 doi:10.20944/preprints202208.0442.v1

Article

Buffalo on the Edge: Factors affecting Historical Distribution and Restoration of *Bison bison* in the Western Cordillera, North America

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Abstract: The historic western edge of bison (*Bison bison*) range and the ecological processes that caused its formation are frequently debated with important implications for bison restoration in the Western Cordillera of North America. We test the hypothesis that a combination of bottom-up habitat suitability and top-down harvest pressure from Indigenous peoples were important processes in forming the western edge of bison distribution. Using 9,384 historical journal observations from 1691 – 1928, we employ MaxEnt ecological niche modelling to identify suitable bison habitat across the Western Cordillera from bottom-up climatic, land cover, and topographic factors. We then use mixed-effect logistic regression to test if bison occurrence in journal records can be in part explained by the abundance of Indigenous humans, wolves, or grizzly bears, in addition to MaxEnt-derived habitat suitability. We find support for our hypothesis because of the limited suitable habitat in the Rocky Mountains that likely prevented westward bison dispersal from core habitat, and there was a negative relationship between bison occurrence and human harvest pressure. On this basis, we propose that intensive human harvest from large Indigenous populations in the Western Cordillera, subsidized by other wildlife, salmon, and vegetation resources, is an underappreciated socioecological process that needs to be restored alongside bison populations. Co-managing bison with Indigenous people will also mitigate the adverse effects of overabundant bison and maximize the ecological and cultural benefits of bison restoration.

Keywords: bison; restoration; socio-ecological processes; indigenous harvest; maximum entropy modelling

1. Introduction

In the period ~CE 1750 to ~ CE 1880 Eurasian colonization of western North America caused one of the greatest near extinctions ever documented. Within a century, *Bison bison*, commonly called the buffalo, once numbering in the millions across the grasslands and woodlands of Great Plains, were reduced to less than 1000 animals [1]. Humans' role in the bison overkill are well-documented [2], and researchers mapped the spatial pattern of extirpation [3,4] within years of its occurrence (Figure 1). The political ramifications of this slaughter of the continent's largest land-mammal helped stimulate conservation by the national governments of both United States and Canada, including designating wildlife a public resource [5,6], and withholding massive areas as public lands mandated for the sustainable use of wildlife and plant resources [7–9].

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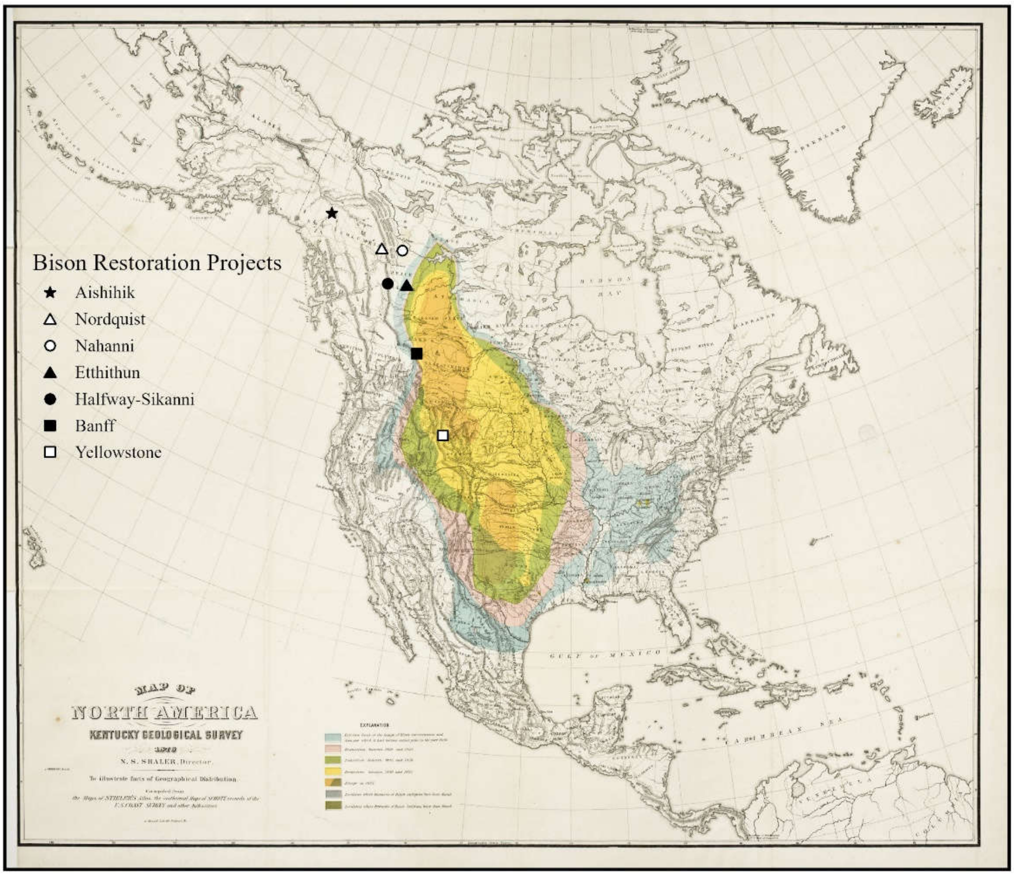

Figure 1. Range contractions of the American bison during the period pre-1800 to 1875 mapped by Joel Allen of the Kentucky Geological Survey in 1876 [3] showing locations of Western Cordillera restoration projects described in this paper.

