-YELL-27818) and in 2016 (CW-2016-07-24-090). In the 1920s, Yellowstone National Park wranglers stampeded a domesticated herd of bison across the Lamar valley grasslands to thrill park visitors. The haystacks for winter bison feed are visible on the center right. Modern wildlife conservation policies now allow bison to roam freely within the park but in the absence of Indigenous predation Yellowstone's total bison numbers have increased from a few hundred in the 1920s to over 5000 by the year 2005 [262,263]. Intense herbivory has altered long-term vegetation and hydrology patterns by reducing or eliminating the sagebrush cover in the foreground, the riparian zone in the mid-ground, and the aspen clones in the background [268,271,475] . Degradation of grassland productivity over time is reducing bison population carrying capacity [535].

*Blue Mountains*- The ~CE 1800 potential bison dispersal event resulted in bison being observed as far west as the Blue Mountains (Ecoregion 6.2.9) in Oregon (Figure 6.2.3.1). How do current conditions here compare to those in the past? This landscape was impacted by Indigenous depopulation and periods of high cattle and sheep stocking during European settlement degraded rangelands in many NW ecoregions. This was followed by a period of intensive logging, then ongoing reduced fire frequency increasing conifer forest cover [417,536–538]. Since the 1930s, elk and other ungulates, once relatively rare here (Figure 6.2.3.2) have increased in numbers. For example, in ~CE 2010 the Starkey Experimental Forest in 2010 managed a combination of elk, deer and cattle at a stocking rate of approximately 11 AU/km$^2$ (equivalent of ~10 bison/km$^2$). Herbivory at this intensity reduces cover of aspen and willow [539–541] and often grasses such as blue-bunch wheatgrass and Idaho fescue—species that may be poorly adapted to ongoing intensive grazing [20,30,31]. A further interaction is the effect of current herbivory levels on beaver, and hence salmon habitat on headwater streams [542].

Thus, the Blue Mountain ecoregion that was once likely strongly contributed to the functioning of a broader ecological corridor that facilitated both human subsistence and bison movements westward is now altered.

Contemporary NW livestock and wildlife winter range guidelines for native grasslands (e.g. blue-bunch wheatgrass, rough fescue, needlegrass) recognize the importance of the long-term low herbivory-high fire regime, and generally recommend very low stocking levels of riparian zones (<1 AU/km$^2$), low stocking levels during spring growing season on many ranges (<2 AU/km$^2$), low densities on dry grasslands 2-4 AU/km$^2$, and only moderate densities 4-6 AU/km$^2$on good sites, but again only for 4-6 months of use in late spring and summer, with all ranges be carefully managed in the spring growing season and that ~30-40% herbaceous matter be retained [73,83,90,532,543–545]. Once herbivore numbers are reduced, prescribed burning or forest thinning can be considered to further enhance vegetation recovery [86]. However, despite these more conservative stocking guidelines there is a disturbing pattern of reduced elk reproduction rates across the west that may be tied to forage nutritional decline [546].

*National Bison Range* - The NBR lies in the area Canadian Rockies Ecoregion (6.2.4) extending into northern Montana. The ecoregion historically had low bison abundance, and only rarely were bison observed west of the continental divide (Figures 6.2.1.4,6.2.1.1). Historically, cool season perennial grasses (bluebunch wheatgrass, Idaho fescue, and rough fescue) were likely dominant, but the native flora of the Flathead grasslands was likely impacted by Pablo-Allard herd, increasing from <10 bison brought in from eastern Montana ~1873-74 to over 700 head by 1912 [54,68]. In the past few decades the reserve has been stocked at approximately ~4 bison/km$^2$ (~350 bison on 77km$^2$) [547]. There are reports of intense NBR grazing in past years, and rough fescue, the most susceptible native species, has very low cover [548].

*Sun River Game Range* - This windswept elk winter range on northern Montana's eastern slopes was likely an area historically used by bison moving westwards when heavy snows covered the Great Plains [48,53,331,390,491]. Since the 1920s it is important winter range for elk summering in mountain meadows in the upper Sun River and migrating down valley in the late fall. Researchers report 2150 elk (1290 AU) using about 80 km$^2$ (~16 AU/km$^2$) for 5 months in winter and early spring causing ongoing major declines in rough fescue cover [83].

*Southwest Alberta prairie, foothills and mountain valleys*- Historically, bison using the Great Plains in this region would migrate, or be herded by Indigenous peoples towards the foothills where snow-depths were less [6,48,197]. Grassland productivity and cattle grazing studies provide estimates for sustainable herbivory on rough fescue and other palatable grasses in the region. Estimates allow for retaining >50% grassland forage and litter for grassland diversity and nutrient cycling [543]. Wilms et al.'s [549] long-term research on cattle herbivory on rough fescue grassland in southwestern Alberta reported that stocking at a "light" rate (1.2 AUM/ha, or ~20 AU/km$^2$) for 32 years (May to November) did not affect vegetation composition. A modest increase in stocking rate (1.6 AUM/ha, ~27 AU/km$^2$) led to a marked decline of rough fescue from 38 to 21% of basal area, and fescue was nearly eliminated when stocking at of 2.4 AUM/ha (40 AU/km$^2$). Researchers currently recommend that native grass communities on the plains, late spring and summer months productivity can support ~10-13 AU/km$^2$, for foothills areas this decreases to ~6-8 AU/km$^2$, and for mountain valley grasslands decrease further to ~4-6 AU/km$^2$ [87,550,551]. This estimated capability is based upon average climatic conditions during the peak productivity months of June to August, with recommendations to avoid riparian areas, and not graze cattle in most foothill and mountain areas in winter through early spring to retain forage for wildlife and avoid erosion in wetland areas. Use of prescribed fire is not discussed in existing guidelines, and satellite images show substantial impacts of herbivory on riparian zones depending on existing pasture stocking levels.

*Western Cordillera: Beaver, Bison, Cows and Fish*- Numerous studies (several reviewed above) describe patterns of herbivory by bison, other ungulates (elk, deer, moose), and domestic stock over time on trembling aspen, riparian/wetland willow, and dependent beaver colonies and aquatic ecosystems in western foothills, mountains and plateaus [90,136,261,268,272,475,540,541,552]. Summarizing, historical journal observations, beaver harvests of the fur trade, and the photographic record demonstrate historic abundance of beaver in several ecoregions (e.g., 6.2.4 Canadian Rockies, 6.2.9 Blue Mountains, 6.2.10 Middle Rocky Mountains) and recent declines with increases in domestic stock and wildlife numbers. The threshold for declines of aspen, willow and dependent beaver colonies appears to be about 2 AU/km$^2$ (e.g., ~1.5 bison, 2 cows or 3 elk) in the broader landscape. Hot wildland fires at higher stocking levels can eliminate long-lived root clones by top-killing residual tall stems followed by intense browsing mortality of the root suckers [274]. In cases where aspen and willow cover is very low, herbivore stocking must be reduced to <1 AU/km$^2$ for recovery [86,553]. Many studies recommend fencing riparian zones or aspen groves to restore vegetation to protect aquatic ecosystems [270,554,555]. In extreme cases, stream-downcutting and resulting riparian zone drying may cause irreversible wetland loss—creating a new stable state [330].

*Banff National Park (BNP)* – The park was established in 1885, and starting in 1898 and for decades thereafter maintained captive bison paddock as a tourist attraction [68,556,557]. The Canadian Rockies ecoregion (6.2.4) created a sharp demarcation to the western edge of bison range (Figure 6.2.3.1) caused by a combination of steep terrain, narrow valleys, deep snow, dense forests, and Indigenous hunting [22,35,392]. Historical observations (CE 1800- CE 1859) for of bison in the park and immediately adjacent lands are sporadic with <100 animals or sign of bison observed in >200 journal days [109,500]. Archaeological data shows a similar trend of sharply decreasing zooarchaeological evidence of bison within the mountains compared to nearby foothills and plains [392,493,558]. Similar to other valleys in the Rocky Mountains adjacent to low elevation grasslands, its likely Indigenous peoples contained and hunted bison in various terrain traps [53,233,261,390] -- essentially using the valleys as large pounds. People appear to have routinely burned valley bottom grassland habitat corridors into the mountains [317,493], On this basis, biologists initially recommended that if Parks Canada did consider restoration of bison to Banff, it should be a low number managed by Indigenous people as a sink population at the edge its range [559,560]. The project would thus largely be most significant from a cultural perspective.

Prescribed burns done along the eastern slopes of BNP beginning in 1984 restored substantial potential bison habitat. During this period a substantial wolf population recolonized the region, resulting a >50% decline in elk numbers and migration into the park from adjacent areas [561], and recovery of vegetation from decades of elk herbivory (Figure 6.2.3.5). A subsequent forage analysis indicated that the proposed restoration area could support >500 bison, but researchers specifically documented that collateral ecological impact on native species, or human social effects were not evaluated [562]. In 2017 an experimental population of 16 bison were reintroduced. The environmental assessment referenced Indigenous peoples only in reference to potential archaeological site impacts by wallowing bison [563]. By summer 2024 the population was >140 with an annual rate of increase of >25%. As with Yellowstone's bison herds, grizzly bear and wolf predation is insignificant. Bison densities now exceed 5/km$^2$ on winter range for the period October to June. Official long-term population objectives remain unspecified with potential ecological and social impacts of various bison population levels under investigation. Active Indigenous participation in the project is now ongoing [119] with a traditional harvest of ~3 bison in November, 2024.

Figure 6.2.3.5. Bison cows and young calves moving up the Red Deer valley, Banff National Park in May, 2021. Parks Canada had burned this area twice in the previous 20 years. Historically, this ecoregion (6.2.4-Canadian Rockies) was at the western edge of bison range [22] with low-densities of bison (Figures 6.2.1.4, 6.2.3.1). Indigenous use of fire was likely important to maintain valley-bottom bison habitat [122,317,558]. Early journalists only sighted <100 bison within the mountains in several trips into this and adjacent watersheds between 1800 and 1850 [109]. Narrow valleys, deep snowpacks and Indigenous hunting likely limited bison numbers [22,35,500]. Most ecological effects will likely occur in spring when high densities of bison are restricted to valley bottoms prior to snow melt at higher elevations. CW photograph.


Figure 6.2.3.6. Coyote Creek meadows in the Red Deer valley Banff National Park in 2002 (a.) and b. 2023 (b.). Aspen had not regenerated to >2m height here since the 1940s. Parks Canada burned these slopes at least twice between 1994 and restoring bison to the region in 2016 [119]. Saplings did not reach >2m in height until elk densities declined to <1 $km^2$ in ~2005 due to a combination of wolf, bear and cougar predation and human hunting in nearby out-of-park areas [561]. Proposed restoration population targets for bison of >100 for this area [562] will likely again limit aspen regeneration and potentially impact nearby valley-bottom fescue grasslands (visible in the background of the earlier photograph). CW photographs.

# 6.3 The North

## 6.3.1 North Overview

Figure 6.3.1.1 shows northern ecoregions [418] overlaid by the north-northwest and north-northeast transect locations. Figure 6.3.1.2 shows locations of eco-cultural biomes for the area, and locations of select Indigenous groups for the historic and/or current period. Broadly, the north has a central intrusion of boreal and mixed plains, a wooded extension of the Great Plains to the south and occupied historically with high densities of bison to the south, but declining northward (Figure 6.3.2.4a). On the west is the mountainous coastal salmon region, with numerous rivers with productive fisheries flowing into the northern Pacific including the Stikine and the Yukon (Figure 6.3.2.4c).

Morgan [99] described three broad bison movement patterns on the northern plains: 1) western herds that wintered in the Rocky Mountain foothills and moved eastwards out onto the plains in spring (described in Section 6.2 above); 2) central herds that wintered in the aspen parklands and boreal mixed-wood north of the plains, and moved southwards onto the plains in summer, and 3) eastern herds that wintered in the woodlands near Lake Winnipeg and southwards near the Red River, and migrated westward out onto the plains in summer. Although this places the summer population center for this current species of bison on the grasslands of the Great Plains, the *Bison* genus has a long affinity with north. Bison are well adapted to cold conditions, and snow depths up to a meter, and can persist in a range of habitats from tundra to forests to wet meadows. Over the Pleistocene epoch evolving bison species ranged from northwestern Europe, east across the steppes, over the Beringia land bridge and into the steppes of North America. As recently as >3-10K years BP (sources vary) the Eurasian steppe bison (*Bison priscus*) still occupied Alaska and northern Canada and apparently interfaced with *Bison bison* near the Peace River in Alberta [564–566]. Why did these bison disappear? Why the modern bison not disperse northwards to take its place? These questions may be partially evaluated with the historical dataset.


Figure 6.3.1.1: Northern ecoregions [80,81] overlaid by center lines for north-northwest and north-northeast transect locations. See Table 5.1.1.1 for ecoregion descriptions and sample sizes.


Figure 6.3.1.2: Main eco-cultural biomes for the northern area and the general location of homelands for select Indigenous groups for the historic and/or current period.

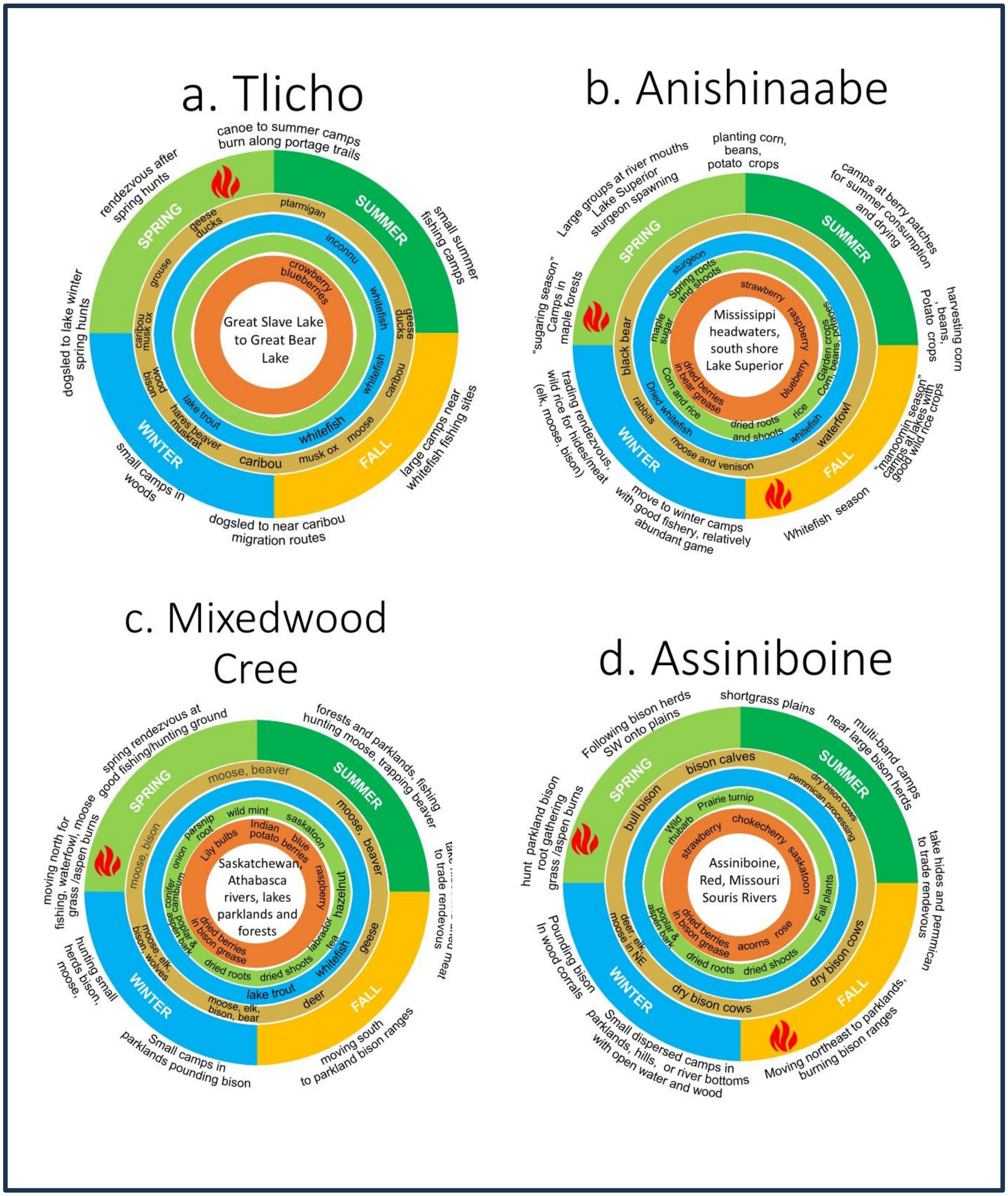



Figure 6.3.1.3: Seasonal rounds of resources used for 4 Indigenous groups and regions: a. Tlicho [567,567], b. Anishinaabe [568–571], c. Mixedwood Cree [56–58], d. Assiniboine [572,573].

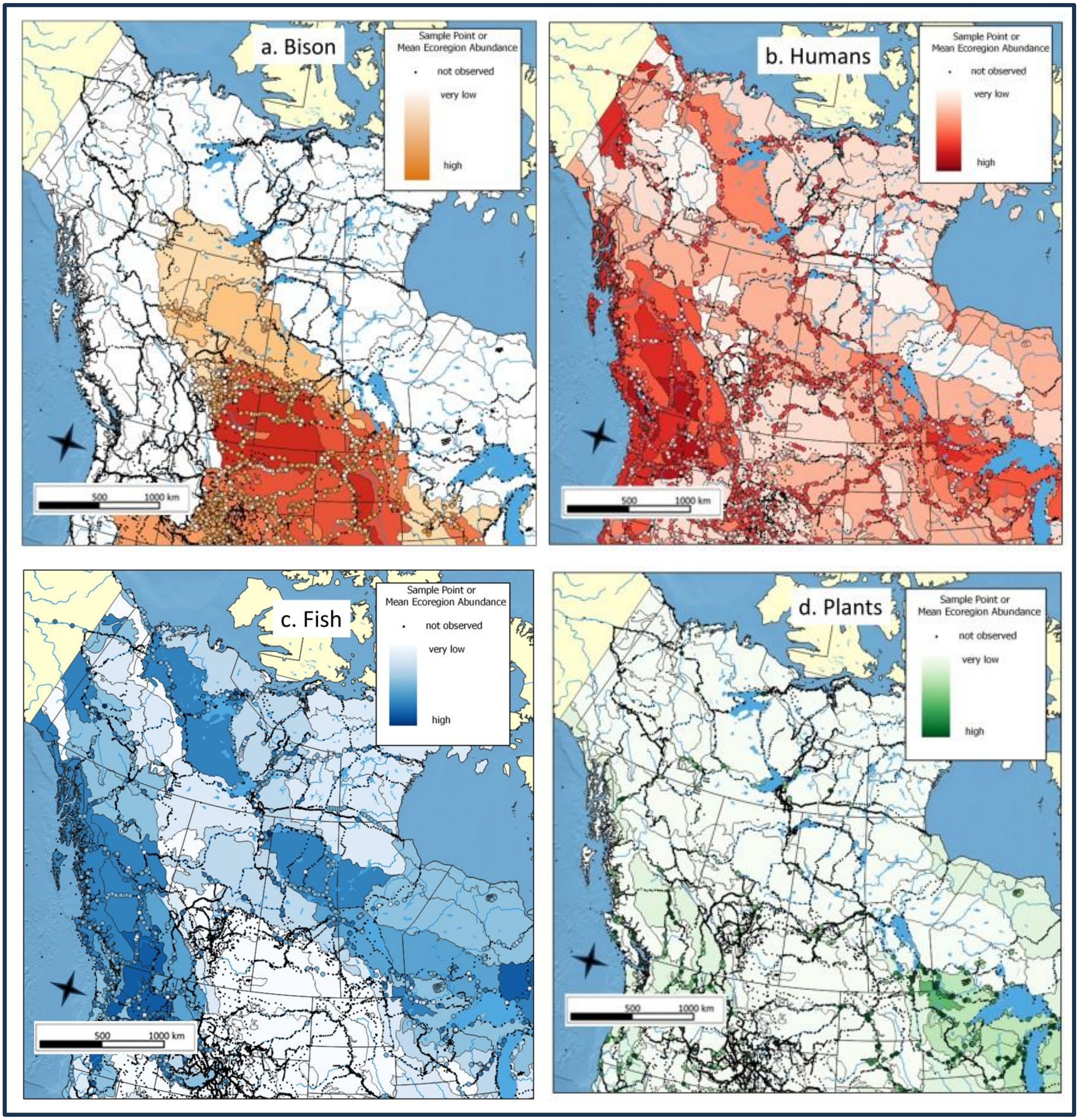



Figure 6.3.1.4: Average daily abundance indices from historical journal observations for a. bison, b. humans, c. fish, and d. plants observed in historic journals for the northern area of bison range.

## 6.3.2 North-Northwest (NNW) Transect

This transect runs NNW (Figure 6.3.2.1.) along the eastern edge of the Cordillera from source bison populations on the grasslands of the Great Plains in the upper Missouri and Saskatchewan river basins, though moderate to low bison densities of the Peace, Slave, and Mackenzie rivers to areas that historically likely had no bison in the Cordillera on the headwaters of Laird and Yukon rivers. Average ecoregion species abundance indices are mapped (Figure 6.3.1.3) and graphed (Figure 6.3.2.1).

### *NNW high abundance region*

On the NNW transect, bison were most abundant in the High Plains (9.4.1), Northwestern Glaciated Plains (9.3.1) and Aspen Parkland and Plains (9.2.1) ecoregions. These areas have high grass cover, low tree cover and relatively low numbers of Indigenous peoples (Figure 3.2.1.2). Colpitts [408] terms this as the "Pemmican Bioregion" for here, in summer and fall, Indigenous people traditionally procured large, nutritious stores of bison meat and fats that was mixed, dried and preserved with berries for winter use. As fur traders expanded up the rivers from Hudson's Bay, Lake Winnipeg and across the plains, they traded European goods for pemmican to feed their hard-working boatmen. In the late 1700s. In early summer large bison herds would aggregate in the southern xeric mixed prairie of the region grazing on *Bouteloua gracilis*, an early-maturing shortgrass [71,99]. Human actions increased bison numbers here in three ways. Most importantly, this was an inter-tribal buffer zone between the Siksika, Piegan, Pikuni on the west, the Cree on the north, the Assiniboine on the east, and the Gros Ventre to the south [6,408]. This deterred large communal hunting groups from using it. Secondly, cultural burning was frequent here for warfare or to influence bison movements [175]. On the northern plains, these fires occur usually in spring and fall, and are driven by warm and dry winds from the southwest or southeast winds—reducing forest cover on the northern interface of the grasslands with the aspen parklands [325,332,574]. Low tree cover reduced human presence in winter, favoring use by large bison herds [172,408]. Finally, Morgan [8] proposed that Indigenous peoples that frequently using the grasslands deliberately minimized predation on beaver to maintain riparian zones and water flow that would sustain both people and bison during drought periods.

Not only did the central grassland zone and its immediately surrounding woodlands provide a refuge for bison, the quality habitat and low human predation here also sustained an abundance of herbivores like moose, elk, and pronghorn (Figure 6.3.2.5), and predators like grizzly bears and wolves [22]. In the early 1800s, Harmon [575] observed the relationship between human hunters and wolves:

> *The wolves know the effects of a discharge of a musket ; and when a hunter fires his gun, at a buffaloe or deer, in a few minutes, from ten to twenty of them will rush to the spot whence the report proceeded ; and, at some times, they are so pinched with hunger, that while standing beside his game, it is with difficulty that the hunter preserves it from being devoured by them* (pg 420 in 1820 version).

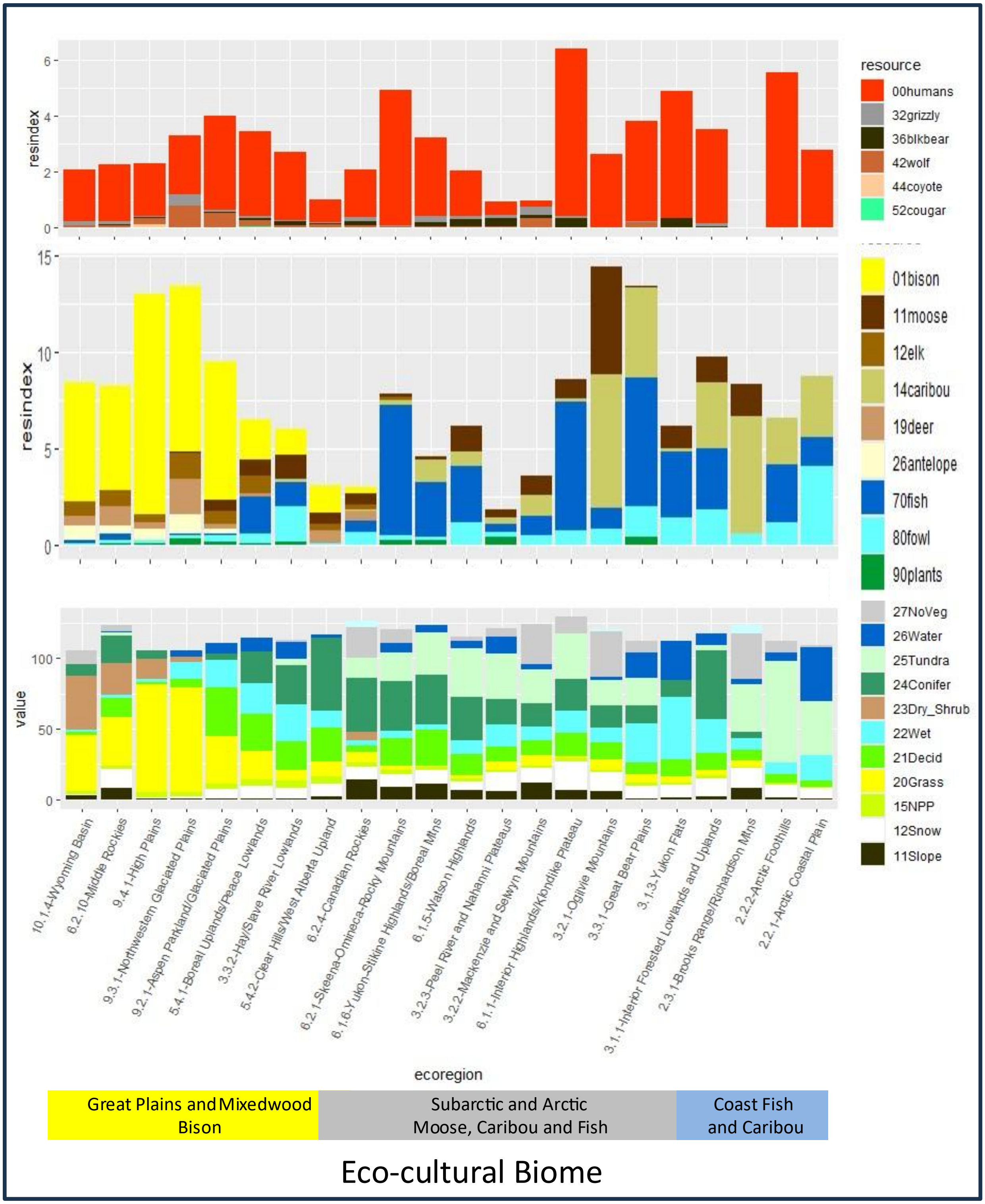



Figure 6.3.2.1. North-northwest transect average ecoregion biophysical values and resource abundance indices. See Table 4.1 for variable descriptions and Table 5.5.1 for ecoregion descriptions and journal observation sample sizes.

### *NNW migration and dispersal patterns*

Several historical and ethnological studies describe bison migratory patterns to the north-northwest [6,36,99,172]. As noted above, bison were attracted to early green-up of grasses on the central plains and remained here in large groups until the fall. In winter, many herds in the central plains moved northwards into the aspen and mixed-wood forests near the North Saskatchewan River [99]. European traders termed this the "rising of the buffalo", and recognized this depended on the severity of the winter and depth of snow [408] and Indigenous burning [172]. A fall burn would remove forage and block bison movement [172] whereas areas burned the previous spring and early summer would have rejuvenated forage that might attract bison northwards [315]. Once bison entered the aspen parkland ecoregion (9.2.1, Figure 6.3.2.1) they encountered the winter camps of Cree and other peoples and were herded into wooden "pounds" by communal hunts that caused high mortality. When large herds came in off the plains, they might pass right through this periphery of human camps and continue further into the forests to the northwest. Here, the predominance of humans, and other predators lay to the south, but Woodland Cree might pursue and herd bison further north into their homelands (Figure 6.3.2.2). In the winter of 1755, fur-trader Anthony Henday observed this pattern of human and bison movement while camped in the parklands near SW of today's Edmonton, Alberta [576]:

> *January 11, 1755: Moderate freezing weather, travelled none, killed 2 beaver; the winter has set in in earnest…*
> *January 13: Travelled none. Indians employed hunting: killed 6 buffalo, saw many going Westward…*
> *January 17: … this day pitcht 10 M to ye westward, here we travel as the Cattle Goes*

Once in the mixed woods, bison would be hunted and dispersed into lower densities, and possibly become relatively non-migratory, and would not move back towards the plains in the spring [36].

This pattern of bison dispersal west and northwest driven by humans may have been interrupted by the establishment of permanent fur trading posts along the North Saskatchewan River after ~CE 1790. Hudson's Bay Company trader James Bird in a letter to fellow-trader James Pruden wrote in January 14, 1814 that:

> *It has occurred to me that the great scarcity of Buffalo latterly experienced in these upper settlements has been, in a great measure occasioned by the situation of Carleton House. The Indians form an almost uninterrupted Line from that place to you and thereby render it impossible for the Buffalo to obtain access to this River.* [577]:202

### *NNW low to moderate abundance region*

Bison dispersing northwards entered a massive tongue of plains covered with a mix of forest, marshland and small meadows with relatively low bison density, that extends >1000 km north to Great Slave Lake (Figure 6.3.2.1). On the south, this was Cree territory, here a mix of plains and boreal cultural traits (Figure 6.3.2.3c) [56,57,99,315]. Further north are the vast mixed-wood ecoregions (e.g., 5.4.1 Boreal Uplands/Peace Lowlands and 5.4.2 Clear Hills-Northwest Alberta Uplands, 3.3.2 Hay/Slave River lowlands) where grass cover and bison abundance declines substantially, and deciduous forest (aspen and poplar), wetlands and conifers increase (Figure

6.3.2.5). Human numbers (Cree and Dene nations) were relatively low, sustained by fish, fowl, and moose, and hunting bison when it was available [217,567,578]. Routine use of fire was likely important to maintain connected grassland bison habitat to high bison density areas to the south. A broad swath of relatively frequent fire (20 to 80-year fire frequency, Figure 5.2.1.1) existed along the northwest transect from Edmonton northwards towards to Great Slave Lake (Figure 3.2.1). Mair [579]:78 traversed this area in 1899, reporting that north of Lesser Slave Lake:

> *There is reason to believe that vast areas at present under timber were once prairies, fed over by innumerable herds of bison whose paths and and wallows can still be traced in the woods. Indeed, very large trees are found growing right across these paths, and this fact, not to speak of the recollections of, or traditions, of very old people, points to extensive prairies at one time rather than to an entirely wooded country.*

Historically, routine Indigenous burning in early spring likely maintained this corridor [217,218,315], but large recent wildfires in 2001 and 2011, where spring drought, hot temperatures, and strong southeast winds drove burns over 50 km from northwest of the Athabasca River towards Lesser Slave Lake [574,580] show that regional biophysical factors are also important. Further north and west Leverkus et al. [581,582] describe historic fire regimes and vegetation mosaics favorable to bison, other large herbivores, and numerous other species.

Historic bison densities were very low in some heavily wooded areas along well used travel routes. For example, in May 1791 Alexander Mackenzie advised Philip Turnor that there were few bison along the main Rocky Mountain portage route, and that Philip Turnor should follow the Christina River to the west to obtain meat. Turnor's [583,584] journal describes no bison along frequently travelled routes, but low densities of hard-to-hunt bison on nearby rivers. In contrast, two intertribal buffer zones had moderately high bison abundance [109]: 1) Slave River- Samuel Hearne in 1772 [583], Mackenzie in 1789 [219], Peter Fidler in 1791/92 [583], and others report numerous bison along the Slave River south Great Slave Lake in Dene territory that was being routinely raided by the Cree to obtain captives during this period; and 2) Peace River Prairies- In 1793 Mackenzie [585], followed by several other traders [217] describe abundant bison on the grasslands of the Peace River in the buffer zone between the Cree and Saulteaux to the east and the Sekani (Tl'azt-en) peoples to the west (Figure 6.3.2.2). These bison herds were distant from the large herds on the plains, and due to smaller herds (less competition), and different habitat conditions developed morphologically into the wood bison ecotype [40].

The broad zone of low to moderate bison density did not persist after European contact, and as James Hector observed in 1858 [198,586], this was one of the first large areas on the continent where bison where early extirpation occurred. Although Hector's Indigenous informants attributed bison's demise to a widespread wildlife disease, lack of corroboration elsewhere makes this suspect. More likely was the over-killing of bison after ~CE 1790 to supply the small fur trade posts on the Peace River prairies [217], and Fort Chipewyan, the major emporium of the north on Lake Athabasca [587]. As described above, it is also possible that Indigenous bison hunting and more intense use of fire adjacent to trading posts along the North Saskatchewan started to block the bison dispersion northwest from the plains [172,577].

