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SCALED ECOLOGY: A FRAMEWORK FOR EVALUATING CONSERVATION OF
WILDLIFE ECOLOGICAL PROCESSES

A Thesis Presented to the
Graduate Faculty of the Biology Department
and the
Faculty of the Graduate College
University of Nebraska

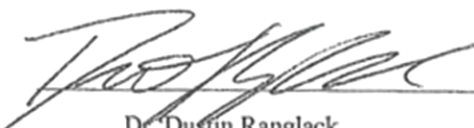
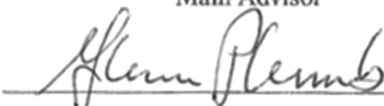

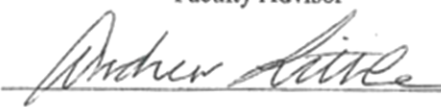
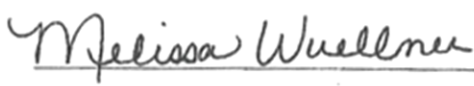


In Partial Fulfillment
of the requirements for the Degree
Master of Science
University of Nebraska – Kearney

By:
Johanna A. Hodge
August 2023

THESIS ACCEPTANCE

Acceptance for the faculty of the Graduate College, University of Nebraska, in partial fulfillment of the requirements for the degree, Master of Science, University of Nebraska at Kearney

Supervisory Committee

Name	Department
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 Dr. Glenn Plumb	IUCN-SCC-BSA
 Dr. Jayne Jonas-Bratten Faculty Advisor	UNK-Biology
 Dr. Andrew Little	UNL-School of Natural Resources
 Dr. Melissa Wuellner	Biology
	 Supervisory Committee Chair
	 Date

DEDICATION

“My gratitude to him is as boundless as the Pacific Ocean.”

Yann Martel, *Life of Pi*

This thesis is dedicated to my best friend and Lieblingsmensch Anthony. We have faced different challenges in our 5 years together, but this one is by far our crowning achievement. Yes, this is as much your achievement as can be considered mine. You were there after losing three of the greatest loves of my life, and the lifestyle collapse that followed. More importantly, you have been here with me while I work to build something new from the rubble. Through every moment of loss, every moment of doubt, every turn to find a taller wall to scale, you have been there to keep me going. You have been as relentless as the North Dakota wind, all with a smile, a good joke, and a warm embrace. Let it be known that your tenacity, love, and dedication know no bounds, and I am forever grateful.

ACKNOWLEDGEMENTS

I would like to thank my committee members Dr. Glenn Plumb, Dr. Dustin Ranglack, Dr. Andrew Little, Dr. Melissa Wuellner, and Dr. Jayne Jonas-Bratten for their support on this project. I would like to give a special thanks to Jayne for providing the much-needed support and guidance over the last crucial months for me to complete this project. Although stepping into the main advisory role at the end of my time at UNK, you became a grounding force without whom I may not have succeeded. Dustin, thanks for providing opportunities to get out with bison in any way you could, because of course, it is all for them (and it kept me sane). Glenn, thank you for your thoughtful insight and dedication to this project, and to me, even through your own battles. It will always be cherished.

To my dearest friends Melissa Thompson, Kate Sedlacek, Andrea Martinson, and Jess Geary, your consistency has been a welcome umbrella against the rains of life, and the most warming comfort. I am grateful to have your friendship. Melissa, I know if not for our years together at THRO, all the bison jams we encountered, and working toward bison baseball cards because “they deserve fame too”, I wouldn’t be here. To my sissy, Jillian Gibson, through the chaos of our lives getting even busier, we found a way to capture any moments we could, which blossomed into our relationship as sisters, and friends, growing more than it has been able to in years. Thank you.

Lastly, to the indigenous plains’ tribes, I acknowledge that my work on this project, no matter how much good it may do, did not adequately lift your voices, whose histories are so familial to that of the great plains’ bison. Incorporating your voices, experiences, and knowledge into all conservation research is necessary as we all work to make our home a better place. I recognize that the future of bison conservation is reliant too, on the decolonization of bison management, and putting bison back in your hands. I would also like to acknowledge that I completed this project in Kearney, NE on the occupied indigenous land of the Pawnee Nation and Očeti Šakówiŋ, who in the 1870’s were forced from their home here on the Platte River, and now reside in Oklahoma. I have cherished my time among the cottonwood, as I found moments of peace beside this serene river, and often contemplate how it has changed my life as it likely shaped yours since time immemorial.

ABSTRACT

Ecological processes are scaled in time and space, including those associated with wildlife. Understanding the ecological processes of wildlife species and their contributions to ecosystems is crucial for effective conservation. This study focuses on American bison (*Bison bison*) as a case-study species to explore the holistic scaling of wildlife ecology. A PRISMA-style literature review was conducted to gather and map the scaled ecology of bison. An AIC best-fit analysis was conducted to assess the scaling of total bison ecology considering 7 different models. The results rejected the null model and identified the best-fit model as a combination between fencing and subspecies with a cumulative weight of 68%.

Unfenced wood and plains bison appear to have all reported ecology conserved in management, with plains bison limited in dispersal and range expansion. Fenced plains bison show the largest area of concern as multiple ecological processes appear to not be conserved in most herds. Fenced plains bison are also kept at the highest densities of all groups, potentially removing opportunities for ecological expression, or forcing bison to express these processes differently than unfenced herds, as the spatiotemporal association of ecology for fenced bison was low compared to unfenced herds ($R^2 = 0.13$). Considering the entirety of bison ecology in conservation efforts and management solutions, especially for bison managed behind fences will likely contribute to efforts of measuring for ecological functionality and address the implications of animal husbandry practices mirrored in bison management. The study methodology can be applied to any species. Scaling the total ecology of species across spatiotemporal gradients provides a comprehensive understanding of their ecological processes and facilitates targeted conservation measures. By incorporating scaled ecology into conservation practices, managers can better conserve wildlife species and contribute to their long-term sustainability.

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CHAPTER I

INTRODUCING A FRAMEWORK FOR SCALED ECOLOGY

Ecological processes occur across scales of time and space, as seen in fire regimes (Morgan et al., 2001; Taylor et al., 2020), meteorology (Thompson et al., 2001), hydrology (Skøien et al., 2003), land-use/cover change (Soranno et al., 2014, 2015), and climate change (Peters et al., 2011). Individual processes of wildlife ecology such as movement ecology (Gurarie and Ovaskainen, 2011), determinants of home range size (van Beest et al., 2011), and herbivory (Shingley, 2007) are scaled in time and space as well. In the case of herbivory, individual foraging bites occur on very small scales of time and space that then result in patch-wide heterogeneity because the animal can chew and move while looking for the next best bite to take (Shingley, 2007). This patch-wide heterogeneity creates patterns of landscape use over longer periods of time and space (Shingley, 2007).

Wildlife are often the engineers or facilitators of environmental processes through their syn / autecology and contribute to the maintenance of unique habitats, communities, and ecosystems (Byers et al., 2006; Dehling et al., 2021; Geremia et al., 2019; Jones et al., 1994; Knapp et al., 1999). In cases of keystone species such as grey wolves (*Canis lupus*), bison (*Bison bison*), or prairie dogs (*Cynomys* spp.), their contributions to driving ecological processes are elevated (Bond, 1994; Duchardt et al., 2021; Geremia et al., 2019; Knapp et al., 1999; Kotliar et al. 1999). Since ecological processes are scaled in time and space, the wildlife species that drive these processes may have scaled ecology as well, creating spatiotemporal structure of a species total ecology. In this context, mapping

a species' ecological processes over time and space to assess whether there is structure to an entire species' ecology could provide valuable insight for species conservation.

Global Change Theory (GCT) states that changes occurring in the environment across the globe can disrupt ecological systems in substantial ways (Peters et al., 2011). One of the fundamental propositions that GCT draws upon is the interaction of spatial and temporal hierarchies, derived from the principles of hierarchy theory mentioned by Allen and Starr (1982). Peters et al. (2011) highlights that past research by ecologists dominated specific spatial grain and temporal extents of environmental processes, creating assumptions that most of these were locally driven. In response, Peters et al. (2011) proposed the importance of understanding processes as they occur across spatial and temporal scales to best understand patterns and inform management and research actions. Furthering this need is the understanding that mapping ecological processes across time and space cannot be fully achieved by scaling down large-scale processes to explain small-scale processes, nor the reverse (Peters et al., 2011).

The entire breadth of species ecology is rarely explicitly incorporated through spatiotemporal scales when conducting research or management solutions however, as much of these focus on species abundance and distribution (Cadotte et al., 2011; Prach et al., 2019; Sanderson et al., 2008; Tulloch et al., 2016), and is further removed from known migratory species (Albers et al., 2023). The gap of information on holistic species ecology across space and time could have negative effects on restoration and conservation management practices by either missing important aspects of ecology entirely or disproportionately favoring others. Further, it creates a concerning problem

regarding the future management of wildlife in the face of challenges such as climate change, urban development, agricultural and fuel necessities, in an unknown future.

A reference model of the ecology of wildlife over time and space would be a useful tool to guide and support conservation and restoration efforts, particularly for range-restricted species. Large mammals face spatial restriction due to physical, political, and economic boundaries globally, the effects of which cause concern for their futures (Bluhm et al., 2023; Fortin et al., 2020; O'Neil et al., 2022; Vynne et al., 2022).

American bison, as they are spatially restricted in most locations (Freese et al., 2007; Rogers, 2021; Sanderson et al., 2008), provide a unique case in which to explore this theoretical framework of scaled ecology. Evaluating the totality of bison ecology as it occurs on spatial and temporal scales may open doors for increased recognition of large- and small-scale necessities within wildlife species' ecology to improve conservation efforts.