Today, the parks, protected areas, and public lands of North America's Western Cordillera, stretching from the Rocky Mountains westward to the pacific from Yellowstone to the Yukon, provide one of the greatest opportunities for restoration and conservation of bison and many other species. Yellowstone in the United States and Banff in Canada are birthplaces of the world's first national park systems, and both played roles in the initial efforts to save the American bison from extinction. Moreover, these parks are the cores of an area that now constitutes one of the planet's largest areas of public lands—a network that provides ecological connectivity from along the Cordillera from Yellowstone to the Yukon [10]. These parks and other public lands are also the homelands of Indigenous peoples and provide ecosystem services, natural resources and recreational opportunities for millions of local and regional residents. Furthermore, they are heavily visited by domestic and international travellers, providing an opportunity to observe, hunt, and study in the wilds of world-renowned scenery.

However, the restoration of bison in the Western Cordillera is complicated by two interacting phenomena: one socio-ecological, one socio-political. First, for most of its distance dividing Atlantic and Arctic watersheds from those draining to the Pacific, the Cordillera also formed a historical range-edge for bison [4] as shown by Figure 1. The causes of this long-term range edge are debated [11,12], but Indigenous humans may have been partially involved in creating a source-sink ecosystem—bison were abundant across the prairies and woodlands to east of the cordillera, but possibly due to human harvest [4], were rare on the western slopes of the mountains and in coastal areas. Many of the west's potential areas for bison restoration lie in the low-density "sink" areas with vegetation and other ecosystem attributes being potentially ill-adapted to high numbers of a large and gregarious herbivore [13]. Secondly, the early establishment and management of national parks and other public lands followed a tradition of removal of Indigenous and other human influences [14,15], and in parks, ongoing programs of "natural regulation" allow wildlife populations to rise and fall unimpeded by management [16,17]. In situations where historically Indigenous human hunting might have maintained low bison densities, creating few ecological impacts, modern management may allow high numbers of bison, elk and other herbivores that greatly impact ecosystems[18–21].

In this paper we further inform effective bison restoration in the Western Cordillera by testing the hypothesis that in this region, high top-down human harvest acting in addition to low bottom-up habitat suitability historically limited bison abundance. Variations of this hypothesis has been proposed and debated since the mid-20th century CE [11,12,22], but has yet to be tested with quantitative analysis of a large dataset. We first present historic information on bison, human, wolf (*Canis lupus*) and grizzly bear (*Ursus arctos*) abundance and distribution from a biome-scale database of daily observations from the first-person journals of early non-Indigenous travellers. Second, we conduct analyses of this data to test how bottom-up habitat suitability and top-down processes, namely wolf and bear predation and Indigenous harvest, could have limited bison distribution in the Western Cordillera. Third, we review the demographics and range areas of bison restored on the edge, or outside of historic range, to test whether the growth of these populations is limited by their location. We then discuss restoration of bison in accordance with bottom-up and top-down ecological processes, and long-term human influences.

2. Materials and Methods

2.1. First Person Journal Observations

Our analysis required specific observations on bison locations and abundance, human cultural practices, and the abundance of other predator species present in historic landscapes. Historic bison, human, wolf (*Canis lupus)* and grizzly bear (*Ursus arctos*) occurrence and abundance was indexed using the first-person daily wildlife observations obtained from the journals of European mariners, fur traders, trappers, and government mappers for the period CE 1691-1860 in southern Canada and northern United States, and CE 1770-1928 in northern Canada and eastern Alaska (Figure 2). Methods followed Kay's procedures for tallying observations from the Lewis and Clark journals [23]. For bison, wolves and bears, three measures quantify the observations of journalists. First is animals seen where a value of 1 was assigned if journalists reported old sign, 2 if the sign was fresh, and 3 if they actually saw the animal. The second index was animal obtained where either the exact number killed is recorded, or where "some" or "a few" is recorded as 3, "several" as 7, and "many" as 10. Third, is herd or group size. Where journalists report sighting large numbers of a species, a value of 10 is assigned, 5 for moderate amounts. Animals seen, killed, and herd/group size are 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 total kill numbers for the period. For humans, if old sign was observed this is assigned a 1, fresh sign a 2, and if the journalists actually saw people a 3, or a 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 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. For all analyses, we excluded observations where wildlife or location data quality were rated as no data. The complete database for these observations (in spread sheet and Google Earth format) is available in the Supplementary Data, and is available at: https://lensoftimenorthwest.com/themes/lens-northwest-files/google-earth-map-journal-wildlife-observations/.

To visualize large-scale trends in bison, human, wolf and grizzly bear abundance based on historic journal observations, we averaged abundance indices for North American ecoregions [24,25] mapped for our study area (Figure 3). We used an ecoregion scale because they are useful for delineating terrestrial biodiversity patterns for global land-use planning and conservation across taxa [26], and have recently been used in studies of large mammal restoration [27]. Where ecoregion boundaries extend beyond the study area, the mean resource index includes observations from across the ecoregion.