### *NNW edge of range and beyond*

The historic limit of bison's range on the north correlates with taiga ecoregions (Figures 6.3.2.1) with decreasing grassland cover, and the abundant fisheries lakes of the Canadian Shield, Athabasca Lake, Great Slave Lake, and the river systems and deltas associated with this fishery (Figure 6.3.2.4). The Dene cultures here were highly skilled fishers [567,578] with great skill in obtaining fish even in the winter[488]. These societies such as the Tlicho also had access to moose, abundant caribou to the north and other smaller game such as fowl, beavers, and hares (Figure 6.3.2.3a). Fed by these alternate resources, these people would kill the few bison that dispersed northwards and were a highly preferred source of meat and hides. The edge of bison range is partially demarcated by the Mackenzie-Slave-Athabasca-Churchill rivers canoe trade route, used to the north by the Dene, and to the south by the Cree. These people were master birch bark canoe builders, using them to rapidly access almost all streams and lakes, and to transport meat and hides back to central camps. Bison's size and value to humans made it prime prey near this waterway.

Further to the northwest, these adverse conditions for bison continue, and intensify near the salmon-bearing streams such as the Yukon, or along the Arctic and Pacific coastlines. During much of the Holocene these northern regions were occupied by steppe bison (*Bison priscus*), originally connected to a large Eurasian source population by the Beringia land bridge and overlapping with the modern plains bison's ranged as far south as near the Peace River [588,564] in the early Holocene. Over the last 10K years the vast open meadowlands of steppe vegetation have gradually shrunk [589]. Figure 6.3.2.5 shows that modern ecoregions are dominated by a complex pattern of boreal forest and wetlands at lower elevations, and tundra, rock, and ice in higher areas. Over time, human numbers have increased [590,591], dependent on fisheries, caribou and moose (Figure 6.3.2.4). The combination of changing habitat and intensifying human predation likely led to the extinction of the steppe bison and blocked the dispersal of modern bison further northward. However, if human mortality sources are managed, modern bison can be successfully introduced into areas with favorable habitat in the Yukon and Alaska [22,592].

### *NNW mutualistic interactions*

The historic presence of bison along NNW transect is one of the clearest examples of a potential human-bison mutualism zone on the continent. Here a combination of variable human hunting, burning, and perhaps facilitated mutual benefits to both bison and humans.

*<u>Herding and movement corridors</u>*- As described above, bison migrating northwards were observed being followed by Indigenous groups encamped at the edge of the plains. In spring, Woodland Cree bands moved north back into mixed-woods to fish and hunt [57]. Possibly a traditional use pattern was to encourage bison to move northwards as far as possible into their homelands. Also, as described above, the Cree burned movement corridors in the spring along the Athabasca and Peace rivers which could have facilitated bison herding [218]. Is it possible that the Cree restricted their spring hunting of bison moving north to protect the resource for subsequent use? Another hypothesis is that pre-contact Cree traders travelling rapidly by canoe down the Athabasca, Slave, or other rivers in their vast territory periodically transplanted bison calves into more northern areas. Whatever the mechanism, low densities of bison extended well north-northwest of high

densities of bison on the plains. This range rapidly contracted southwards in the early 1800s, simultaneously with hunting to supply fur trade posts, and Cree territory contraction southwards.

*Community-scale interactions*- Clearly many ecological communities were dependent on native people's role in the burning large areas between the stable grasslands in the south and the northern edge of bison range. The 20-80 year fire frequency (Figure 5.2.1.1,[593]), often created by Indigenous spring burning [144,218] maintained not just meadows for bison habitat, but numerous forage species for humans and other species.

*Beaver conservation*- Indigenous people's conservation of beaver may have been higher on the prairies on the south end of this transect, but less moving northwards. Traders report that the Assiniboine and Gros Ventre on the plains were poor beaver hunters, preferring to take wolves, foxes, and buffalo robes [224]. Archaeological sites on the northern plains show little evidence of Indigenous beaver use [8]. The northern Cree and Dene nations were excellent beaver hunters--providing the mainstay for the European trade. By the mid-1800s intensive harvesting had depleted beaver numbers across vast boreal areas [105,152].

*Population and biome-scale regulation* – Based on the human herding and community-level interactions described above, it is possible that a NNW massive area—possibly up to 6 ecoregions between the northwest grasslands and Great Slave Lake —had a persistent bison population due to a process of human-bison mutualism that can be summarized as follows:

- Low human presence on the northern Great Plains due to lack of wood and other resources allowed high growth rates of bison;
- Human burning ("the fires of spring") maintained prairies and corridors of high-quality habitat from the Great Plains on the south north to the Peace River. Most of this land under control of Cree;
- Winter snows stimulated the "the rising of the buffalo" where they moved northwards off the plains into the parklands. Here, humans would surround them on the south, moving them further northward into the fire-created northern corridors and smaller prairies.
- Bison could persist in inter-tribal buffer zones where mortality rates were low such as occurred along the Peace and Slave rivers in historic period. If bison were locally extirpated, they would be replenished eventually from another wave from the Great Plains to the south. In addition, small herds might not be detected if they remained at low densities away from human travel routes.
- Indigenous hunting of the steppe bison likely played a role in its extinction and certainly influenced connectivity from high quality habitats on the lower Yukon River to its southern range boundary on the lower Liard and middle Peace rivers. Human's mutualism role here for modern *Bison bison* would then be a case of "apparent competition" [131,594,595] where the actions described above, combined with hunting of steppe bison possibly tipped the balance in its favor of the southern species.

### *NNW modern analogs*

Bison populations have either been maintained or restored in many NNW ecoregions. Bison densities further northwards decline likely due to lower grass cover, and higher rates of predation mainly by humans, but also wolves, grizzly and black bears.

_Buffalo National Park at Wainwright (BNPW)_- The Government of Canada's first major bison conservation effort took place in a national park of ~511 $km^2$ established in 1908 to as rangeland for bison purchased from Pablo Allard in Montana and moved north into Canada by in railway cattle cars [556]. Although located in the Aspen Parkland (Ecoregion 9.3.1) the area was predominantly sand ridges, "poor grass", "scrubby poplar", and "ground cedar" unsuitable for cultivation agriculture-- conditions of an ecotone to the Northwestern Glaciated Plains (Ecoregion 9.3.1) to the south. Brower [596] provides further details on the rise and demise of the conservation herd. With winter feeding and an absence of predation from Indigenous people, wolves, and bears, numbers expanded rapidly from the original 748 bison transferred to the park between 1909 and 1912 to over 2000 by 1916. During the period 1922 to 1932 the population ranged between 4242 (8.3/$km^2$) and 8832 (17.8/$km^2$). At the bison population peak, the park also held 30 moose, 368 elk, and 1293 deer. Government scientists recognized a wildlife over-population crisis with damage to the habitat and declining bison health and size. Heavy grazing and trampling in the early spring were particularly damaging by removing new grass shoots, causing water erosion, and favoring weed-growth. The serious overpopulation and a lack of political support for slaughtering the surplus forced BNPW to transfer bison north to Wood Buffalo National Park. Many of these animals were infected with bovine tuberculosis. Due to ongoing serious declines in range forage quality and quantity, the "Buffalo Park" at Wainwright was closed in 1939. Brower [596]:189 summarizes a newspaper report that encapsuled the effort:

> *…the journalist suggested that the effort at one time occurred under natural conditions, evidence shows that from the onset there was nothing natural about the Buffalo National Park effort to conserve the bison. One of the few conservationist principles followed by the park was to grow the herd as rapidly as possible, and this directive had disastrous consequences. In fact, the effort to protect the plains bison cannot be considered conservationist at all. Rather than ensure the permanence of the plains bison, management decisions made throughout the park's existence threatened the very future of the species.*

_Grasslands National Park (GNP)_- The park lies in the Northwest Glaciated Plains (Ecoregion 9.3.1, Figure 6.3.2.1), in southern Saskatchewan. This was historically a high abundance ecoregion for bison (Figure 6.3.2.5). In 2006 an initial herd of 71 bison was released into a 181 $km^2$ paddock on the west side of the park. The herd is managed by capture and removal at numbers of 400-500 (~2.5 bison/$km^2$), but bison typically use only the northeast portion of the park during summer (~42 $km^2$, or >10 bison $km^2$) [528]. The park website [597] explains population management:

> "*This target allows the park to prudently manage its herd according to the lowest biomass production predictable for the area (i.e. the poorest environmental conditions), while ensuring long-term retention of genetic diversity. Bison were initially reintroduced to restore the historic 'grazing regime' of large herbivores in a portion of the West Block of the park. Bison grazing, in combination with fire, creates a diverse mosaic of habitats, which can benefit many grassland species.*"

Historically domestic stock apparently stripped most riparian zone vegetation from along the Frenchman River. This has recovered in some pastures outside the park, but within the park current bison stocking levels are likely too high for willow and poplar recovery [270,554]. No substantial beaver activity is currently evident on satellite images or recorded in research accounts.

*Elk Island National Park (EINP)*- The national park lies in the highly productive Aspen Parkland ecoregion (9.2.1, Figure 6.3.2.1) near Edmonton, AB, maintaining both plains and wood bison ecotypes in a total fenced area of 194 $km^2$ with few wildlife predators. The 2006 survey on the park's main paddock (134 $km^2$) counted 959 animals (476 bison, 72 moose, 333 elk, and 78 deer) for a density of ~7AU/$km^2$. Managing herbivore densities at this (or even higher levels in past times) has impacted upland plant communities, beaver, songbirds, and likely deer and moose [274,598–600]. These studies indicate that although EINP staff routinely ignite prescribed fires, herbivory and fire interact to reduce beaver abundance. Fire and herbivory also interact to degrade, not enhance traditionally used plant resources such as berry-producing shrubs, but this requires further investigation. However, all these studies recognize that the parkland ecoregion vegetation communities in EINP are exceptionally productive, and the observed rates of herbivory will not likely cause irreversible ecosystem trends.

Figure 6.3.2.2. Bison in Elk Island National Park. Individual populations of wood and plains bison ecotypes are managed in separate paddocks that maintain genetic diversity. Herbivory in combination with prescribed burning impacts vegetation, beaver, and associated species [274].

*Prince Albert National Park (PANP)*- About 300-400 bison occupy ~1000 $km^2$ of the SW corner of the park (density <0.35 bison/$km^2$) with highest numbers near the park's boundary with farms and ranches [601,602]. The region is 85% forests (mostly aspen, some spruce), 10% meadows, and 5% waterbodies. The bison forage >70% in the meadows, and periodically on adjacent farmlands outside the park. Dominant forage species are a combination of grasses and sedges: *Agropyron* *spp.. Carex atherodes, C. aquafilis, Calamagrostis inexpansa, Hordeum jubarum***,** *Juncus balticus and Scolochloa festucacea*. Bison numbers appear to be limited by wolf predation within the park, and human harvest outside [603,604]. There are no reports of recent vegetation degradation, although in the 1970s the condition and extent of dry fescue meadows was of concern due to a combination of fire suppression and cattle grazing [605]. Domestic stock was removed and in the past few decades PANP staff have burned large areas of the range [122]. Meadow extent appears to have increased. Aspen and shrub regeneration, and beaver activity appear to be prolific (2020 Google Earth image).

*Cattle and Bison in Northern Deciduous Woodlands*- Moving northwards into the Aspen Parklands and Boreal Lowlands (Ecoregions 9.2.1, 5.4.1) cattle producers face an issue of sharply increasing deciduous forest and decreasing grassland cover (Figure 6.3.2.1). Historically grasslands were maintained by a fire frequency of less than 40 years (Figure 5.2.2.1), but aggressive fire suppression and forest management to produce wood fiber has decreased area burned with a current fire frequency >500 years [122,179]. Most forest removal is now done by machinery. If cattle stocking is the management objective, a combination of tilling, reseeding, and aggressive herbivory can be used to limit woody plant reproduction from remaining roots [606]. Pastures stocked at >100 AU/km$^2$ (>10-20 AUM/ha) on an annual basis will suppress growth or eliminate most woody plants, but pastures have relatively low range health with low productivity and numerous weeds [607,608]. In contrast, if wood fiber production is the objective, summer cattle stocking at ~1.0 to 4.0 AUM/ha (20 to 80 AU/km$^2$) appears to cause minor reductions on trembling aspen and balsam poplar regeneration >4m in height [609,610]. Bork et al. [611] investigated the effects of various mixes of herbivore densities (cattle, bison, elk, deer) on trembling aspen in 6-week trials in paddocks with combined stocking levels of 1.63-1.82 AUM/ha (~110-140 AU/km$^2$). The native ungulates, particularly elk and bison, had the most negative impacts on aspen saplings. Their research indicates that native and domestic ungulates appear to have different functional effects on woody plant dynamics in savanna ecosystems.

*Halfway-Sikanni*- The northern Rocky Mountains have a long history of Indigenous burning and more recent prescribed burning that maintained rangelands for bison and other herbivores [581,582]. In 1971 a herd of 48 plains bison ecotype became established northwest of Fort St. John, BC near Pink Mountain in Ecoregion 6.2.1 Skeena-Omineca-Central Rocky Mountains (Figure 6.3.1.1). Initial annual population growth rates were high (>10%). By 2006 the herd numbered ~ 1300 over 1513 km$^2$ with a management target of 1000 to 3000, managed by Indigenous sustenance and limited entry hunts [612,613]. Range expansion westward was ongoing. By 2022 the population had declined to <500 or <0.3/km$^2$ [614]. Wolf predation is rarely observed [615], but in the past Indigenous human predation rates were high in mountainous terrain at the western edge of historic range [22], and this may again be an important source of bison mortality for this herd.

*Wood Buffalo National Park*- WBNP, on the border of northeast Alberta and the Northwest Territory has the largest free-roaming bison herd in the world. In the 1800s, small remnant herds of the wood bison ecotype existed in the area. By the 1950s, subsidized with plains bison transplants from the south, the park held an estimated 10,000 to 12,000 bison [616]. The population then began to decline, and by mid-1990s had declined to <2000 due to potential combination of predation (wolves and Indigenous harvest), introduced cattle diseases (tuberculosis and brucellosis) and habitat change [617–619]. The population then began to increase, possibly due to reduced predation [238].

Relative bison habitat use has been consistent over time with generally highest densities (.208-1.661/km$^2$) on the ~4815 km$^2$ of Peace Athabasca delta grasslands and marshes, moderate densities (0.091-0.201/km$^2$) on ~5485 km$^2$ of mixed meadows and forests along the Slave River, and low densities (0.01/km$^2$) in 18,180 km$^2$ uplands forests. These densities are low compared to other bison or cattle ranges. WBNP and surrounding ecoregions still have frequent fires [22,593,620]. No adverse effects from herbivory, fire, or their interaction are reported for WBNP plant communities or beaver.

Figure 6.3.2.3. Bison on the Salt Plains in Wood Buffalo National Park. Bison numbers declined rapidly in this region during the early fur trading period, but a small number or the wood bison ecotype persisted along an inter-tribal buffer zone between the Cree and the Dene nations near the Slave River. (Photo: Mike Drew/Postmedia Network).

*Mackenzie Bison Sanctuary (MBS)*- In 1963 eighteen wood bison were transplanted into the area northwest of Great Slave Lake, Northwest Territories. The population expanded to about 2400 in 1989 over a range of about 12,000 km$^2$ (0.2 bison/km$^2$) before declining to ~1900 animals. The population expanded by a cyclical pattern-- when the population density exceeded ~ 0.55 bison/km$^2$ in an existing range, animals would again disperse to expand the range, and the cycle began again. In other words, the colonization occurred through a series of increases in local areas followed by pulses of dispersal and range expansion [621]. As with other areas in NW Canada, high fire frequency continues here[122,179,620]. No adverse effects on plant communities from herbivory, fire, or their interaction are reported.

*Aishihik, Yukon Territory*- As described above, the steppe bison (*Bison priscus*) likely existed along the upper Yukon River until <3000 years BP before extinction possibly due to vegetation change and increased human occupation in the region [589,591]. The territorial government transplanted wood bison northwest of Whitehorse, YT, with the herd reaching a population of ~500 animals in 1999, and ~1470 in 2014 (~0.115 bison/km$^2$ over ~12,000 km$^2$ of range. Other ungulates on this range are moose (~0.173/km$^2$), caribou (~0.215/km$^2$), and mountain sheep (~0.063/km$^2$) [622]. At these relatively low population densities plant community impacts and direct herbivore competition for forage are unlikely due to different patterns of ungulate herbivory and habitat use [622–624]. However, bison are a popular species for winter human hunters, and some interactions could occur between wolf use of human hunter access trails, or opportunistic human hunting of non-target species (e.g., apparent competition). Possibly these types of interactions contributed to local past extirpations of bison or caribou (depending on the area) due to different pre-historic Indigenous hunting systems [132,179,625].


Figure 6.3.2.4. Aishihik bison herd in the Yukon Territory, Canada.

## 6.3.3 North-Northeast (NNE) Transect

> *These Ojibwa ate "Buffalo Rucheggan mixed with fat": what may be surprizing they traded most of it from the pedlers who had more of it than they could use, as the fire country through which they pass is so plentiful of that kind of provision.* (Fur trader James Sutherland 1785, quoted by Colpitts [408]:19).

In 1691 Hudson's Bay Company trader Henry Kelsey was the first European to see bison on the northeastern plains [110].He, like those following him recorded that the "fire country" or grasslands had many bison-- but only a short distance to the north-northeast their range ended abruptly. Historic observations repeatedly show that bison abundance declined dramatically in a northeast direction from the Red River (of the north) and headwaters of Mississippi moving into the wide terrestrial corridor between Lake Superior and Lake Winnipeg (Figures 6.3.2.4a, 6.3.3.1). Although some habitat still existed, the bison did not. This may have resulted from a combination of changing vegetation from grasslands to northern hardwoods, increasing human numbers, and a broad range of foods available for Indigenous people. However, as Sutherland observed in the quote above, the Indigenous people liked their buffalo meat, and the 1700s fur traders helped serve this demand with pemmican they carried back east.

### *NNE high abundance region*

The Northwestern Great Plains and Glaciated Plains (Ecoregions 9.3.3, 9.3.1, Figures 6.3.3.1) had numerous bison and would likely be the source population of any bison moving to the NNE. During the 1700s the region west of the Mississippi on of the Red and Minnesota rivers was likely in a buffer zone between the Anishinaabe, Assiniboine, and Lakota peoples (Figure 6.3.2.2) with productive bison herds infrequently visited by large communal hunting groups [257,468,626]. Hickerson [135,569] further describes abundant wildlife in a buffer zone between warring Chippewa (Ojibwa, Anishinaabe) and the Santee Sioux at ~ CE1750 CE in northern Minnesota.

### *NNE migration and dispersal patterns*

Information on bison movement patterns here is scanty. From interviews with Indigenous and Metis guides, accounts from Long's [627] and Hind's [626] expeditions describe a long-term pattern of large herds of bison summering in the center of the Great Plains west of the Assiniboine River that then moved in the fall to the southeast, wintering in the hills on the western side of the Red River valley. This migration pattern was possibly driven by human hunters who wintered in villages in woodlands to the east of the plains but followed the bison westwards onto the open plains each summer. The adoption of the horse by the Indigenous peoples, and later two-wheeled carts by the Metis and Sioux increased the length of these hunting expeditions onto to the plains [408], pushing bison further west. There is little evidence of bison either migrating or dispersing to the north-northwest into woodlands nearer to Lake Superior, although in the 1738, La Verendrye [490] observed bison approaching closer to Lake Manitoba and Winnipeg than in subsequent times.

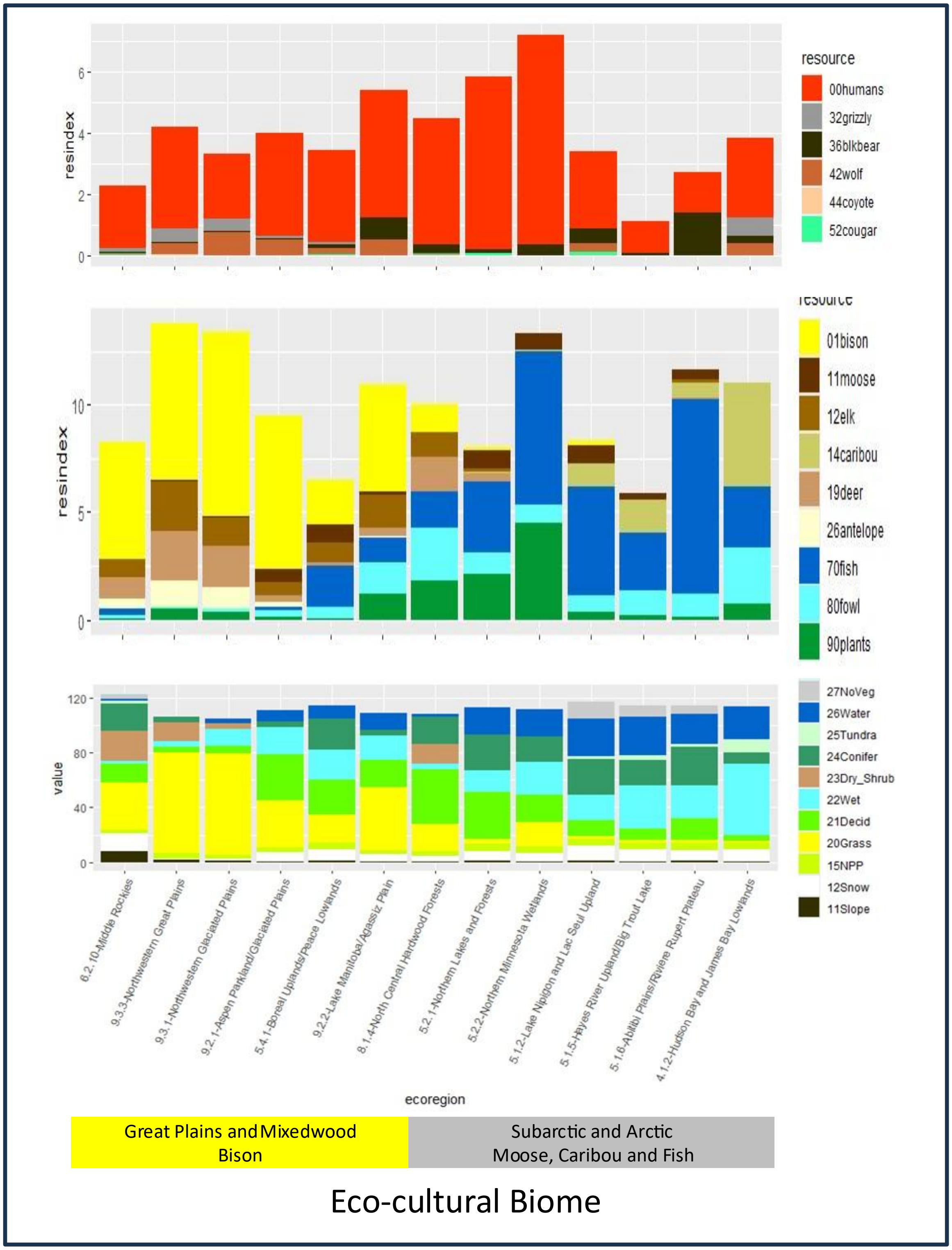



Figure 6.3.3.1. North-northeast transect average ecoregion biophysical values and resource abundance indices. See Table 4.1 for variable descriptions and Table 5.5.1 for ecoregion descriptions and journal observation sample sizes.


Figure 6.3.3.2. A view from near the Custer Black Hills expedition camp along the Cannonball River on July 6, 1874 (Devereux Library Archives, Illingworth-803) and the same scene, now near Heil, North Dakota on July 6, 2008 (photograph by Paul Horsted with permission from Page 51 in *Crossing the Plains with Custer* by Paul Horsted with Ernest Grafe and Jon Nelson, Custer, SD: Golden Valley Press, 2009). The historical image shows a riparian zone lightly impacted by herbivory, but likely frequently burned.

### *NNE low to moderate abundance region*

Unlike the NNW transect, the NNE does not a large area of low to moderate densities of bison. Only the North Central Hardwood Forests (ecoregion 5.2.2) had low historic bison abundance, with only traces of bison in ecoregions further to the NNE (Figures 6.3.2.4a, 6.3.3.1).

### *Edge of NNE range and beyond*

Although grasslands extend into NE hardwood forest and northern Minnesota wetlands (ecoregions 8.1.4 and 5.2.2), historical bison presence was negligible (Figure 6.3.3.1). The sharp edge of bison range here possibly is related to unique ecosystem conditions—these ecoregions hold many resources for abundant people-- wild rice, small corn fields, white fish, sturgeon [628–631]. Moreover, rice and corn were easily stored and then traded with bison hunters such as the Lakoda and Cheyenne on the edge of the plains  [468]. This likely increased both the number of hunters and the intensity of their bison predation rate. Assuming a few dispersing bison did permeate further into this zone, the Canadian Shield ecoregions to the NNE had very little bison habitat, and many lakes and waterways that made most the landscape easily accessible to Cree in canoes (Figure 6.3.3.3). These people were sustained by fish, low densities moose, caribou and black bear, and in tough times, hares and grouse [125,488]. Any bison approaching from the southeast would likely been methodically tracked and killed.

Figure 6.3.3.3: Woodland Cree village in 1880 at Oxford House, Manitoba. (Robert Bell, Geological Survey of Canada, National Archives Canada). Bison did not occur here likely due to poor habitat quality and high densities of humans using the waterways in ecoregions along the southern edge of Canadian Shield.

### *NNE mutualistic interactions*

Humans-bison- There is little historical evidence of historic human-bison mutualism along the NNE transect. After the 1600s, both the Dakota, then the Anishnaabe (Ojibway) advanced towards the bison herds on the plains on the upper Mississippi [468,630,632]. The buffer zones between these antagonistic nations provided some refuge from human predation. Indigenous people here lit fires along the transect that provided habitat bison and other species [285,633,634], but high densities of Indigenous hunters fed by alternate resources described above may have made these areas ecological traps. At a landscape and population level, the width of the low to moderate bison abundance zone was possibly too narrow for interactive population-scale management of bison.

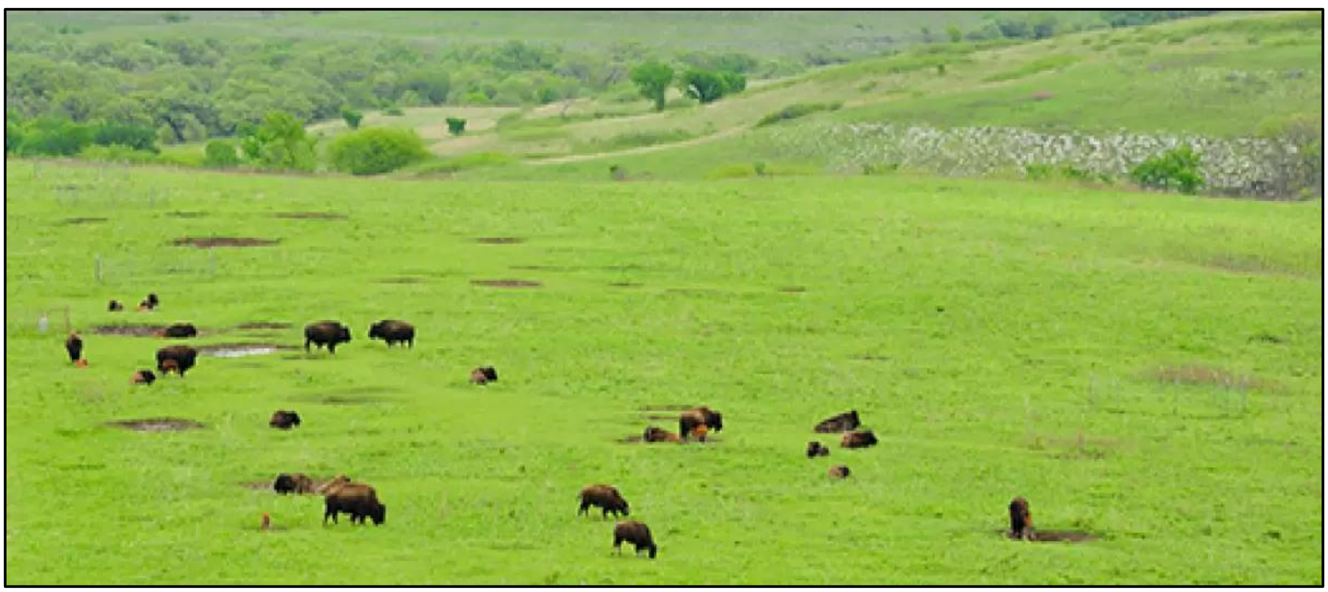
Beaver conservation- Humans had intimate knowledge of beaver ecology along the northeast transect. In the south, beaver influenced the water levels and vegetation cover near ponds and shallow lakes used by the Anishnabbe and  other peoples for the harvest of wild rice [635–637]. Feit [638] describes use of traditional knowledge by the James Bay Cree to transplant beaver to restore populations in trapped-out regions.

# 6.4 The East

## 6.4.1 East Overview

Figure 6.4.1.1 shows eastern ecoregions [418] overlaid by the northeast and southeast transect locations. Figure 6.4.1.2 maps the three main eco-cultural biomes for the area-- Great Plains Bison, Northeast Hardwoods and Conifers, and Southeast Conifers and Piedmont, and locations of select Indigenous groups for the historic and/or current period [11,12,306]. Seasonal rounds for four eastern Indigenous groups (Figure 6.4.1.3) show a strong dependence on the “three sisters”—corn, beans, melons—for at least part of the year for groups near or east of the Mississippi River [246,247,639–641]. Eastern Indigenous peoples routinely used fire to prepare agricultural fields, and maintain native cultural plants and wildlife habitat [70,640]. Moving further west, the Sioux, Cheyenne, Osage and others ventured out on the plains to obtain bison [46,59,642].

The east region had a broad interface with the plains along the Mississippi River with a central intrusion of grasslands into the modern Kentucky, with a gradient of high bison on the plains declining to the east (Figure 6.4.1.3a). Ecoregions along the Mississippi River, Gulf of Mexico and along the east coast had high human abundance, sustained by abundant fish and plant resources (Figure 6.4.1.3b-d). Further, as described above in Section 5.4.2, the east experienced a series of major human depopulation and re-distribution events in the late pre-contact and contact periods [400] that favored bison expansions into the region, and may have resulted by 1700 CE with one of the broadest distributions of the species during the Holocene. Figure 6.4.1.4 maps abundance indices from historical journal observations for humans, bison, and fish and plant resource use.



Bison herd grazing on tallgrass prairie at the Konza Prairie Biological Station in the Flint Hills (ecoregion 9.4.4) of Kansas. This ecoregion has very high productivity, providing carrying capacities >20 AU/km$^2$ for ranchers during a period of spring-early summer grazing, and relatively high year-round stocking for conservation bison herds. Historically the region had low to moderate densities of bison likely due to Indigenous harvesting. Photo Credit: Barbara Van Slyke


Figure 6.4.1.1: Eastern ecoregions [80,81] overlaid by center lines for northeast and southeast transect locations. See Table 5.1.1.1 for ecoregion descriptions and sample sizes for historical journal observations.