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CHAPTER II

FENCING AND SUBSPECIES DIFFERENCES IMPACT ECOLOGICAL EXPRESSION OF AMERICAN BISON: A SYSTEMATIC REVIEW TO INTRODUCE THE FRAMEWORK OF SCALED ECOLOGY

INTRODUCTION

Spatial-temporal scaling

Ecosystem dynamics are driven and maintained through environmental and ecological processes structured in time and space as identified in hierarchy theory (Allen and Starr, 1982), and expanded on in Global Change Theory (Peters et al., 2011). Within wildlife ecology, processes like herbivory (Shipley, 2007), movement (Gurarie and Ovaskainen, 2011), and home range size (van Beest et al., 2011), each operate at differing scales of time and space. Considering that individual wildlife ecological processes are scaled, the totality of species ecology may have structure in time and space as well, offering insight to wildlife conservation efforts.

Range-restricted species, particularly large mammals, are of great conservation concern, as they often play irreplaceable roles in their ecosystems that drive cascading environmental effects (Bluhm et al., 2023; Fortin et al., 2020; O’Niel et al., 2022). Large mammals are often migratory as well, adding another level of uncertainty to conservation approaches (Albers et al., 2023). Mapping species ecology as it occurs across scales of time and space may highlight areas of greater conservation concern and contribute to science-based restoration efforts. American bison (*bison bison*) provide an optimal case study for this framework of scaled ecology, as they are spatially restricted large mammals that are temporally influenced by management actions and are of cultural and

environmental importance (Freese et al., 2007; Pejchar et al., 2021; Redford et al., 2016; Rogers, 2021; Sanderson et al., 2008).

Bison ecology and management

Bison are one of the notable examples of large mammalian preservation and conservation of the 20th century with over 350,000 individuals present today after eradication efforts left the population decimated to a few hundred individuals in the late 1890's (Boyd, 2003; Hartway et al., 2020; Meagher, 1986; Rogers, 2021; Shaw, 1995). While this level of recovery is a notable achievement, the challenge of conserving bison as wildlife within their historic range persists as 96% of bison undergo selection for commercial purposes, with only 4% managed as wildlife (Bates and Hersey, 2016; Boyd, 2003; Freese et al., 2007; Sanderson et al., 2008). The numerical success of bison restoration is captured in The IUCN Red List Assessment of endangered species, which lists American bison as “near threatened” (Aune et al., 2017). The disparity in numerical bison success and wild restoration success has been recently recognized by the IUCN and has contributed to the new Green Status Assessment that tracks past and current conservation efforts of the species to understand recovery potential (Grace et al., 2021). The assessment has identified American bison as a “critically depleted” wild taxon in their historic range (Rogers et al., 2022). The distinction is in part due to the restrictions on even the wildest of conservation herds as animals that move outside boundaries can be subject to varying control actions due to local and state regulations, biological concerns, tribal influence, as well as divisive public concern (Clark et al., 2016; Lolika et al., 2018; Pejchar et al., 2021, Rogers, 2021). Under these pressures, bison are extensively

restricted, most notably in spatial capacities, as they are managed on small landscapes with highly fragmented populations relative to historical conditions (Boyd, 2003; Freese et al., 2007; Hartway et al. 2020; Pejchar et al., 2021; Rogers, 2021; Sanderson et al., 2008).

The system of bison populations maintained on small landscapes requires an increased level of management intensity that compares to that of many modern animal husbandry practices, to include fenced boundaries, supplemental feeding, vaccinations, lethal removal of trespass individuals, and round-up and removal of “surplus” animals (Bailey, 2013). Such practices are known contributors to domestication, and further remove bison from ecological functionality and conserved wildness (Bailey, 2013, Freese et al., 2007; Rogers, 2021; Sanderson et al., 2008). These contributors coupled with most bison populations existing for commercial purposes creates potential conflicts in the promotion of ecologically wild bison, as many people are only exposed to bison as an extension of husbandry (Bailey, 2013; Freese et al., 2007, Rogers, 2021; Sanderson et al., 2008).

According to Sanderson et al. (2008), conservation success can only be obtained when large herds of bison roam freely in their historic range on large unfragmented landscapes that allow significant ecological functions to occur unhindered. While many herds are not capable of reaching a state indicative of ecological recovery based on this definition due to physical, political, or cultural restraints, bison are still acting on the systems to which they belong. Bison in this way contribute to various levels of ecological importance such as arthropod abundance and diversity due to wallows, or soil nutrient

cycling due to dung and urine distribution among others (Knapp et al., 1999; McMillan et al., 2019; Truett et al., 2001). This implies that some aspects of bison ecology are being conserved, but to what degree is widely variant across populations and even more difficult to quantify (Sanderson et al., 2008). In turn, the lack of established support for total ecological conservation highlights the likelihood that some ecological processes are not conserved in managed bison herds.

Objectives and hypothesis

To examine potential consequences of practical operational and management considerations for ecological restoration of wild bison, I incorporated a coarse-filter approach to explore the scaling of bison ecology and: 1) systematically reviewed relevant peer-reviewed literature to place bison ecological processes on scales of time and space, 2) created a heuristic model of bison ecology over time and space, and 3) explored aspects of the current management paradigm that influence the spatial-temporal scaling of bison ecology to identify if management needs to adapt to conserve the holistic ecology of bison. I hypothesize that holistic bison ecology is scaled in time and space, offering certain processes within small spatial and temporal scales, and other processes at large spatial and temporal scales. These processes are likely influenced by intensive/complex management practices. If supported, identifying which ecological processes are conserved under current management paradigms and which are not will possibly allow conservation efforts to incorporate all of bison ecology into research and management solutions, creating opportunities for managers to better conserve bison as wildlife into the future, as well as address the mirrored animal husbandry practices on

bison conserved as wildlife. This exploratory approach may additionally benefit wildlife conservation globally, as it can easily be applied to any species of conservation concern.

METHODS

Objective 1 - Literature collection and search

I performed a systematic review of scientific literature on bison ecological processes following a-priori inclusion/exclusion criteria (Figure 1). Primary literature was provided by the International Union for the Conservation of Nature (IUCN) Bison Specialist Group (BSG) compiled between 2016 and 2021, after an initial presentation by Plumb et al. (2016) at the 2016 American Bison Society meeting, where the research questions for this study were first identified. The BSG proposed that wild bison exist on a scale of management intensity and complexity, and wild bison conservation now and into the future similarly relies on the ability for bison to fully express their natural biology over scales of time and space. Until now, the collective representation of bison ecology over time and space has not been available, so identifying how much of bison ecology is being conserved under the current paradigm has been impossible.

The BSG provided 164 sources of scientific literature spanning the years of 1889-2020. For comprehensive bison status assessments and large compilation reference material I reviewed both the record and the literature cited material for the record. Only one iteration of reviewing records from literature cited material was performed as a deterrent for encountering excess duplicate literature cited material. For complimentary literature input, a database search was performed following PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines (Page et al., 2021). Using the advanced search engine of Google Scholar between December 2022 and January 2023, I searched for records that must include the word “bison” and at least one of the words “ecology” OR “activity” OR “genetics” OR “habitat” OR

“demography” OR “spatial” OR “temporal”. Of the 6,750 results, I reviewed the first 300 records in order of most recent publication and by relevance to the search terms as a pre-defined ceiling.

Literature Screening

Ecological research associated with commercial bison industries was excluded. While American bison management occurs on a spectrum of wildness due to varying intensity and complexity (Rogers, 2021), I only included records on bison herds that most closely matched the criteria for “wild” as used by Aune et al., (2017) and Rogers (2021) to minimize inclusion of deviations from natural bison ecological processes to which commercialization might and often does contribute (Bailey, 2013). Additionally, some ecological processes were omitted from analysis due to the lack of spatial and temporal scaling within relevant literature. Bison ecology associated with disease, for example, is well studied and an important factor in the conservation of wild bison. However, most literature on this topic did not include spatial and/or temporal data that could be incorporated within the parameters of this study, and thus was not well represented within the review.

Of the 1,076 total records, I removed records prior to screening as they were easily identified as research pertaining to European bison (*Bison bison bonasus*) (n = 33). I then removed records for which qualitative or quantitative bison ecology data could not be identified based on review of title, abstract, and results (n = 557). In this second tier of the exclusionary process, I removed duplicate records (n = 173), with 313 records remaining. These records underwent a more comprehensive review to identify those that contained quantitative temporal or spatial data associated with the ecological processes (Table 1). In this portion of the review, records were removed that were highly specific to bison temporal ecology, spatial ecology, or both, but did not have extractable data for the purposes of this study due to methodology parameters of research or vagueness of ecological process association (n=156). After this review,

157 records were included (Appendix A), and 919 records were excluded (Appendix B). Of these records, 108 were from the BSG list review, and 49 from the database search (Figure 1).

Quantitative and qualitative coding

Data from literature was categorized within broad ecological processes (Appendix D) of activity and behavior, movement, habitat interactions, and demography and genetics, with 26 ecological components of each process nested within (Table 1). These groupings encompass current known key elements of bison syn / autecology (Truett et al., 2001; Freese et al., 2007; Sanderson et al., 2008; Gates et al., 2010; Plumb et al., 2016; Geremia et al., 2019). Qualitative and quantitative information was gathered to enhance understanding and identify data patterns (Table 2).

Temporal scales were measured through the length of days in which the process was measured, the days of recurrence on a 365-day basis identifying the timeframe from the end of an ecological process to when it begins again, as well as maximum and minimum values for both if provided. In cases where days of occurrence were not stated, but implicit terminology such as ‘season’, ‘month’, ‘mid-month’ were used, I used 90 days, 30 days, and 15th day of the month, respectively for coding. Further, implicit terminology such as ‘early month’ or ‘late month’ was regarded as the 7th day of the month, and 23rd day of the month respectively.