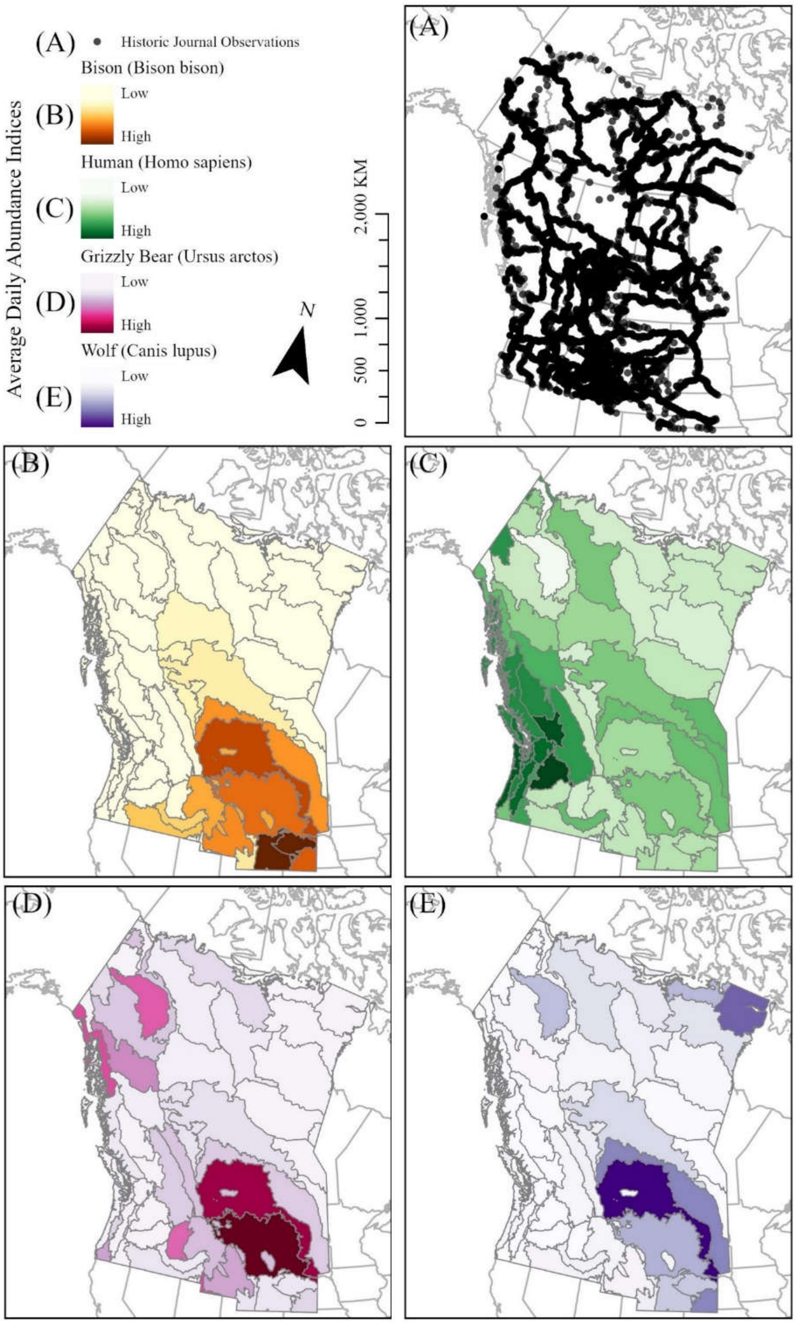

Figure 2. Location of historic journal observations from CE 1691-1860 in southern Canada and northern United States, and CE 1770-1928 in northern Canada and eastern Alaska (A) and the mean abundance indices per ecoregion of (B) bison (*Bison bison*), (C) humans, (D) grizzly bears (*Ursus arctos*) and € wolves (*Canis lupus*). Abundance was indexed following on the methods of Kay (2007), based on sign, harvest and group size.

2.2. Journal Data Analysis

2.2.1. Bottom-Up Effects on Bison

We first accounted for the effect of bottom-up factors on bison distribution by constructing an ecological niche model for bison using maximum entropy modelling (MaxEnt) [28]. We predicted that bison distribution would be largely explained by

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bottom-up modelling, but expected that the addition of top-down factors (see below) would further improve the model and thus provide evidence of their importance in defining historic bison range. MaxEnt has been widely used to estimate habitat suitability and thus predict the geographic distribution of a variety of species [29], including both European and North American bison [30,31]. The output of MaxEnt modelling provides an estimated probability of species occurrence based on environmental variables, and we join others in referring to this as synonymous to habitat suitability [29,32,33].

To represent bottom-up factors that could affect habitat suitability, we collected a series of land cover, topographic and climatic predictors in ArcGIS Pro version 2.4.0 [34]. The temporal span during which land cover and climatic predictors were measured does not reach back to time periods when bison were observed and reported by journalists, and land cover and climate have both changed significantly over recent centuries [35]. Our analysis assumes that these variables have remained static over time, which we believe to be acceptable because we applied current data measured at a large scale (raster pixel size = 100 square kilometers) to describe the general land cover and climatic characteristics of locations where bison were reported. For land cover variables, we reclassified the MODIS 2005 land cover map into grass and treed areas at a 250m cell size [36], and calculated their proportional area within each pixel. To capture topographic variation, we calculated terrain ruggedness using the USDS North America Elevation 1-km resolution grid [37]. We calculated a curvature grid in ArcGIS, then used a moving window analysis to determine the standard deviation of curvature within a 3 km radius of each 1-km cell to produce a measure of topographic variability, with high values indicating more rugged terrain [38]. We then averaged ruggedness values within each pixel. Lastly, we collected five climatic variables and averaged their values within each 1-km pixel [39]. We considered annual precipitation as snow and mean temperature of the coldest month to be indicative of snow depth and winter severity, which have been previously shown to affect bison distribution [40,41]. The other three climatic variables were mean annual solar radiation, mean summer precipitation, and mean temperature of the warmest month, which we considered indicative of primary productivity and thus forage availability for bison.