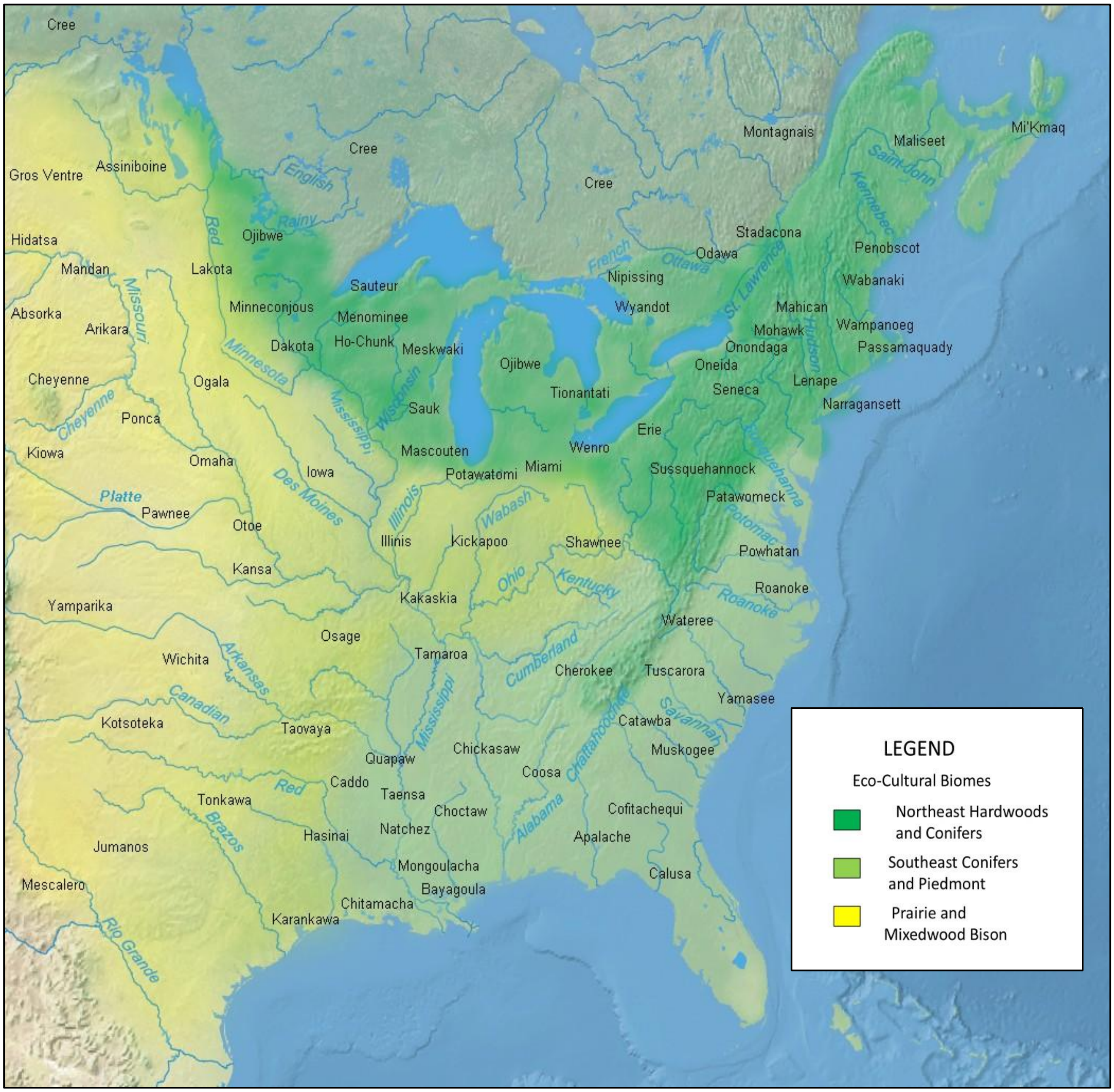



Figure 6.4.1.2: Main eco-cultural biomes for the eastern area and the general location of homelands for select Indigenous groups for the historic and/or current period.

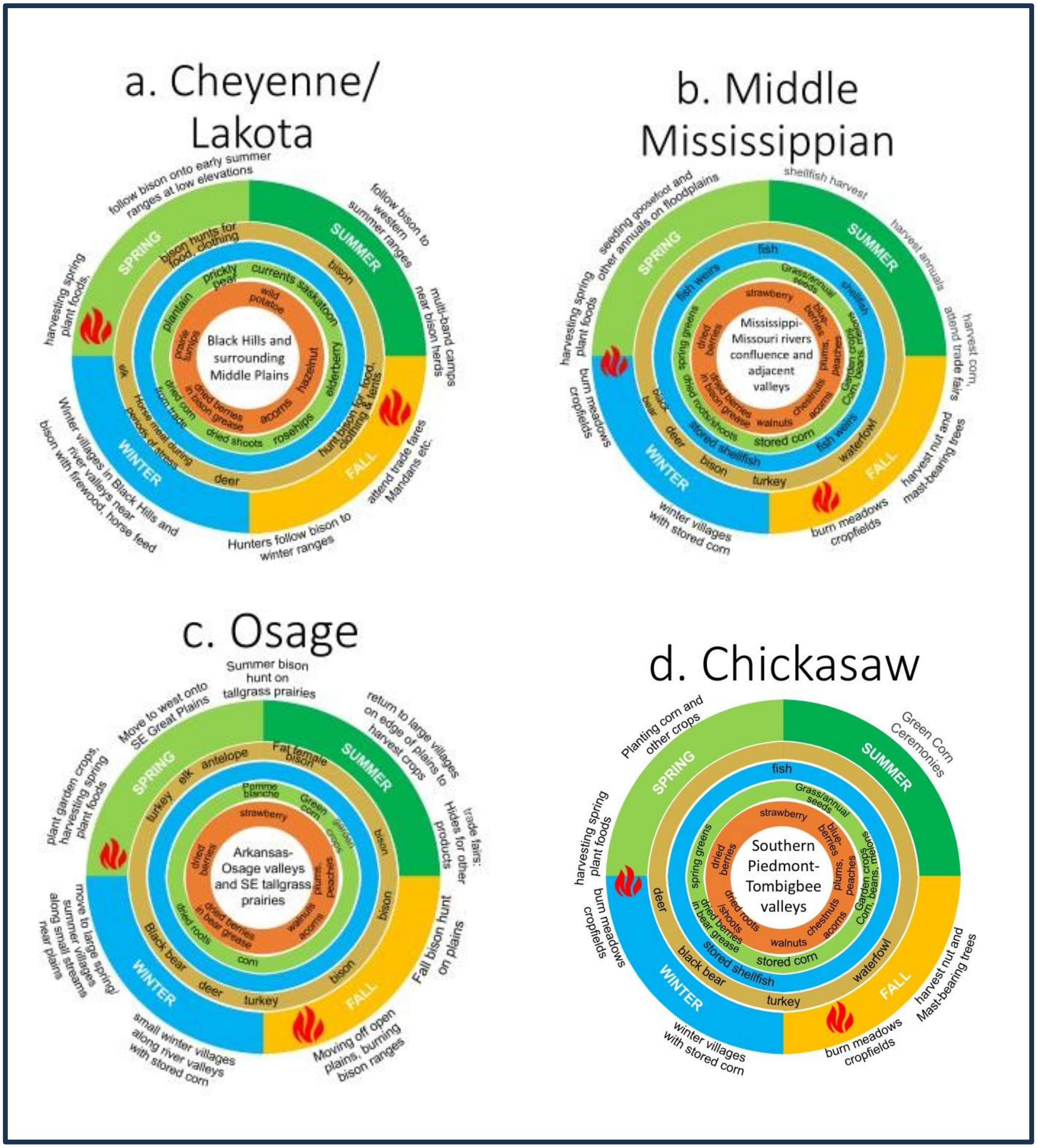



Figure 6.4.1.3: Seasonal rounds of resources used for 4 Indigenous groups or regions: a. Cheyenne and later the Lakota Sioux in the Black Hills and surrounding central plains [46,643–645], b. Middle Mississippi peoples [246,247,641,646,647], c. Osage on the southeastern Great Plains [59,642,648–651], and d. Chickasaw on the Southern Piedmont and Tombigbee valleys [246,646,647,652].

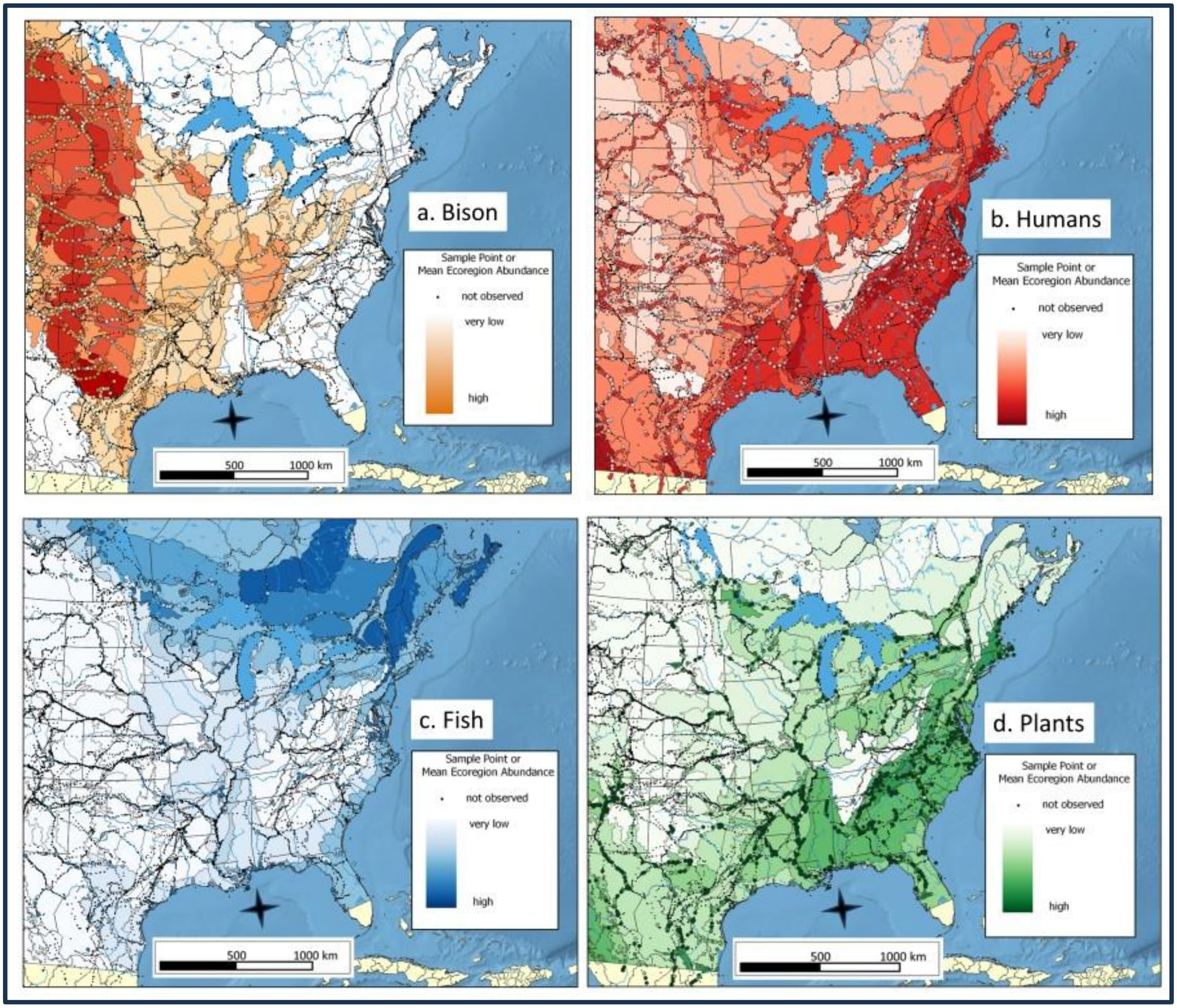



Figure 6.4.1.4: Average daily abundance indices from historical journal observations for a. bison, b. humans, c. fish, and d. plants observed in historic journals for the eastern area of bison range.

## 6.4.2 Northeast (NE) Transect

The NE transect runs from high abundance bison populations on the the prairies of upper Missouri River eastwards through a broad tallgrass plains-hardwood forest ecotone with moderate bison densities near the Great Lakes, Illinois, and Ohio, then across the Appalachian Mountains to New England's Atlantic coast (Figure 6.4.1.1). Average ecoregion abundance indices are mapped (Figure 6.4.1.4.a-d) and graphed (Figure 6.4.2.1). The northeast had an early, strong human population decline, followed by great population changes as several nations moved westward in front of an Iroquois expansion. These cultural convolutions may have created unique conditions for bison moving eastward far into the Great Lakes and western Appalachian region [61,250]. Although many researchers believed that grassland habitats were relatively rare across the NE (e.g., Sanderson and Boyer for Manhattan [653]), the past few decades of assembling traditional and historical knowledge, combined with dendrochronological studies show that fire and grassland cover was relatively abundant [70,339,654].

### *NE high abundance region*

The closest large source population for bison expansion to the northeast was five ecoregions of the northwest and central great plains (9.3.3, 9.3.1, 9.2.1, 9.4.2 in Figure 6.4.1.1) of the broad prairies along the lower Missouri above its confluence with the upper Mississippi (near modern-day St. Louis). During the early historic period, this region was the western side of a circle of war zones as the Sioux-Lakota tribes expanded westwards [46,467,468] . To the north lay their enemies the Cree, Sauteur and Assiniboine [655]. To their west were the Arikara along the Missouri. Southwards and eastwards were their foes the Nadoussioux, Mesquakies, and Mascoutens [468]. When these fissures between nations lay adjacent to high densities of bison, the herds could move east with minimal hunting pressure.

### *NE migratory and dispersal patterns*

Like the pattern reported for the north-northeast on the Red River (Section 6.3.2), in winter bison likely moved eastwards to wooded areas along the Missouri, Minnesota, Des Moines and Mississippi rivers although this needs documentation from historical observations. Cold, snowy conditions could push bison into or even through the territories of Indigenous peoples wintering here. In these zones people could herd them off the plains and into wooded areas or sheltered valleys safer for human travel, and where communal hunting pounds using combinations of wood fences and terrain were possible. If so, bison annual movements in the NE partially followed patterns of communal bison hunting reported on the headwaters of the Yellowstone, Missouri, and Saskatchewan rivers in the northwest (Section 6.2.3). For example, in his military survey report for September, 1855 Warren [655] describes the Sioux using the terrain on the southern edge of the Black Hills to contain a bison herd for their upcoming winter hunt:

> *they were encamped near large herds of buffalo, whose hair not being sufficiently grown to make robes, the Indians were, it may be said, actually herding the animals. No one was permitted to kill any large bands for fear of stampeding the others, and only such were killed as straggled away from the main herds. Thus, the whole range of buffalo was stopped so that they could not proceed south, which was the point towards which they were travelling. The intention of the Indians was to retain the buffalo in their neighborhood till their skins would answer for robes, then to kill the animals by surrounding one band at a time..*

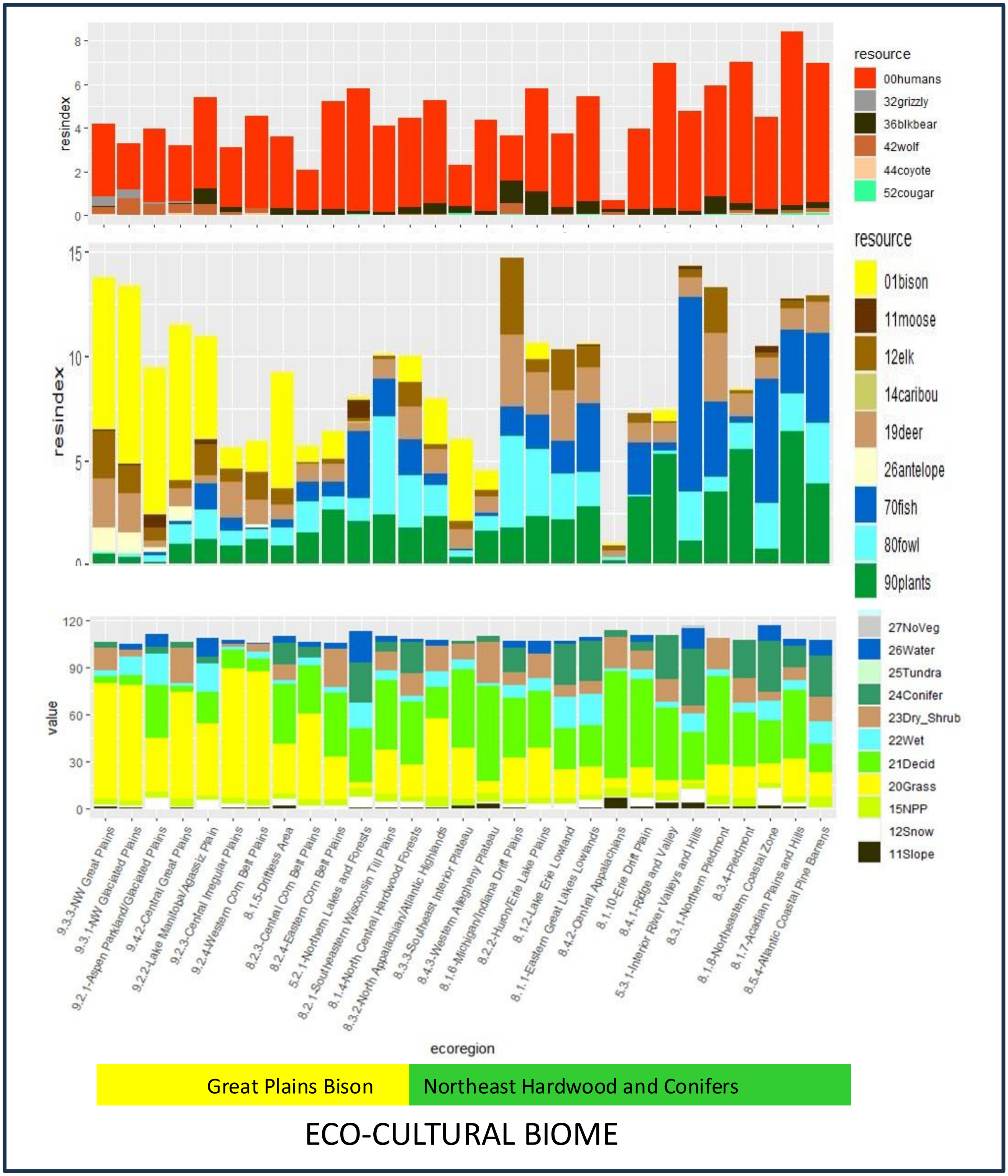



Figure 6.4.2.1. Northeast transect average ecoregion biophysical values and resource abundance indices. See Table 4.1 for variable descriptions and Table 5.5.1 for ecoregion descriptions and journal observation sample sizes.

Morrissey [61] proposes that periods of drought on the central shortgrass and mixed grass prairies were important in "pushing" bison eastwards and northwards into the tallgrass. Drought and fire could both interacted to increase the palatability of tallgrass, and helped reduce growth of woody species, thus favoring bison movements eastward. A further factor that could have favored vectors for bison movements south-eastward from the plains towards Lake Michigan was the establishment in the 1600s of two deadly (for humans) buffer zones between the warlike Lakota and other nations- one zone to between groups in the north (Assiniboine, Assinnabe (Ojibwa), Cree and another to the south between groups to the south (Oneida, Illinis, Iowa) [468,569,632]. Abundant bison from the west entered these buffer zones, and with less human predation, survived to colonize regions further east. Then as they advanced further to the southeast, Haynes [182] describes evidence of how bison linked rich habitats:

> *Bison trail systems are well known east of the Mississippi River-- in fact, some were used by white settlers to lay out early roads and rail lines long after the bison were gone. The trails are imprinted in landscapes where animals regularly sought optimal resources by periodically re-distributing themselves nonrandomly. One very visible trail system connecting resource megapatches is preserved today as the Buffalo Trace in Indiana, also called the Vincennes Trace and Clarksville Trace, where US Route 150 follows it. The Natchez Trace Parkway from Mississippi to Tennessee is laid out along another old long distance bison trail.*

An interesting idea is that these trails, presumed to be long-term "natural" migration were, like the Indigenous herding of bison near the Black Hills described above, routes for people hazing bison herds east for harvest and trade.

#### *NE low to moderate abundance region*

During the period post ~900 CE, a broad area of low to moderate bison density (Section 5.4, >5 ecoregions, Figure 5.4.1.1d) spread eastward towards the Appalachian Mountains [61,250]. Historic observations show some ecoregions had moderately high bison abundance such as 8.1.5 Driftless Area and 8.3.3 Southeast Interior Plateau. Three phenomena may be interacting here: 1) Early human depopulation due to collapse of Cahokia and the middle Mississippi cultures, followed by epidemics and warfare after ~1500 CE [360,656,266,357]; 2) indigenous burning that created grasslands [657] , and 3) Inter-tribal buffer and warfare zones which may favor both fewer people and lighting of more intense and frequent fires. How these changes interacted to allow bison to spread eastwards would be complex and location-specific, but bison could spread east anywhere a source population was adjacent to expansive grassland habitat and relatively low human predation risk. One hypothesis for bison expansion into the Driftless Ecoregion is that the collapse of the Middle Mississippi created intense warfare zones around remaining villages that were lightly hunted but frequently burned [658].

The epitome of bison diffusion eastwards were the herds recorded by early European travellers in the mid-1700s [659,660] on the Southeast Interior Plateau (Ecoregion 8.3.3) — today's Kentucky grasslands. Archaeologists term this landscape "the vacant quarter" for the period ~1300 to 1700 CE, and Delcourt and Delcourt [246] hypothesize that the collapse of the Mississippian culture here was created by overuse of woodlands, intensive agriculture and other factors. This cultural collapse left a large area of cultured grassland, lightly used by humans, and colonized by bison dispersing from the west.

*NE edge of range and beyond*

The ecological and cultural conditions of the northern Appalachian Mountains limited bison's eastward expansion (Figure 6.4.1.4a). Patterns of Indigenous land use and culturing were significant [246,661], the area of grasslands decreases, valleys are narrower, and for any bison that did permeate the mountains, their hides and meat would have exceptional value to Indigenous and European hunters otherwise limited to mainly deer and black bear. Moreover, high densities of people along the east coast who were sustained by fish and plants (Figure 6.4.1.4b) had demand for hides and meat supplied through long-standing Indigenous trade routes across the mountains, first to neighboring nations, and later to the Dutch and English colonies. Again, mainly deer and some beaver were central to the "skin trade" [200], but any bison encountered at the edge of their range would be preferentially taken due to volume of meat and quality of the hide.

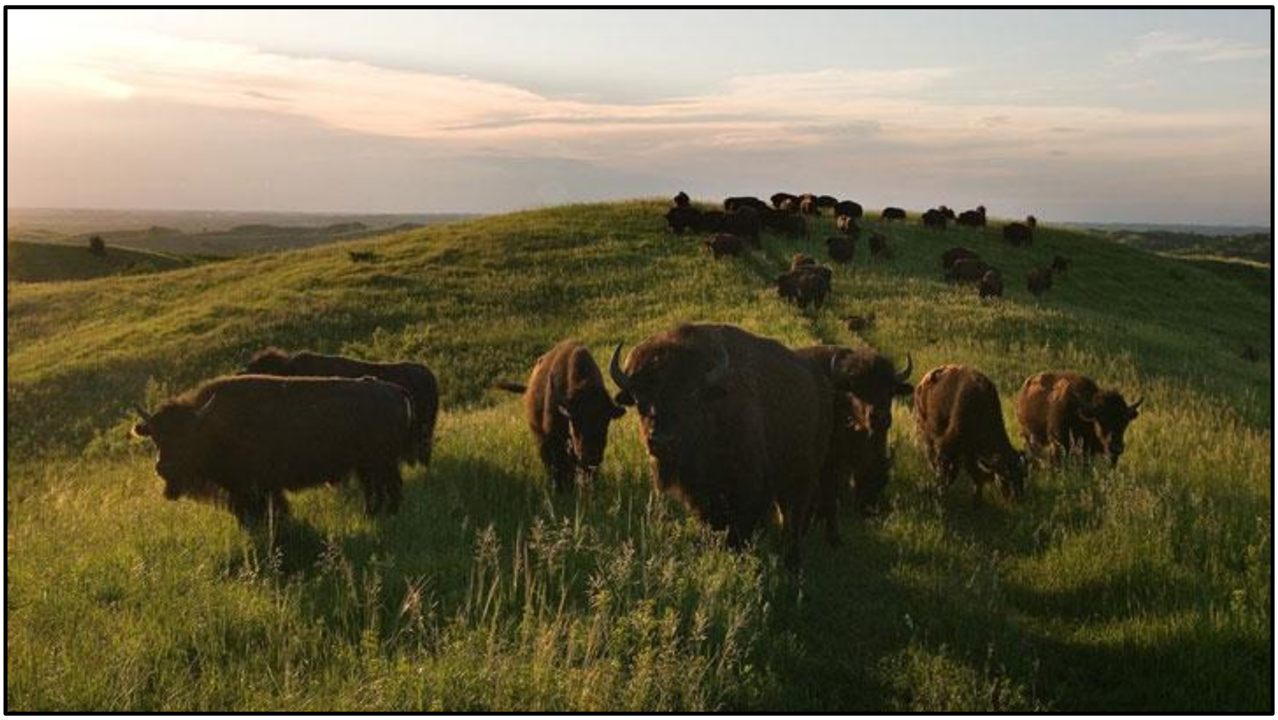


Figure 6.4.2.2. Bison in the Loess Hills of Iowa (photo Chris Helzer, Iowa Natural Heritage Foundation). The Nature Conservancy is working its Broken Kettle Grasslands Preserve and partnering local ranchers to maintain >30,000 ha of tallgrass prairie on the western edge of the state. Historically, although this ecoregion (9.2.3 Central Irregular Prairie) was highly productive, it may have had only moderate densities of bison (Figures 6.4.1.4a, 6.4.2.1) due to Indigenous hunting and its proximity to downstream population centers.

## 6.4.3 Southeast (SE) Transect

The SE transect reaches from abundant historical bison populations on the on the prairies of today's Texas and Oklahoma across the watersheds of the Arkansas and Red rivers to the Mississippi, then eastwards over the southern Allegheny Plateau and Appalachian Mountains to the Atlantic piedmont and coast (Figure 6.4.1.1). Average ecoregion abundance indices are mapped (Figure 6.4.1.4 a-d) and graphed (Figure 6.4.3.1).

The historical journal database [109] holds ~850 observations for 6 expeditions into the southeast region prior to 1600 CE (Figure 6.4.2.3a): 1528-32 de Vaca [204,205], 1539-42 de Soto [208,209], 1559-61 de Luna [399], 1565 Hawkins [662], and 1566-68 Pardo [663]. These daily accounts provide evidence of numerous Indigenous peoples of many nations (Figure 6.4.1.2) largely subsisting on maize with some deer and fish (Figure 6.4.1.3). As Allen [2] well-described in his 1876 analysis of bison range, although people along the edge of the region had bison hides, and recounted about bison presence to the north and west, the journalists did not observe any live bison on these early southeast trips. Over the next century, Indigenous populations declined precipitously across the southeast due to combination of disease, warfare, and slave-taking [360,66,400,361]. In contrast, bison numbers increased, and by the 1686 Delgado expedition [664] the buffalo spread across the south as far east as Florida [18,665,66], and for the next 7 decades bison were seen routinely near the ridge and south of the Appalachians (Figure 6.4.2.3.b). Where were the source populations for these bison? How did they spread so rapidly across the south?

### *SE high bison abundance region*

Historical journal observations place the closest high abundance area for SE bison in the Great Plains ecoregions (9.4.1 High Plains, 9.4.6 Edwards Plateau, and Central Great Plains 9.4.2) with high grass cover and low human density (Figure 6.4.2.2). Moving eastwards, bison abundance declined even as net primary productivity of the tallgrass prairies increases [69]. Possibly bison mortality increased due to higher numbers of Indigenous peoples in a more diverse landscape of mixed grasslands, dry shrublands, and woodlands. This rapid decline of bison density was a long-standing situation, evident in archaeological sites for the period CE 500 to 1700 ([67], see Figure 5.4.1.2 above) and earlier in time [362]. During the historic period, the seasonal round of the Osage Nation (Figure 6.4.1.3c) created hunting pressure along this eastern edge of heavily used range [642].

### *SE Migratory and dispersal patterns*

Allen [2] describes that on the central southern plains, bison "never moved more than a few hundred miles" to the south in winter, and returned north or northwest in the summer. Near the eastern edge of densely occupied range, bison possibly either moved east in winter on their own accord into wooded areas or were perhaps herded in this direction by Indigenous hunters. For example, during a September-October, 1719 trip north of the Red River, de la Harpe's party ignored advice of their guide, and attempted to hunt an isolated herd of bison in the Quachita Mountains [666]. They were immediately attacked by local people that likely had a propriety interest in the animals and that may have even herded them from the west for winter use.

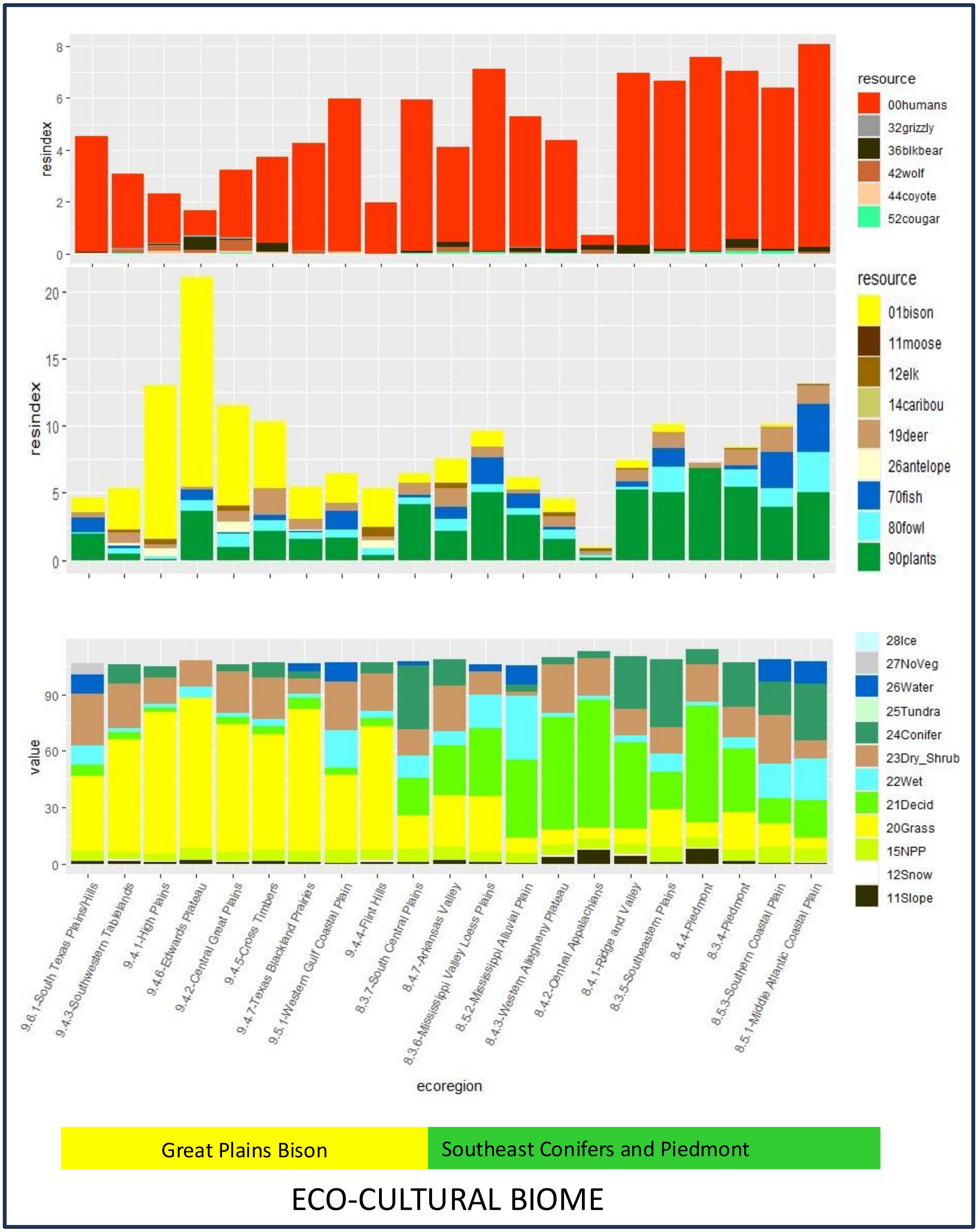



Figure 6.4.3.1. Southeast transect average ecoregion biophysical values and resource abundance indices. See Table 4.1 for variable descriptions and Table 5.5.1.1 for ecoregion descriptions and journal observation sample sizes.