For spatial information, identification of the total spatial scale (km²) to which the bison population had access was collected, the observed spatial scale (km²) of the ecological process, and the minimum and maximum values of observed spatial scales, if provided, were recorded. If explicit spatial scales were not provided, but implicit scales such as “steps” or “number of wallows” or “seasonal range” were used, average step length provided by literature, average wallow size provided by literature, and a box encompassing the minimal amount of area

described by the literature on a provided study area map were referenced, respectively. In cases where distance (km) was provided for an ecological process, I searched for information pertaining to movement or migration corridors associated with the study population to identify approximate areas of known use to convert to area (km²).

Objective 2 - Heuristic model

Since spatiotemporal data points counted for only 49% of all the data points extracted from literature review, I prepared boxplots depicting ecological components over space and time separately to include all extracted data compared to the subset of spatiotemporal data points used in further analyses (Figure 1). The boxplots provide a visual tool to highlight the extent of variability in some ecological components that may or may not have been captured in analyses. Additionally, the boxplots provide insight into ecological components that are commonly recorded on only a temporal or spatial scale, as opposed to spatiotemporally, and how those processes may be similar or different respective of time and space.

To visually depict bison ecology over time and space, the information gathered on spatial and temporal scales of ecological processes was graphically depicted with time in days as the independent variable, and space (km²) as the dependent variable both denoted by log₁₀ increments. All secondary ecological components that provided at least 3 spatiotemporal data points (Table 1) were plotted as averages with standard errors. To clearly identify where bison ecological processes are being conserved based on the current management paradigm, a representation of the current spatial parameters of bison populations conserved as wildlife was overlaid on the model showing the median, 1st, and 3rd quartiles of available space (Rogers, 2021). Temporal parameters were displayed as indicators of substantial disruption of bison ecology that often occur depending on the spatial scale at which populations are managed.

Temporal restrictions are rarely impervious boundaries, as they are hard to measure and cannot be extensively confined (Albers et al., 2022). However, most plains bison populations are managed intensively through seasonal or annual roundups that alter the population demography and behavior in various ways (Bailey, 2013; Rogers, 2021).

Statistical analysis

I tested seven models comparing descriptive characteristics of bison populations extracted from literature review to address my hypothesis of scaled bison ecology. The explanatory variable was time, and the response variable was space in all models but the null, which had the y- intercept, but did not have an explanatory variable. The models included: 1) a null to challenge stochasticity; 2) a standard regression across all data points over time and space; 3) comparing data that was implicitly or explicitly extracted from literature review; 4) whether the observed population was fenced; 5) comparing subspecies; 6) the US EPA level I ecoregion (Environmental Protection Agency, 2022) associated with the observed population; and 7) a combination of fencing and subspecies. The combination of fencing and subspecies was captured by a single factor with 3 levels, as there were no fenced wood bison herds found in literature review. Following the method of maximum likelihood for identifying data pattern drivers and applying it to the spatiotemporal scale of bison ecological processes from literature review, I performed an Akaike's Information Criterion (AIC) model selection approach (Akaike, 1973; Anderson and Burnham, 2002) on records for which both spatial and temporal information was reported and provided adequate sample size for each model variable being tested.

Spatial and temporal data were \log_{10} transformed to meet the assumptions of normality. Models containing factors were run as equal or unequal slopes depending on whether the interaction expressed significance. From results of an AIC model selection test, Delta AICc (Δ)

scores indicate the differences between the identified best-fit model among those which were tested to the next best identified model, and so forth. For this experiment I chose to include only those models which provided a Δ score of < 2 (Anderson and Burnham, 2002). After plausible model selection, I conducted a pairwise analysis to consider points at average ± 1 standard deviation in which slopes may be significantly different from each other over time.

RESULTS

Objective 1 – Literature review

Of the 157 records included after review, 459 total data points were contributed (Appendix A). Of these data points, 49% ($n=224$) had both a temporal and spatial scale for the quantified ecological process, 17% ($n=78$) provided only the spatial scale, and 34% ($n=157$) provided only the temporal scale (Figure 1). Of these, 21 of the 26 identified ecological components had at least 3 data points necessary for use in analysis (Table 1). Movement was the most prominent ecological process present in literature review, with 153 total data points, and demography/genetics was the least with 35 total data points (Table 1). Of the records that provided only spatial scale or temporal scale for an ecological process, habitat interactions and activity/behavior were the most common, respectively (Figure 1, Table 1). Data extraction from literature review resulted in findings from 44 locations across North America (Figure 2).

Of the 224 spatiotemporal data points, 20% were observations from Yellowstone National Park (YNP), 14% from Wood Buffalo National Park (WBNP), 10% from the Mackenzie Bison Sanctuary (MBS), and the remaining 56% split among 34 locations. Year of publication ranged from 1941-2022, with 79 primary authors. Frequency of publication year was relatively equal between 1980 and 2020 (Figure 3). Unfenced populations accounted for 70% of data points, of which 51% were of the wood subspecies. In total, 64% of populations were of the plains

subspecies. Observations within the U.S. equaled 55% of data points, and the rest were from Canada. From record extraction, 37% of data points explicitly provided a temporal and spatial scale for an ecological component, whereas 63% provided implicit scale such as “week” or “season” for temporal scales and “steps” or “number of wallows” for spatial scales. Maximum and minimum amounts for spatiotemporal data and recurrence days were not well provided overall so they were omitted from analysis. Of the U.S. EPA level 1 ecoregions (Environmental Protection Agency, 2022), 29% of the data points occurred in the Taiga, 8% occurred in the Northern Forests, 31% occurred in the Northwestern Forested Mountains, 28% occurred in the Great Plains, and the remaining 3% occurred across others. Fenced plains bison occupied 95% of data extracted from the Great Plains, unfenced plains bison occupied 65% and 75% of data extracted from Northern Forests and Northwestern Forested Mountains, respectively, and unfenced wood bison occupied 100% of the data extracted from the Taiga.

Objective 2 - Heuristic Model

Ecological components averaged at occurring across scales between 100-1,000 km², and over 10-1,000 days, although in some cases maximum values exceeded 10,000 km² and 10,000 days respectively (Figure 4). Of the bison populations identified as being conserved as wildlife and recognized through systematic analysis by Aune et al., (2017) and Rogers, (2021), 25% of bison herds are managed on ≤ 50 km², with the majority of these experiencing some sort of seasonal management such as pasture rotation or periodic confinement (Figure 4, Table 5). The median of bison herds are managed on ≤ 195 km², where between the 25th and 50th percentile, intensive management occurs often through annual gathers of the entire herd that often change the population demography in various ways (Figure 4, Table 5). Herds existing on ≤ 1278 km² make up 75% of all conservation herds. Of the herds existing between 195 km² and 1278 km², the majority are commonly managed on decadal scales through free-chase hunting permits

established by long-term written management plans that do not require invasive management actions for the entire herd often (Figure 4, Table 5). These populations are also somewhat controlled naturally through established predators and environmental conditions such as disease (Gates et al., 2010; Government of Northwest Territories, 2019a; 2019b). Supplemental boxplots depicted over space and time show little deviation from ecological component averages when comparing all data points for a dimension (spatial or temporal) to those which had both a spatial and temporal dimension (Figures 5 and 6). On the temporal scale, spatiotemporal points of intraspecific aggression, hierarchical social dominance, and range expansion highlight the higher range of extracted temporal occurrences, with parturition highlighting the lower range. On the spatial scale, spatiotemporal points on fire aggregate around the median value for the extracted spatial occurrences.

Statistical analysis

Results from the AIC analysis indicate that of the 7 models provided, the best-fit model carrying 68% of the model weight was the combination between fencing and subspecies (Adjusted $R^2 = 0.49$, F-stat = 42.19 on 5, df = 211, p-value $< 2.2e^{-16}$), with the next best-fit model identified as ecoregion with Δ only slightly greater than 2 (Table 3). For the pairwise analysis, bison subspecies that were fenced / unfenced had significant differences at varying temporal thresholds. At -1 standard deviation from the mean (less than 1 day after back-transformation), the spatial scale of fenced plains bison differed significantly from unfenced wood bison within 95% confidence ($p = 0.0365$, Table 4, Figure 7). At the mean (roughly 40 days after back-transformation), all species – fence levels were significantly different at 95% confidence (Table 4, Figure 6). At +1 standard deviation (roughly 6 years after back-transformation), unfenced plains and unfenced wood bison were significantly different from fenced plains bison ($p < 0.01$ for each), but not from each other ($p = 0.09$, Table 4, Figure 7).

DISCUSSION

Scaled ecology

For the first time to my knowledge, the comprehensive ecology of a wildlife species has been mapped across comparable scales of time and space. The overall objective was to map instrumental bison ecological processes as they occur across scales of time and space to reveal whether the species' holistic ecology contains scaled structure. Through literature review, heuristic visual modeling of bison ecology, and AIC model selection, I found that bison ecology is scaled in time and space, with the combination of subspecies and fencing improving model fit.

Differences in the expression of bison ecology between subspecies are minor but are congruent with Bergmann's rule that an increase in species mass results in increased spatial needs between closely related species (Clauss et al., 2013; Noonan et al., 2020) which is known to be true between plains and wood bison (Gates et al., 2010; Larter and Gates, 1994). The scaled expression of ecology by unfenced plains bison and unfenced wood bison is virtually identical, suggesting an overall species trend regardless of ecological separations between subspecies. While there were no studies in literature review on conservation populations of wood bison managed with fencing, the most prominent finding of this research is the effect fencing has on the expression of plains bison ecology across scales of time and space. The low spatiotemporal association of ecological components ($R^2 = 0.13$) suggests that fencing is either preventing plains bison from expressing portions of their ecology, pressuring them to express these processes in different ways than unfenced herds, or indicates that research on these herds does not adequately report the full range of ecological component expression. The impact of fencing on plains bison ecology is an expected one however and supports the growing research on the adverse effects of fences on wildlife ecology (O'Neill et al., 2022; Laurance and Oosterzee, 2019; McInturff et al., 2020; Wilkinson et al., 2021).