We split bison journal observations (N = 1,654) into training (75%) and testing (25%), and used the kuenm package in R [42] to calibrate 17 candidate models using the *kuenm_cal* function, select the best models with *kuenm_ceval*, and then create final models using the full set of occurrences and selected parameters using *kuenm_mod*. We created candidate models including all possible combinations of environmental variables, 14 values of regularization multiplier (0.1–1.0 at intervals of 0.1, 2–5 at intervals of 1, 8 and 10), and linear, quadratic and product feature classes. We excluded hinge or threshold feature classes in an attempt to minimize overfitting by limiting model complexity [43]. We evaluated models based on statistical significance (partial ROC) [44], omission rates (E = 5%) [45], and model complexity (AICc ≤2 from top model) [46]. To evaluate the relative contributions of our environmental predictors, we determined the percent contribution of each variable toward model fit [30], and generated marginal response curves to evaluate the effect of these variables on bison habitat suitability. Finally, we generated 10 replicates of the top selected model, averaged their logistic outputs, binned the values into 10 equal interval categories, and projected this across our study area to quantify bison habitat suitability on a scale from 1 (low suitability) to 10 (high suitability).

2.2.2. Top-Down Effects on Bison

To test the hypothesis that top-down processes acted in addition to bottom-up habitat suitability to limit bison distribution in the Western Cordillera, we modelled the relationship between the presence of bison and the abundance of three species that consume bison (humans, wolves and grizzly bears) using mixed-effect logistic regression [47]. If bottom-up factors were adequate at explaining historic bison distribution, we would expect that top-down factors would fail to significantly explain any variation in bison distribution. We assume that the abundance of humans, wolves and grizzly bears is representative of the harvest or predation intensity that they pose towards bison at each location.

For each journal observation for which data was available, we rated bison presence as 1 if any evidence of bison was observed, or 0 if not. We then used the *glmer* function from package lme4 [48] to model presence/absence as a function of habitat suitability as determined from the MaxEnt logistic output value at the observation location, and the observed abundance index value for humans, wolves, and grizzly bears. All predictors were mean centered and scaled to a standard deviation of 1, and we verified that no predictors were highly correlated ($r^2 > 0.6$). We also included the journal observer as a random effect to account for spatial and temporal autocorrelation within journal expeditions. We then used the *dredge* function from package MuMIn to identify the top model(s) based on the most parsimonious combination of predictor variables ($\Delta AIC_c < 2$ from top model [49]. We evaluated model fit of our top selected model(s) based on conditional and marginal R^2 values using the *r2* function from the package performance [50]. We conducted all statistical analyses in *Rstudio* version 2022.2.3.492 [51,52] and considered results significant if p values < 0.05.

2.3. Cordilleran Bison Restoration Project Demographics and Outcomes

Finally, we test whether the historic edge of current bison range has limited the success of current restoration projects by summarizing the range area and demographics (current population estimates, carrying capacity, growth rates) of bison in populations outside of historic core distribution. We predicted that the current outcomes of these projects may provide further insight to the processes delineating historic bison distribution.

3. Results

3.1. Historical Range and Abundance of Bison

Of 9,384 journal observations where wildlife and locational data were robust, bison were reported 1,841 times. Bison were mostly reported as sightings (81.2 %), but other evidence of their presence was also recorded (18.4 %) based on traditional ecological knowledge acquired from guides or other Indigenous people, feces, tracks, or wallows. Humans were reported as seen or encountered on 3,272 journal observations, and in another 438 records evidence of humans was observed without encountering people. Evidence or visual sightings of wolves or grizzly bears were less frequently reported in 183 and 243 journal observations, respectively.

Across ecoregions (Figure 2), bison abundance largely followed the proposed historic distribution (Figure 1) and centered around the Great Plains ecoregions. Bison were rarely observed in the Rocky Mountain ecoregions and only extended west of the Rocky Mountains in the south end of the study area. In contrast, humans were most abundant west of the Rocky Mountains. The abundance of wolves and grizzly bears was reportedly highest in the same area as bison, the prairie ecoregions, although both were also reported farther north in the region.

3.2. Factors Affecting Bison Distribution

As predicted, bottom-up factors were strong predictors of bison occurrence based on MaxEnt modelling. All 17 candidate models were statistically better than the null model and 14 of these met omission rate criteria, but examination of model complexity revealed a single top model (average area under ROC curve = 0.84, omission rate at 5 % = 0.041, AIC = 33162.96). The predictor with the highest contribution to model fit was the proportion of grass (48.9 %), followed by the mean coldest month temperature (23.9 %), mean annual radiance (9.5 %), the proportional tree cover (7.7 %), ruggedness (4.1 %), mean warmest month temperature (3 %), precipitation as snow (2 %) and mean summer precipitation (0.9 %). Marginal response curves (Figure A1) indicated that habitat suitability was positively correlated with mean annual solar radiance, negatively related to mean summer precipitation, precipitation as snow, ruggedness, the proportional tree cover and mean warmest month temperature, and that intermediate values of mean coldest month temperature and proportion of grass yielded the highest habitat suitability values.