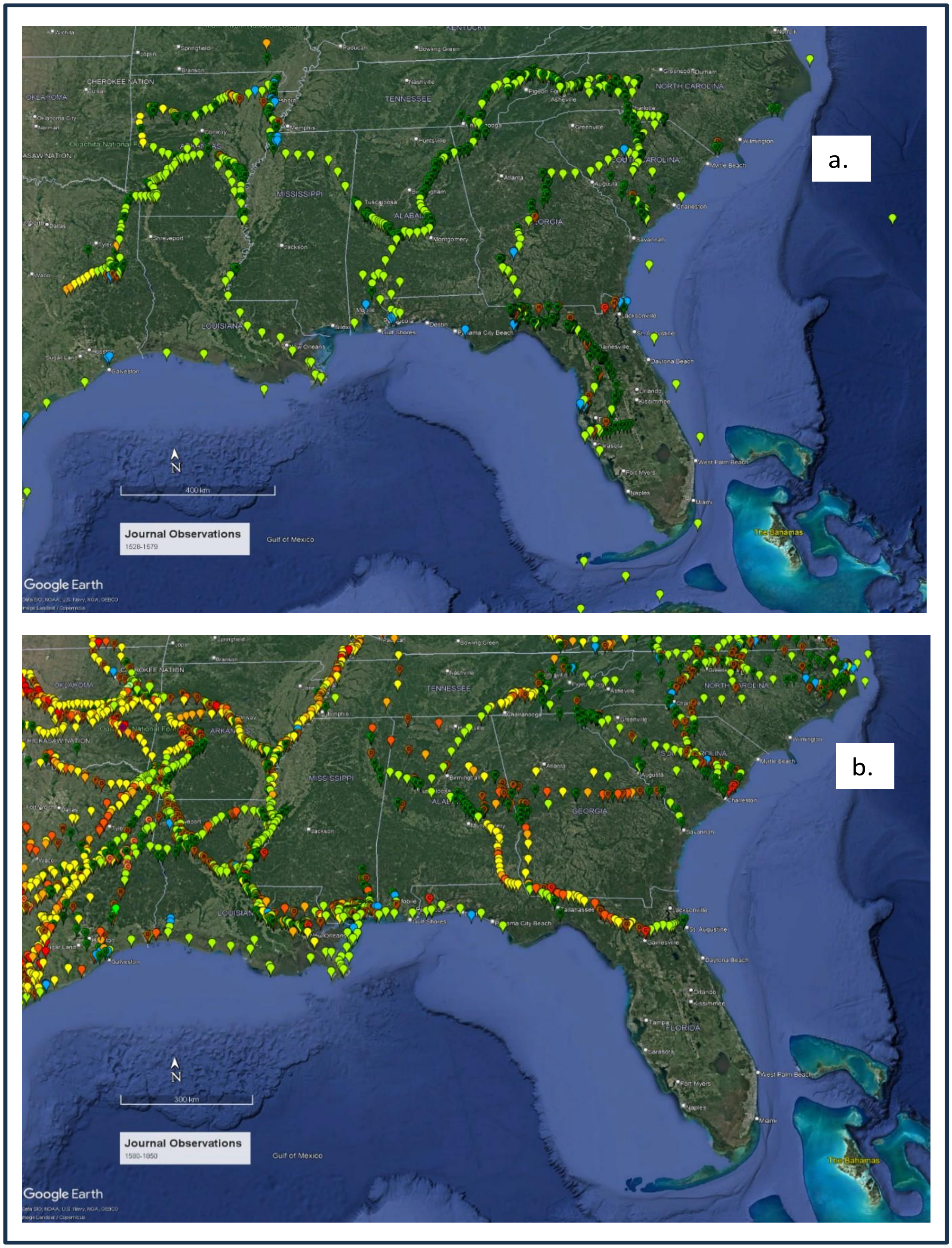



Figure 6.4.3.2. Historic journal bison observations (red and orange markers) for the Southeast region for the periods: a. before CE 1600 and b. after CE 1600. Yellow indicates potential bison range but no bison observed, light green markers indicate southeast locations generally outside of bison range with no bison or other resources observed. See Journal Observations database for other codings and individual traveller routes and data [109].

Prior to ~1300 CE it is unlikely that southeast bison dispersing east could persist for sustained periods in the lower Missouri, Arkansas or Red River valleys. For the dense societies of people along the Mississippi River, Smith [113] describes that long-term sustainability followed a general pattern of:

> *1) a primary reliance for protein on a set of animal species and species groups (deer, fish, migratory waterfowl) that combined both a high biotic potential and relative immunity from over-exploitation; and 2) a coherent and integrated overall strategy of restructuring vegetation communities in ways that enhanced and expanded the habitats of many plant (and some animal) species that were important sources of food and raw materials*

The further dispersal of bison across the Mississippi and eastward was likely triggered first by an early Indigenous depopulation (~1300-1500 CE) along the middle Mississippi that reduced human hunting and allowed bison nearer to the river, followed by a further major depopulation (~1570-1670) that favored bison's crossing of the river valley and into Appalachian watersheds [66,362]. An intriguing hypothesis is that Indigenous peoples may have even captured and transplanted bison calves to establish new herds in pastures and villages south and east-- nearer to Spanish, French and English trade houses that purchased bison's meat, smooth hides, robes, and even their woolly hair (see Section 6.4.4 below).

### *SE low to moderate abundance region*

The SE area is unusual in that by the early 1700s it has a broad area of 9 ecoregions that have relatively low bison abundance (Figures 6.4.1.4 and 6.4.2.2) at long distances from the source population to the west. These ecoregions have relatively high forest cover, many alternate resources for humans (plants, fish, fowl, deer), and apart from 8.4.2 Central Appalachians, relatively abundant people. In other areas (e.g. west, northwest, north-northeast, ecoregions with this low number of bison usually be rapidly hunted to extinction. Three conditions could favor small bison herds: 1) relatively broad and intensely-observed buffer zones between Indigenous villages, and particularly between Indigenous groups and European settlements engaged in taking slaves [66,361], 2) frequent infusions of bison either through dispersal or movements, or possibly Indigenous introductions of semi-domestic bison from the west (see above) along with European cattle from the east, and 3) routine burning to maintain grasslands and shrublands [70]. Indeed, during his 1716 expedition from the Florida coast to the Apalachicolos along the Chattahooochie River, Diego Pena observed mixed herds of branded cattle and bison in depopulated areas with frequent meadows and shrublands [667,109].

### *SE edge of range and beyond*

Prior to ~ CE1500 bison range in the southeast was west of the Mississippi valley, and even after its major expansion eastwards to its maximum range ~1700 CE, bison did not reach the Atlantic Ocean [2]. Numerous people, first Indigenous then European, sustained by fisheries and plants (Figures 6.4.1.4 c, d, 6.4.2.2) had high demands for meat and hides. In coastal ecoregions, only low numbers of white-tail deer could persist under this level of human predation (Figure 6.4.2.2), so ancient Indigenous trade routes reached across the Appalachians to further supply the demand for these products [668,669]. This pressure from coastal societies, combined earlier with middle Mississippi cultures had probably long restrained bison movement east coast.

### 6.4.4 East Region: Potential Human-Bison Mutualistic Interactions

Is there evidence of a long-term mutualistic relationship between humans and bison along the eastern edge of their range? A simple answer would be no--- even though there was ample habitat, Indigenous hunting clearly made it impossible for bison to reach the Atlantic Coast, or before CE 1600, even much of the Mississippi River valley. However, a more complex relationship might be, like other regions around the bison frontier, there were varying areas, at least a few decades where humans created a mutualistic habitat and a predation regime. Here, at least for a time, the numbers of both people and the buffalo were relatively stable—each species supporting the other. Likely over the long-term archeological studies [67,362] indicate this mutualistic zone was on the eastern side of ecoregions in the oak savanna on the edge of tallgrass prairie (from north to south: 9.2.3 Central Irregular Plains, 9.2.4 Western Corn Belt Plains, 9.4.4 Flint Hills, 9.4.5 Cross Timbers, 9.4.7 Texas Blackland Prairies, Figure 6.4.1.1).

#### *East: Bison herding, containment, domestication and escapes*

The Great Lakes and western tributaries to the Mississippi River provided an efficient way for Indigenous peoples to move bison products, and even live bison eastward. Fleets of long dugouts that had long plied these waters [406]. In 1673 Joliet and Marquette [401] observed while on the Mississippi:

> *"canoes all in one piece, fifty feet long and three broad, in which three men can embark with all their baggage. They manage it more elegantly than we do ours. They have such a large number of these that in a single village one sees as many as 180 together."*

Clearly people could transplant bison (orphaned calves) at will. The early French settlement of the Mississippi was economically driven by a plan to employ Indigenous peoples raise and harvest bison to supply the European hide market. The plan proposed by La Salle was to establish a tannery on the lower Ohio River, then use barges to move the heavy hides downstream. As historian Richard Gross [670] describes, La Salle clearly recognized that the freight could not go upstream back to Canada:

> *Their plan all along was to ship furs down the Mississippi River. He (La Salle) explained that shipping buffalo hides back to Canada through the Great Lakes would be altogether impossible. Use of canoes was not economically feasible because each canoe could only transport twenty bison hides per trip. The value of the hides would not even cover the expense of the canoe and men.*

To me it seems logical that earlier cultures would use their fifty-foot canoes in a similar way to move hides, meat, and even live bison downstream. Urban centers such as Cahokia [358] would, like subsequent European cultures, have a high demand for these products-- and Indigenous peoples clearly had the water transport to deliver them. It is entirely likely that similar many other examples in Indigenous North America, bison were moved and domesticated closer to these centers of demand, and escapes facilitated routine sources of bison dispersal across much of the east. The tribes may have managed these eastern bison carefully, but this changed in times of war. For example, La Salle writes:

> *The Oxen are becoming scarcer since the Illinois have been at war with their neighbors, as both sides kill them and hunt them continually*. ( [666]Vol2:97)

Indigenous peoples near the coast appear to have may raising both bison and cattle. Pena, on his trip though Florida and Georgia frequently encountered both species. For ~Sept 8, 1716 near the St Johns River, he records:

> *On the prairie there were seen more than three hundred cattle [rezes,] buffalo and a few cows. Five buffalo, two cows and eleven deer were killed. I wish to mention the characteristics of buffalo and domestic cattle. Be it known that the difference is slight between the buffalo [cibolo] and cattle [rez bacuiia]. There is however difference, in that cattle have hair, and buffalo, wool. The horn of the buffalo is small and thick, resembling those of a goat. The buffalo is high in the forequarters, but similar, and breeds just like cattle. Now the flesh is better than that of the cow, the fat is thinner and is tinged with flavor of mutton*. ([667]:18)

After the great human depopulation events of ~CE 1500s occurred, these types of human-bison mutualism likely led to the rapid major range expansion towards the coasts of the Atlantic and Gulf of Mexico.

### *East: beaver conservation*

Like other peoples on the plains, Indigenous nations occupying the eastern edge of the plains where bison were relatively abundant appear to have recognized the importance beaver in maintaining sources of water [8]. Trader Jean Baptiste Truteau ascended the lower Missouri River 1794-95 and recorded that the tribes on the Cheyenne River and its region— the Kiowa, Arapaho, Pawnee, and Cheyenne did not know how to trap or dress beaver [225]. A Cheyenne traditional story warns against sickness caused by eating, or even touching beaver [671]. Grinnell [226] attributed the beaver's sacred status with the Cheyenne due to its link with water:

> *The beaver was reverenced to some extent… no doubt because of the intelligence which was attributed to it, from the fact that beaver built dams to raise waters streams, and houses to live in. It is said that in old times beavers were not often killed, and that no Cheyenne woman would dress or even handle a beaver skin.*

Similarly, the Osage Nation living on the southern plains told an origin story that:

> *A snail living on the banks of the Arkansas River married a beaver's daughter. They became the ancestors of the Osage living on the river. Therefore, until the very late days of the beaver trade the Osages had no part in it.* [672]

Further east, archaelogists have recently began to recognize that beaver dams and ponds may have been important in the formation and maintenance of Alabama's black prairies where corn was raised [673].

### *East: community scale interactions*

A combination fire and herbivory created the "shoreline of grass" well-described by Morrissey [61]:20-42 for the transition from the tall-grass prairies to eastern woodlands. This oak savanna ecotone was a broad zone of interaction where human burning and hunting could theoretically regulate both bison and human habitat and numbers. This region roughly approximates the warmer and dryer sites in the 10 to 30-year fire frequency zone mapped in Figure 5.2.1.1.

Dendrochronologists such as Abrams, Guyette and Stambaugh have, over the last few decades, greatly refined our understanding of human's role in determining the fire frequency and season of burn in these oak savannas [290,650,674,675]. Brose [283] synthesized numerous tree-ring studies on the ecology of oaks. Collectively these showed a pre-settlement mean fire interval of ~13 years, shortening to ~6 years during periods of European settlement, and after 1900s increasing to >40 years. Nearly 80% of fire scars are in the dormant period (fall, winter, spring) suggesting human ignitions, and this matches the early traveller's observations on the season and cause of fires (Table 5.2.1.1). Compared to dense oak forests, repeated fires, regardless of season, and combined with carefully managed grazing can greatly increase the forb and grass groundcover and biodiversity [94,676–678].

Historically this regime of fire and herbivory at the edge of tallgrass prairie provided a rich range of plant resources for traditional human use, bison, and other wildlife. For example, the seasonal round of the Osage near the confluence of the Canadian and Arkansas rivers (Figure 6.4.1.3c) including a diversified food supply of nuts (walnut, pecan, chestnut, walnut, hazelnuts), berries, papaws, lily roots, deer, elk, bison and bears, hardwoods such as walnut, hickory, pecan, chestnut, hazelnut, and oak source of nuts, berries and papaws, lily roots, yonkapin (wild lotus root), and deer, elk and sometimes bison, and bears. Crops of corn and gourds were also important [59,642].

*East: biome or large population scale regulation and stability*

The tallgrass prairie on the eastern edge of the Great Plains is the productive grassland in North America [69,679]. Clearly Indigenous burning helped maintain it by nutrient recycling and reducing and removing woody plants such as oaks and juniper [680,681]. Likely due to human predation bison abundance was not as high here as on the drier mixed and shortgrass prairie to the west, but the habitat was there for periods of necessity such as drought. Thus, this eastern "shoreline of grass" may have had continental significance for human-bison mutualism through the through two key regulatory mechanisms with feedback described in Section 2.4.3 above: 1) variable human predation on bison, and 2) variable habitat management dependent on fire use and herbivore density. Is there evidence these mechanisms occurred along this eastern ecotone?

<u>Variable Predation</u>- There is ample evidence that the human-bison predation pattern east of the Mississippi and Missouri rivers would help to stabilize both bison and human numbers. Each spring, Indigenous peoples from the Red River of the North to the Red River of the South (Figure 6.4.1.2) would leave their winter camps, and travel--sometimes in large groups--westward into the heart of summer buffalo habitat on the grasslands (Figure 3.1.1.1). From north to south, examples of people following this seasonal round included the Assiniboine [572], Crow [222,519], Lakota [46,468,632], Pawnee [682], Kansas [666]V6.9:410-450, and the Osage [59,642]. Depending on the Indigenous group, these annual human hunts might occur after planting crops near their villages, then loading up provisions (e.g., pemmican, corn) on dogs in earlier times, horses in later, and going up streams or across country in search for bison. The location of the hunt and number of bison taken would likely fluctuate depending on bison distribution and abundance with less bison taken when bison were further from the Indigenous camps on the edge of the grasslands. Core bison numbers would remain in the center of the grasslands, but surplus growth would be harvested on the edges.

Variable Habitat Management- Similarly, Indigenous fire use could be adapted to maintain an optimal zone of woodlands on the eastern edge of the range. Likely fire use was carefully constrained in southern regions to maintain some woodlands but fire frequency increased during times of warfare as per the fire history studies described above. Further north, fire use likely had to be more aggressive to maintain an optimal cover of woodlands that provided winter habitat for both humans and bison and might attract bison to freshly burned areas.

### 6.4.5 Eastern Region Modern Analogs

Few bison populations have been restored in eastern biomes or on the eastern edge of bison range. However, the existing restoration efforts for both grasslands, fire, and bison are informative. Here I review a potential source population area for the eastern region (Black Hills) and tallgrass prairie studies in long-term moderate abundance regions.

#### *Black Hills, South Dakota*

The Sioux called the region "our meatpack" [46] and as described in Section 6.4.2 above, they were observed using the ridges and valleys of terrain adjacent to the hills to contain herds of bison for winter use [655]. The legend of abundance Black Hills wildlife grew with the accounts of the Custer's 1874 expedition and the following gold rush. With the establishment parks, this led to bison restoration in both Custer State Park and Wind Cave National Park. But was this legend of a wildlife cornucopia on the plains accurate? Unfortunately, I have yet to find a detailed first-person journal accounts from within the hills during the mid-Sioux period [109]—apparently this was terra incognita for establishment of trading posts and most non-Indigenous travellers.

The 1874 expedition of US Army into the Black Hills led by George Armstrong Custer provided a legacy of photography, and then re-photography (Figure 6.4.4.1). This was clearly a case where the camera caught up with massive cultural change. The last Sioux were just leaving the Black Hills, and due to their previous presence virtually no Europeans had entered hills prior to the 1870s. The last of their "lodge trails" are still visible in a blow-up of the old image (Figure 6.4.4.2). As researcher Charles Kay has reminded me, Illingsworth's images of the expedition are a priceless rarity for the BC era on the Great Plains— as Kay terms the time "before cows". Illingworth had excellent photographic equipment, clearly knew how to use it, and was fortunate to travel during a period of clear weather, with little smoke, which was unusual for dry season the central plains. The quality of the historic images and their potential use for ecological research stimulated an excellent re-photography project by Donald Progulske and Richard Sawell in the 1970s. Their report *Yellow Ore, Yellow Hair, Yellow Pine: A Photographic Study of a Century of Forest Ecology* [683] was one of the earliest comprehensive repeat photography research projects focusing on ecological changes, and stimulated a host of other studies across western North America and the world [684]. More recently, Ernest Grafe and Paul Horsted returned to the Illingworth photographs to produce high quality images in the book: *Exploring with Custer: The 1874 Black Hills Expedition* [685], giving increased resolution to our knowledge of historical herbivory impacts and beaver use [555,643,686] and fire history [644,645,687].

Illingworth's historic image number 809 helps illustrate an amazing story of the ecological and cultural history of the Black Hills. Surrounded by the windswept Central Plains, the Black Hills provided shelter and sustenance to native peoples for many centuries. As historian Royal Hassrick describes, as the Sioux moved westwards in the late 1700s "their dependence upon the modified woodland environment may have accounted for their determination to wrest the Black Hills country, which they later called their 'meat pack' from the Kiowas, the Cheyennes, and the Crows" [46]:189. Here, in this secure location in in the core of their territory, for more than a century until Custer's arrival, the Sioux would maintain their home camps, sheltering in the winter, and moving out on to the plains in other seasons when conditions were favorable to hunt bison and other wildlife. The photographic evidence of nearby campsites in the zoomed in portion of Illingworth's view below are the trails paralleling Custer's wagon trains (Figure 6.4.2.2). These are freshly used tracks made by people on horseback dragging travois made from the lodge poles also used for tipis. Note the incised center part of the trail, made by horses, and the drag marks from the dragged poles adjacent to them. The Sioux would carry all their possessions and children in the travois. Indeed, historian Ernest Grafe documents several members of Custer's expedition describing freshly used "lodge trails" as they passed through this area of the Black Hills, and on the same day the photograph was taken, the expedition encountered a small Sioux camp of 5 lodges of men, women and children further down the valley. One of Custer's fellow-travelers remarked: "How pretty the little village of clean white tepees nestling in the valley below appeared " but soon after this sighting, a minor skirmish occurred with Custer's troops, and the Sioux families abandoned their camp and fled into the hills [685].

What does a blow-up of the 1874 photograph (Figure 6.4.2.2) tell us about historic bison use? Well first, there are not numerous deep, braided parallel trails indicating abundant, routine bison use. Moreover, there is little sign of wallows, or deep depressions made by bison rolling in the soil, that would occur if bison used the area routinely in summer. Perhaps one wallow is in the scene in the upper center right area near the wagons. Also, the willows and other shrubs along the streams show no signs of intensive browsing or trampling damage from bison or other large herbivores such as elk. However, the streams were occupied by numerous beavers [688] and the reason Illingworth even took this photograph is that he had time to ascend the hill above the valley while the wagon drivers built corduroy bridges across streams swollen with beaver dams. George Grinnell, the expedition's zoologist recorded for his description of beaver [689]:82:

> *This species was common on all the large streams which we crossed on our way to the Black Hills, in many places having by means of their dams retained a plentiful supply of water when the creek both above and below was dry. They were also numerous in the Hills, as their dams and houses in many of the streams bore witness*.

The observed low bison use within confines of the Black Hills is in good harmony with many historical accounts that large groups of bison were generally found out on the plains, not in wooded hills routinely used by humans for shelter and to hunt other species such as deer [6,8,45,99,188]. However, the Black Hills did provide a secure location for relatively high numbers of Native Americans, and their periodic forays out on to the plains would have partially altered bison behavior over a broad area. So, that the Sioux called the Black Hills their "meat pack" is likely in reference to its central location in buffalo country, not that the hills themselves were routinely used by bison. However, the terrain within the hills could be viewed as a local mutualism zone where bison could seek refuge in a bad winter on the plains, and fine quality habitat.

The historical photograph (Figure 6.4.4.1a) also clearly shows the effects of the long-term fire regime. Fire ecologists Brown and Sieg [644] tallied numerous fire scars collected from Black Hill's ponderosa pine. Burning was most frequent along the edges of meadows, with average fire intervals of 10-12 years, and the position of the fire-scars in the annual tree growth rings indicated that most these fires occurred in the dormant season (late August to May). This is a sign that many of these fires were outside the lightning season, thus lit by people. From the historic view, we can also see that many of these fires were relatively low intensity "maintenance burns" that burned the meadows and their edges, but did not advance far into the adjacent forest. In fact, Brown and Sieg observe that fire was twice as frequent in more open grasslands as the interior forests. This high fire frequency occurred throughout the Sioux's occupancy period of the Black Hills, continuing during the onslaught of the Black Hill's gold rush. However, by the 1890's the amount of burning began to decline. After one large-area fire in 1910, burning almost ceased entirely [644]. This predates efficient fire suppression--indicating that cultural change could be an important factor.

What does the fire frequency tell us about historic bison use of the Black Hills? Like the evidence of few bison trails and wallows, and dense stream-side shrubs described above, frequent historic fires support the idea that bison numbers were usually relatively low. If high numbers of bison did routinely occur, they would have herded in meadows and valley bottoms and reduced the grass cover that allows for frequent burning. This doesn't appear to have occurred during the Indigenous times. In contrast, compare the effects of modern high bison numbers in Yellowstone National Park that have reduced grass and shrub cover, reducing the fuels available for low severity, shoulder season fires (Figure 6.2.3.4). Similarly, along Castle Creek, several decades of harvesting hay, intensive cattle grazing, and possibly high winter elk use are likely factors in the disappearance of the stream-side shrubs visible in 1874 (Figure 6.4.4.1b).

Managers of bison herds in Wind Cave National Park (WCNP) and Custer State Park (CSP) in the southern Black Hills inherited a similar legacy of decades early settler high domestic stock grazing, then declining fire frequency. Moreover, when the parks restored bison, elk, and other ungulates, the perception of high historic numbers within the hills themselves combined with and bison species conservation. Today, the ecological effects of these policies are clear. Bison and other ungulate densities are extremely high (Table 6.4.1.1). Shrubs and palatable woody browse is badly degraded, especially near streams [686] , and this occurs even outside the parks where both cattle and ungulate use is high (Figure 6.4.1.1b). Beaver and beaver ponds-- so abundant in Grinnell's observations during the 1874 Custer expedition (see above)—are now extremely rare in the parks. The condition forage for ungulates is declining. Keller [690]:325 gently recommends for Custer State Park:

> *Managers may consider removal of forage by the ungulate assemblage might be above 35% for some forage species, especially in years with lower-than-normal spring precipitation. It might be prudent to monitor plant species that were most sensitive to increases in ungulate populations. Forage species that our model indicated have a tendency to be overutilized at current stocking densities include big bluestem, blue grama, needle and thread, sedges, common yarrow, northern bedstraw, and woodland shrubs.*

Table 6.4.1.1: Approximate number of ungulates and AU equivalents for Custer State Park for the period 2009 to 2010 [690] and for Wind Cave National Park for [686]

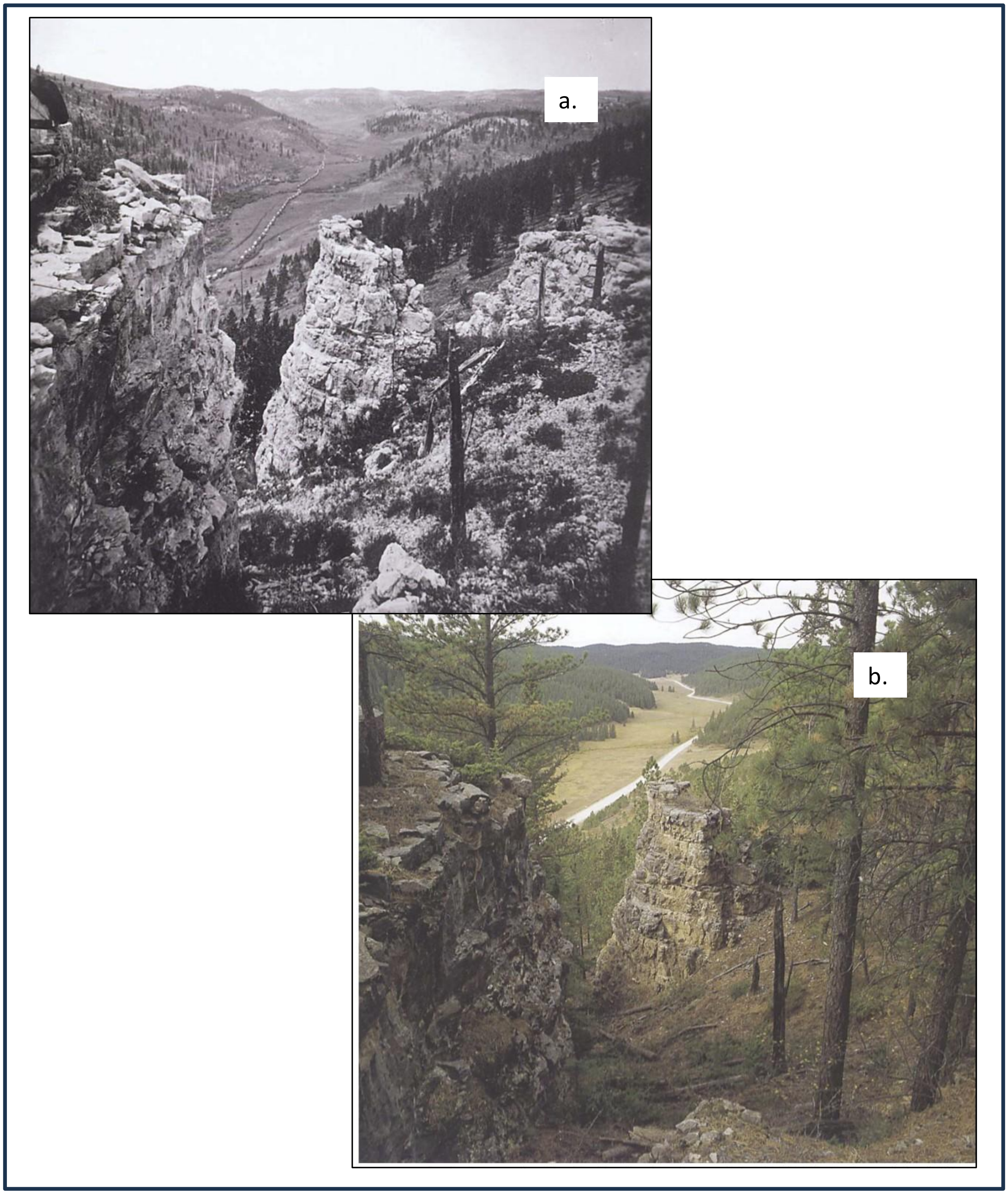



Figure 6.4.4.1 The Custer Expedition wagon train descending the Castle Creek valley on July 26, 1874 (photograph by William Henry Illingworth, Devereux Library Archives, Illingworth-809), and the same location photographed by Paul Horsted in 2000 page 175, Ernest Grafe and Paul Horsted, Exploring with Custer ). The US Forest Service cleared tree growth in the foreground to make possible. Observe the “then versus now” position of the burnt snags in the lower right foreground of the images– their exact positioning shows precise skill in repeat photography.

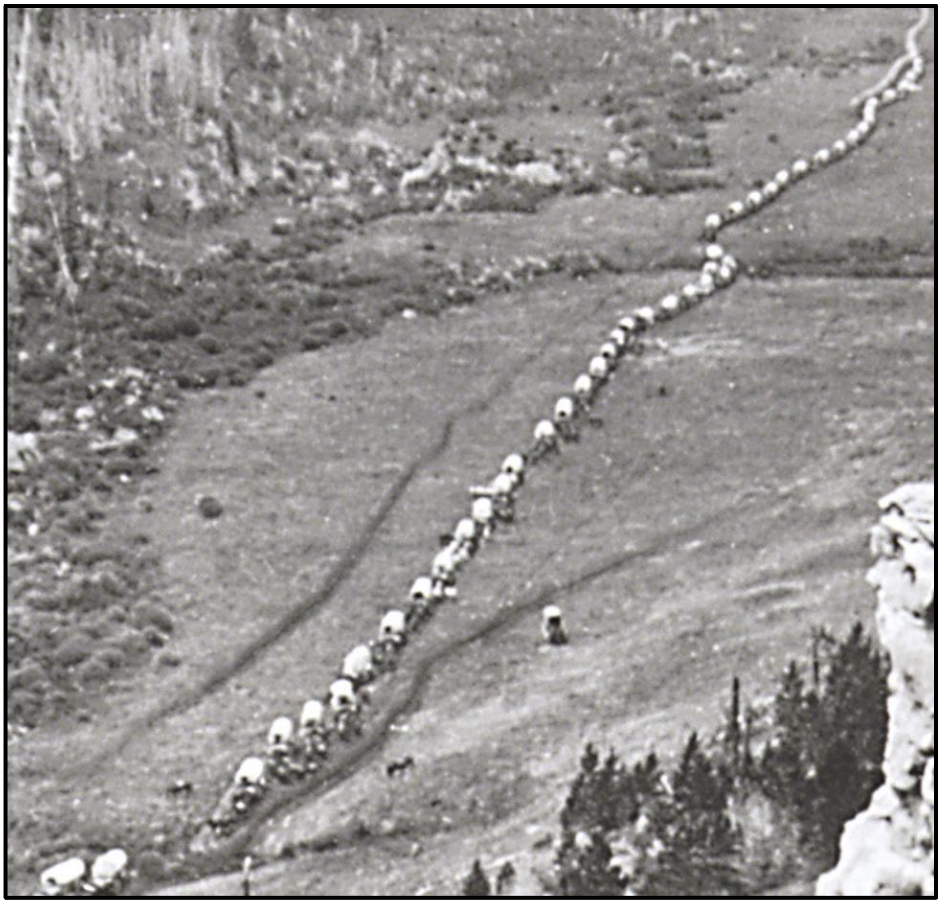


Figure 6.4.4.2. A blow-up of the Illingworth-809 image showing the "lodge trails", or paths made by horses dragging travois on either side of the wagon train. A potential bison wallow is visible in the central upper right, but the shrubs show no sign of animal browsing or trampling. Dense riparian zones heavily used by beaver were common in the Black Hills at the time of the Custer 1874 expedition [688].

Table 6.4.1.1: Approximate number of ungulates and AU equivalents for Custer State Park for the period 2009 to 2010 [690] and for Wind Cave National Park for [686]

| Species | Custer State Park | | Wind Cave NP | |
|---|---|---|---|---|
| | Number | AU/km$^2$ | Number | AU/km$^2$ |
| Bison | 900 | 3.1 | 450 | 3.9 |
| Elk | 550 | 1.2 | 800 | 4.2 |
| White-tailed deer | 860 | 1.2 | 50 | .2 |
| Mule deer | 285 | 0.4 | 150 | .5 |
| Pronghorn | 220 | 0.3 | 60 | .2 |
| Bighorn Sheep | 38 | 0.1 | | |
| Feral burros | 38 | 0.1 | | |
| Total | | 6.3 | | 9.1 |

### *Badlands National Park*

During the period ~1985-2015 the park managed about 500-1000 bison in a large paddock (344 $km^2$) of shortgrass prairie or a density of ~2.1-4.3 bison/$km^2$ [25,691]. Prior to park establishment in the 1930s, the area was heavily grazed by domestic stock [692], and at current bison stocking levels there is scant evidence of riparian zone vegetation or regenerating deciduous shrubs [693]. Proposals to increase numbers and area occupied by bison conclude that given existing intense herbivory impacts on vegetation, further detrimental effects by increasing numbers would be unlikely [691].

Badlands National Park in South Dakota. Photo credit: NPS Carl Johnson

### *Curtis Prairie*

Tallgrass prairie once predominated >8 ecoregions on the eastern edge of the prairie biome from Manitoba south to Texas. Tallgrass once spread across most of south Wisconsin but over 90% has been converted to agriculture [657]. This was the primary habitat linking large herds of bison on the Great Plains eastwards to small groups south of Lake Erie [61] and further SE into Ohio and Kentucky. For >75 years the ~30 ha grassland near the University of Wisconsin has been a center of tallgrass prairie restoration research [694]. Restoration techniques including mowing, seeding and burning, but not herbivory treatments. A pioneering research finding was that routine prescribed fires (<5-year cycle) are highly important to reduce woody plant dominance. A detailed review of individual species coverages over time [695] quantified ongoing vegetation changes. Surveys in 1976 and 2002 reported continual increases in native species, but more recent surveys show a major loss of drier prairie species. The classic indicator tallgrasses are declining the most— >70% decline in of Indian grass (*Sorghastrum nutans*) and a 50% decline in big bluestem (*Andropogon gerardi)*. Potential causes may be due to increased run-off from nearby urbanization and regional precipitation. From social perspective, the Curtis Prairie ecological restoration sought to promote humans as essential, ongoing participants in ecosystem maintenance. Jordan [696] commented about fire use on Curtis Prairie:

> *'I'll tell you one of the reasons why that's so beautiful – it's because these burns dramatize our integral relationship with these classic ecosystems. They say 'If you don't do these burns this prairie will disappear'. So you belong on these prairies…and maybe you belong on the planet."*

### *Nachusa Grassland, Illinois*

Researchers rate this tallgrass prairie reserve managed by the Nature Conservancy as one of North America's more outstanding examples of ecological restoration, recognizing that a combination of fire and bison herbivory are necessary processes [697]. In 2014, American bison (*Bison bison*) were reintroduced to Nachusa in a phased approach and since 2018 the herd has been managed at about 100 adult animals year-round on 600 ha of grazing area (~16 bison/km$^2$). Researchers show that bison grazing has maintained or increased grassland diversity, although non-native plant cover has increased [698]. Similarly, with a combination of prescribed fire and bison herbivory there have been increases in grassland bird species diversity [699]. Review of Google Earth images over time suggest that riparian zone vegetation and beaver pond cover has not declined over time as might be expected at high bison densities, but time will tell. Likely highly productive tallgrass prairies can sustain higher bison densities than historically occurred and still maintain both fire and wetland processes.