Objective 1 – Literature review

From literature review, some insights into how ecological processes are measured and reported in research were gained. Ecology research differed between large herds on large landscapes and small herds on small landscapes. For instance, WBNP and YNP contributed 42% ($n = 192$) of data points in this project, yet only 9% ($n = 18$) of these data points focused on small-scale ecology (avg $< 10 \text{ km}^2$). Similarly, 90% ($n = 156$) of large-scale processes (avg $> 100 \text{ km}^2$) were studied on large spatial sanctuaries ($> 1000 \text{ km}^2$). Research on these processes within smaller, spatially restricted herds would be useful in understanding how bison exhibit these processes differently as an adaptive necessity of ecosystem engineering specific to physical confinement (Geremia et al., 2019; McInturff et al., 2020), or if they simply do not express them at all. To capture the reality of how ecology scales in time and space, ecological processes need to be measured in both dimensions, but many processes were highly spatial or temporal in the reported literature. Habitat interactions were predominantly spatial, and activity / behavior was predominantly temporal in research, respectively. The boxplots indicate that range expansion, group size, and inter-specific aggression could use more spatial reporting, and fire, movement within feeding patches, and dispersal could use more temporal reporting. Spatial and temporal reporting on both components of demography and genetics is needed. Research could approach mitigating these single dimension differences in ecological process reporting.

Some literature provided insight into areas of research that would benefit from more in-depth association with total bison ecology. For example, within literature the spatiotemporal characteristics of the “rubbing” behavior by bison does not yet provide applicable landscape effect. As Coppedge and Shaw (1997) found in their work, bison clearly preferred certain age and species class of tree for rubbing. They note that it is likely that bison pre-1800’s reduction had a substantial effect on woody vegetation extent and composition within the Great Plains (Coppedge

and Shaw, 1997). However, it is difficult to extrapolate what that effect might have been (and more importantly what it could be today) without understanding the spatial and temporal characteristics of this behavior. Bowyer et al. (1998) was close to providing this by identifying that rubbed trees only occurred within 5 meters of the forest edge, and rubbed trees were spatially distributed roughly 7 meters apart from one another. Even so, the temporal association of tree rubbing as a process was not examined within the study model (Bowyer et al., 1998). If the species and age preferences of trees by bison for rubbing was studied through the spatiotemporal lens, we would better understand the larger ecosystem effects that bison have on forest/meadow edges for purposes of encroachment, invasive species mitigation, and potential effects on birds regarding nest success with access to fur left behind during rubbing events (Bailey, 2013).

Similar occurrences were found in relationships between bird species, bison abundance, and fire effects without providing spatial parameters useful in understanding total ecological effects (Powell, 2006), bison movement patterns without designating the type of movement (McMillan et al., 2021), weather dependent movement that, while providing general understanding of temperature increased movement values, failed to provide the level of detail needed for more scaled application (McMillan et al., 2022), and interspecies interaction that relies on spatial and temporal scales but does not report them (Simon et al., 2019). These records, and others like them, provide insightful and important contributions to bison ecology but fail to provide information that can be explicit enough to apply to an understanding of total bison ecology across scales of time and space. The research conducted in this study minimally provided literature that identified spatial-temporal placement of geneflow and introgression. It is likely difficult to map the spatial occurrence of genetic ecology since it is intertwined with dispersal and sexual selection, so approaching the spatiotemporal scaling of demography and genetics may be more challenging than other aspects of their ecology. However, the research surrounding the

impact of isolation on population genetics is well-covered and has had a prominent effect on the research and management of conservation herds that will continue (Giglio et al., 2018; Hartway et al., 2020).

By leaning more heavily on compiled material from the BSG, there is a possibility of over selective literature that highlights certain areas of bison ecology more prominently than others, as well as a possibility of missing literature through the BSG compilation process. Additionally, the low ceiling of literature gathered from database searches may have resulted in a large sector of literature uncaptured in my analysis. This is also true of the methodology of the database search as it only used a single database (Google Scholar), and retrieval of some articles was limited by accessibility. Expanding research in these areas could be beneficial to capturing the total known ecology of bison today. However, given these limitations, the high occurrence of duplicate records found in the database search ($n = 68/300$) suggests that a large portion of records pertaining to bison ecological processes were retrieved. Explicit ecological component observations over time and space were rarely the focus of ecological studies on bison from literature review. Even so, the nonsignificant ($p = 0.4716$) difference between slopes from the AIC analysis indicates that there is likely little deviation between bison ecology that was explicitly or implicitly extracted, and thus provides a measure of quality control from data collection.

Objective 2 – Heuristic Model

To visualize scaled bison ecology, I created a heuristic model to represent where ecological processes and components occur on average scales of time and space. From placement of ecological components as averages, the model does depict the scaling across time and space I expected to see and provides a new perspective to view species ecology. However, the model

revealed itself to be somewhat misleading in its display due to minor factors that were beyond the scope of this project to address but identified important features and adaptations that should be considered moving forward. Since this model was built with an overall species-aggregate approach, the model does not account for population size, even though this is one factor that greatly differs between fenced and unfenced populations (Rogers, 2021) and between subspecies (Larter and Gates, 1994). For instance, the herbivorous use of landscapes and the way bison employ their ability as ecosystem engineers (Geremia et al., 2019) changes depending on the population visiting grazing sites at any given time.

The heuristic model includes bison populations across multiple ecoregions. Ecoregion differences contribute to changes in the way bison interact with their environment, such as the differences in the length of the growing season between the Taiga and the Great Plains (Mekonnen et al., 2016), annual precipitation (Maurer et al., 2020), and temperature and snow cover (Sheppard et al., 2021). Range productivity is a large indicator of spatial necessity for large herbivores, and bison are no exception. The composition of energy sources on the landscape greatly influence bison use and movements within their home range (Babin et al., 2011). Home range sizes for adult female wood bison can triple in size between that of high and low range productivity (Larter & Gates, 1994), so visualizing all populations through the coarse filter approach doesn't capture the total reality of this process over time and space.

Expression of ecological components in the heuristic model was limited by sample size. I chose to include any ecological processes that contained at least 3 spatiotemporal datapoints for the model. Due to the expansive breadth of data collection, the model strength could greatly improve if spatiotemporal points for each individual ecological component were increased, with more equity across total processes and components. The gap of extractable ecological process and component data in relevant literature highlights the possibility that management actions for wild

bison populations may be lacking supportive information on bison ecological processes, or in scientific reporting.

The first approach to mapping bison ecology on a visual model has provided valuable information that can be incorporated in subsequent versions. Maximum and minimum values of ecological components or polygons will likely better represent the individual scale of ecological components as they contribute to holistic ecological scale. Separating subspecies from the visual representation will more closely represent the holistic ecology of each to better infer conservation and management progress. Additionally, assessing ecological processes as they occur across population density, as it is a known influence on the scale of ecological expression (Plumb et al., 2009; Taper et al., 2000) would be beneficial in the heuristic model, but the approach to ecological process extraction from literature review did not provide an approach to include it. If approached using finer details such as local range productivity, ecoregion, and population size, the model will very likely provide a more useful visual for individual managers.

Scaling and current management practices

The results of this study identified scaling of temporal management disturbances associated with the scaling of spatial limitations among conservation herds. Seasonal disruptions occur for most bison managed on $\leq 50 \text{ km}^2$ as many of these sanctuaries are partitioned into various pastures that require animal rotation, which is known to increase human habituation and domestication (Bailey, 2013). Annual gathers similarly do this, but add excess stress to animals (Caven et al., 2022) in herds existing between 50 km^2 and 195 km^2 . Removals such as these likely disturb the expression of demographic based ecology post-gather (Zanette and Clinchy, 2020) as male and female bison in varying age classes utilize the landscape in different ways (Rosas et al., 2005). However, herds existing on more than 195 km^2 are mostly subject to annual to decadal

management plans that align more with that of traditional wildlife management (Egerton, 1964; Ranglack and Du Toit, 2016; Sanderson et al., 2008). As a management tool, modifications like those mentioned previously to the heuristic model may provide visual identification to highlight where conserving bison ecological processes is occurring, and where processes are being forced to be expressed differently / excluded based on individual management boundaries. Managers can then adapt to better conserve bison into the future, through spatial expansion or ecological process manipulation.

Objective 3 – Bison management paradigm

To identify where management is and is not conserving bison ecological processes, I first approached using the heuristic model as a foundation for reference. However, since the heuristic model was somewhat misleading at face value, I instead compared ecological processes that were recorded based on the AIC best-fit model variables of unfenced wood bison, unfenced plains bison, and fenced plains bison to the spatial availability of conservation herds. Unfenced wood bison were unsurprisingly the group that appeared to have all reported ecological components conserved under the management paradigm, as many herds have vast, unfractured landscapes to fully express their ecology. Unfenced plains bison were similar, yet ecology associated with dispersal and range expansion doesn't appear to be well captured as unfenced plains bison are essentially "terrestrial castaways" (Ritson, 2019) that have no protection if they leave conservation areas. Fenced plains bison ecology was the least conserved under the current management paradigm. Most fenced plains bison exist below the median for spatial availability of conservation herds at 195 km², but at the highest densities at 13.4 bison per km² on average. Ecological components such as migration, dispersal, range expansion, predation-based flight, and seasonal range movement appear to not be conserved within these herds. In some of the data gathered from fenced plains bison, movement within seasonal ranges reached areas that almost

matched that of total available space to the population, suggesting that total allotted space for fenced populations may be inadequate for the densities they are managed at. Unfenced plains bison predominantly occupy space between 195 km² and 1278 km² at densities of 0.4 bison per km², but some such as YNP are above the 75th percentile of 1278 km² and contain densities of roughly 0.23 bison per km² on average. Unfenced wood bison only occupied available space above the 75th percentile of conservation herds at densities of 0.22 bison per km². It is possible that since fenced bison are occupying allotted landscapes at roughly 13 times that of unfenced bison on average, the ecological expression of these herds is diminished, contributing to the regressed scale seen from analysis, but was beyond the capability of this study to determine.