Habitat suitability varied across the study area with the highest values occurring on the Great Plains east of the Rocky Mountains (Figure 3). The Rocky Mountains and higher elevation areas had much lower habitat suitability, as did areas in the far north and near the coasts. However, several areas in the Western Cordillera exhibited high habitat suitability, including the grassland interior plateau of British Columbia and the plains of Idaho and Washington state.

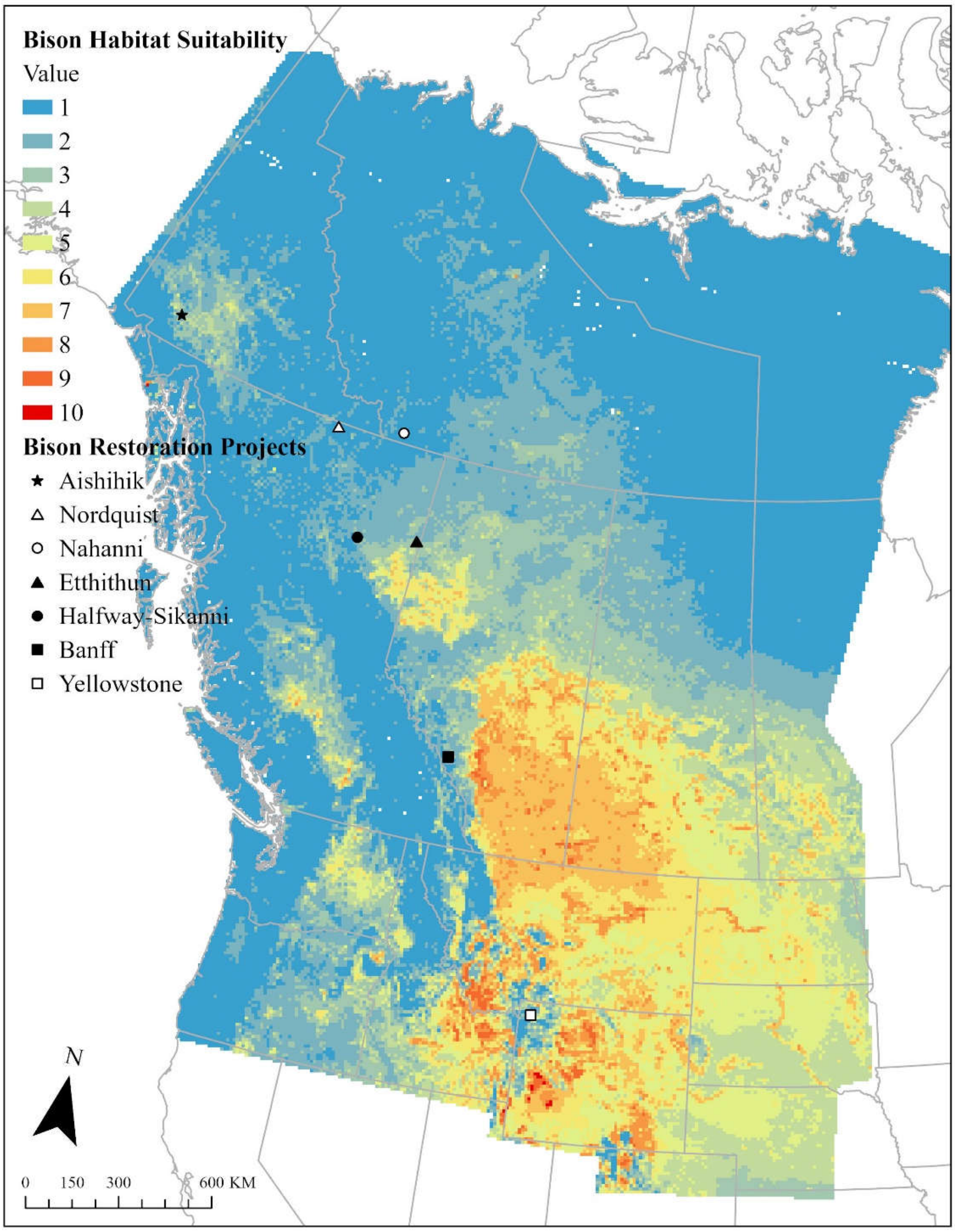

Figure 3. Bison habitat suitability as determined through MaxEnt modelling of bison occurrences based on historic journal observations. Models were constructed in R using the *kuenm* package and used climatic, land cover, and topographic variables as bottom-up predictors of bison occurrence.

Top-down factors were important predictors of bison occurrence, as mixed-effect logistic regression analysis of bison presence revealed a clear top model (>5 AIC_c from the next model) that included all predictor variables (Table 1). The conditional R^2 value was 0.520 while the marginal R^2 was 0.322, suggesting reasonably good model fit. Bottom-up habitat suitability, quantified based on MaxEnt output values, was the strongest predictor of bison presence, as expected. Of the top-down effects on bison distribution, only human abundance was negatively related to bison occurrence, while a positive relationship existed between the abundance of wolves and grizzly bears and bison presence (Table 1).