### *Flint Hills, Kansas: Bison Reserves and Cattle Ranchers*

Lying on tallgrass prairie of Kansas and Oklahoma, the Flint Hills ecoregion (9.4.4, Figures 6.4.1.1, 6.4.5.3) has a unique history of cattle grazing, widespread use of fire, bison restoration and detailed research (e.g., [273,679,700–702]). Sproule [703] describes the current cattle industry where ~ 1 million ha is burned annually early in spring, then immediately "double-stocked" at ~17.5 AU/km$^2$ (1-700 lb yearling/2.5 acres) for 90 days before finishing. Two reserves conduct bison and fire research: the Konza Prairie (KOPR) with ~200 bison in a 1012 ha paddock (~19 bison/km$^2$) [700] and the Tallgrass Prairie Reserve (TAPR) with reported densities of: ~1000 bison and calves in ~4200 ha paddock during the period 2000 to 2001 (~24 bison/km$^2$) [702], and 73 bison in a 445 ha paddock (~16.4 bison/km$^2$) in 2010 [704], and ~2000-2500 bison in a 94 km$^2$ paddock (~21bison/km$^2$) from 2010-2012 [705]. Flint Hills research projects are unique in focussing on "pyric herbivory" or the interaction between burned areas and herbivore (bison and cattle) movements and fitness as measured by weight gain, and the allocation of tallgrass prairie biomass cycling between fire, grazers, and other processes is an ongoing focus of research [273,679]. Current management at high stocking levels (>15 AU/km$^2$) could be higher than early historic times where the Flint Hills were at the eastern edge of core bison range (Figures 6.4.1.4a, 6.4.2.2). Fuhlendorf et al. [273] describe the interaction between herbivore density and fire:

> *A critical determining factor to the effects of pyric herbivory is the relationship of grazing pressure to the number of fires and the amount of area burned each year. If large areas are*

> *burned and grazing pressure is low, then the animals will create grazing lawns within the burned patch as the vegetation outgrows that animal's ability to forage throughout the entire burned area. If small areas are burned or grazing pressure is heavy, then the animals will uniformly consume most of the vegetation growing in the recently burned area and then return to areas burned in previous years. In addition, if fires are many and dispersed, they can contribute to the dispersal of herbivores, whereas if they are few and large they can lead to congregations of grazers....*

Both cattle and bison managers increasingly recognize that the traditional time of spring, dormant season burning should be expanded to other seasons to vary fire intensity, plant response, and grazer distribution [706,707]. For example, on TAPR attempts to mimic pre-European conditions with prescribed fires on a 3-5 year cycle randomly across internal patches (100-600 ha) with 80% dormant-season (40% fall and 40% late spring) burning, and 20% growing season fires [273,708]. A long-term study comparing bison versus cattle grazing on KOPR describes that bison tended to increase biodiversity due factors such as more varied foraging preferences, less utilization of grasses, and wallowing [709] .

Figure 6.4.5.3. Tallgrass Prairie Reserve in the Flint Hills of Oklahoma and Kansas, an ecosystem with high net productivity where vegetation cover is influenced by high herbivory and frequent fire.

The importance of fire versus herbivory is accentuated by the increase in woody plants across the Flint Hills due to reduced fire frequency and intensity, partially related to reduced anthropogenic use of fire, high herbivory levels removing fuel, and landscape fragmentation— similar to ecoregions on the southern Great Plains [710]. Ratajczak et al. [711] describe increases in eastern red cedar (*Juniperus virginiana)* cover and decline in tallgrass species with fire intervals > 3 years, and changes that may be irreversible when intervals >20 years. Prescribed fire can reduce the rate of woody plant cover increases in grasslands (Figure 6.4.5.4).

Figure 6.4.5.4. Using prescribed fires to reduce eastern red cedar cover on the Konza Prairie in the Flint Hills.

A further set of indicators for the tallgrass prairie is the condition of streams and riparian zones [712]. Prairie native fish populations are generally in serious condition with many species either extirpated or declining in abundance. Along eastern streams, beaver are either relatively abundant on reaches where domestic stock does not graze, or relatively rare where grazing occurs [713]. Alterations to the landscape caused by changes in land use, land cover and hydrology have contributed to habitat degradation. For example, a recent assessment of TAPR [704] rated the condition and trend of steams as of concern due to these factors, and satellite images of TAPR and other regions of the Flint Hills show cattle and bison impacts along streams. After nearly a century of low abundance, beaver were rated as abundant in the Flint Hills in 1987 [714]. However, only scattered evidence of beaver use (ponds or dams) is visible today in satellite images. The Kansas Grasslands Land Coalition currently has an initiative to recognize the ecological role of beaver in the Flint Hills [715].

# 7. SYNTHESIS

## 7.1 Bison Biogeography Problems and Human-Bison Mutualism

North American bison distribution and abundance has traditionally been approached as:

- a "bottom-up productivity" problem where forage type or productivity are key predictors (e.g., [23,27–29,228]).
- a "top-down" predation problem where humans, wolves, and bears are most influential. In particular, Indigenous hunting is recognized as important in many regions (e.g., [4,34,39,137,138,241]).
- an interaction of top-down and bottom-up factors both interact to determine distribution and abundance (e.g., [39,238,618,716]).

Although each of these explanations have their merits, four key are flaws are evident:

- Indigenous knowledge and populations- although all bottom-up, top-down and interaction explanations require some level of human action (e.g., hunting, habitat creation through fire), Indigenous knowledge or humans acting as an intelligent agent explanations remain underexplained. Moreover, human numbers at a biome level appears to have been relatively stable across the Great Plains suggesting persistent feedback and regulatory mechanisms.
- Stability of bison distribution and abundance- although there is variation in time, bison numbers and range have remained remarkably stable over the last few thousand years, and this is certainly interesting when compared to the fate of other large mammals facing human predation earlier in the Holocene.
- Persistence of habitat quality- Bison are large mammals with potential large impacts on their habitat when abundant. Riparian zones and native perennial grasses are particularly susceptible to trampling or intense herbivory. These communities appear to have thrived prior to recent times.
- Availability of water- Many studies of historic bison distribution and abundance assume that surface water was generally not limiting and instead focus on precipitation's effect on grassland production. Although this may apply to many some areas of pastureland today, the situation was vastly different in the past. Historically, across the Great Plains water sources were often distant, ephemeral, dependent on climate and season, and could be a location of high predation risk for bison. Beaver were likely important species controlling water supply.

One approach that addresses these flaws is to recognize that likely over the last 15K years humans, bison and beaver likely had interactions that led to ecological and cultural stability. Simply put, the hypothesis is:

*Humans, beaver and the buffalo are long-term mutualists. Humans, through fire use and conserving beaver contributed additions to the essentials of bison habitat—forage, water and winter cover. More importantly, by regulating bison populations with predation, humans kept the bison from degrading habitats. In return, the buffalo could provide many humans with nearly everything—food, clothing, shelter and for some cultures, a complete circle of life.*

## 7.2 Research Approach

This study required an interdisciplinary approach of linking traditional knowledge of seasonal rounds with "western science" theories of optimal foraging, niche construction, and ecological mutualism. I then developed a conceptual model of human-bison interactions and evaluated this with ~30,000 daily/multi-day historical journal observations by early European travellers and fire history information from ~200 tree-ring and peat bog studies. Then I compared long-term bison and beaver abundance and plant community conditions for natural ecoregions with current domestic and wildlife density estimates and impacts on rangelands and riparian vegetation.

## 7.3 Key Findings

A group of >20 biophysical and social (human abundance and resource use) spatial covariates were evaluated at both the continental (Table 5.4.2.3 above), and regional transect levels (Figure 7.3.1) for their potential influence on bison distribution and abundance. In addition, bison abundance may be inversely linked to human abundance, so may have varied temporally when Indigenous populations declined in several regions after ~CE 1200.

### 7.3.1 Biophysical Influences on Bison

As observed in many studies (e.g. recently by [22,23]), ecoregion grass cover is by far the best predictor of long-term bison abundance and distribution. North America's central grasslands provide forage for bison, and a refuge from human predation due to lack of alternate resources and rigorous conditions in winter. Ecoregions with highest bison density generally have grassland cover >50% (Figures 5.4.2.5a, 7.3.1). Increasing deciduous woodland cover around the periphery of grasslands as determined by fire frequency (Figure 5.4.2.3) is a key determinate of decreasing bison and increasing human abundance, and the transition from high density bison populations on the Great Plains to lower density populations in peripheral zones. Other biophysical factors that may be important depending on the continental region include:

- Terrain (slope)- mountain terrain (high mean slope in ecoregions) sharply reduces bison abundance, partially due to human predation in rugged terrain [233,389,390,499].
- Snow- high winter snow depths similarly reduce bison abundance [22] likely due to difficulty to obtain forage and increased efficiency of human and wolf predation [41,237].
- Conifer cover- areas of dense conifer are associated with smaller bison herds, less forage, and possibly greater sources of alternate resources to support predators.
- Four-legged predators (wolves, bears)- on the Great Plains these predators are more abundant in high bison density areas likely as scavengers and inefficient predators. In northern ecoregions with low bison densities, deep snowpacks, and alternate prey (caribou and moose), wolves and grizzly bear predation may be more significant [237,615,717] .
- Productivity (NPP)- Highly productive ecoregions can clearly support higher densities of bison in the absence of predation (see modern analogs in Section 6). However, historically, highly productive ecoregions had many alternate resources that supported high densities of humans [118,367], and thus ironically, less bison.
- Water (historical map not available)- Sources of surface water would likely have historically been one of the most important determinants of bison abundance.

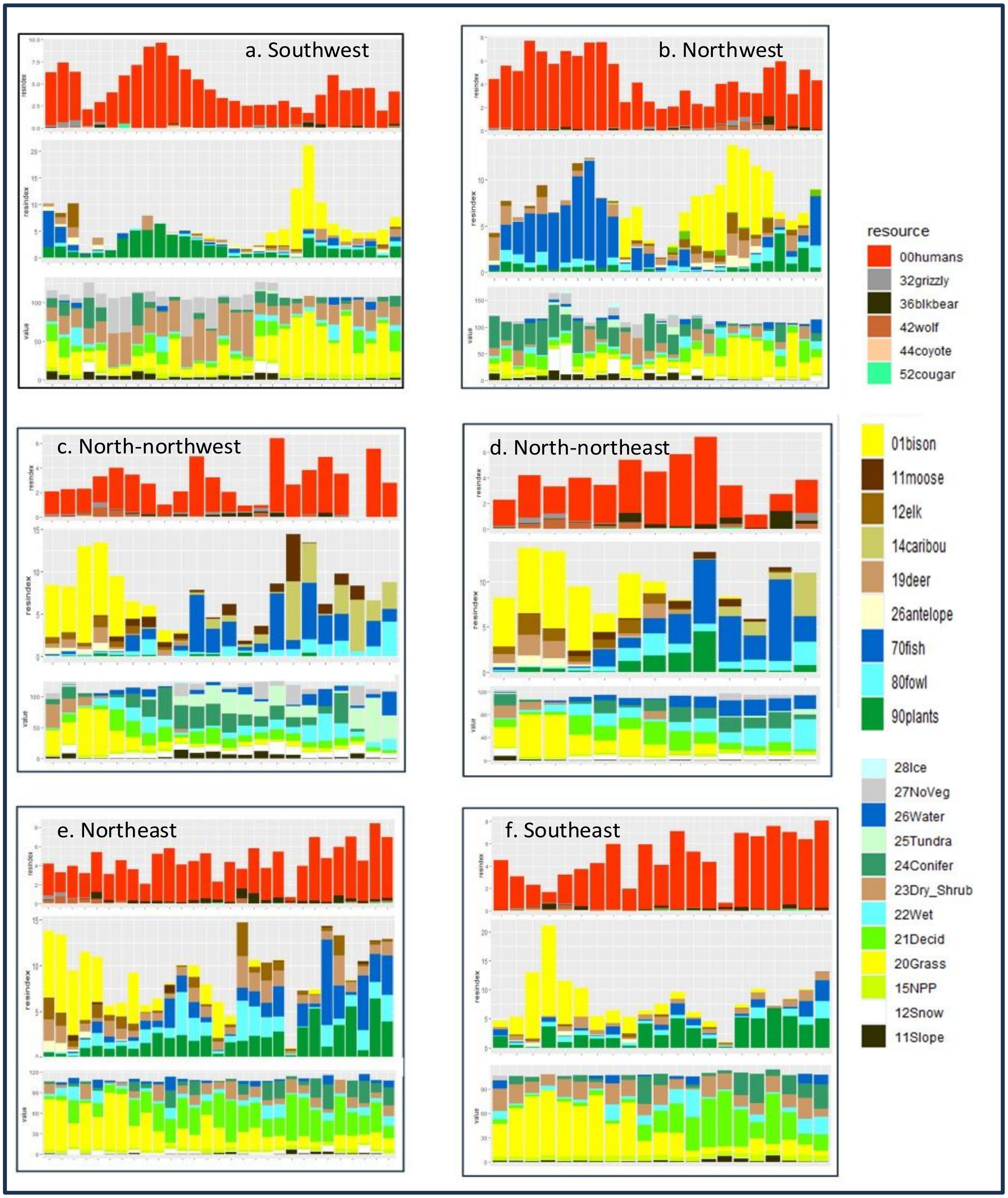



Figure 7.3.1: Biophysical and cultural variables for ecoregions plotted for six transects from core bison habitat on the Great Plains to the continental coast with the Pacific Ocean (transects a and b, running from right to left), to the Arctic, north Pacific and north Atlantic oceans (transects c and d), and Atlantic Ocean (transects e and f). For each transect, top bar graph is the abundance index for top consumers, middle graph is abundance index for resources used by humans, bottom graph is ecoregion cover, and productivity, snow depth and slope indices. See Table 4.1.1 for variable descriptions, and Section 6 for transect locations and ecoregions graphed.

## 7.3.2. Cultural Influences on Bison

Human abundance and access to alternate resources (wood, plants, fish, fowl) were important determinants of bison density at the edge of the grasslands. Human densities increase as grasslands transition to deciduous woodland with cover >20% (Figures 5.4.2.5c, 7.3.1). Increasing woodland cover is largely determined by a declining frequency of human-caused fires, with parklands and savanna providing Indigenous peoples with necessary shelter, cooking heat and fencing for bison pounds. Higher human densities (abundance indices >4-5 ) determine the edge of bison range.

Human abundance at the edge of bison range is largely determined by the availability of alternate resources. Unique geographies for alternate resource availability occur by continental region (Section 6, Figure 7.3.1):

- a. Southwest transect- A post-1200 decrease in human numbers in the SW was followed by bison becoming numerous on the Texas plains. Moving westwards plant resources (predominantly corn production along the Rio Grande River) are associated with sharp increases of human numbers near the edge of bison range (Figure 7.3.1a). Human abundance, limited sources of water and forage, and hide-trading networks limited bison expansion of the arid southwest [201,450,451,453]. Further west in California, bison colonization was likely constrained by abundant humans utilizing fish and plant resources [451,718,719].
- b. Northwest transect- Bison were abundant in the ecoregions of the northwest plains, but the range was sharply demarcated by the Rocky Mountains, and numerous people to the west supported by fish (salmon) and plant resources [4,22,35,136,720]. A ~CE 1780-90 Indigenous depopulation caused by smallpox [344] may have followed by an increase in bison numbers west of the main range of the  Rocky Mountains on the headwaters of the Snake and Missouri rivers (see Section 6.2.3).
- c. North-northwest transect- Bison numbers appear to have been limited by decreasing frequency of human caused fires (Section 5.2), with increasing woodland cover [581] only maintained smaller herds of bison that are more easily decimated by human hunting. Moving further northwards, several ecoregions had relatively abundant humans supported with alternate resources (particularly fish, but also moose and caribou). Rugged terrain and deep snow may have further facilitated human hunting [22].
- d. North-northeast transect- High bison numbers on the northeast plains rapidly decline moving northeast towards the edge of the range in ecoregions near the Great Lakes where high numbers of humans are supported by plants (wild rice) and fish [569,636]. Further north in the ecoregions of the Canadian Sheild, bison abundance limited by bare rock, snow and lakes. Although human numbers decline, these people were supported by a suite alternate resources-- fish, moose, caribou, waterfowl and smaller mammals such as snowshoe hare [125,629].
- e. Northeast transect- In a seeming paradox, bison numbers declined rapidly moving eastward from the less productive short and mixed grass grasslands into the more productive tallgrass prairies [61]. Today, in the few areas where native grassland remain,

these grasslands can support very high densities of herbivores (e.g., >15 AU/$km^2$) [698]. Of course, historically, this more productive habitat was occupied by abundant humans of the Middle Mississippi societies, supported by a broad range of alternative resources including the "three sisters" (corn, beans, melons), other plants, fish and shellfish [246,247]. These peoples also would have had a strong demand for bison meat and hide products, and during the Cahokian period trade networks to obtain these products extended well into the Great Plains [129,358]. With the collapse of these societies, bison range expanded ~CE 1450 across the Mississippi, and southeastward into the grasslands of Illinois, Indiana to northern Kentucky (Section , but these pioneer populations were soon exterminated by intense Indigenous hunting to supply the expansion of European trade in the east [66,250].

- f. Southeast transect- Like the northeast, despite its productive ecosystems and expansive historic grasslands [70], in the southeast bison become rare in the archeological record anywhere within 200 km of the Mississippi River [362]. Similarly, several early expeditions prior to ~1600 CE observed numerous people subsisting largely on cultivated plant resources (corn, fruit trees etc.), but no bison in the region from the lower Osage, Arkansas and Red Rivers, across the Mississippi and on to the Atlantic Ocean [204,208,360,664] . However, by ~1600 CE a massive human depopulation occurred [360,652], and in the 1600s bison were periodically reported east of the Mississippi almost to the Atlantic Ocean in Florida [18,66]. Historical accounts suggest that some of sightings may have semi-domesticated herds (Section 6.4.4).

### 7.3.3 Human-Beaver-Bison Mutualism: Biophysical and Cultural Interactions

Perhaps it is tautological that two dominant species with strong interactive processes (e.g., bison and human seasonal movements, human use of fire, variable human predation on bison) must, over thousands of years be mutualistic for co-existence. R. Grace Morgan stresses to us in her book "Beaver Bison Horse" [8] the importance of deep human values in this process with her hypothesis of Indigenous beaver conservation on the plains. Mutualism requires variable ecological and social processes with feedback that stabilize and regulate population growth of participants. For the human-bison case, four potential mutualism processes were evaluated in this study:

- Variable and adaptive human use of fire- Indigenous people likely started almost all fires in pre-European times following the practice of "burn early, burn often, burn light" --often occurring early in drying periods, and centered on grasslands and meadows created habitat for bison and a broad range of other resources for humans. On the periphery of the central plains, these fires created a parklands and savannas jointly used by both bison and humans. By varying the timing and intensity of fires, humans could create optimal conditions and stability of this habitat [146,243].
- Human conservation of beaver- Availability of water was a likely limiting factor for bison across many North American central, grassland ecoregions. Indigenous plain's peoples recognized the importance of beaver in maintaining water sources, and conserved them accordingly [8,98].
- Variable human-bison predation rates- Seasonal rounds from numerous Indigenous groups on the ecotone between the plains and woodlands show an adaptive, flexible pattern of hunting dependent on weather and bison density (ref Figures). Dependent on habitat creation and human seasonal rounds, humans could vary predation mortality. Similarly,

bison could adapt movement patterns and densities in response to human risk— forming large, highly mobile herds on the plains, and low densities of small herds in woodlands [6,10,61].

- Human protection of habitat from high bison densities- Bison, as the continent's largest herbivore could, through foraging or trampling, greatly alter habitats such as dry grasslands or riparian zones. Moreover, through intense foraging, bison could remove herbaceous fuels for fire, lengthening fire cycles, and allowing increases in woody vegetation. By regulating bison numbers, and influencing movements, humans protected many habitats from bison overuse. In many situations, these areas might provide critical habitat for bison during critical periods of drought or extreme winters [31,532].

### 7.3.4 The Spatial Scale and Complexity of Human-Beaver-Bison Mutualism

Mutualism is typically evaluated at fine, local scales. An important recent advance in ecological understanding is that across broader scales, species interactions can vary from symbiotic to antagonistic, with the "footprint of mutualism" occurring in limited areas under special circumstances [178]. North American human-beaver- bison mutualism as proposed by Morgan [8,98] may be an interesting example of a complex and variable footprint that occurs at a continental scale, and has varied spatially over many centuries. Depending on the location, different processes dominated but the overall population-level effect, for humans, bison, and other ecosystem components was a form of stability and mutual benefit to the species.

Following Morgan's model and the bison abundance pattern described here, we can recognize three broad spatial zones of varying human-beaver-bison mutualism:

- Dry central grasslands- These were the core areas of highest bison density, and potentially strongest traditional aversion of humans to hunting beaver. The benefits for beaver from human mutualism would be strongest through lower predation on beaver, and reducing bison herbivory impacts along streams caused by: 1) direct killing of bison entering riparian zones, and 2) a potential behavioral response of bison minimizing their risk by avoiding riparian zones near water as much as possible( e.g., creating a "landscape of fear" [721,722]). In return, beaver's benefit to humans would also be highest by maintaining sources of water and riparian zones and attracting bison from nearby plains.
- Parklands and savanna on the periphery of the plains- Depending on the amount of surface water and riparian habitat, mutualism interaction could be as above. Probably the most important process was the overall strong reduction in bison numbers that reduced herbivory impacts on beaver habitat at perhaps a broad regional scale.
- Northern and eastern woodlands- With low densities of bison, large areas of wetland, and low densities of bison mutualistic interactions between the three species would be minimal.

## 7.4 Refining the Humans, Bison, Beaver and Fire Relationship

> *We Blackfoot always have known about the "web of life" as you call it. Everything is connected. You touch one species, and all the others feel it. Bison, beavers, wolves, fire—they created our world and held it together.* Elder Narcisse in conversation with Christina Eisenberg [723]:192

Morgan [8] further reminds us that the buffalo did not live in isolation, with their numbers simply estimated by the amount of grass. By taking a holistic view, she makes us consider that people depended on the bison, but the bison depended on both grass and water, and the beaver helped create sources of water. The beaver in turn was linked to humans through fire effects on its food (aspen and willow), and the value people placed on the streams it maintained versus just its pelt. In other words, we need to consider both bottom-up effects (e.g., availability of grass and water), and the top-down effects of human predation and conservation. Moreover, in the human-bison food web, the beaver was certainly a keystone species (e.g., a species whose abundance /biomass is low, but ecological effects are large [724]). We need to consider under what conditions beaver existed. Can the beaver give us a long-term perspective of human-bison mutualism over much of the continent? Could we use the presence of beaver to quantify historic bison abundance?

### 7.4.1 Multiple Stable States

Across North America, wildlife and range managers have often assume that historically bison, elk, and other herbivores, and currently their modern analogs, domestic horses, cows and sheep can exist with abundances approximately regulated by the amount of forage, and this level of herbivory will maintain relatively stable ecosystems [168,169,514]. However, across the continent, great changes can take place in landscapes where other influences (e.g., frequent burning, periodic flooding by beavers, intense predation on herbivores from humans, bears, wolves) were once important. Managers of ranges with domestic stock increasingly recognize the need to maintain biomass for wildlife, nutrients, watershed protection, or as fuel for fires to reduce shrub encroachment [72,73,412]. Unfortunately, in some ecoregions, particularly in the southwest, intense historic grazing by domestic may have shifted vegetation and watershed conditions into a new "stable state" where recovery of native plant communities is impossible even with dramatic reductions in stocking levels [267,469].

Recognition that intense herbivory by native herbivores such as bison, elk, and deer can also degrade ecosystems has been slower. Aldo Leopold's early research on the effects of abundant deer on the vegetation and watersheds of Kaibab Plateau [482] was a precursor to numerous studies in western national parks on the effects of intense herbivory on plant communities—particularly the impacts of high elk numbers on grasslands, aspen, riparian willow and other wildlife [89,725–727]. Initially, following Leopold's lead, research has often focussed on "trophic cascades" where native predators (e.g., wolves, bears, cougars but not humans) were most considered important in reducing ungulate herbivory impacts [513,728,729]. However, the long-term role of Indigenous human hunting and burning is increasingly recognized [91,119,136,730]. As described in this report, this may be essential to understanding bison distribution, abundance and impacts on ecosystems.

Like the impacts of intensive domestic stock grazing, researchers recognize the potential for multiple stable states when herbivory impacts are intense. For example, in Yellowstone National

Park where wolves, grizzly bears, and cougar predation occurs on elk and bison, but humans hunting remains prohibited, Hobbs et al. [330] recently describe that:

> *.. the restoration of large carnivores to the food web failed to restore riparian plant communities on Yellowstone's northern range, supporting the hypothesis that this ecosystem is in an alternative stable state caused primarily by the extirpation of apex predators during the early 20th century.*

In accordance with Morgan's hypothesis for the significance of beaver , the general process researchers identify for a state change in Yellowstone's riparian areas is intense herbivory, first by elk in the period 1940 to 1995, followed by increasing bison densities, removal of riparian woody species important for beaver, and then ongoing erosion and incision of waterways (Figure 7.4.1.1) which dries out meadows and further decreases the potential for woody plant recovery [89,91,268,475,552].


Figure 7.4.1.1: Incised stream channels on Yellowstone's northern range (adapted from Beschta et al. [475]. Beaver were historically common in these streams but declined rapidly in the 1920s due to competition for woody plant forage with elk increasing numbers of elk [89,552]. Elk numbers declined after reintroduction of wolves in 1995 and willow regeneration did occur in some streams at upper elevations. However, bison numbers then began to increase at this time, limiting riparian zone recovery on most winter ranges.

Surveys of beaver abundance South Dakota, Dieter and McCabe [731] also report two potential stable states:

> *Livestock grazing, which has caused a dichotomy in habitat conditions along the Big Sioux River, can influence beaver activity.... Dieter... found 27 (82%) of the 33 active beaver lodges along a portion of the Big Sioux River were located in ungrazed habitat, although only 40% of the study area was ungrazed.*

Similarly to riparian shrubs, trembling aspen abundance in western ecoregions also follows a pattern of two relatively stable states, abundant regeneration where herbivory from elk, cows, or bison is low, little regeneration where it is high, and often only a weak response when the number of herbivores is lowered (due to full or partial restoration of predation or reduced domestic cattle stocking) [90,271,539,599,732]. Herbivory levels may need to substantially reduced before aspen will regenerate (Figure 7.4.1.2).

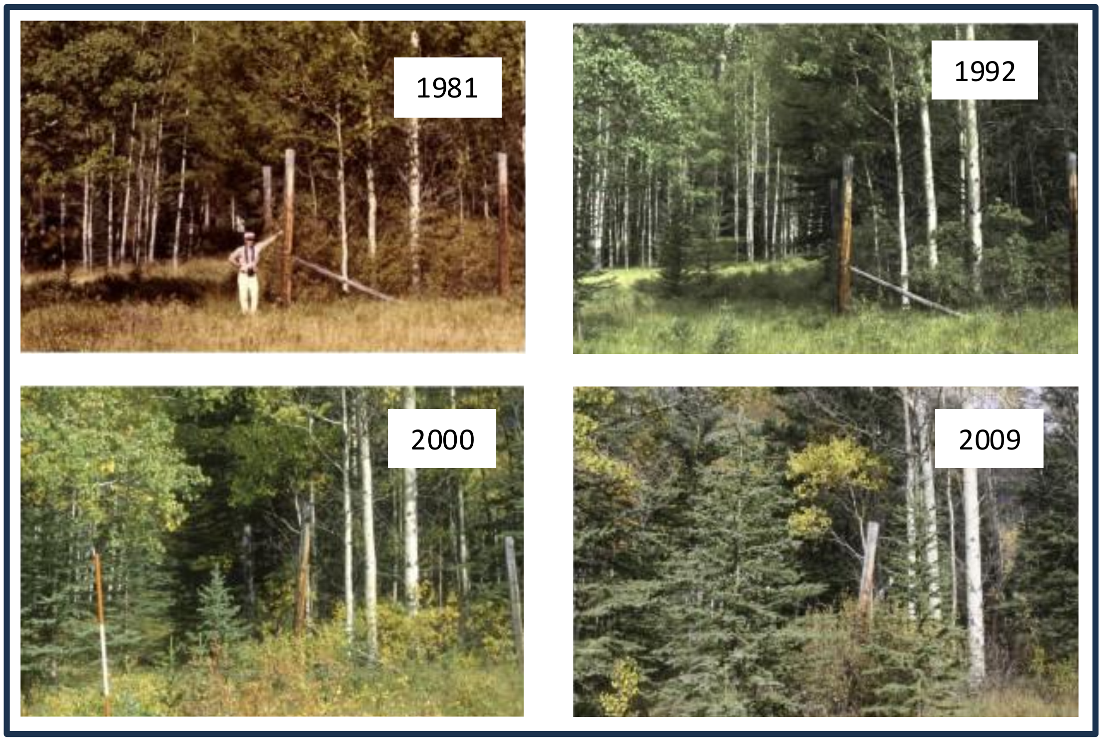



Figure 7.4.1.2. The 10.5 Mile Wildlife exclosure in Banff National Park showing changing herbivory effects and forest succession. Trembling aspen saplings (and other woody species) outside the exclosure did not reach >2m height for >60-year period (CE 1940 to 2000) due to elk herbivory. Due to wolf predation elk numbers declined after 1990 indexed <1 pellet group /100 $m^2$ (~1 elk/$km^2$) with abundant aspen saplings>2m after that time. The main influence on vegetation change is now forest succession caused by ongoing fire suppression, with white spruce beginning to dominate the plot. Historically these valley-bottom meadows were routinely burned by Indigenous people [317] . (Photos: Canadian Wildlife Service, Cliff White).

White et al. [86] explored the transition processes between these states with different elk densities and fire frequencies for 9 watersheds in the Canadian Rockies (Figure 7.2.1.1). In general, aspen abundance was greatest when elk densities (as influenced by wolf and/or human predation) were low, and fires were frequent, and aspen densities were low when elk were abundant, and fire occurrence further reduced regeneration. Two relatively stable states occurred because dense vigorous aspen stands are rarely foraged on by elk (perhaps due to predation risk avoidance), and could tolerate elk densities of up to 3/$km^2$,(3 pellet groups/100$m^2$) whereas once stand structure is degraded, herbivory is intense on the few remaining stems, and ungulate density needs to be very low (e.g., <1 pellet group/100 $m^2$ or approximately <1 elk/$km^2$ or 0.8 AU) before aspen regeneration from sprouting can occur [86].

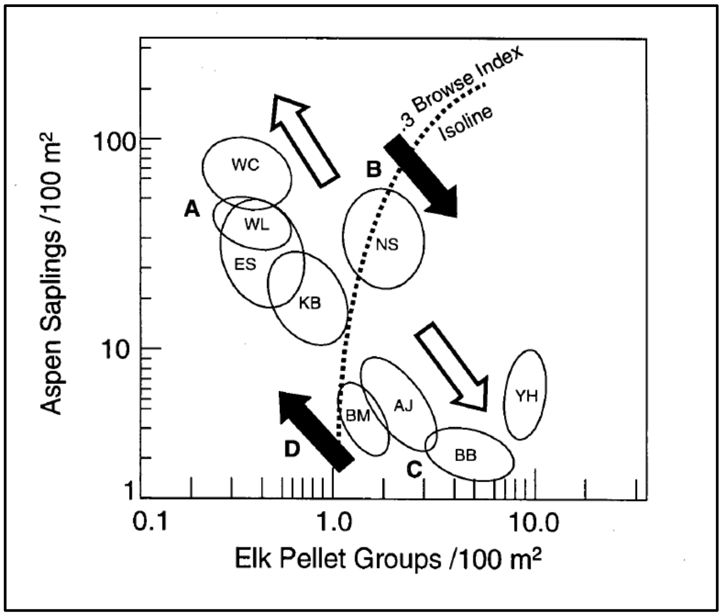



Figure 7.4.1.3: Two stable states of aspen saplings as a function of elk density (indexed by pellet groups) and herbivory (black arrows), and fire (white arrows) for nine watersheds in the Canadian Rockies (from White ). When aspen saplings are abundant, such as in the WC, WL, ES, and KB watersheds, elk rarely enter dense thickets, and fire regenerates even denser thickets (State A). High elk numbers and intense herbivory results in declining aspen density (NS watershed) and fire (B) results in a transition at B at ~3 pellet groups/100 m$^2$ (~3 elk/km$^2$), and at densities above this both herbivory and fire maintain the low aspen stable (C) state with no saplings. Elk densities must be very low (<1 pellet group/100 m$^2$, or <1 elk/km$^2$) at D to allow aspen regeneration.