Bison conservation and management adaptations

Bison conservation is faced with multiple complex challenges that include genetic diversity issues (Hartway et al., 2020; Oppenheimer et al., 2021), mirrored animal husbandry practices that effect social perception, acceptance, and thresholds for free-roaming wild bison (Bailey, 2013; Pejchar et al., 2021), state varied wildlife categorization creating policy issues for protections, disease transmission and resource competition (Bailey, 2013; Bruczyńska et al., 2022; Plumb et al., 2009; Ranglack et al., 2015; Turner, 2020), and underrepresented involvement of indigenous peoples' considering their heavily intertwined history with bison (Hessami et al., 2021; Holt, 2018; Mamers, 2019; 2020;). Efforts and social support to restore America's largest land mammal across its historical range persists despite these challenges (Faselt, 2022; Pejchar et al., 2021; Zier-Vogel and Heuer, 2022) and sentiments of the species reaching a threshold of conservation / ecological restoration possibility (Huggins and Morales, 2023; Redford et al., 2016). For American bison, the IUCN Green status Assessment which "assesses the impact of past, current and future conservation actions to measure their conservation success and actual or potential recovery of the taxon" (Grace et al., 2021), highlights that conservation gain has the

potential to increase from the current standing of 17% to 22% for the species, and recovery potential for wild bison across their historic range is achievable beyond current management (Rogers et al., 2022).

For situations where spatial expansions are feasible, utilizing shared stewardship techniques (Symstad et al., 2019), incorporating socio-political boundaries to identify optimal locations for conservation connectivity (Faselt, 2022), and the removal of internal fencing between adjacent populations (Stone and Miller, 2013) could alleviate many stressors for management and bison alike. Efforts for conservation utilizing the inclusive Bison Management System (BMS) (Martin et al., 2022) and cross-jurisdictional / habitat crediting programs (Iranah et al., 2022; Pejchar et al., 2021), are greatly encouraged as 90% of grasslands are privately owned (Martin et al., 2021). Free-roaming herds may provide opportunities for states' economies through hunting that aligns with more traditional wildlife management (Ranglack and Du Toit, 2016) and moves away from common roundup practices. In areas where natural predators are present or will become present, free-ranging herds have additional opportunities to reach ecological restoration milestones (Jung et al., 2023). Increased presence of indigenous knowledge in science and management highlight bison as a centerpiece of cultural significance as many tribes work to decolonize and heal generational wounds (Mamers, 2019; Mueller et al., 2021; Henri et al., 2021), as well as gain leverage for the future of nations' food sovereignty (Pietrorazio, 2021, Ruelle et al., 2022; Shamon et al., 2022). Progress is constantly made toward understanding, securing, and minimizing the risks associated with free-roaming herds and the transmission of disease (Padilla, 2022; Szcodronski and Cross, 2021) which if incorporated with holistic conservation connectivity (Faselt, 2022), may ease pressures and fears of livestock ranchers. Spatial expansion is ideal for most conservation herds, but understandably it is not

feasible for all. Managers of these herds, however, still have avenues in which to address ecological conservation for the benefit and future of the species.

Solutions to mitigating the consequences of spatially limited sanctuaries are becoming more relevant in research. In situations where expansion is not feasible, changing culling operations to mirror more natural predation (Zanette and Clinchy, 2020), and genetic augmentation to avoid inbreeding and loss of genetic diversity through meta-population management strategies (Hartway et al., 2020). Where bison gathers must remain, moving toward genetics-based removals in place of demographic based removals can better secure allelic diversity across populations (Giglio et al., 2018). Even still, approaching bison management through the ecological process lens may be more beneficial to the species over the long-term (White and Wallen, 2012). Some appropriate depopulation in certain herds, and the use of landscape fire to promote dynamic movement patterns (Coffman et al., 2020; Fuhlendorf et al., 2009) may alleviate density-based increases in spatial needs for ecological processes.

With spatial expansions and fine-tuned management manipulation progressions, the ability to incorporate bison ecology as it occurs across scales of time and space to management in the future will continue to move toward achieving ecological functionality for the species (Sanderson et al., 2008). Measuring ecological functionality was one challenge Sanderson et al. (2008) posed. While mapping bison ecological processes and components across time and space does not provide the solution to this difficult conservation challenge, it likely adds a level of demonstrable progress, since bison that cannot express the full suite of their ecology, are unlikely to have total ecological functionality.

Wildlife conservation

The future will bring known and unknown challenges, and wildlife conservation requires dynamic and innovative approaches to address them, as we continue to uncover the interconnections of global environmental processes and spatiotemporal scale described in GCT (Peters et al., 2011) and hierarchy theory (Allen and Starr, 1982). Evaluating wildlife ecological processes on a spatiotemporal scale is one of many useful tools for this reality; one in which total ecology can be measured, and more comprehensive understanding of species needs can be accomplished. This project utilized bison as a case-study species for this framework, but its applications are applicable across all species. Working toward conserving ecological expression, and eventually ecological functionality, will likely be a great tool in improving species management. In identifying total ecological needs, holistic conservation practices are more feasible, and our confidence in what we are conserving for the future is more secure.

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FIGURES AND TABLES

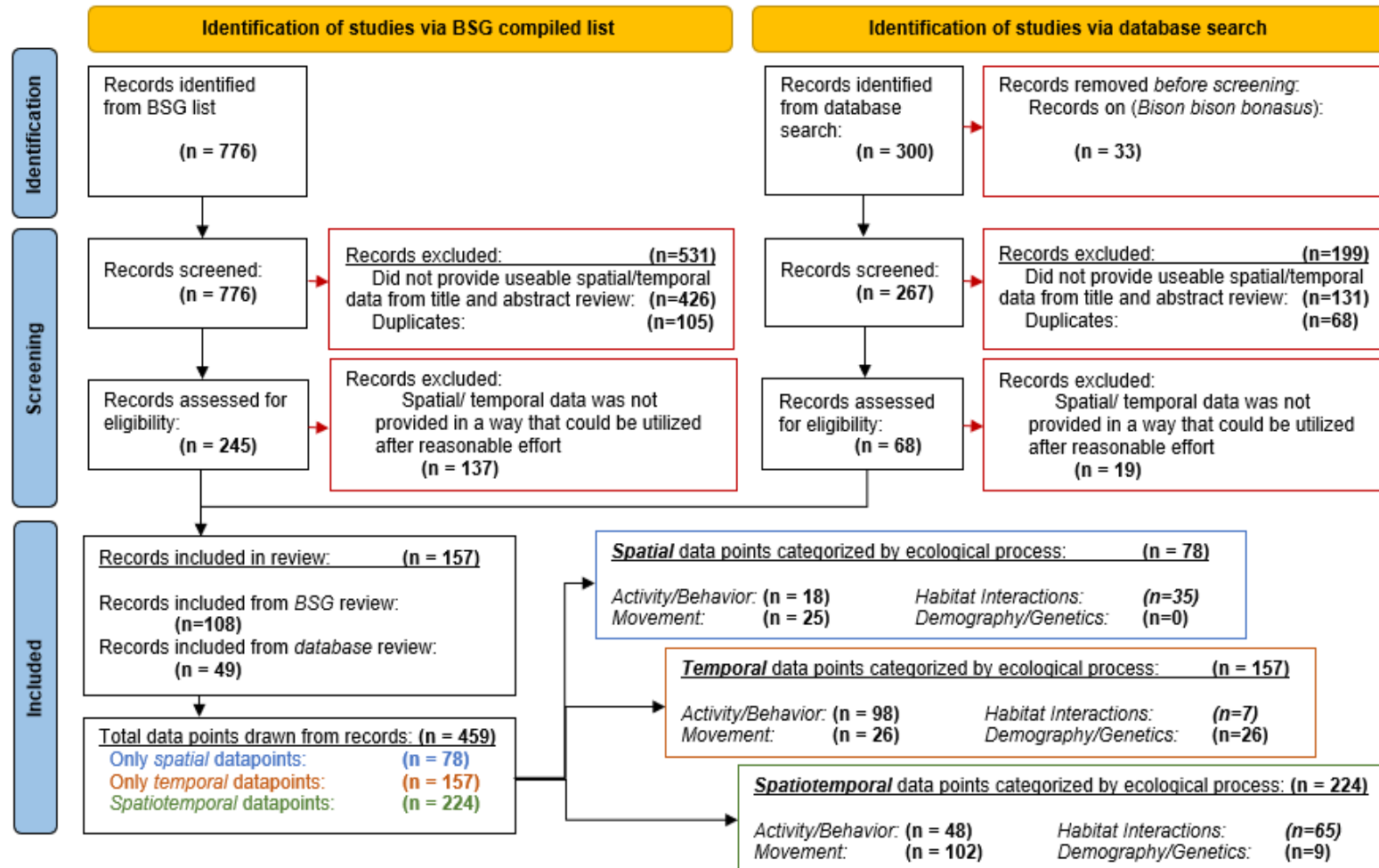


Figure 1: PRISMA-style flowchart (Page et al. 2021) displaying inclusion/exclusion criteria for bison ecological process records from database search and precompiled BSG list.