Table 1. Top mixed-effect logistic regression model predicting bison presence or absence in historic journal records as a function of MaxEnt habitat suitability and the abundance of humans, wolves, and grizzly bears.

Predictors	*Estimate*	*Std. Error*	*p*
(Intercept)	-2.68	0.182	< 0.001
Bison Habitat Suitability	1.44	0.0595	< 0.001
Human abundance index	-0.214	0.0410	< 0.001
Wolf abundance index	0.0878	0.0305	< 0.001
Grizzly bear abundance index	0.188	0.0370	0.004

3.3. Cordilleran Bison Restoration Project Outcomes

Table 2 summarizes demographics for seven ongoing bison restoration projects in the Cordillera. Although all native non-human predators occur in all areas, annual population rates of increase are generally high (>10%) when populations are <50% of carrying capacity. The exceptions are those projects such as Nordquist and Nahanni that are bisected with highways causing high bison mortality [53]. Generally, where carrying capacity is estimated from habitat quality, the estimated density is higher than for those where it is determined from social criteria. There is no apparent relationship between demographics of projects either on the edge, or those outside historic bison range. For example, although the Aishihik project in the Yukon is several hundred kilometers NW of the historical bison range boundary, both population growth rates and potential population totals comparable to those in or near historic range.

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Table 2. Demographics for select current bison restoration projects in the Western Cordillera, North America.

Location and sub-species [references]	Estimated Range (km^2)	Population Estimate (year)	Estimated carrying capacity (K, bison/ km^2)	Observed annual rate of increase (%) at ≤ 50% K	Remarks
Yellowstone, WY, MT **Plains Bison** [17,54,55]	9,400	4,500 (2018)	.405	12	All native predators except humans. K determined by habitat quality and demographics, population c. 2010 >75% of K (counts of ~4000), large impacts on grasslands, woody plants and hydrologic indicators, emigration rate out of park is increasing
Banff, AB **Plains Bison** [56–58]	1,200	80 (2020)	.480	30	All native predators except humans. K determined by habitat quality, current increase rate very high due to high female-to-male ratio of the founder herd, current population <100 but increasing rapidly
Halfway-Sikanni, BC **Plains Bison** [59–61]	3,200	1,233-1,371 (2006)	.500	10-38	All native predators present including humans. 48 plains bison escaped in 1971, population ~1300 in 2006, K socially determined to minimize range expansion
Etthithun, BC & AB **Wood Bison** [53,60,62,63]	5,000	181 (2010)	No information	15-20	All native predators present. First Nations allocated permits to take bison to discourage range expansion to conflicts with industry and agriculture
Nordquist, BC **Wood Bison** [53,60,63–66]	1,400	117 (2010)	No information	<5%	All native predators present including humans. A total of 49 bison released in 1995 at Aline Lake, by 2010, range mainly along 170 km Alaska Highway, population limited by traffic accidents
Nahanni, NT & BC **Wood Bison** [67,68]	11,700	431 (2011)	No information	~8%	All native predators present including humans. Slow growth since establishment, limiting factors appear to be drowning, traffic accidents, hunting, and perhaps tooth wear due to diet high in silica
Aishihik, YT **Wood Bison** [69–73]	11,000	1,106-1,385 (2011)	.125	10-20	All native predators present. Socially determined carrying capacity to minimize conflicts with Indigenous land uses and competition with other species

4. Discussion

Our analysis of historical journal observations provides key information for bison restoration in the Western Cordillera by supporting the hypothesis that top-down human harvest pressure, in addition to bottom-up habitat suitability, likely created a sink population dynamic in this region. First, we found that bottom-up factors largely explained bison distribution and highlighted a large band of low-suitability habitat in the Rocky Mountains that isolated otherwise suitable areas in the Cordillera from the core bison range on the Great Plains. Second, we identified a negative relationship between bison occurrence and the abundance of Indigenous humans even when bottom-up habitat suitability was accounted for in models, which suggests that harvest pressure was also an important determinant of the western limit of bison distribution. We propose that the historical occurrence of high-density bison populations in the Western Cordillera was ecologically nearly impossible due to limited habitat connectivity and consistent human pressure, which created an ecological trap for bison that emigrated west from core populations. The rapid expansion of bison populations restored to areas of historically low habitat suitability provides further support of our hypothesis that top-down human harvest limited bison distribution rather than environmental factors or non-human predators, and this presents risks for ecosystems that are not historically adapted to high bison numbers. Based on our findings, we propose that maximizing the ecological and cultural benefits of bison restoration will require the re-establishment of Indigenous harvest as a key socio-ecological process to create sink bison population dynamics in the Western Cordillera [74,75].

4.1. Processes Limiting Historic Bison Distribution

With a MaxEnt ecological niche modelling approach, we identified a large core area of highly suitable bison habitat from the Northwest Territories southward along the Rocky Mountains into the Great Plains, encompassing the historic bison distribution mapped by Allen [3] and Roe [4] (Fig 1, 3). Within this region, both recognized subspecies of North American bison existed: a migratory "plains" variant occurred in high numbers on the grasslands of the southern Great Plains, which then integrated to a more sedentary "wood" variant that had low densities in the mixed and boreal forests of the northern Great Plains and mountain foothills [1,4,76,77]. On the Great Plains, traditional ecological knowledge and numerous accounts of early journalists provide evidence of plains bison herds numbering in the tens of thousands [23,78,79]. The reported abundance of plains bison and relative scarcity of wood bison were likely linked to various bottom-up and top-down factors acting across their range.