Figure 7.4.1.4: Aspen in a recently recovered high density state with abundant saplings and suckers (State A in Figure 7.4.1.3) on Coyote Creek in Banff National Park (see Figure 6.2.3.6 above). Within a few years of recovery, these rare aspen groves were discovered and being utilized by an expanding population of restored bison. Sustained use at >3 bison km$^2$ will likely lead to degradation of the clones. Parks Canada photograph.

Hebblewhite et al. [553] synthesized these results to interpret the effects of differential wolf densities on elk, aspen, willow, and beaver densities demonstrating two stable states depending on elk densities: 1) areas near Banff, AB townsite with many people, few wolves, many elk (>5/$km^2$), and few aspen, willow, and beaver, and 2) areas away from Banff townsite with few elk (<1 elk/$km^2$) and abundant aspen, willow, and beaver [86,733]. The ungulate herbivory-aspen/willow 2-stable state model was also extended to evaluate the cover and condition of >30 common northwest woody plant species in Banff National Park including saskatoon, red-osier dogwood, Douglas maple, balsam poplar, choke cherry, common wild rose, buffaloberry, and snowberry. All these shrubs tend to have a similar "presence/absence" pattern to various herbivory levels. Similar to aspen and willow, ~1 AU/$km^2$ is an important threshold for palatable shrubs of these species in this ecoregion [734]. Similarly, current research year-round bison use of American Prairie Reserve pastures shows riparian zone (willows) and upland vegetation (snowberry) recovery when bison density <1 $km^2$ [527].

Figure 7.4.1.5 extends the elk-aspen analysis above to a preliminary bison density multiple stable states model based upon ecoregion vegetation cover and bison density. Early historic photographs taken in the late bison, the pre-cattle era clearly show prolific evidence of fire, and copious willow and aspen regeneration and resulting beaver activity (Figures 6.4.1.1, 6.4.2.2). The evidence is strong that a low herbivory/frequent fire stable state was the norm. From modern North American range and wildlife studies (Section 6) where we can quantify herbivore densities and impacts (e.g., [72,87,268]) we can predict potential thresholds. In general, the less cover a plant community has in an ecoregion, the more susceptible it will be to overall ecoregion bison densities due to concentrated use on these types. Grassland winter ranges, riparian zones, or deciduous groves (e.g. aspen) are particularly at risk. For ecoregion with low productivity bison population thresholds would be likely be <1-2 AU/$km^2$ (e.g. ~1-2 bison/calf pairs) on core ranges to maintain vigorous aspen and willow communities, and their associated riparian zones and beaver ponds. In highly productive ecoregions (e.g., aspen parklands, tallgrass prairies, bison densities could likely higher (e.g., 3-5 AU/$km^2$ ) before plant community degradation is evident. For example, Elk Island National Park in the highly productive aspen parkland ecoregion maintains bison densities in excess of 3/$km^2$ along with a total of >5AU/$km^2$ of elk, deer and moose (Section 6) with moderate, but acceptable impacts on beaver and plant communities according to its management objectives [598,600,735]. Similarly, for Nachusa Grasslands in the highly productive Central Corn Belt ecoregion, researchers report that recent high densities of bison (~17/$km^2$) are not altering plant communities [698,699], but this is a recently introduced herd into an area with abundant wetlands and beaver ponds.

Important for ecosystems influenced by both bison herbivory and frequent fire is how burning influences plant regeneration. For areas in the light herbivory, non-degraded state, fire will generally rejuvenate grasslands, and young vigorous shrub willow, aspen, oak and other shrublands while removing conifer competition. However, once degraded, fires may not even burn, or may remove the last surviving palatable woody species important for beaver or other species.

Once bison and beaver habitats are degraded by herbivory (perhaps in combination with fire), they can enter a new stable state where vegetation recovery can be difficult--grassland native plant composition generally shifts to less productive, grazing tolerant perennials and annuals, aspen groves and oak savannas disappear, conifers may become more common due to altered fire regimes. In riparian zones herbivores may have to be excluded by fenced exclosures [272,477,554,736] , or if water tables have lowered, artificial dams might be considered [737,738] (Figure 7.4.1.6).

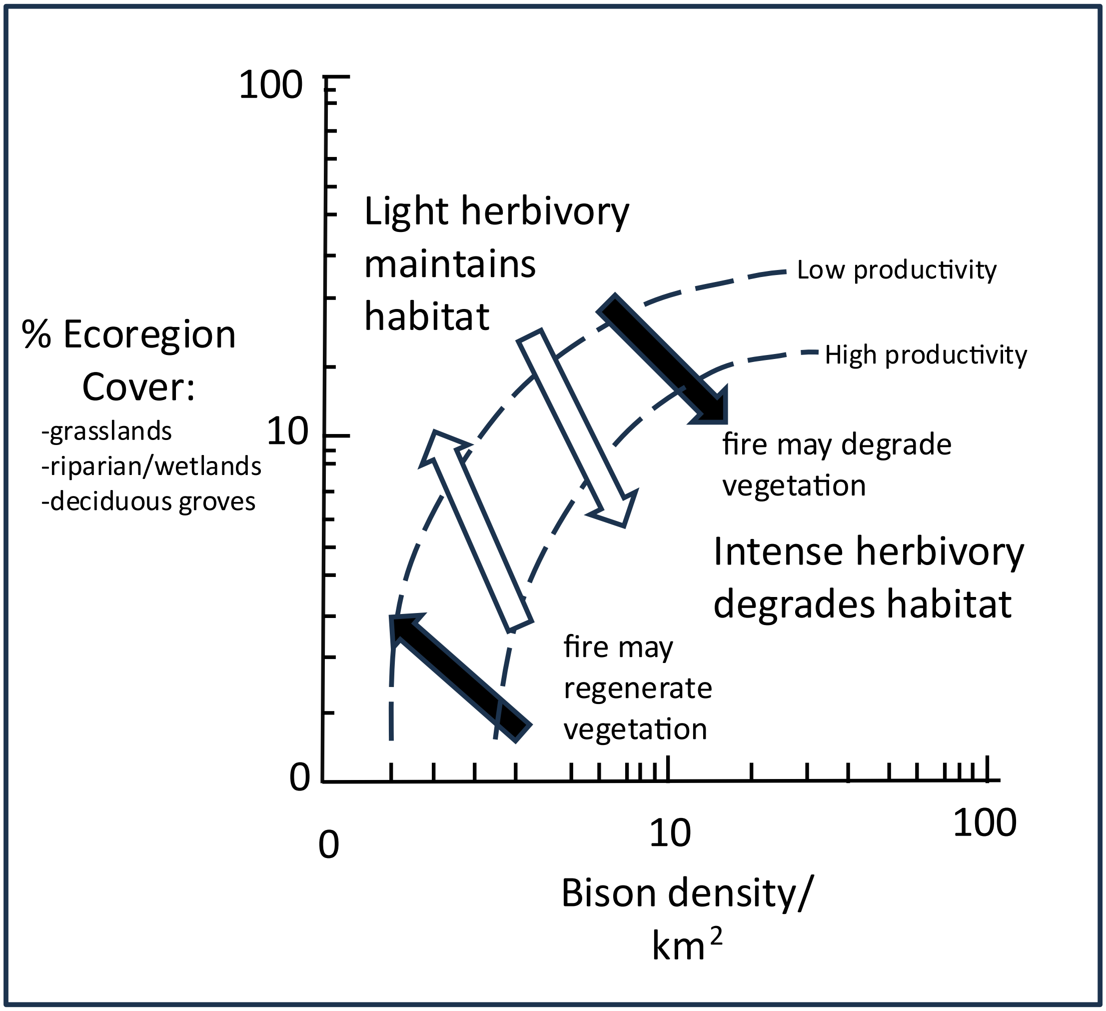



Figure 7.4.1.5: A generalized multiple stable state model for ecoregion cover, productivity, and bison density. Open arrows indicate changes in bison density; black arrows indicate fire occurrence. When area of cover type is limited bison may concentrate in it causing habitat degradation. Rare habitat types on the Great Plains (riparian zones, deciduous groves) could be degraded at even low bison densities. In mountain ecoregions, grasslands, riparian zones, and deciduous groves often have low cover and are found on limited areas of winter range. Bison densities >1-3 $km^2$ can degrade habitats. High productivity ecoregions (e.g. tallgrass prairies, aspen parklands) may have higher thresholds before degradation occurs.

Hobbs et al. [330] summarize the difficulties of recovery in Yellowstone's beaver and riparian zones from a high herbivory stable state created by abundant elk and bison if human and other predator's interactions are not considered:

> *The promotion of ecosystem restoration by restoring apex predators suggests there is a "quick fix" for losing them from food webs. We have shown that the ecosystem state that emerged following the loss of large carnivores from the food web resisted reversal after they were restored. It is clear that maintaining the ecosystem services of large carnivores by preventing their extirpation may be a more successful strategy than trying to restore those services after a long absence of apex predators from the food web.*

Figure 7.4.1.6: Ocate Creek cattle exclosure near Wagon Mound, New Mexico. See Figure 6.2.2.2 for a satellite image view. This creek has broad reaches of incising arroyos both above and below the cattle exclosure. With cattle excluded and dams (see bottom of photograph), riparian zones and beaver can be restored, allowing floodplain aggradation during floods. At the recovered stable state, low levels of cattle (or bison) use are sustainable. If fencing was removed, likely stocking densities would need to be maintained <~1-2 AU/km$^2$ to prevent another cycle of degradation based on research on multiple stable state research on wildlife and domestic stock herbivory in willow and aspen vegetation types [86,90,330,553,733]. (Further information for Ocate Creek at: https://nmbeaverproject.org/ ) .

## 7.4.2 Extending the Time Frame of Understanding Human-Beaver-Bison Potential Stable States

As described above, deciduous woody plant condition is proving a reasonable indicator of long-term large mammal herbivory and trampling effects, and recent changes due to alterations of changing herbivore abundance and fire regimes. Interpreting these interactions can be extended back in time at least 100 years with dendrochronology or historic photographs (e.g., Figures 6.2.3.4, 6.4.2.2). Researchers are also providing greater understanding on the longevity of aspen clones and potential herbivory and fire interactions that can potentially kill these long-lived organisms [86,552,739] .

For an even a longer perspective, quantifying the counteracting processes of stream aggradation and incision can give multi-century integrations of the effects of factors such as parent material, climate, herbivore density, beaver dams and land use [740]. This research is advancing in the southwest [267,470,741], northwest [269,272,542,742], and as described above the winter ranges within Yellowstone National Park [268,330,475] and Banff National Park [553,733,734]. Similarly, detailed research has been conducted in the aspen parkland ecoregion [8,274]. However, almost all these areas were outside or on the edge of core bison range, so evaluations of potential moderate to high bison (or cattle) density effects on long-term stream morphology may not be relevant to understanding the effects of long-term fluctuations in bison density.

Recently, bison restoration to relatively high densities has occurred in several areas where historically bison likely had relatively moderate to high densities (see Section 6) and where altered stream processes could be occurring (e.g., American Prairie Reserve, Grasslands National Park, Black Hills, Badlands National Park). For example, Figure 7.4.2.1 a,b shows ongoing stream incision in a tributary to Sage Creek in Badlands National Park. This region was heavily grazed by domestic stock both prior and after protected area establishment in 1929. Possibly the streams of park had entered a stable state of ongoing arroyo formation and degraded riparian zone at the time of establishment and subsequent bison restoration in 1963. Although bison densities have been managed at relatively conservative levels (~2-4 bison/$km^2$ (Section 6.4.5)), as is evident in the satellite images, channel incision continues, and a multiple stable state model (e.g Figure 7.4.1.3) would suggest that very low densities of bison (e.g., <1/$km^2$) might be required for riparian zone recovery.

From this perspective, a reasonable hypothesis is that over the long-term bison populations fluctuated, often to low levels, even in the core of historic bison range. These periodic lows maintained riparian vegetation structure and beaver populations even as bison densities might rise again to 1-3 bison/$km^2$ without greatly degrading native vegetation. Indigenous hunters would then likely be attracted to these regions of relatively abundant bison, again reducing numbers to allow an increase willows and beaver. A variety of research tests of this hypothesis could be proposed in the dry central grasslands including following up on Morgan's studies of beaver abundance at various herbivory levels [8], mapping present and hypothetical past stream profiles, varying bison stocking by watersheds to potential riparian recovery stocking levels and dating soil profiles in streamside zones understand the frequency of aggradation versus incision over multi-century periods .

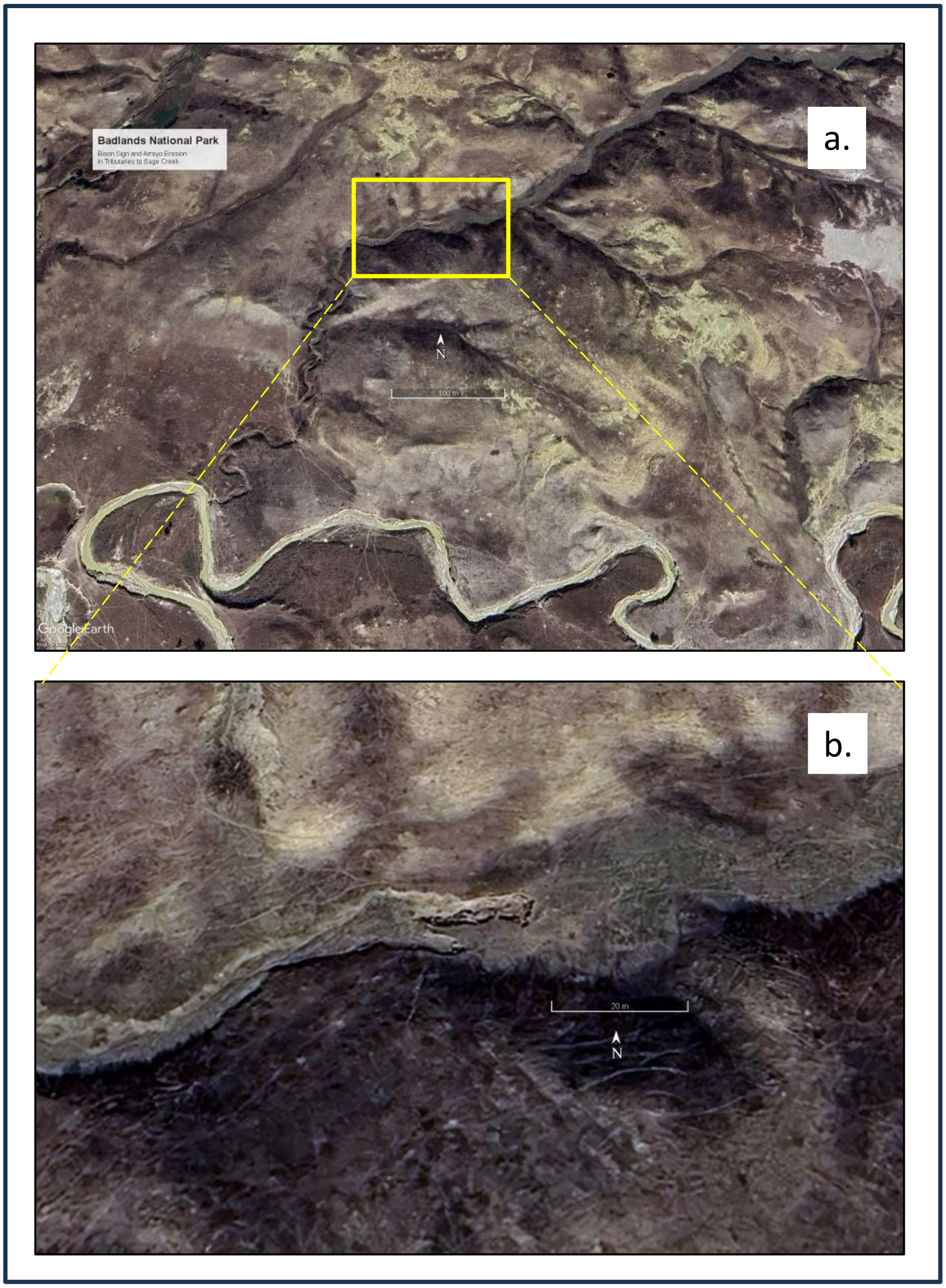



Figure 7.4.2.1: A tributary to Sage Creek in Badlands National Park (a) showing an expanded view of the channel incision zone (b) in what may have in the past been a riparian zone with planar flows and soil aggradation (Google Earth Image dated 2024-09-24 downloaded 2025-04-18). Research on long-term patterns of stream aggradation and channel incision [740] may help refine knowledge of historic riparian zones and bison and beaver abundance.

### 7.4.3 How Many Bison Historically?

The research described above may provide some context for bison abundance of the long-term. For the historical and immediate pre-European contact period, Shaw [39] observed "bison populations were neither stable or pristine", and much of this variation was tied to changes in human populations on the continent. Moreover, given the magnitude of the number of Indigenous people that died after ~ CE 1150, the resulting historical bison distribution as mapped by Allen [2] in Figure 1.1, and further refined in this paper (Figure 5.4.1.1) was likely approaching a maximum continental extent of bison distribution and abundance for the period after CE 500. Traditionally, researchers have used some version of "bottom-up" range capacity (e.g., grass productivity) and domestic stocking levels to estimate total historic bison abundance. Originally pegged at nearly 60 million bison by Ernest Thomas Seton in the early 1900s [27], subsequent researchers have revised this downwards based upon variable habitat quality, availability of water, and some consideration of predation [10,28,234]. However, Flannery [232]:342 remarks on the paradox of even a lower population estimate:

> *If there were just 30 million buffalo (an estimate on the low side) on the plains, then Indians could have taken 2.1 million animals in an average year and not reduced the population. As most estimates put the total number of plains Indians around 200,000, and no more than 400,000, <u>that's a lot of buffalo per Indians per year</u>.* (CW emphasis)

From the data and analysis in this report we can assess a combination of "bottom-up" and "top-down" (e.g., bison predation) influences on abundance. Specifically, there are five key sources of information to make revised population estimates:

- Archaeological evidence of bison in various ecoregions in the period ~ CE 0100 to ~CE 1500 (e.g. [67,250,362,452] provides reasonable evidence of bison relative abundance in most ecoregions for the prehistoric period.
- Historical journal documentary evidence of wildlife abundance [109] (Figure 5.4.1.1 this study) provides an estimate of <u>relative</u> abundance of across ecoregions during the early-mid historic period. This is contrast to previous assessments where bison abundance is based upon a simple demarcation of the range edge, and potential abundance of bison in ecoregions often based upon a "bottom-up" estimate of low (for woodlands) or high (for grasslands) productivity as indexed by the historic or current densities of domestic stock [27–29,37,39,234,431].
- Historical photographic evidence from the mid to late 1800s shows vegetation conditions in the pre-bison extinction period, and before domestic stock introduction. These photographs (e.g., Figures 6.3.2.2, 6.4.1.1 in this report) show little evidence of herbivory, but abundant effects of fire [136,251,534].
- High fire frequency requires that fuel is not limiting. For ecoregions utilized by bison, this requires low bison densities to leave provide herbaceous fuels for burning [251].
- Repeat photography studies from the period of increasing wildlife and domestic stock abundance after the 1880s show degradation of grasslands, riparian zones and deciduous forests [91,414–416,685,743].

- Extensive current research provides information on the effects of wildlife or domestic stocking densities on plant communities (e.g., [72,412,551,744]) and described for select areas in Section 6 above).
- Finally, we can consider Morgan's [8] hypothesis that Indigenous peoples had a tradition of conserving beaver across many arid and semi-arid grasslands and evaluate bison densities required maintain necessary riparian zones. As described above, this indicates <1 bison/km$^2$ for previously heavily impacted areas, but higher density scenarios (e.g., 1-3 bison/km$^2$) could be possible in an upper stable state with a landscape of dense riparian willow, aspen or other beaver foods.

Figure 7.4.3.1 graphs scenarios for approximate total continental bison numbers (see details in Appendix A). These are estimated from ecoregion totals from the CE 1400s to 1700s based upon extrapolating from the observed historic bison abundance index (Section 5.4) for 3 scenarios:

- High- bison densities with a maximum ~10-20 bison/km$^2$ in high abundance ecoregions (based upon cattle stocking on the for southern plains) then simply scaling this using the ecoregion historical journal abundance index as a proxy to modern day high domestic stocking estimates for the most grassland regions, and high estimates for bison in wildland environments in wildlands and boreal ecoregions (see "Modern Analogs" in Section 6);
- Moderate (50% of high densities)- could likely approximate bison density under moderate predation risk or in intertribal buffer zones.
- Low (25% of high densities)- areas with high predation risk from humans or other predators.

The range of populations predicted using this method is lower than previous continental calculations summarized by Shaw [39] . The estimates here are based upon the relative abundance baseline data from the journal observations assuming maximum numbers in an ecoregion, and recognition that human, wolf, and bear predation could have reduced bison numbers from 25% to 50% from this baseline. Under the low to moderate scenarios, most ecoregions likely had densities of bison <1/km$^2$ (Table 7.4.2.1 (Appendix A). These low densities would maintain vegetation conditions favorable for periodic burning, vigorous communities of aspen, willow and beaver [34,86,90,251,274,330,553,733], and associated availability of water [8,330]. Historic bison population numbers in the 10-15 million range are estimated by Shaw [29] and Geist [41], and Kay [251] provides evidence the population numbered even less. The results presented here suggest that based upon historic vegetation condition, the presence of beaver, and variable bison densities across the continent that the lower population estimates may be valid.

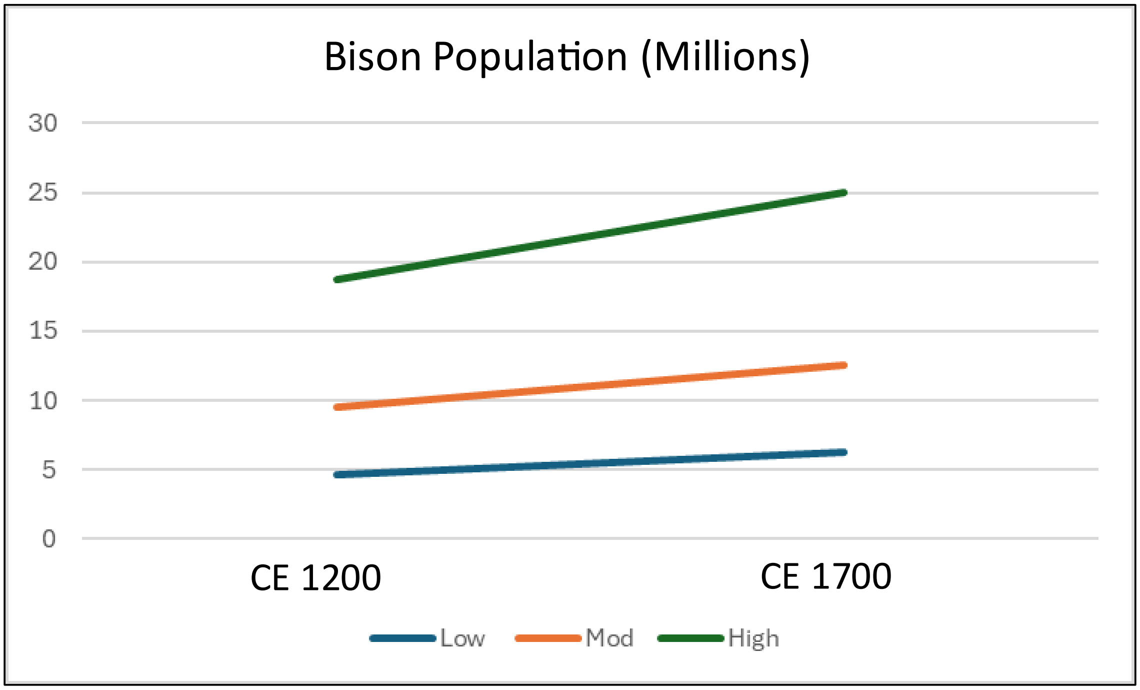



Figure 7.4.3.1: Bison population scenarios depending on scaling of historic abundance index to modern cattle and bison population estimates for ecoregions and ecological effects. The increase from 1400s to 1700s reflects bison dispersal into many ecoregions following human depopulations. Estimates in the low and moderate range would likely be favorable for riparian zones and beaver (e.g. <3 bison $km^2$) even in ecoregions with generally high bison densities.

Table 7.4.3.1: Modelled ecoregion bison population density for mid-population scenario (Appendix A). Asterisk indicates likely increasing bison density during the period ~CE 1200-1700.

| Biome | High (>3 bison/km$^2$) | Moderate (1-3 bison/km$^2$) | Low (<1 bison/km$^2$) |
|---|---|---|---|
| Great Plains | 9.4.6 Edwards Plateau* | 6.2.10 Middle Rockies* | 5.4.2 Clear Hills and Western Alberta Upland |
| | 9.4.1 High Plains | 6.2.6 Cypress Upland | 9.2.4 Central Irregular Plains |
| | 9.3.1 NW Glaciated Plains | 9.4.5 Cross Timbers* | 3.3.2 Hay and Slave River Lowlands |
| | 9.4.2 Central Great Plains | 9.2.2 Lake Manitoba and Agassiz Plain | 8.3.8 East Central Texas Plains* |
| | 9.3.4 Nebraska Sand Hills | 9.4.4. Flint Hills* | 9.6.1 Southern Texas Plains/Interior Plains-Hills* |
| | 9.3.3 Northwestern Great Plains | 9.4.7 Texas Blackland Prairies* | 9.2.3 Western Corn Belt Plains |
| | 9.2.1 Aspen Parkland-North Plains | 9.5.1 Western Gulf Coast Plain* | 8.2.3 Central Corn Belt Plains* |
| | 10.1.4 Wyoming Basin | 5.4.1 Mid-Boreal Uplands/Peace Lowlands | 5.4.3 Mid-Boreal Lowland and Interlake Plain |
| Southwest-Great Basin | | 6.2.14 Southern Rockies | 10.2.4 Chihuahuan Desert* |
| | | 9.4.3 Southwestern Tablelands | 10.1.5 Central Basin and Range* |
| | | | 6.2.13 Wasatch and Uinta Mountains* |
| | | | 10.1.6 Colorado Plateaus |
| | | | 10.1.7 Arizona/New Mexico Plateau* |
| | | | 12.1.2 Piedmonts and Plains with Grasslands* |
| Northwest Coast-Plateau | | 10.1.3 Northern Basin and Range | 6.2.15 Idaho Batholith* |
| | | 10.1.8 Snake River Plain | 6.2.4 Canadian Rockies |
| | | | 6.2.1 Skeena-Omineca-Rocky Mountains |
| | | | 6.2.9 Blue Mountains* |
| Subarctic-Arctic | | | 5.1.1 Athabasca Plain/Churchill River Upland |
| | | | 3.4.5 Coppermine River and Tazin Lake Uplands |
| | | | 3.3.1 Great Bear Plains |
| Northeast Woodlands | | 8.1.5 Driftless Area* | 8.2.3/8.2.4 Eastern/Central Corn Belt Plains* |
| | | 8.3.2 Interior River Valleys and Hills* | 8.1.4 North Central Hardwood Forests* |
| | | | 8.4.3 Western Allegheny Plateau* |
| | | | 8.2.2 Huron/Erie Lake Plains* |
| | | | 8.4.1 Ridge and Valley* |
| | | | 5.2.1 Northern Lakes and Forests* |
| | | | 8.2.1 Southeastern Wisconsin Till Plains* |
| | | | 8.4.2 Central Appalachians* |
| | | | 8.1.1 Eastern Great Lakes Lowlands* |
| Southeast Woodlands | | 8.3.3 Interior Plateau* | 8.4.5 Ozark Highlands |
| | | 8.4.9 Southwestern Appalachians* | 8.4.7 Arkansas Valley |
| | | | 8.4.8 Ouachita Mountains |
| | | | 8.4.6 Boston Mountains |
| | | | 8.3.6 Mississippi Valley Loess Plains* |
| | | | 8.5.2 Mississippi Alluvial Plain* |
| | | | 8.3.7 South Central Plains* |
| | | | 8.3.5 Southeastern Plains* |
| | | | 8.5.3 Southern Coastal Plain* |
| | | | 15.4.1 Southern Florida Coastal Plain* |
| | | | 8.3.4 Piedmont* |
| | | | 8.5.1 Middle Atlantic Coastal Plain* |

## 7.4.4 Broad Scale Human-Bison-Beaver-Water Interactions

The analyses in this paper focus on forage, human predation and fire as primary drivers of historical bison density. What's missing, and especially in the center core bison range? Well, as any rancher, or Gwen Morgan's research on beavers would tell us: "WATER!"[8]. Baker recognizes the link between beaver and willow and riparian zones in the inter-mountain west:

> *Because beaver facilitate willow establishment and survival processes, and willow is important as food and construction material for beaver…., we suggest that beaver and willow are mutualists.*[745]

With the preliminary understanding of multiple states described above for herbivory impacts on willow and aspen (Section 7.4.1 and 7.4.2 above), we can extend Morgan's and Baker's concepts of mutualism to linking humans to bison to willow/aspen to beaver and ultimately to water at broader landscape scales. In other words, human predation maintained low bison densities across most ecoregions, this reduced bison trampling and browsing of riparian vegetation, this in turn provided forage and dam-building material for beavers (willow and aspen) and ultimately maintained stable stream flows in many of the continent's central grasslands and drought-prone ecoregions. From the multiple stable states models described above, this effect would most pronounced when ecoregion bison densities were held at <1/km$^2$ but might also occur at slightly higher bison stocking densities if fear of predation kept herds on uplands above the riparian zones. Researchers report that bison in modern herds tend to distribute themselves further from water than domestic cattle and could potentially cause less riparian impacts [527,528].

Do we have other examples of broader scales of bison density that we can link to a humans-bison-beaver interactions? Kay's (2007) tabulations of the Lewis and Clark CE 1804-1806 expedition provide a useful case history. The daily records of human and wildlife abundance (Moulton) provide a relatively fine-scale dataset to evaluate human density versus bison density. Using the same abundance index that this study is based upon, Kay grouped days on the route into 55 segments where they observed similar human densities (Figure 7.4.3.1a). The pattern is clear. Bison were only observed in travel segments where humans were rare, and in many regions (e.g. west of the Rocky Mountains), even where humans were few, bison were not observed. If we assume that beaver would be present when the bison abundance was <3 (e.g. ~ 3/km$^2$), and particularly abundant when bison were <1 (e.g. <1/km$^2$), it's likely that beaver would have been present to abundant in most of Lewis and Clark's travel segments.

Other researchers describe the same general pattern of bison versus human abundance in the Lewis and Clark's journals, especially in the Columbia basin west of the continental divide where humans were abundant, and this likely resulted in not just low bison numbers, but also few other large ungulates such as elk and moose [34,138,241]. And as would be expected with low impacts from large herbivores pressure, and Indigenous people that likely valued salmon streams, the western ecoregions were exceptionally rich in beaver-- driving a trapping war between the American mountain men coming from the east, and the Hudson's Bay Company established Fort Vancouver and several other trading posts in the region [103,215].

Kay's [137] analysis of the Lewis and Clark journals provide even more key insights to bison abundance. While travelling along the Missouri River through the Great Plains, the expedition crossed several inter-tribal buffer zones between tribes at war. In each case, the daily abundance index of deer, then elk, then bison numbers rise as the expedition left the village of one group and reach the center buffer zone, then decline, bison first, then elk and deer as they reach the next Indigenous villages (Figure 7.4.3.1b). Again, this pattern of abundant wildlife between tribes at war has been previously recognized [135,219], but Kay's detailed daily analysis gives us some ability to evaluate the breadths of several zones, the general density of bison, and the optimal foraging priorities of humans. selection method. Along the Missouri, Kay's graphs suggest that <20% of the region lay in buffer zones where bison were periodically abundant (e.g., abundance index of 10, or ~10 bison/km$^2$, so if Indigenous people were conserving beaver, bison trampling or browsing in riparian zones would not be a concern in most areas. Moreover, tribal buffer zones changed over time, so recovery would be periodically possible.