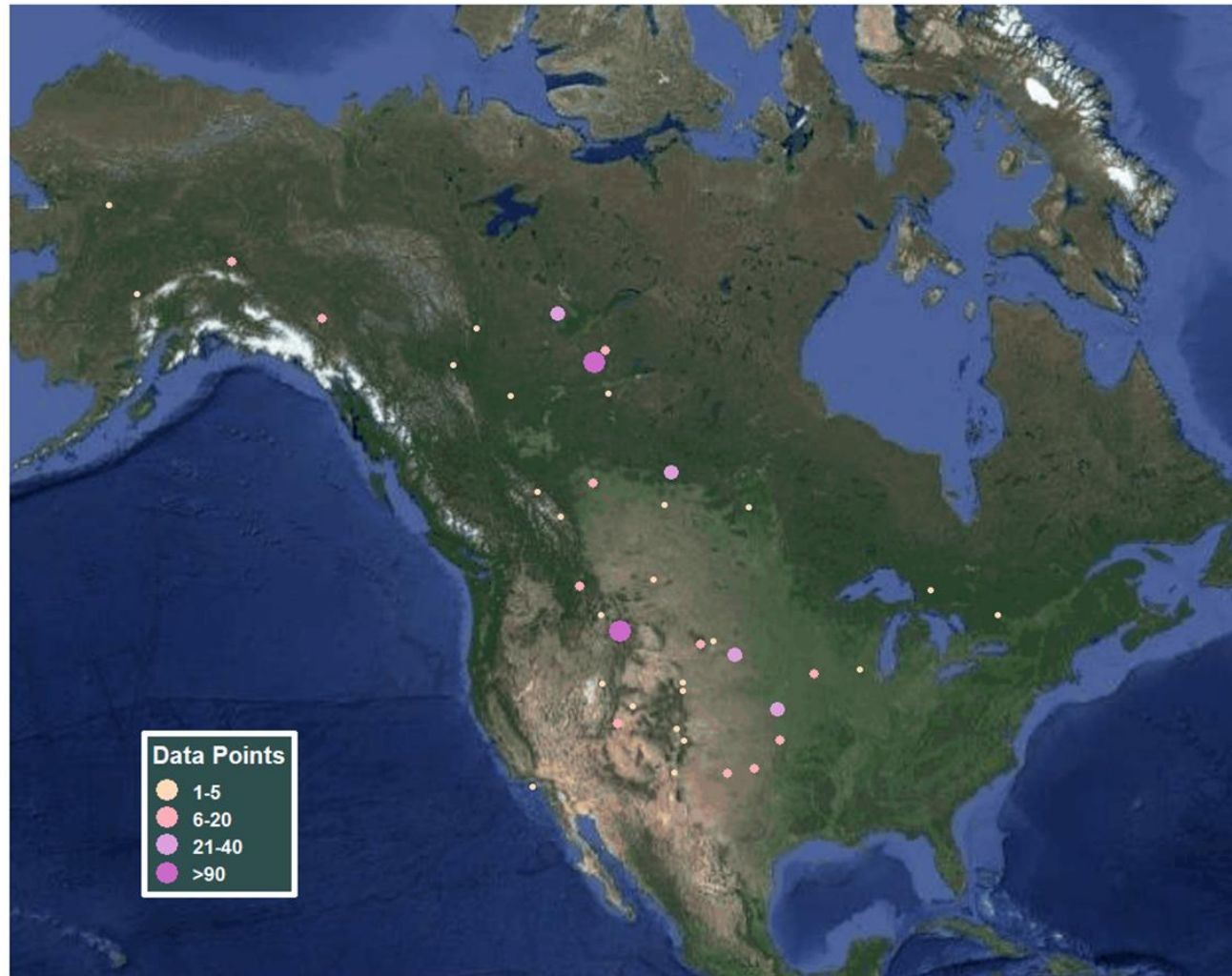


Figure 2: Map of North America showing the different locations where data was extracted from literature review. The number of data points that the location provided is denoted by color and size of points.

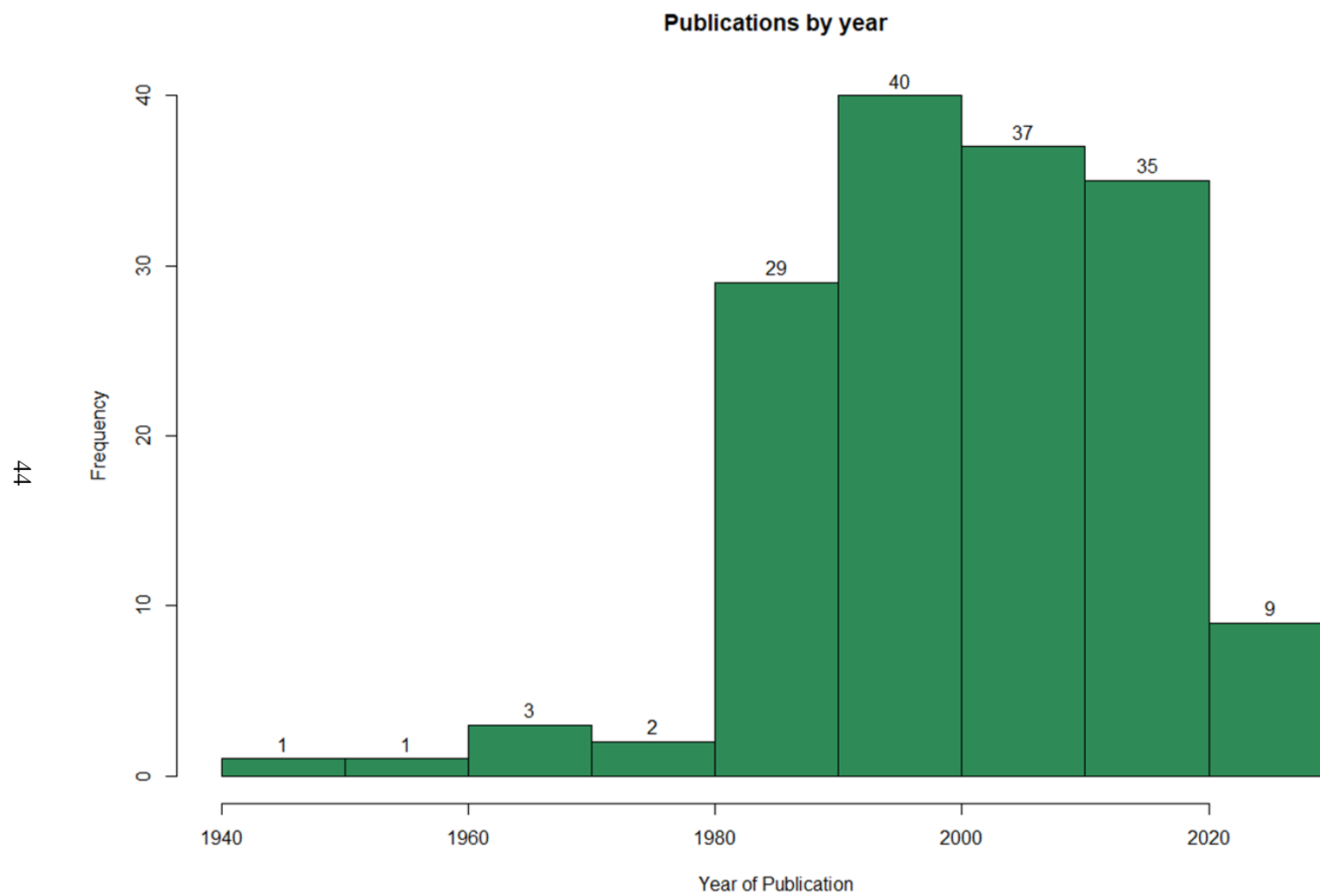


Figure 3: Publications after exclusion process from literature review ordered by decade. Information gathered spanned an equitable coverage of 4 decades.