Within the core range, the Great Plains provided ideal habitat for plains bison, where their abundance can be attributed to a combination of factors including high forage availability from expansive grasslands [80,81], favorable climatic conditions [30], a lack of geographic barriers to formation, movements, and dispersal of large herds [81,82], and areas that provided refuge from human harvest [80,82]. Indigenous groups in this area were heavily dependent on bison [2,83,84], but over-harvest was likely limited because bison found refuge spatially in intertribal buffer zones between conflicting Indigenous groups [23,85], and temporally during winter when large areas were mostly inaccessible to human hunters because of unavailable firewood and shelter on the exposed prairie [82,86,87]. Further north and west in forested areas, the wood bison likely persisted due to spacing in low densities, occupying inter-tribal buffer zones, and good connectivity and periodic dispersals from plains bison herds to the south and east [23,77]. Source-sink wildlife population dynamics likely operated within this core area, both between and within plains and wood subspecies, to allow for abundant bison in many areas [23,79,88,89].

In contrast to the high numbers of bison found throughout the core distribution, numerous studies report few bison west of the Rocky Mountains, although periodic dispersals did occur through low passes from the core population on the plains [3,4,79,88]. Two factors made long-term occurrence of high numbers of bison west of the Rocky Mountains unlikely: a lack of connected suitable habitat preventing colonization, and consistent and effective human harvest pressure from Indigenous peoples [12,22,88]. Our MaxEnt niche model identified a paucity of suitable habitat in the Rocky Mountains (Figure 3), likely discouraging the westward dispersal of bison from the core area of high habitat suitability. Furthermore, the topography of the foothills and mountains and deep winter snowpack provided opportunities for Indigenous people to harvest bison using natural traps and jumps [90–92], which probably eliminated many groups of bison that ventured into these areas. Indeed, recent studies have shown that Indigenous groups, especially those of the Blackfoot Confederacy, used the topography of the Rocky Mountains extensively to hunt bison [93,94]. A considerable corridor of connected habitat existed in southwest Montana and northern Wyoming, and indeed herds of bison were observed in the plains of southeastern Idaho west of the Rockies (Figure 2). However, bison were not observed north in the grassland interior region of British Columbia or only rarely seen on the plains of eastern Washington and Oregon, although large tracts of suitable habitat existed in these regions (Figure 3). High numbers of Indigenous peoples lived in these regions supported by abundant plant and salmon resources [95–97], and our analysis and other research [23,79,88,89] demonstrates that high human abundance is negatively related to bison occurrence. In these sink regions, bison persistence in relative isolation from a source population, while facing considerable harvest pressure, was highly improbable. Similarly, we suggest that the relatively recent extirpation of bison (<3000 BP) in Alaska and Yukon may be associated with increasing human numbers [98,99], and development of hide trade routes from the Liard and Yukon rivers to the Pacific coast [100,101].

We acknowledge several limitations of our analysis that should be considered when interpreting our findings. First, as mentioned in the methods, covariates used in MaxEnt models assume that climatic and land cover variables measured in the 21st century are representative of historical patterns. While we believe that this assumption is appropriate for modelling broad-scale trends in bison distribution, local climate and land cover changes [35] make more detailed interpretations of our habitat suitability model potentially perilous. Second, historical journal observations are almost exclusively written from a male, colonial perspective. While the records of some journals describe traditional ecological knowledge shared by Indigenous guides or groups encountered when travelling, the often do not describe plant use, or female perspectives on seasonal resource availability. Future research requires further Indigenous knowledge of historic bison and other resources to better understand the nuance of historic human-bison interactions [6,92,95,102–104].

4.2. Implications for Bison Restoration in the Western Cordillera

Despite these bottom-up and top-down limits imposed on historical bison distribution, recent restoration projects have achieved rapid bison population growth in areas that were historically on the fringe or outside of what we identified as suitable habitat (Figure 3, Table 2). The success of these projects demonstrates that bison are clearly adapted to thrive in a broad range of climates, vegetation conditions, and predators, even if snow depth [40], forage quality and availability [105] and non-human predation [106] influence their localized spatial distribution. Recent studies have also demonstrated remarkable plasticity in bison diets across North America [107,108], providing further evidence that bison can thrive in a variety of conditions. Lastly, MaxEnt ecological niche modelling based on fossil records of bison and historic climates demonstrated that much of North America was suitable bison habitat over the past 20,000 years [30]. Although bison have demonstrated their ability to thrive in conservation herds outside of their historical range, their potential to degrade local ecosystems that have not recently sustained bison presents a challenge for responsible bison management.

Restoring bison has numerous benefits, but over-abundant populations of large herbivores can have detrimental ecological impacts through intense herbivory on ill-adapted vegetation species [18–20,55,74], direct and apparent competition with other species [109], disease transmission [1,20], and detrimental cultural effects through human injury and damage to cultural resources [70,110]. Therefore, bison restoration in the Western Cordillera without also adequately restoring the key socio-ecological role of Indigenous harvest is likely to lead to challenges for conserving ecological integrity and human-wildlife conflict. Our findings add to a large body of recent evidence demonstrating that Indigenous people were a key ecological force shaping North American landscapes by affecting the abundance of large mammals [23,79], cultivating and gathering plant and animal species [103,111], and manipulating fire regimes across the continent [102,112–114]. Acknowledging and restoring the role of Indigenous bison harvest in creating source-sink population dynamics is therefore needed for all bison restoration initiatives, and especially those at the edge of historic bison range.