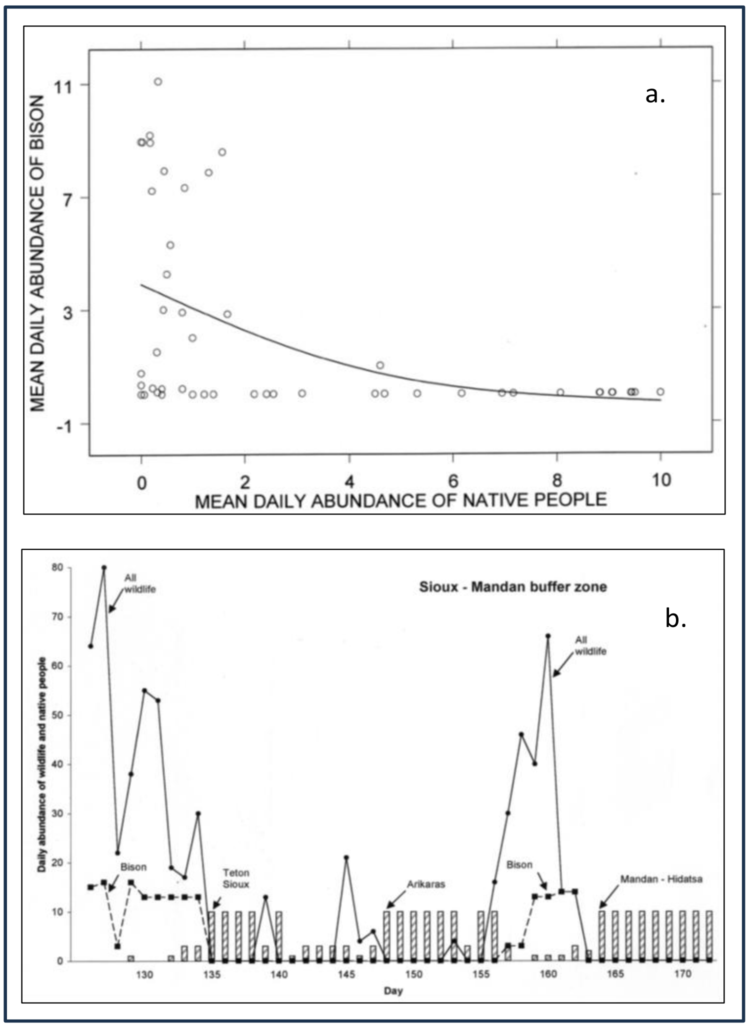



Figure 7.4.4.1. Wildlife abundance as recorded by the Lewis and Clark expedition adapted from Kay [137]: a.) mean daily abundance of bison for travel segments and mean daily abundance of people. B) Daily abundance of native people, all wildlife and bison related to mean daily abundance of humans and intertribal buffer zones.

## 7.4.5 Pyric Herbivory: Interactions between Fire and Herbivores

As described above, in the past heterogenous herbivory from bison and other herbivores likely resulted in many areas with relatively light browsing and grazing impacts that favored aspen, willow, other woody species and beaver. Then what was the other process that might reduce shrub and tree encroachment? When herbivore numbers are lower, fire becomes an increasingly important factor in removing litter, and regenerating grasses, forbs, and shrubs [273,708]. Clearly fire was frequent across most of North American bison range, and especially in several ecoregions with the high densities of bison (Figure 5.2.1.1). Humans lit by far the majority of these fires, and following the general anthropogenic pattern of "burn early, burn often, burn light" [146]:52, most of this burning occurred in the dormant seasons (see Section 5.2.1) when conditions were cooler and moister. Can we evaluate the relative importance of this historical fire regime versus herbivory in maintaining vegetation and wildlife habitat? Historical photographs (Figure 7.4.5.1 or see Section 6 for other examples) show that these fires were usually not intense on the periphery of grasslands or in riparian zones, regenerating patches of willow and aspen, while not burning others. Under low levels of herbivory and "light burning" many areas would be unburned, and woody shoots in burnt patches would grow back rapidly, soon reaching heights of ~2m that are optimal food and building material for beaver [733]. On the grasslands themselves fires would be patchy, but have higher coverage in ungrazed areas, removing accumulated dried litter, dung, woody plant shoots, and stimulate new growth ([100,708]. These recently burnt patches in turn attract higher bison use, thus maintaining a cycle of distributing herbivory across a grasslands [100,702]. The current high densities of domestic stock and wildlife described in Section 6 remove fuel and alter the potential to restore long-term fire frequency, seasonality, and intensity.

Figure 7.4.5.1. A historic landscape shaped as by "pyric herbivory" along the Yellowstone River below Pompey's Pillar in c. 1880. The river is a fuelbreak from fires spreading from the south (left side of photograph). This allows a comparison of riparian zone and moist area woody plant cover and height under different fire frequencies, but likely similar herbivory regimes. At this location, fire frequency appears to play a larger role than browsing or trampling of woody plants. Photographer L. A. Huffman also obtained images of one of the last bison hunts about 50 km north of this location [746].

## 7.4.6 Active Human Conservation?

How altruistic were people in potential human-beaver-bison mutualism? The degree of conservation in human's interaction with both species has long been of interest to researchers [152,638]. Grace Morgan's [8,98] research described in Section 3.3.3 concludes that people were keenly aware of the need to conserve beaver and sources of water in the dryer regions of bison's range. Did this awareness also apply directly to relationships with bison? Certainly, the anecdotes from journalists provide examples of what could be perceived as pre-meditated conservation:

- Burning bison ranges to remove competing woody vegetation, and stimulate forage production that attracts bison [626].
- Sparing cows with calves, killing barren cows without calves [198,223].
- Herding bison to new pastures [655].

Alternately the human-bison relationship could simply be similar that of a long-lived pragmatic couple—it just worked. Bison thrived on the habitat that human burning and beaver conservation provided, and at the human-created stocking levels that preserved the habitat. Moreover, they had a refuge from human predators on the treeless plains in the center of the range. Humans thrived on bison hides, meat and bone and the cultural conditions required to obtain it-- the Blackfoot, Lakota and Comanche peoples were some of the tallest peoples on the continent, and their lifestyle is romanticized and celebrated by current cultures around the world [366,468]

As an example of simple practicality, lets return to Captain Earl Warren's 1855 observations of the Lakoda's careful guarding of a buffalo herd of bison within favorable terrain near the Black Hills Sioux herding bison (Section 6.4.2). Warren [655]; writes that Sioux were keeping the bison here until their hair was grown enough to make good winter robes, and that his command needed to respect the Chief's wish and change the course of his troopers…

> *For us to have continued on… we might have deflected the whole range of the buffalo fifty or one hundred miles to the west, and prevented the Indians for laying in their winter stock of provisions and skins, on which their comfort, if not even their lives depended. Their feelings towards us, under the circumstances were not unlike what we should feel towards a person who should insist on setting fire to our barns.*

Human behavior while herding bison into pounds or terrain traps shows economic efficiency in bison procurement, not conservation. To maintain predictability of bison behavior responses [99], all animals trapped were killed. For example, in his journal from his 1792-93 winter sojourn with the Blackfoot in the Canadian Rockies foothills, Peter Fidler [197] describes the need for total mortality because:

> *. . . should those that escape be at any future time in a band of Buffaloes that they might be bringing to the pound, by their once being caught in a trap would evade going into it again for in general when a single one breaks out of the Dead Man all the rest will follow.*

After his experiences with the Cree pounding bison, McDougall [747]:282 recounted:

> *Not one buffalo is allowed to escape. The young and the poor must die with the strong and fat, for it is believed that if these were spared they would tell the rest, and so make it impossible to bring any more buffalo into a pound.*

Brink [48]:39-42 and Colpitts [408]:84-94 further emphasize that hunting bison was skilful and hard work, and the animals chosen for killing and processing at any given time and place provided the best sources of nutrition and other products required.

So, ultimately, it's probably best to recognize that humans and bison were simply a well-matched couple for the time and the place. Their relationship survived "hell and high water" (and more importantly drought) for >10K years [23]. The reason both species were highly entwined and persisted on the continent was that active direct human conservation of bison was not required. Both species had adaptions that guaranteed their persistence in core range areas, but "the footprint of mutualism" [178] determined the ultimate range boundary for bison, and population densities for both species in many ecoregions. They were each, independently, simply optimal foragers [124,174] --and it worked.

But there was a key "middleman" in this relationship—the beaver. Across most the great plains it was water, not grass that often limited bison numbers [8,740]. By recognizing this, and conserving the beaver, Indigenous peoples not only supported bison numbers, but they also created riparian habitats where bison would be sure to congregate nearly daily. Again, this was a simple economic trade-off. Refrain from hunting a smaller animal often hard to find in river banks, in return get the fruits its hard work creating surface water flows that attracted a much larger animal to narrow valleys, wooded areas, and draws where it was easy to hunt [48,233,390]. And possibly human's greatest benefit to the beaver on the plains was not just that they not intensely hunt them, it was that humans hunted the bison that could degrade their habitat—keeping them to a lower number, and altering their behavior to avoid riparian zones as much as possible [528]. For people, this was simple trade-off, but it was also complex form of mutualism. But again, it was optimal foraging, not active human conservation measures that was the driver for the human behavioral pattern [124].

Figure 7.4.6.1. Bison and beaver ponds on the tallgrass prairie, Nachusa Grasslands, Illinois. Highly productive grasslands may be able to maintain riparian zones and beaver at higher densities of bison than occurred historically. In the past human predation sharply limited bison numbers in these ecoregions.
Photograph: https://www.enjoyillinois.com/explore/listing/bison-tours-at-the-nachusa-grasslands/

## 7.5 Bison Restoration: Aesthetics, Politics, Economics, and Ecology

> *It is a melancholy contemplation for one who has travelled as I have, through these realms, and seen this noble animal in all its pride and glory, to contemplate it so rapidly wasting from the world, drawing the irresistible conclusion too, which one must do, that its species is soon to be extinguished….*
>
> *And what a splendid contemplation too, when one (who has travelled these realms, and can duly appreciate them) imagines them as they might in the future be seen (by some great protecting policy of government) preserved in their pristine beauty and wildness, in a magnificent park, where the world could see for ages to come… .What a beautiful and thrilling specimen for America to preserve and hold up to the view of her refined citizens and the world, in the future ages! A nation's Park, containing man and beast, in all the wild and freshness of their nature's beauty.* (George Catlin in present day South Dakota in 1832, in Brower)

The North American bison is iconic— stamped on the American nickel, the country's national mammal, an international conservation story from near extinction to numerous restored populations, all with strong social, ecological and economic support, jointly shared by Mexico, Canada, United States, their citizens, and their governments. But surprisingly we still know so little of its long-term ecology--- where the buffalo roamed in great numbers, and where they didn't-- and why? The species is now a poster child for wilderness, but does a human-bison mutualism model provide a better understanding of bison's past and better prospects for its future?

### 7.5.1 Aesthetics and Politics

The International Union for the Conservation of Nature's status survey of the North American bison conservation clearly recognizes the unique past and present social dimensions of the buffalo:

> *Few species enjoy a history as rich in archaeology, palaeontology, story and legend, oral and documentary history as the American bison. Nor is there another North American species for which the cultural and political significance of an animal is so great. For thousands of years various forms and populations of bison have coexisted with humans in North America, providing sustenance and shaping human social and economic patterns, and influencing national history and international political relationships*. [5]:9

The aesthetic images arising from this legacy [748,749] lead to nostalgia for large herds of buffalo roaming vast grasslands. Certainly, historic bison numbers were high in 8 ecoregions. However, most of the bison's distribution was in low to moderate densities over 58 ecoregions (Table 7.4.2.1, Figure 5.4.1.1, Appendix A). Moreover, bison are promoted to the public as "ecosystem engineers" or other metaphors for agents of great ecological or hydrological change [24,530]. Again, that applies to several ecoregions, but not everywhere. In fact, at low densities, beyond seeing the obvious signs of their presence (tracks, trails and chips), heavily hunted bison are secretive and not routinely observed—even in open country. The proposal that in many regions, mutualism might have long-linked humans, bison, beaver and fire further strains the idea of imagining large herds roaming many areas of the continent. Both beaver and fires require low to moderate levels of herbivory to maintain biomass. The norm, especially in open woodlands, hills and mountains on the periphery of the plains was small, widely spaced herds, and many of these bison may have had small home ranges compared to the more migratory bison on the plains [10,36].

Moreover, the “bison in abundance” aesthetic often results in political direction for conservation and restoration projects to manage for numerous bison. A comparison of “modern analog” bison restoration projects described in Section 6 (Table 7.5.1.1) shows that current project population and population density targets do follow the general pattern of historic ecoregion bison densities with highest on central grassland, and lower in the periphery. However, the observed or management target densities are above the modelled ecoregion densities that would maintain native plant and animal communities. This problem is most acute in mountain restoration projects such as Yellowstone and Banff) where snow depths concentrate high numbers of bison in the winter and spring on valley bottom grasslands and riparian zones, or for small parks managed for high wildlife numbers such as those in the Black Hills (Figure 7.5.1.1), or Elk Island and Grasslands national parks (see Section 6).

Figure 7.5.1.1. Bison in Custer State Park in the Black Hills. The riparian zone along the stream has few remaining willow or other woody plant species. Deciduous trees or shrubs persist in wildlife exclosures or as isolated large individuals resistant to browsing damage. Historically, beavers were abundant in the Black Hills but are now relatively rare. Contrast the streamside vegetation in this image with conditions when the Sioux occupied the area (see Figure 6.4.4.2). (Photo: Black Hills Visitor Magazine)

Table 7.5.1.1. Select bison restoration projects (from Section 6) stratified by biome and ecoregions. Historic bison density modelled at the low to moderate ranges scaled from of the historic abundance index (Appendix A) that would possibly maintain observed historic biomass and fire regimes, vegetation (e.g., aspen, willow, saskatoon), and wildlife (e.g., beaver). Restoration bison density is reported numbers or management objective range for population. One AU is equivalent to 1 domestic cow with calf. Appendix A describes modeling assumptions and limitations for historic densities.

| Biome | Project (Ecoregion) | Modelled historic density range (bison/km$^2$) | Observed or target restoration project density (bison/km$^2$) | Remarks |
|---|---|---|---|---|
| Great Plains Mid-Rockies | American Prairie Reserve (9.3.1 NW Glaciated Plains) | 2.15-4.19 | ~5 (summer) | In rotational paddocks for spring and summer grazing season, hay-fed in winter [528] |
| | American Prairie Reserve (9.3.1 NW Glaciated Plains) | 2.15-4.19 | 2.5-3.7 (year round use) | Light stocking in several large paddocks, annual rotation, riparian recovery described [527] |
| | Grasslands National Park (9.3.1 NW Glaciated Plains) | 2.15-4.19 | ~2.5 >10 (NE area) | Bison concentrate on NE portion of park in summer[528], high riparian impacts |
| | Northern Plains tribal herds (9.3.1 NW Glaciated Plains) | 2.15-4.19 | ~9 | Mean density for of 4 tribal herds (Belknap/Peck/ Blackfeet/Rosebud), production/conservation [750] |
| | Buffalo National Park (9.2.1 Aspen Parkland) | 1.77-3.64 | 8.3-17.8 | Park established from 1908-1936, closed due to serious range degradation [596,751] |
| | Elk Island National Park (9.2.1 Aspen Parkland) | 1.77-3.64 | 3.6 (bison) ~7 AU (all wildlife) | Bison numbers high for genetic conservation, negative beaver/vegetation impacts [274,599,600] |
| | Yellowstone National Park (6.2.10 Middle Rocky Mtns) | <1.35-2.71 | 0.405 (total range) ~2-8 (core ranges) | >95% historic bison sightings <YNP elevation, high current ecosystem impacts [89,263,529,730] |
| | Black Hills parks (6.2.10 Middle Rocky Mtns) | <1.35-2.71 | 3.1-3.9 (bison) 6.3-9.1 AU (other) | Managed for high densities of several species, vegetation impacts observed [686,690] |
| | Badlands National Park (9.3.3 NW Great Plains) | 1.83-3.66 | 2.1-4.3 (bison) (year-round use) | 500-1000 bison across Sage Ck area, vegetation effects monitored |
| | Natusha Grasslands, IL (8.2.3 Central Cornbelt Plains) | 0.19-0.83 | ~17 (bison) (year-round use) | ~100 bison on 600 ha, historic densities low, no negative ecological effects detected yet [698] |
| | Flint Hills and Tallgrass Prairie (9.4.4 Flint Hills) | 0.72-1.45 | ~16-24 (varies by period) | Productive grassland [679,700,702,705,752], historically not in high density bison range |
| | Prince Albert National Park (5.4.1 Boreal/Peace lowland) | 0.52-1.05 | <0.35 | Bison concentrate on SW corner of park boundary near agricultural lands[602,603] |
| | Wood Buffalo National Park (3.3.2 Hay/Slave R Lowlands) | 0.32-0.64 | 0.21-1.66 (meadows) 0.01-0.02 (forests) | Highest bison densities on Peace-Athabasca delta meadows [237,238,618] |
| Southwest-Great Basin | Vermejo Ranch, New Mexico (6.2.14 Southern Rockies) | 0.60-1.20 | ~1.0 (summer) ~1.5 (winter range) | High elk densities (~3/km$^2$) likely impacting vegetation [474] |
| | Rio Moro National Wildlife Refuge (9.4.3 Southwestern Tablelands) | 0.78-1.57 | ~13.5 | Bison managed by Polaque Pueblo, beaver restoration research ongoing [478,479] |
| | San Luis Valley (6.2.14 Southern Rockies) | 0.60-1.20 | ~7.7 | Population likely exceeds carrying capacity [480] |
| | Janos Biological Reserve (10.2.4 Chihuahuan Desert) | 0.10-0.20 | >2.5 | Mexico's first bison restoration project, ecological effects being monitored [17,472,473] |
| | North Rim-House Rock (10.1.7 Arizona NM Plateau) | 0.02-0.04 | 0.1-0.2 | Bison increasingly impacting Grand Canyon NP vegetation, population culling ongoing [481,484] |
| | Henry Mountains (6.2.13 Wasatch Uinta Mtns) | 0.04-0.07 | ~0.32 | Bison densities highest at mid elevations, above cattle range [486] |
| Northwest Plateau | National Bison Reserve, MT (6.2.4 Canadian Rockies) | 0.08-0.15 | ~4 | Historically bison not observed in area, possibly high current ecosystem impacts [547,548] |
| | Banff National Park (6.2.4 Canadian Rockies) | 0.08-0.15 | ~0.5 (total range) >5 (winter range) | >90% historic observations E of park, current mgmt. targets [119,562], high impacts likely |
| | Halfway-Sikanni (6.2.1 Skeena Omineca Rocky Mtns) | 0.01-0.02 | <0.1 (total range) | Historically at west edge range [22], limited draw and Indigenous sustenance hunts [612–614] |
| Subarctic Arctic | Mackenzie Bison Sanctuary, NWT (3.3.1 Great Bear Plains) | <=0.01 | 0.2 | Historically bison only observed in southern area of ecoregion [621] |
| | Aishihik , Yukon Territory (6.1.5 Watson Highlands) | 0.00 | 0.115 | Bison not observed in historic records [622,716] |

## 7.5.2 Economics

There are probably few greater truisms when disentangling past and present cultural-ecological processes than “follow the money”.  For modern societies bison are big business. The economics of a mechanized hide and meat trade led to near-extinction of the species in the 1800s [15] and today it has created a revival to numbers >200,000, but where >90% are in commercial herds managed as a luxury meat product competing with beef [5]. The link between bison and agriculture is even more complex. Likely the deep-aesthetic image of ecosystems supposedly resilient to “bison in abundance” still frames an argument for managing both commercial herds of both bison and cattle at relatively high stocking rates, although modern range researchers and managers increasingly recognize potential impacts [72,73,412,753]. An irony here though is that cattle stocking rates and management practices have, in turn been used as a basis for estimating the carrying capacity for “wild bison” in some restoration efforts. Projects informed by domestic cattle guidelines often propose bison densities more than the estimated historical conditions above (Figure 7.5.1.1).

In parks, economics has long been a primary driver for nature conservation [754,755]. In the 1900s many parks placed bison in display paddocks for public viewing [556,557]. This attracted visitors, helping build a tourism industry with hotels, buses, guides and park rangers [755]:17, 75-79. Even as the use of “paddocks in parks” fell in disfavor and bison were allowed to roam, the tradition and public expectations of wildlife viewing has continued to drive an industry that advertises and depends on seeing bison, elk, and other species—and these are often human-habituated, foraging near roads or crowds of tourists [756].  This requirement for easy wildlife viewing and a nostalgia for views of “tranquil nature” in turn leads to opposition from many economic stakeholders to culling and Indigenous hunting. This creates conundrum for managing a species such as bison that likely depended on human predation and burning for its very existence and sustainability.

A further economic issue for bison (and bison habitat) is the funding and motivation of conservation groups. Buffalo’s cachet has for over a century drawn concerned citizens into movements to conserve and restore the species. However, the aesthetics and politics of “bison in abundance” can lead to the species being a poster child for fund raising and continued lobbying to expand conservation areas and relieve the impacts of super-abundant herds. Here’s an abridged example of conservation-group fund-raising pitch to buy more bison habitat. This could apply to many herds:

> *Bison are naturally migratory; … bison cross vast amounts of land and are instinctually driven to leave the harsh, high elevation(s)… in the winter and seek lower elevation habitat that is more conducive to calving and finding winter forage*

Every restoration herd listed in Table 7.5.1.1 has its citizen proponents and opponents, but if the project’s existing bison are degrading their existing ecological community, it should be the mutual concern of all to reduce numbers to sustainable levels while the societal debates about expanding their range are ongoing. Humans, bison, nor the hundreds of other native species will benefit during these decadal discussions if the core habitats and boundary zones of existing protected ranges are destroyed by an advancing juggernaut of starving buffalo during droughts or tough winters. The priority for conservation groups should be to support herd managers in efforts to protect their existing lands. This can serve as a model for how bison could thrive on additional habitat [757].

Finally, let's consider costs of managing bison in wildlands. These days, buffalo don't come cheap—especially on the southern ranges of the continent. Even in an optimal scenario where bison numbers are relatively low, human access is close, and there a willing supply of hunters, doing the hunts managing the hunts can still be costly. In the wildlands of parks where many wild bison may live, wheeled vehicle use is often restricted. Using horses or mules to pack out large quarters of meat, even for a few kilometers is costly. Sadly, packing your all possessions and most your grubstake on dogs, mules, horses or oxen is becoming a lost art. Perhaps the ideal scenario to fully involve Indigenous people will be to allow them sustenance hunting and prioritize them as the guides and outfitters for limited-draw commercial hunts. Again, for most ecoregions and restoration projects, when managing by hunting, recognize that fewer bison is better. In worse case scenarios, many bison herds are managed by roundups, drive fences, holding facilities, and then shipping for slaughter. With wild bison, this is all costly, visible to the public, and often leads to high controversy. In most cases less bison will be better—and for most landscapes this will reflect processes of long-term human-bison mutualism.


Figure 7.5.2.1: Satellite view of Badlands National Park bison handling facility during the September, 2024 buffalo roundup. The park manages a herd of ~500-1000 bison with an annual increment of ~50-100 per year. Managing high numbers of bison is costly.

### 7.5.3 Bison Restoration: Ecology, Genetics and the Land

The IUCN report *American Bison: Status and Conservation Guidelines* [5] provides a comprehensive review of the species' history, ecology and restoration. Here I will describe additional perspectives through recognition of the broad-scale influence of Indigenous peoples, and the variable population densities that may have occurred.

*Ecology: Bottom-up or Top-Down?*

Two statements in the IUCN report provide important context:

> *The ecological scope of the species was limited only by its habitat requirements and specialised diet. An obligate grazer, grasses and sedges present in grasslands and meadows are the mainstay of the American bison's diet and habitat.*[5]:1

> *No other wildlife species has exercised such a profound influence on the human history of a continent. As the great ice sheets receded, and grasses and sedges colonised the emerging landscape, beginning 14,000 years ago, bison, then human cultures followed. Widespread and abundant…, bison were a staple resource for more than 12,000 years in the subsistence economies of successive cultures of Native North Americans.*[5]:2

The human-bison mutualism hypothesis fundamentally reverses this bottom-up perspective. Humans, through use of fire, were the primary agent that created and maintained sedges and grasses for bison forage. People, not habitat were the widespread and consistent factor that determined where bison could persist—much good habitat was never occupied. Bison may have been a staple resource in some parts of the continent, but across most of its range the long-term abundance of the species was determined by alternate food and shelter resources for humans, the territorial buffers and coalitions between cultures, and the resulting human densities from these factors.

With this understanding, we can consider this perspective from the IUCN report:

> *Bison can best achieve their full potential as an evolving, ecologically interactive species in large populations occupying extensive native landscapes where human influence is minimal and a full suite of natural limiting factors is present*. [5]:2

Clearly this ideal might partially represent the ecology of large herds in the continent's central grassland ecoregions, but even here it is useful to consider that the quality of range forage was often determined by burning, and the presence of water was partially tied to the activities of beaver—both under some human influence [8,252]. Moreover, when bison densities became high on the central grasslands, they would disperse to the peripheral parkland and savanna ecoregions where human predation was high. Elsewhere on the continent, although some contiguous populations may have been numerous in total across a vast area, bison density was generally low—often very low. Further, in these areas Indigenous burning, and other mutualism processes such as herding or even temporarily capturing and transplanting bison could influence distribution and abundance. Perhaps the greatest contribution humans made in these peripheral areas was create good habitat (parklands and savannas) and protect it from degradation by hunting that kept bison numbers low. In regions adjacent to the central grasslands, this routine hunting over time favored individuals or herds that rapidly moved back to the central plains when the stress of droughts or a severe a winter decreased [6,8,172,188]. This bison migration pattern, and resulting periods of low herbivory impact, maintained high quality habitat around edges of the prairies.

### *Role of Four-Legged Predators*

The human-bison mutualist hypothesis consigns other predators (wolves, grizzly bears, black bears, cougars) to nearly an irrelevant role. Statistically, this is supported at the continental scale by the positive correlation of wolves and grizzly bears with historical bison abundance (Section 5.4.2). These predators were are more abundant when bison are abundant-- indicating a possible general dependence on bison for meat or carrion in the center of the range [22], but with few or undetectable negative effects of their predation on bison numbers here or elsewhere. Low bison predation rates by wolves and bears is also the experience of current southern restoration projects in Yellowstone [530] and Banff [119,758]. Both these parks have relatively abundant wolves and bears, and both carefully manage human predation or removals. Yet, in neither case do wolves or bears predators yet demonstrate capacity to regulate bison population growth rates.

For northern restoration projects (e.g., Halfway-Sikanni, Wood Buffalo, Mackenzie Bison Sanctuary, Aishihik) the situation is more complex. In the historic dataset there are few journal accounts that would indicate predation effects by wolves or bears, but human predation is routinely described where bison occurred (e.g., along the Peace, Slave and Athabasca rivers). Currently, bison hunting (Indigenous sustenance and permit draws) and carnivore harvesting (by trapping or hunting) is ongoing in most northern regions. These bison populations all have lower densities than southern herds (Table 7.5.1.1), and there are alternate sources of prey such as moose and caribou. Some research projects have concluded that wolf predation (particularly of calves and subadults) combined with habitat quality and climate (e.g. snow depth/condition) can reduce bison numbers in northern regions [237,717].

Thus, for the long-term continental perspective a tentative hypothesis is that historically wolf and bear predation might have reduced bison numbers in some areas, depending upon: 1) bison density as influenced by the more significant effects of habitat and human hunting and density, 2) human hunting of the predators themselves, and 3) availability of alternate food sources for these predators/omnivores which again were influenced by humans (hunting and burning). Further analysis of the historical journal dataset [109] might provide some evidence to evaluate these potential relationship and their relevance to current restoration projects.

### *Ecology, Genetic Diversity and Evolution*

The main driving forces of evolution in any population are genetic mutation, natural selection and gene flow and genetic drift. Species genetics influence epigenetics, or rapid changes to morphology or behavior that can provide inheritable adaptions to changing environments. Both genetic and epigenetic processes all vary by population density, connectivity and selection forces. The massive source-sink dynamic of overall North American human-bison interaction (Figure 3.1.1.1) suggests an astounding array of potential genetic and epigenetic influences on bison. A high quality, annotated chromosome-level bison genome has recently been developed [759,760], but genetic and epigenetic linkages remain largely unknown or theoretical. With reference to the ecological models, long-term species and community interactions, and population densities described in this report, I will briefly (and tentatively) consider some potential long-term and future implications for bison conservation.

Mutation is a permanent change in the DNA sequence of an organism, which can be inherited or occur spontaneously and can have various effects, from being beneficial to neutral to negative. For example, based on their genome analysis, Stroupe et al. [760] identified various mutations across the several genes responsible for rare bison albinism. Various environmental conditions can trigger mutations, and given the wide variety of habitats, elevations, density, and other parameters influencing bison, unique patterns of mutation and genetic change will likely be identified in future.

Gene flow follows movement of individuals or subpopulations and obviously creates genetic structuring. Bison have a varied range of movements from <100 sq km wood bison ranges, to >100 km annual migrations of bison on the Great Plains, to multi-decadal range expansions of >1000 km depending on climate and predation conditions. Based on migration patterns [99,188,331], source-sink population dynamics from northwestern plains (Figure 3.1.1.10) and historic bison abundance (Figure 5.4.1.1) likely the historic main flow of bison was from high density herds on the plains to low density regions in peripheral woodlands, foothills, and mountains, and indeed there are numerous journal accounts reporting this pattern around the whole range (Section 6 above). Moreover, there was likely, through use of fire and herding, ongoing human efforts to enhance or move bison off the plains into surrounding woodlands. Although most gene movement would have been high to low density areas, environmental events (e.g. deep snow winters) or human influences could periodically drive low density bison out of the mountains and woodlands and back onto the plains. Thus, genetic diversity developed in these smaller herds would periodically be returned to the abundant gene pool in the center either through direct movement or breeding with adjacent subpopulations.

Natural selection, including sexual selection, makes possession of some traits more likely for an organism to survive and reproduce. It is usually quantified through “fitness”, or the probability of survival and reproduction in a particular environment. Although genetic or epigenetic controls remain largely unknown, the observations from early journalists and current researchers on the differences between the two ecotypes of plains bison in the south, and wood bison from the north allow surmises of sets of physical and behavioral adaptions to their respective environments that may result from natural selection. These include differences in body mass, shape, pelage, herd size, daily movement distances, and response to predation risk (e.g., [13,24,36,40,41,223,761]. An interesting observation from archaeological data is the synchronicity between gradual diminution of bison living in the large herds on the grasslands with the body size of ephemeral populations in the Pacific northwest [78,385] . This allows interpretations of natural selection processes on the plains, and potential gene flow patterns from source bison populations on the plains to sink populations in the west.

Genetic drift- This is defined as the variation in the relative frequency of different genotypes in small populations, owing to the chance disappearance of particular genes as individuals die or do not reproduce. Drift may have not been a major factor in the wide-ranging, high-density bison populations on the central Great Plains. However, for most its historic range, bison densities were lower, and often much lower (Figure 5.4.1.1, Tables 7.4.2.1, 7.5.1.1), and these small herds were not highly migratory [10,36]. Under these conditions genetic drift was likely, and natural selection would in turn favor unique subpopulations with adaptions to their local environment. Some of these individuals would periodically disperse back into the core population increasing genetic diversity.

Genetic conservation through metapopulation management- The modern bison species and ecotypes arise from a variety of genetic processes of long-term historical high-density source population on the center of the Great Plains surrounded by low-density herds in numerous ecoregions with a diversity of habitats and predation conditions, and then a genetic bottleneck due to near extinction reduction to <1000 [762,763]. Due to land use development, particularly on the Great Plains [179], it now impossible to restore this metapopulation system at its former continental scale. The future is likely isolated populations managed with conditions and densities reflective of their ecoregion's habitat and predation patterns [604,764]. Periodic transplants may be required to maintain diversity. The greatest difficulty will be to establish a high-density core population where forage and intra-species competition are the primary regulatory and evolutionary forces [40,41,78,79]-- a conservation population that could be a primary source for transplants to surround regions. The proposed eventual expansion the American Prairie Reserve may partially serve this purpose [525,765]. In the surrounding lower density sink populations, human-bison mutualism was in the past, and will in the future continue to drive genetic diversity. The general way forward may be to link knowledge of Indigenous seasonal rounds for ecoregions and biomes (Section 2.1, Section 6) to bison predation, herding, harvest and habitat management.

*Restoration: "Who will speak for the land?" (and water!)*

In a recent critique of bison restoration and ecosystem management, past Range Society President Jenny Pluhar reminds managers and researchers that the essence of managing large herbivores is to conserve the landscape that sustains ecosystem productivity [757]. For the >10K years of North America's human-beaver-bison mutualistic relationship. Indigenous people helped sustain the land—burning the vegetation early and often and optimally foraging by intensively hunting bison whenever possible. This level of predation was beneficial not just to humans, but as mutualism with many other species, preventing degradation of grasslands, riparian zones, beaver, and sources of surface water. Aggressive killing may seem like heresy to some of the many modern managers and stakeholders now engaged for bringing the buffalo back from the brink of extinction, but ultimately bison and the ecosystems they depend on are doomed if we fail to understand long-term ecological states and processes, and the Indigenous ways that influenced them.

Rangeland researchers have long-recognized the negative ecological impacts of large herbivores over-abundance [267,469], but on many North American landscapes the economic realities of the agricultural industry often constrain management options. Never-the-less, private and corporate owners recognized the importance of sustaining the land and have recently been at the professional forefront to conserve or restore the productivity of ecosystems grazed by large-herbivores. In contrast, public land managers, with different set of constraints often dictated by diverse groups of stakeholders, often fail to maintain long-term herbivory and fire regimes. Public land managers tend to be drawn to laissez-faire, hands-off "natural processes for native species" fail to fully comprehend the long-term significance of past Indigenous practices [345,534,730].