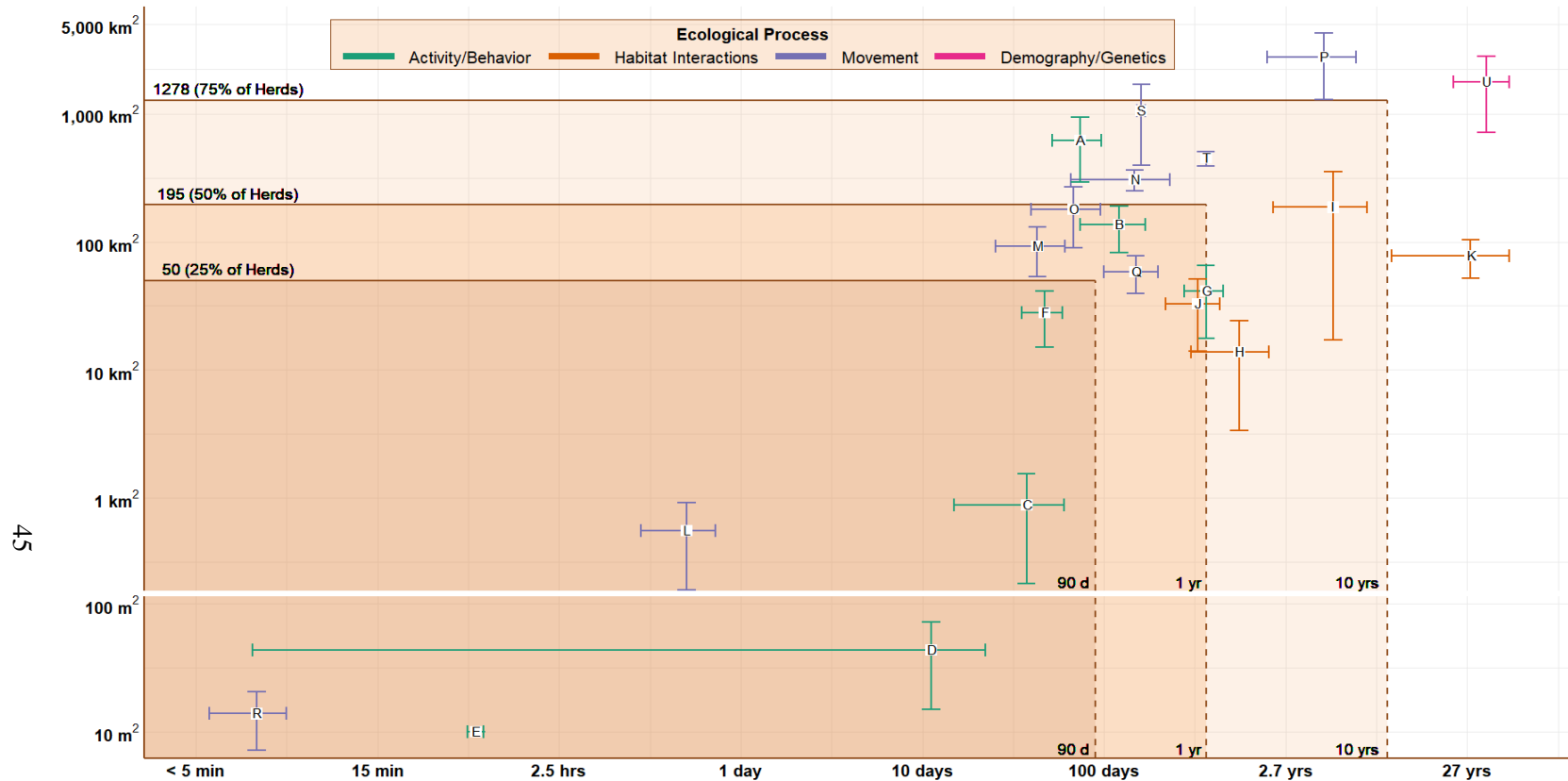


Figure 4: Heuristic model depicting bison ecological processes and components as they occur across scales of time and space. Ecological processes are denoted by color, while individual ecological components are denoted by letters representing the mean, with ± 1 standard error bars for both time and space. Letters correspond to the following: **A** = Flight, **B** = Group Size, **C** = Hierarchical Social Dominance, **D** = Intraspecific Aggression, **E** = Parturition, **F** = Rut, **G** = Social Interaction, **H** = Fire, **I** = Herbivory, **J** = Nutrient Distribution, **K** = Wallowing/Rubbing, **L** = Between Feeding Patches, **M** = Between Seasonal Ranges, **N** = Dispersal, **O** = Migration, **P** = Range Expansion, **Q** = Weather Dependent, **R** = Within Feeding Patches, **S** = Within Seasonal Ranges, **T** = Within Total Range Size, **U** = Population Demography. Of the herds recognized as wild by the IUCN and Rogers (2021), the median, 1st and 3rd quartiles of spatial availability are displayed as solid horizontal lines with values labelled. Temporal parameters for these herds are depicted as dashed lines to indicate that herds below 50 km² are subject to seasonal management actions (90 days), herds below 195 km² are subject to annual management actions (1 year), and herds below 1278 km² are subject to decadal management actions and natural occurrences (10 years) that likely have adverse effects on bison ecology.

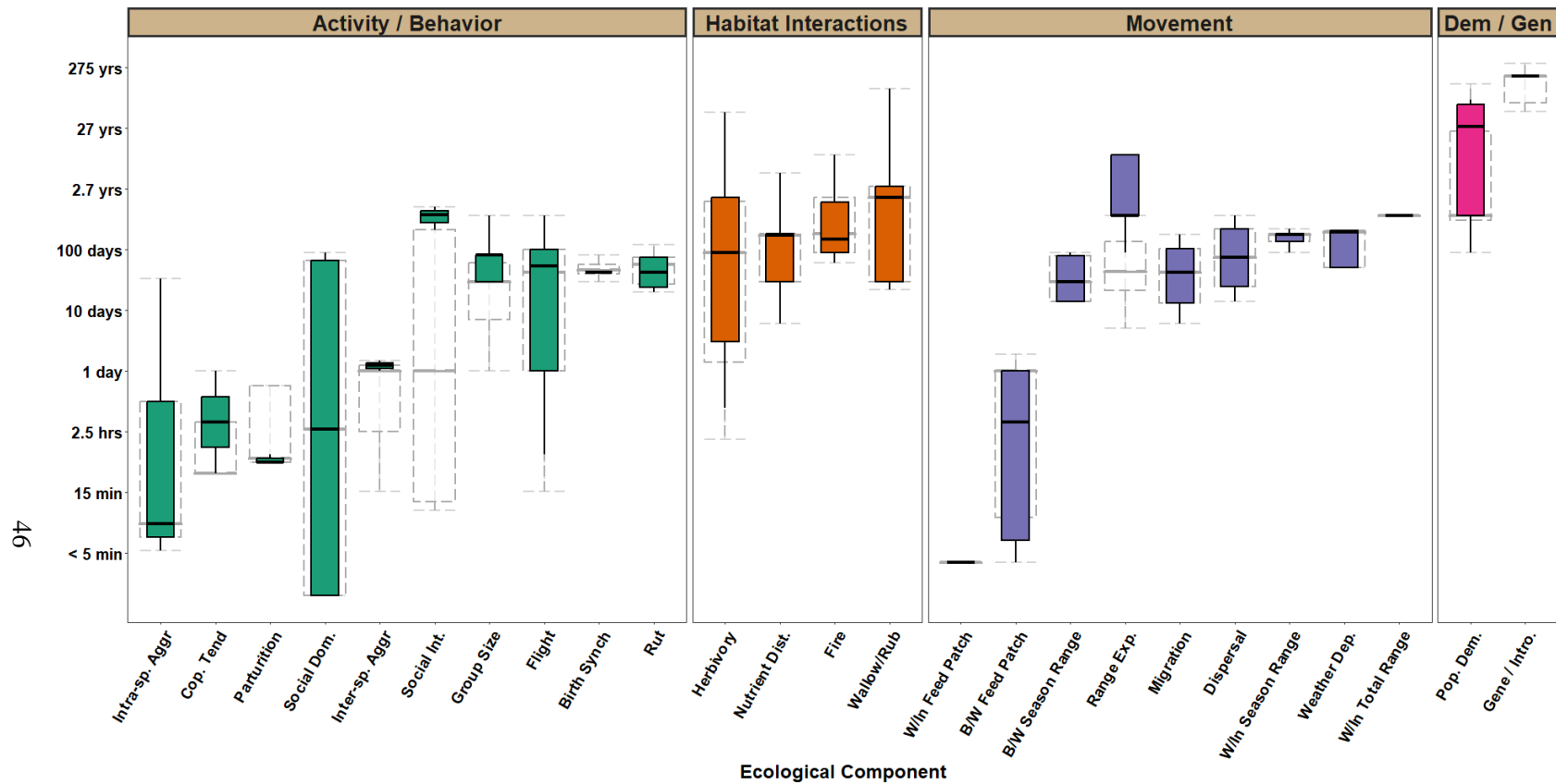


Figure 5: Boxplot depicting ecological components across time. Colors indicate ecological process, labelled above. Dashed boxes indicate the total data extraction for the temporal dimension, where colored boxes indicate the data points that had a corresponding value for the spatial dimension. The colored boxes indicate the data used in analysis. The overlapped boxes allow for a visual understanding of the potential difference in mapping bison ecology based on the data used in this project, and an understanding of the extent to which data used in analysis differs from the totality of ecological processes extracted across single dimensions. Ecological components were ordered by median values of total temporal data points. Ecological components are abbreviated, and full labels are available in Table 1.