Of the bison restoration projects discussed in this paper, Indigenous harvest has been partially restored in Aishihik, Nahanni, Nordquist, Etthithun, and Halfway-Sikanni. These projects should aim to continue to expand the role of Indigenous people in bison management. In the national parks of Banff and Yellowstone, Indigenous harvest has not yet been restored, and this top-down process remains de-coupled from these bison populations. Free-roaming bison have only recently been restored to Banff in 2018 [56,57], and if this project can implement Indigenous harvest early in the project then it may quicky gain the cultural benefits of bison harvest while proactively mitigating adverse ecosystem

 doi:10.20944/preprints202208.0442.v1

impacts [74,115]. In contrast, Yellowstone has had free-roaming bison for over a century [55], and populations have reached a point where ecosystem recovery is challenged by overabundant bison as Indigenous people remain excluded from practicing traditional bison harvest in the park [14,18,20]. Without policy adjustments and management changes, both Banff and Yellowstone are at risk of the ecological and sociological consequences of overabundant bison populations in historical sink areas [18,70,74,110].

We propose that a paradigm shift is needed, one that reverses 19th and 20th century national park policies that excluded Indigenous people from protected areas [14,15] and expands Indigenous bison management in areas where harvest is already permitted. Working with Indigenous groups that have deep cultural connections This is especially important for populations in the mountainous valleys of the Western Cordillera, where human harvest on bison played a significant role in creating a sink population dynamic in these areas. Furthermore, the restoration of Indigenous bison harvest as a top-down process both inside and outside of protected areas would contribute to reconciliation with Indigenous peoples and help reconnect them with cultural practices that have been occurring for time immemorial [115]. Only once bison are co-managed and harvested by Indigenous peoples will their full range of ecological and cultural benefits be restored to the Western Cordillera and across North America.

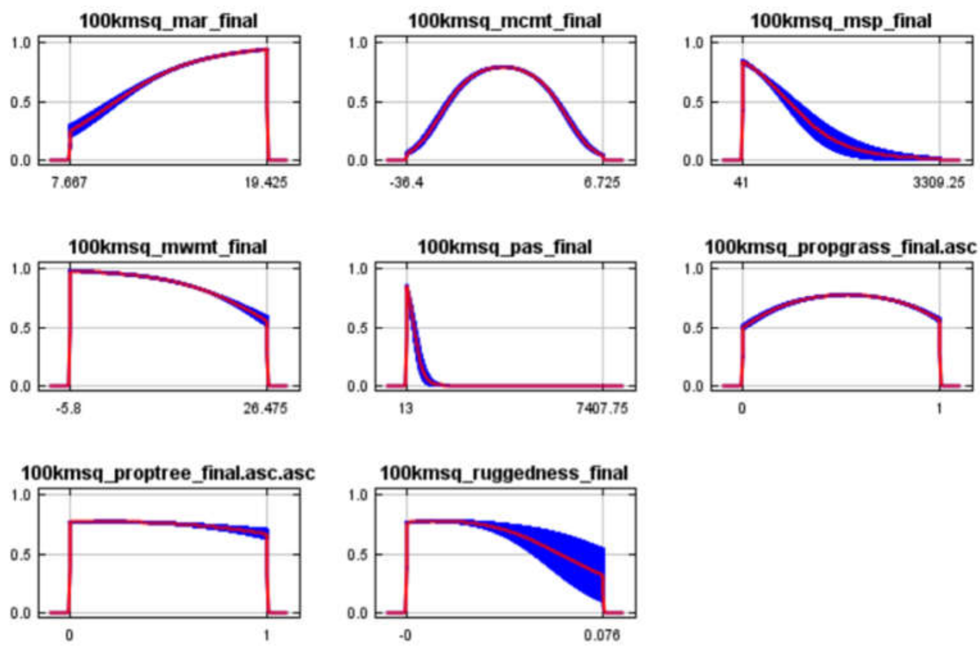
Funding: Parks Canada provided initial funding for historical journal database compilation.

Data Availability Statement: Geospatial data and R code supporting the reported results of this study are openly available on GitHub at https://github.com/jfarr99/Farr_and_White_Historic_Bison_Distribution. The full dataset of historical journal observations is available at https://lensoftimenorthwest.com/themes/lens-northwest-files/google-earth-map-journal-wildlife-observations/ or after 2025 in the Whyte Museum of the Canadian Rockies, Banff, Alberta Clifford A White fonds

Acknowledgments: We appreciate comments from M. Hebblewhite and K. Heuer on earlier drafts of this manuscript. We respectfully acknowledge that this work was conducted on Treaty 7 territory, a traditional gathering place for diverse Indigenous peoples including the Blackfoot Confederacy (comprising the Siksika, Piikani, and Kainai First Nations), as well as the Tsuut'ina First Nation, and the Stoney Nakoda (including the Chiniki, Bearspaw, and Wesley First Nations).

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A



 doi:10.20944/preprints202208.0442.v1

Appendix A Figure A1. Marginal response curves revealing the relationship between predictor variables (x axes) and bison habitat suitability (y axes) as determined by the top selected MaxEnt model.

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