The current cycle of range ecosystem research and management is increasingly appreciative of the complexity of interactions between long-term human cultures, grassland and riparian communities, fire, beaver, and numerous wildlife species [8,73,412,766,767]. There are no better places to recognize these millennium-long cultural and ecological interactions than parks and protected areas where bison are being restored. Canada's 1990 National Parks Act clearly requires managers to "speak for the land." The legislation specifies that the first priority for national park managers is to maintain or restore "ecological integrity" [768], legally defined as:

> *"a condition that is determined to be characteristic of its natural region and likely to persist, including abiotic components and the composition and abundance of native species and biological communities, rates of change and supporting processes"*

and further policy clarification from Parks Canada [769]:7–2 recognizes that

> "*the influence of Aboriginal peoples is fully consistent with … [the] definition of ecological integrity…. this traditional human role is an important element of the ecological integrity of the ecosystems that Parks Canada is mandated to preserve or restore.*"

This type of legislative and policy guidance is being adopted by other governing bodies. Many areas of the northwest, currently perceived as "wild" may again be regarded as ancient indigenous homelands where long-term indigenous seasonal rounds and the potential keystone ecological role of humans are recognized, understood, valued, and in some locations, restored.

Implementing Parks Canada direction for ecological integrity, Heuer et al. [119] describe a framework for ongoing bison restoration in Banff National Park. Parks Canada recognized the importance of restoring the Indigenous fire regime [90,122,770] and for two decades prior to bringing back the buffalo had systematically burned its historical range. Indigenous blessing ceremonies proceeded transplanting 16 bison in 2017 to acknowledge the long coexistence of people and bison in Banff. In 2018 an Indigenous advisory circle was established to help guide management as the herd was allowed to leave their soft-release pasture into the wilds of Banff's northeast corner. In 2020 the Stoney Nakoda Nations [771] proceeded with a biocultural study to link elder's traditional knowledge of the landscape with bison habitat use patterns. Population growth was rapid (>30%). By 2024 the herd numbered greater than 100 and Parks Canada and the Indigenous advisory circle authorized First Nation hunts for up to 10 bison. This eco-cultural approach establishes a good basis for further management, but this will be challenging in this remote area— holding this population at just 200 animals at current growth rates will require removing 40-50 per year [119,758]. In winter and spring bison congregate for extended periods on limited areas of grasslands and riparian meadows at densities that, as predicted in Figure 7.4.1.5 would result in habitat degradation (Figures 7.5.4.1, 7.5.4.2). Perhaps ongoing Indigenous hunting will result in numeric and behavioral responses to alleviate this concern.

Figure 7.5.4.1. Bison herd grazing the rough fescue grasslands of Scotch Camp meadow, Red Deer valley, Banff National Park c. 2022 when the restored population still numbered <100 [119,758] (Parks Canada photograph). Deeper snow depths at higher elevations in the park constrain bison to limited valley bottom areas from December through May. Given summer population carrying capacity estimates [562] of 500 - 1000 for the whole designated range of 1600 $km^2$, and that only ~5-10% of this area is winter range results in stocking densities of >20 bison/$km^2$ (>100 AUM for 5 months grazing ) on these grasslands, including the period of fescue's critical early spring growth. Bison at these stocking densities will degrade fescue grassland productivity [260,549] .

Figure 7.5.4.2. Bison herd on alluvial fan of Coyote Creek in the Red Deer valley, Banff National Park in June, 2022. In spring deep snowpacks at upper elevations constrain bison to low elevation ranges. (Photo courtesy of Vern Dewit Photography). Snow cover blocks bison movements to upper elevations.

## 7.6 The Upshot: The Buffalo's Great Heartbeat and Human-Beaver-Bison Mutualism

This paper provides data and other interdisciplinary information to test the following proposition:

> *Humans, beaver and the buffalo are long-term mutualists. Humans, through fire use and conserving beaver contributed additions to the essentials of bison habitat—forage, water and winter cover. More importantly, by regulating bison populations with predation, humans kept the bison from degrading habitats. In return, the buffalo could provide many humans with nearly everything—food, clothing, shelter and for some cultures, a complete circle of life.*

The key to this relationship was the massive area of North America's central grasslands. Here, where humans could not survive the winter and drought, the bison became the largest land mammal to survive the continent's colonization by humans. From this refuge in the center of the continent, the "Buffalo's Great Heartbeat" -- its capability to survive, reproduce, and migrate — allowed periodic dispersals from great herds on the plains into surrounding deciduous parklands and savannas (Figure 3.1.1). In this peripheral zone, two most the complex processes of mutualism with feed back between humans and bison occurred. Humans, using our species' unique tool, "burn early, burn light, burn often" could adaptively maintain optimal habitat for humans to survive at the edge of the plains, but also a pattern of grasslands between the woods that allowed bison to escaping hostile winters. Secondly, in this peripheral zone, humans could adaptively hunt and herd bison. Some would be killed in pounds for winter food. Others wood be driven further into the nearby forests or mountains for future use. Here, some dispersing bison would escape their human hunters, providing numerous ecoregions and other peoples with a low density, but important source of food, clothing, and shelter. This human hunting had a regulatory function with feedback—humans that hunted too aggressively would be forced to move further out on the plains, take greater risks in a dangerous environment, have poorer hunting success, and eventually retreat back into the woodlands. A final complex mutual relationship occurred further out on the plains.

A near-final act in North America's >10 millennium human-bison mutualistic process began to play out in the early CE 1200s. At first it was probably nothing different from previous oscillations. Drought, disease, economic collapse, or a combination of these reduced numbers of Indigenous people on the periphery of the range, and bison began to expand its distribution, first southwards into Texas, bison range, then southeastwards into the lower Mississippi, eastward towards the Great Lakes and Ohio River, and finally, ~1800 CE a large expansion over the Rocky Mountains onto the Snake River. Possibly at about ~CE 1700 bison numbers were at a long-term high—likely somewhere in the range of 10-25 million (Figure 7.6.1). Then came the astronomic collapse as global, industrial scale hunting reached into the heart of the range and forever silenced the continental-scale of "buffalo's great heartbeat" [15].

However, even if the "heartbeat" from the migratory pattern of a massive North American central population is gone, the individual heartbeats of bison now numbering in the hundreds of thousands are still with us. Most are in commercial herds, but an increasing number are being restored in wild herds to their ancient homeland— it is indeed a great conservation story.

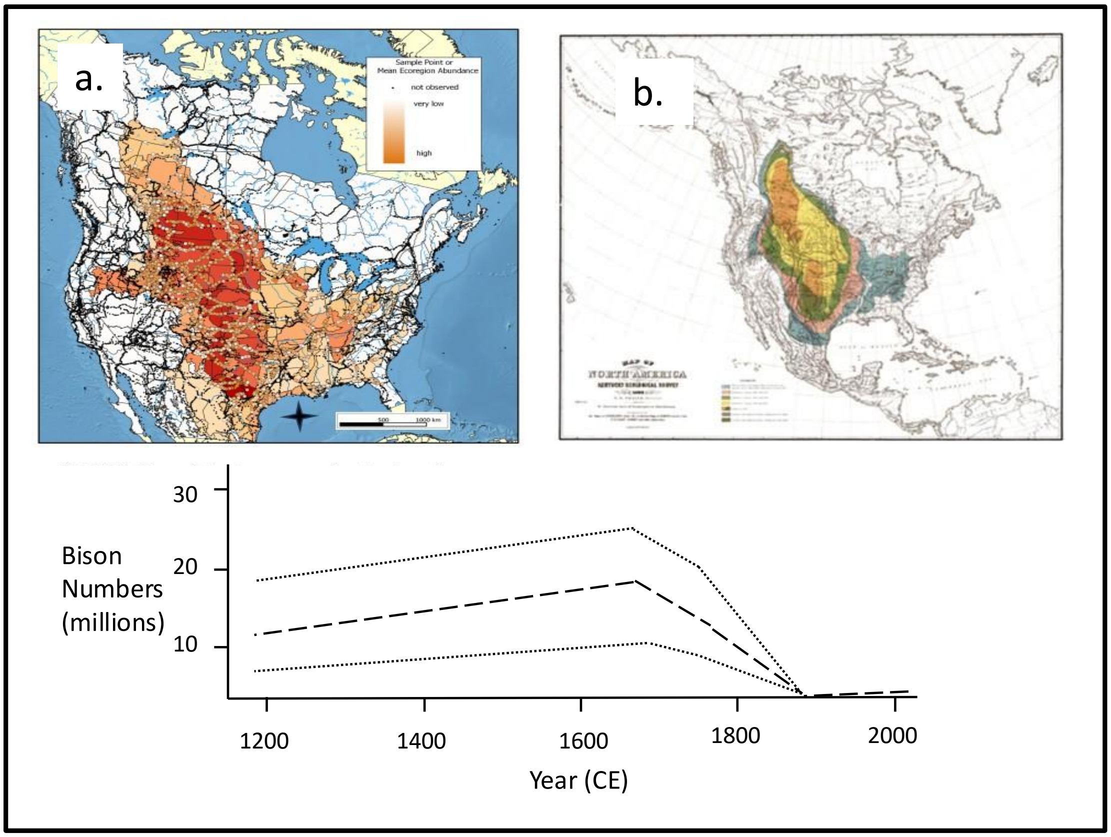



Figure 7.6.1. Estimated abundance and distribution of bison for the period CE ~1200 to 2000 showing: a. period of bison distribution expansion (~CE 1200-1700) around the periphery of bison range (Figure 5.5.1.1 this study) followed by b. period of decline as mapped by Allen [2] showing a potential population range based upon modern analogs where the lower estimate could result in vigorous riparian zones and beaver, and the upper level would provide only marginal riparian habitat (Section 7.4.3 this study).

So begins another cycle of human-bison mutualism—and one where more than ever the close ecological and social links between our species will have to be recognized and valued. Further, for the relationship to be successful, the third partner—the beaver—must also be restored. If there ever was species that was good "family glue", the beaver more than fills this role, especially the more arid prairie and mountain grasslands. The beaver will continue to bring humans and bison together. Its presence signifies ecological and cultural integrity, and a recognition from modern cultures that the long-term Indigenous valuing of the beaver is understood and respected. Beaver abundance along the streams of areas with restored bison is critical sign that modern humans "will speak for the land" and not degrade the habitat for bison (Figure 7.6.1) through ignorance, neglect or lack of respect for our essential role in long-term human-bison mutualism.


Figure 7.6.2: a) Riparian willow, cottonwoods, and aspen along the Madison River in Yellowstone National Park on September 30, 1938 (from an early Kodachrome slide, Cushman Collection, Indiana University Archives P15797), and b) a mixed bison herd (bulls, cows, calves) along the river in c. 2000 (US National Parks Service YELL-16356). This location is approximately 15 km downstream from Madison Junction, the legendary location for an early tourist gathering. This meeting around a campfire helped create "America's greatest idea"- the national parks. Once a rich riparian zone with prime beaver habitat, bison herbivory has reduced cover to weed-infested patches of largely non-native grasses on Madison River's bottomlands.

# 8. LITERATURE CITED

*Note for editing… use just straight "Word" program to reformat… select all then move indents… defaults back, so just do for PDFs, see bottom for pasted version.*

2025-05-25 Lit Cit Version- 771 total citations

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# Appendix A: North American Ecoregion Bison Population Modelling

## Estimation Method

Historic bison numbers are usually estimated assuming they could be related to current domestic stocking estimates, which in turn are related to forage productivity, and not influenced by to predation or risk sensitive foraging. The historic journal observations for humans and other species abundance and habitat conditions, and historic photographs and allow consideration of both bottom-up habitat and top-down predation factors on bison numbers. Modern analogs for the herbivory and trampling effects of bison and cattle management in combination with the historic observations give further information on likely historic densities.

For the preliminary estimates below I simply presume that the index (01Bison) for an ecoregion approximates an upper range of bison density based upon density for high cattle stocking, or for example ~11.40/km$^2$ for High Plains, or ~15.65/km$^2$ for the Edwards Plateau. This might be a maximum stocking under favorable conditions (see Modern Analogs sections above). I then simply scale this to the journal abundance index for other ecoregions as a maximum density (this may be low for some boreal landscapes) and then reduce column by 25% and 50% for bison density estimates that would maintain observed historic vegetation and wildlife conditions (e.g., woody plant cover of aspen, willow etc. and presence of beaver). Using this admittedly rough approximation method, the column numbers in Table A.1 as follows:

**Biome**- Grouping variable, Figure 6.1.1
**Ecoregion**- North American ecoregions
**01Bison**- historical journal index
**Area km2**- area of the ecoregion
**LD1**- potential bison ecoregion density at 25% of maximum (HD2) prior to post- CE 1400 population expansion. Several ecoregions were possibly not utilized by bison at this time.
**LowPop1**- LD1 times area of ecoregion (km2).
**LD2**-potential bison density at 25% of maximum (HD2) during 1700s.
**LowPop2**- LD2 times ecoregion area.
**MD1**- potential bison ecoregion density at 50% of maximum (HD2) prior to post-CE 1400 population expansion.
**ModPop1**- MD1 times ecoregion area.
**MD2**- potential bison density at 50% of maximum (HD2) during 1700s.
**ModPop2**- MD1 times ecoregion density.
**HD1-** potential bison ecoregion density at 100% of maximum (HD2) prior to post-CE 1400 population expansion.
**HighPop1**- HD1 times ecoregion area.
**HD2**- potential bison density at 100% of maximum (HD2) during 1700s.
**HighPop2**- HD2 times ecoregion area.

## Discussion

These rough calculations yield a broad range of populations for two time periods (1400s, 1700s) reflecting the general observed relative abundance of bison from the mid-1500s to mid 1800s, and possible maximum number of bison for ecoregions based upon current stocking rates of cattle for core prairie ecoregions. From the modern analogs described in Section 6 the estimates might be a high for high density ranges, and low for low density ranges. The estimates can also be questioned on bison distribution within the ecoregions versus the routes of historic travellers and observation bias coming from this. In addition, some ecoregions were not fully occupied by bison in the 1700s (e.g., 10.2.4 Chihuahuan Desert, 10.1.3 Northern Basin and Range) so numbers of bison are overestimated by using the total ecoregion area.

Table A.1 Historic bison population estimates for ecoregions.

| | A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Biome | Ecoregion | 01bison | Area km2 | LD1 | LowPop1 | LD2 | LowPop2 | MD1 | ModPop1 | MD2 | ModPop2 | HD1 | HighPop1 | HD2 | HighPop2 | |
| 2 | 1Great Plains | 9.3.1 Northwestern Glaciated Plains | 8.59 | 404,239 | 2.15 | 867,796 | 2.15 | 867,796 | 4.29 | 1,735,591 | 4.29 | 1,735,591 | 8.59 | 3,471,183 | 8.59 | 3,471,183 | |
| 3 | 1Great Plains | 9.4.1 High Plains | 11.40 | 288,175 | 2.85 | 821,379 | 2.85 | 821,379 | 5.70 | 1,642,758 | 5.70 | 1,642,758 | 11.40 | 3,285,516 | 11.40 | 3,285,516 | |
| 4 | 1Great Plains | 9.3.3 Northwestern Great Plains | 7.32 | 356,739 | 1.83 | 652,529 | 1.83 | 652,529 | 3.66 | 1,305,057 | 3.66 | 1,305,057 | 7.32 | 2,610,114 | 7.32 | 2,610,114 | |
| 5 | 1Great Plains | 9.2.1 Aspen Parkland/Northern Glaciated Plains | 7.09 | 326,563 | 1.77 | 578,817 | 1.77 | 578,817 | 3.54 | 1,157,633 | 3.54 | 1,157,633 | 7.09 | 2,315,266 | 7.09 | 2,315,266 | |
| 6 | 1Great Plains | 9.4.2 Central Great Plains | 7.45 | 274,832 | 1.86 | 511,955 | 1.86 | 511,955 | 3.73 | 1,023,910 | 3.73 | 1,023,910 | 7.45 | 2,047,821 | 7.45 | 2,047,821 | |
| 7 | 1Great Plains | 9.4.6 Edwards Plateau | 15.65 | 75,039 | 0.00 | 0 | 3.91 | 293,601 | 0.00 | 0 | 7.83 | 587,203 | 0.00 | 0 | 15.65 | 1,174,406 | |
| 8 | 1Great Plains | 5.4.1 Mid-Boreal Uplands/Peace-Wabaska Lowla | 2.10 | 436,359 | 0.52 | 228,737 | 0.52 | 228,737 | 1.05 | 457,473 | 1.05 | 457,473 | 2.10 | 914,946 | 2.10 | 914,946 | |
| 9 | 1Great Plains | 6.2.10 Middle Rockies | 5.42 | 164,099 | 1.35 | 222,328 | 1.35 | 222,328 | 2.71 | 444,655 | 2.71 | 444,655 | 5.42 | 889,311 | 5.42 | 889,311 | |
| 10 | 1Great Plains | 10.1.4 Wyoming Basin | 6.11 | 132,467 | 1.53 | 202,252 | 1.53 | 202,252 | 3.05 | 404,504 | 3.05 | 404,504 | 6.11 | 809,008 | 6.11 | 809,008 | |
| 11 | 1Great Plains | 9.4.3 Southwestern Tablelands | 3.14 | 198,809 | 0.00 | 0 | 0.78 | 155,826 | 0.00 | 0 | 1.57 | 311,652 | 0.00 | 0 | 3.14 | 623,304 | |
| 12 | 1Great Plains | 9.4.5 Cross Timbers | 5.01 | 88,221 | 0.00 | 0 | 1.25 | 110,583 | 0.00 | 0 | 2.51 | 221,166 | 0.00 | 0 | 5.01 | 442,333 | |
| 13 | 1Great Plains | 9.3.4 Nebraska Sand Hills | 7.45 | 59,032 | 1.86 | 109,964 | 1.86 | 109,964 | 3.73 | 219,929 | 3.73 | 219,929 | 7.45 | 439,858 | 7.45 | 439,858 | |
| 14 | 1Great Plains | 9.2.2 Lake Manitoba and Lake Agassiz Plain | 4.95 | 82,662 | 1.24 | 102,343 | 1.24 | 102,343 | 2.48 | 204,686 | 2.48 | 204,686 | 4.95 | 409,372 | 4.95 | 409,372 | |
| 15 | 1Great Plains | 3.3.2 Hay and Slave River Lowlands | 1.28 | 297,251 | 0.32 | 95,170 | 0.32 | 95,170 | 0.64 | 190,340 | 0.64 | 190,340 | 1.28 | 380,679 | 1.28 | 380,679 | |
| 16 | 1Great Plains | 9.2.3 Western Corn Belt Plains | 0.98 | 227,783 | 0.24 | 55,734 | 0.24 | 55,734 | 0.49 | 111,468 | 0.49 | 111,468 | 0.98 | 222,937 | 0.98 | 222,937 | |
| 17 | 1Great Plains | 9.5.1 Western Gulf Coastal Plain | 2.19 | 90,970 | 0.00 | 0 | 0.55 | 49,808 | 0.00 | 0 | 1.10 | 99,616 | 0.00 | 0 | 2.19 | 199,232 | |
| 18 | 1Great Plains | 5.4.2 Clear Hills and Western Alberta Upland | 1.48 | 121,079 | 0.37 | 44,907 | 0.37 | 44,907 | 0.74 | 89,814 | 0.74 | 89,814 | 1.48 | 179,629 | 1.48 | 179,629 | |
| 19 | 1Great Plains | 9.2.4 Central Irregular Plains | 1.47 | 114,230 | 0.37 | 42,034 | 0.37 | 42,034 | 0.74 | 84,068 | 0.74 | 84,068 | 1.47 | 168,136 | 1.47 | 168,136 | |
| 20 | 1Great Plains | 9.6.1 Southern Texas Plains/Interior Plains and H | 1.05 | 145,733 | 0.00 | 0 | 0.26 | 38,213 | 0.00 | 0 | 0.52 | 76,426 | 0.00 | 0 | 1.05 | 152,852 | |
| 21 | 1Great Plains | 9.4.7 Texas Blackland Prairies | 2.40 | 43,417 | 0.00 | 0 | 0.60 | 26,050 | 0.00 | 0 | 1.20 | 52,100 | 0.00 | 0 | 2.40 | 104,201 | |
| 22 | 1Great Plains | 9.4.4 Flint Hills | 2.89 | 27,914 | 0.00 | 0 | 0.72 | 20,188 | 0.00 | 0 | 1.45 | 40,376 | 0.00 | 0 | 2.89 | 80,751 | |
| 23 | 1Great Plains | 8.3.8 East Central Texas Plains | 1.06 | 55,805 | 0.00 | 0 | 0.27 | 14,812 | 0.00 | 0 | 0.53 | 29,625 | 0.00 | 0 | 1.06 | 59,250 | |
| 24 | 1Great Plains | 8.2.3 Central Corn Belt Plains | 0.74 | 76,413 | 0.19 | 14,141 | 0.19 | 14,141 | 0.37 | 28,283 | 0.37 | 28,283 | 0.74 | 56,565 | 0.74 | 56,565 | |
| 25 | 1Great Plains | 6.2.6 Cypress Upland | 5.42 | 8,243 | 1.35 | 11,167 | 1.35 | 11,167 | 2.71 | 22,335 | 2.71 | 22,335 | 5.42 | 44,669 | 5.42 | 44,669 | |
| 26 | 1Great Plains | 5.4.3 Mid-Boreal Lowland and Interlake Plain | 0.05 | 130,837 | 0.01 | 1,626 | 0.01 | 1,626 | 0.02 | 3,253 | 0.02 | 3,253 | 0.05 | 6,506 | 0.05 | 6,506 | |
| 27 | 2Southwest-Gr | 6.2.14 Southern Rockies | 2.40 | 145,588 | 0.60 | 87,195 | 0.60 | 87,195 | 1.20 | 174,389 | 1.20 | 174,389 | 2.40 | 348,778 | 2.40 | 348,778 | |
| 28 | 2Southwest-Gr | 10.2.4 Chihuahuan Desert | 0.39 | 510,159 | 0.00 | 0 | 0.10 | 50,146 | 0.00 | 0 | 0.20 | 100,293 | 0.00 | 0 | 0.39 | 200,585 | |
| 29 | 2Southwest-Gr | 10.1.5 Central Basin and Range | 0.18 | 309,681 | 0.00 | 0 | 0.05 | 13,944 | 0.00 | 0 | 0.09 | 27,888 | 0.00 | 0 | 0.18 | 55,776 | |
| 30 | 2Southwest-Gr | 10.1.6 Colorado Plateaus | 0.12 | 134,835 | 0.00 | 0 | 0.03 | 4,066 | 0.00 | 0 | 0.06 | 8,133 | 0.00 | 0 | 0.12 | 16,266 | |
| 31 | 2Southwest-Gr | 10.1.7 Arizona/New Mexico Plateau | 0.09 | 150,070 | 0.00 | 0 | 0.02 | 3,198 | 0.00 | 0 | 0.04 | 6,396 | 0.00 | 0 | 0.09 | 12,793 | |
| 32 | 2Southwest-Gr | 6.2.13 Wasatch and Uinta Mountains | 0.14 | 45,648 | 0.04 | 1,602 | 0.04 | 1,602 | 0.07 | 3,203 | 0.07 | 3,203 | 0.14 | 6,407 | 0.14 | 6,407 | |
| 33 | 2Southwest-Gr | 12.1.2 Piedmonts and Plains with Grasslands | 0.02 | 130,711 | 0.00 | 0 | 0.01 | 667 | 0.00 | 0 | 0.01 | 1,334 | 0.00 | 0 | 0.02 | 2,668 | |
| 34 | 4Northwest Co: | 10.1.3 Northern Basin and Range | 4.29 | 141,988 | 0.00 | 0 | 1.07 | 152,271 | 0.00 | 0 | 2.14 | 304,542 | 0.00 | 0 | 4.29 | 609,083 | |
| 35 | 4Northwest Co: | 10.1.8 Snake River Plain | 3.69 | 53,527 | 0.00 | 0 | 0.92 | 49,345 | 0.00 | 0 | 1.84 | 98,690 | 0.00 | 0 | 3.69 | 197,381 | |
| 36 | 4Northwest Co: | 6.2.4 Canadian Rockies | 0.30 | 104,576 | 0.08 | 7,924 | 0.08 | 7,924 | 0.15 | 15,849 | 0.15 | 15,849 | 0.30 | 31,697 | 0.30 | 31,697 | |
| 37 | 4Northwest Co: | 6.2.15 Idaho Batholith | 0.37 | 60,151 | 0.00 | 0 | 0.09 | 5,623 | 0.00 | 0 | 0.19 | 11,246 | 0.00 | 0 | 0.37 | 22,491 | |
| 38 | 4Northwest Co: | 6.2.1 Skeena-Omineca-Rocky Mountains | 0.05 | 139,420 | 0.00 | 0 | 0.01 | 1,568 | 0.00 | 0 | 0.02 | 3,137 | 0.00 | 0 | 0.05 | 6,274 | |
| 39 | 4Northwest Co: | 6.2.9 Blue Mountains | 0.01 | 70,757 | 0.00 | 0 | 0.00 | 195 | 0.00 | 0 | 0.01 | 391 | 0.00 | 0 | 0.01 | 782 | |
| 40 | 5Subarctic-Arct | 5.1.1 Athabasca Plain/Churchill River Upland | 0.04 | 275,310 | 0.01 | 2,712 | 0.01 | 2,712 | 0.02 | 5,425 | 0.02 | 5,425 | 0.04 | 10,850 | 0.04 | 10,850 | |
| 41 | 5Subarctic-Arct | 3.4.5 Coppermine River and Tazin Lake Uplands | 0.02 | 253,082 | 0.00 | 0 | 0.01 | 1,364 | 0.00 | 0 | 0.01 | 2,729 | 0.00 | 0 | 0.02 | 5,457 | |
| 42 | 5Subarctic-Arct | 3.3.1 Great Bear Plains | 0.01 | 332,155 | 0.00 | 0 | 0.00 | 883 | 0.00 | 0 | 0.01 | 1,767 | 0.00 | 0 | 0.01 | 3,534 | |
| 43 | 6Northeast Wo | 8.3.2 Interior River Valleys and Hills | 2.18 | 120,349 | 0.00 | 0 | 0.55 | 65,645 | 0.00 | 0 | 1.09 | 131,290 | 0.00 | 0 | 2.18 | 262,580 | |
| 44 | 6Northeast Wo | 8.1.5 Driftless Area | 5.55 | 47,297 | 0.00 | 0 | 1.39 | 65,616 | 2.77 | 131,231 | 2.77 | 131,231 | 0.00 | 0 | 5.55 | 262,463 | |
| 45 | 6Northeast Wo | 8.2.4 Eastern Corn Belt Plains | 1.35 | 86,762 | 0.00 | 0 | 0.34 | 29,199 | 0.67 | 58,398 | 0.67 | 58,398 | 1.35 | 116,796 | 1.35 | 116,796 | |
| 46 | 6Northeast Wo | 8.1.4 North Central Hardwood Forests | 1.25 | 88,737 | 0.00 | 0 | 0.31 | 27,773 | 0.00 | 0 | 0.63 | 55,545 | 0.00 | 0 | 1.25 | 111,091 | |
| 47 | 6Northeast Wo | 8.4.3 Western Allegheny Plateau | 1.00 | 81,363 | 0.00 | 0 | 0.25 | 20,341 | 0.00 | 0 | 0.50 | 40,682 | 0.00 | 0 | 1.00 | 81,363 | |
| 48 | 6Northeast Wo | 8.4.1 Ridge and Valley | 0.57 | 116,647 | 0.00 | 0 | 0.14 | 16,732 | 0.00 | 0 | 0.29 | 33,464 | 0.00 | 0 | 0.57 | 66,929 | |
| 49 | 6Northeast Wo | 5.2.1 Northern Lakes and Forests | 0.14 | 255,875 | 0.00 | 0 | 0.04 | 9,201 | 0.00 | 0 | 0.07 | 18,402 | 0.00 | 0 | 0.14 | 36,804 | |
| 50 | 6Northeast Wo | 8.2.2 Huron/Erie Lake Plains | 0.81 | 31,543 | 0.00 | 0 | 0.20 | 6,376 | 0.00 | 0 | 0.40 | 12,751 | 0.00 | 0 | 0.81 | 25,503 | |
| 51 | 6Northeast Wo | 8.4.2 Central Appalachians | 0.06 | 62,010 | 0.00 | 0 | 0.02 | 959 | 0.00 | 0 | 0.03 | 1,918 | 0.00 | 0 | 0.06 | 3,836 | |
| 52 | 6Northeast Wo | 8.2.1 Southeastern Wisconsin Till Plains | 0.09 | 31,293 | 0.00 | 0 | 0.02 | 671 | 0.00 | 0 | 0.04 | 1,341 | 0.00 | 0 | 0.09 | 2,682 | |
| 53 | 6Northeast Wo | 8.1.1 Eastern Great Lakes Lowlands | 0.01 | 129,549 | 0.00 | 0 | 0.00 | 282 | 0.00 | 0 | 0.00 | 565 | 0.00 | 0 | 0.01 | 1,130 | |
| 54 | 7Southeast Wc | 8.3.3 Interior Plateau | 3.92 | 123,480 | 0.00 | 0 | 0.98 | 121,035 | 0.00 | 0 | 1.96 | 242,070 | 0.00 | 0 | 3.92 | 484,139 | |
| 55 | 7Southeast Wc | 8.4.5 Ozark Highlands | 1.80 | 106,347 | 0.00 | 0 | 0.45 | 47,793 | 0.00 | 0 | 0.90 | 95,586 | 0.00 | 0 | 1.80 | 191,171 | |
| 56 | 7Southeast Wc | 8.3.5 Southeastern Plains | 0.52 | 329,050 | 0.00 | 0 | 0.13 | 42,499 | 0.00 | 0 | 0.26 | 84,998 | 0.00 | 0 | 0.52 | 169,995 | |
| 57 | 7Southeast Wc | 8.4.9 Southwestern Appalachians | 3.92 | 37,996 | 0.00 | 0 | 0.98 | 37,244 | 0.00 | 0 | 1.96 | 74,487 | 0.00 | 0 | 3.92 | 148,974 | |
| 58 | 7Southeast Wc | 8.3.7 South Central Plains | 0.72 | 152,232 | 0.00 | 0 | 0.18 | 27,268 | 0.00 | 0 | 0.36 | 54,535 | 0.00 | 0 | 0.72 | 109,070 | |
| 59 | 7Southeast Wc | 8.5.2 Mississippi Alluvial Plain | 0.93 | 116,173 | 0.00 | 0 | 0.23 | 27,001 | 0.00 | 0 | 0.46 | 54,002 | 0.00 | 0 | 0.93 | 108,005 | |
| 60 | 7Southeast Wc | 8.3.6 Mississippi Valley Loess Plains | 1.23 | 51,827 | 0.00 | 0 | 0.31 | 15,901 | 0.00 | 0 | 0.61 | 31,803 | 0.00 | 0 | 1.23 | 63,606 | |
| 61 | 7Southeast Wc | 8.4.7 Arkansas Valley | 1.80 | 28,422 | 0.00 | 0 | 0.45 | 12,773 | 0.00 | 0 | 0.90 | 25,546 | 0.00 | 0 | 1.80 | 51,092 | |
| 62 | 7Southeast Wc | 8.4.8 Ouachita Mountains | 1.80 | 26,900 | 0.00 | 0 | 0.45 | 12,089 | 0.00 | 0 | 0.90 | 24,178 | 0.00 | 0 | 1.80 | 48,356 | |
| 63 | 7Southeast Wc | 8.5.3 Southern Coastal Plain | 0.23 | 141,587 | 0.00 | 0 | 0.06 | 8,156 | 0.00 | 0 | 0.12 | 16,312 | 0.00 | 0 | 0.23 | 32,624 | |
| 64 | 7Southeast Wc | 8.4.6 Boston Mountains | 1.80 | 14,176 | 0.00 | 0 | 0.45 | 6,371 | 0.00 | 0 | 0.90 | 12,742 | 0.00 | 0 | 1.80 | 25,483 | |
| 65 | 7Southeast Wc | 8.3.4 Piedmont | 0.07 | 166,124 | 0.00 | 0 | 0.02 | 2,852 | 0.00 | 0 | 0.03 | 5,704 | 0.00 | 0 | 0.07 | 11,408 | |
| 66 | 7Southeast Wc | 15.4.1 Southern Florida Coastal Plain | 0.23 | 22,576 | 0.00 | 0 | 0.06 | 1,300 | 0.00 | 0 | 0.12 | 2,601 | 0.00 | 0 | 0.23 | 5,202 | |
| 67 | 7Southeast Wc | 8.5.1 Middle Atlantic Coastal Plain | 0.01 | 78,470 | 0.00 | 0 | 0.00 | 175 | 0.00 | 0 | 0.00 | 350 | 0.00 | 0 | 0.01 | 701 | |
| 68 | Total | | | 9,531,353 | | 4,662,312 | | 6,259,917 | | 9,514,253 | | 12,519,833 | | 18,766,043 | | 25,039,666 | |

## Appendix B: Species Referred to in Text

In progress.