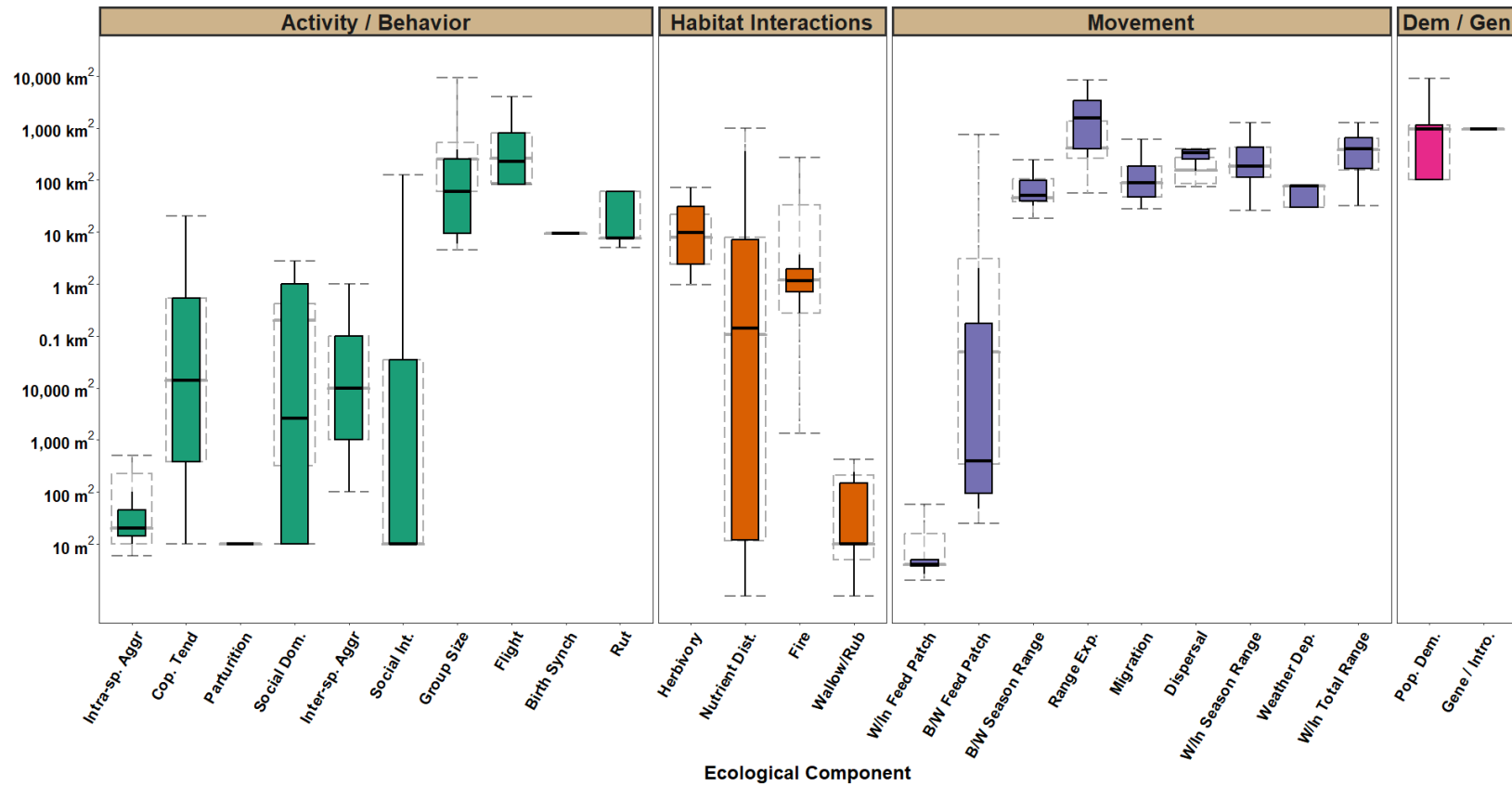


Figure 6: Boxplot depicting ecological components across space. Colors indicate ecological process, labelled above. Dashed boxes indicate the total data extraction for the spatial dimension, where colored boxes indicate the data points that had a corresponding value for the temporal dimension. The colored boxes indicate the data used in analysis. The overlapped boxes allow for a visual understanding of the potential difference in mapping bison ecology based on the data used in this project, and an understanding of the extent to which data used in analysis differs from the totality of ecological processes extracted across single dimensions. Ecological components were ordered by median values of total temporal data points. Ecological components are abbreviated, and full labels are available in Table 1.

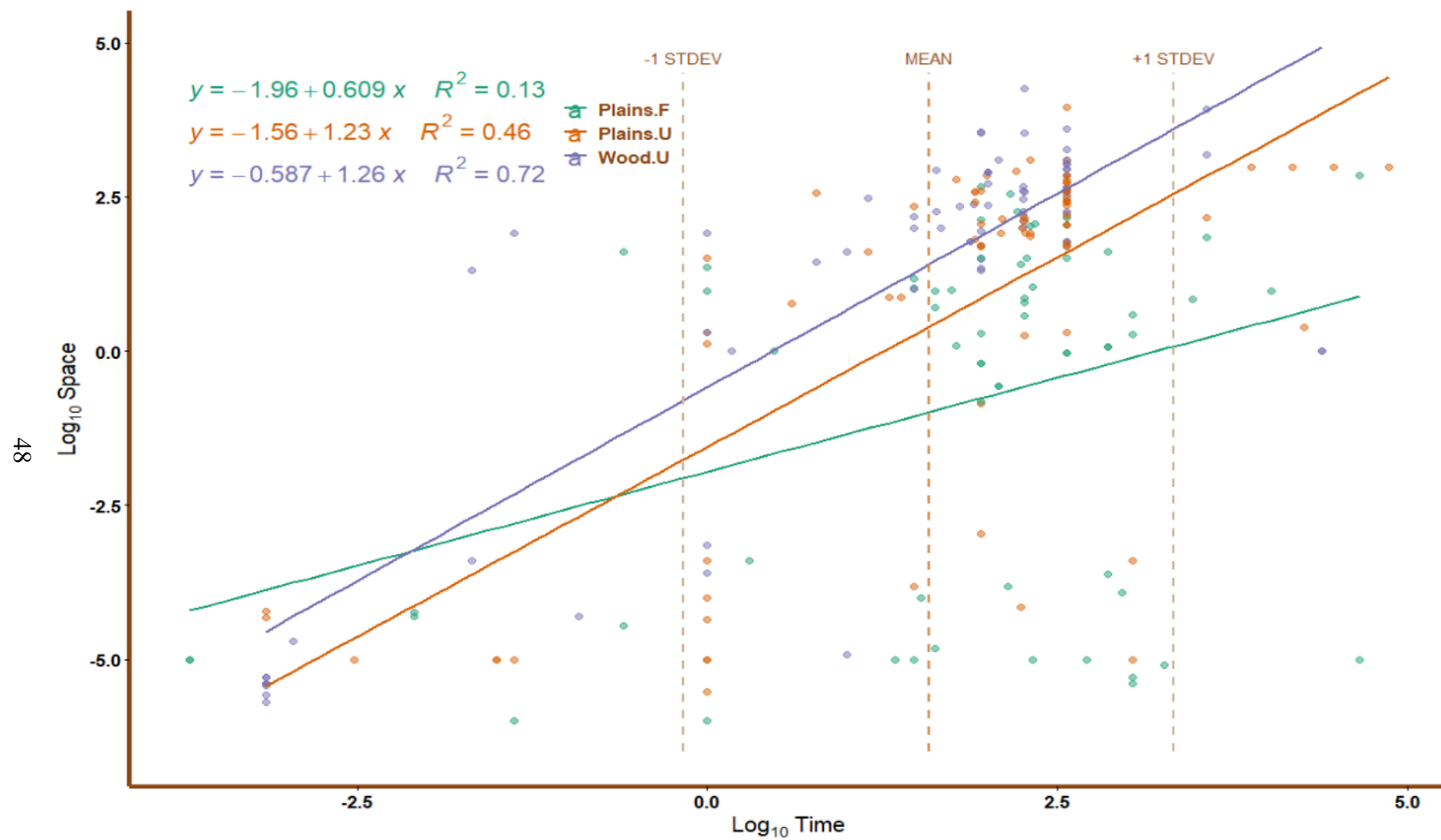


Figure 7: AIC top model showing the slopes for bison ecology based on subspecies and fencing. Dashed lines on the x-axis indicate the mean and ± 1 standard deviation across time. Slopes and R^2 values are provided with corresponding color to plains fenced, plains unfenced, and wood unfenced bison. Values of significance are available in Table 4.

Table 1: Known key ecological processes (bold) enveloping multiple ecological components used to categorize data from literature. The number of data points gathered in these categories is separated by whether the literature provided only spatial, only temporal, or spatiotemporal data. Totals for ecological process data points in each category are bolded in columns and totals for all ecological process and ecological component data points are displayed in the “Total” column.

Ecological Processes, Components, and associated data points extracted				
	# Spatial	# Temporal	# Spatiotemporal	Total
Activity/Behavior	18	98	48	164
Group Size	8	67	9	84
Copulation Tending	0	1	2	3
Birth Synchrony	0	10	1	11
Parturition	0	1	3	4
Rut	0	6	5	11
Hierarchical Social Dominance	3	0	4	7
Intraspecific Aggression	4	0	3	7
Interspecific Aggression	0	1	2	3
Flight	3	6	16	25
Social Interaction	0	6	3	9
Habitat Interactions	35	7	65	107
Wallowing/Rubbing	9	0	9	18
Fire	19	1	14	34
Nutrient Distribution	3	0	21	24
Herbivory	4	6	21	31
Movement	25	26	102	153
Within Feeding Patches	1	0	10	11
Between Feeding Patches	8	1	6	15
Between Seasonal Ranges	3	0	5	8
Within Seasonal Ranges	0	0	27	27
Within Total Range Size	1	0	35	36
Migration	0	0	6	6
Dispersal	7	0	4	11
Range Expansion	5	24	5	34
Weather Dependent	0	0	4	4
Climate Dependent	0	1	0	1
Demography/Genetics	0	26	9	35
Population Demography	0	20	8	28
Gene flow/Introgression	0	6	1	7

Table 2: Categories of information extracted from literature after screening and ultimately included. For quantitative information, the maximum and minimum values of each process were extracted as well if provided. Explicit / Implicit refers to whether records stated temporal and spatial parameters of an ecological component explicitly or implicitly.

Information extracted from literature			
Record Information	Qualitative Information	Quantitative Information	Geographic Information
Publication title	Fenced / Unfenced	Herd population size	General location name
Year of publication	Management sector	Observed population size	Latitude in decimal degrees
Primary author	Subspecies	Total spatial scale available	Longitude in decimal degrees
	Explicit / Implicit	Observed spatial scale	Ecoregion level 1
	Ecological process	Length in days of ecological process	
	Ecological component	Recurrence days of ecological process	

Table 3: Results of Akaike Information Criterion (AIC) model selection. Results are ordered by ΔAIC indicating the best-fit model first. The number of parameters (K) adjusted AIC for small sample sizes (AICc), the difference between the minimum AICc and that model's AICc (ΔAIC), model probability of accounting for variability (AIC Wt.), cumulative sum of model probabilities (Cum Wt.) and the degrees of freedom (df) are provided. Model 1 variables are fenced plains bison, unfenced plains bison, unfenced wood bison, and the \log_{10} transformation for each. Model 2 variables are four identified type 1 ecoregions from data (Taiga, Great plains, Northern Forests, and Northwestern forests) and the \log_{10} transformation for each. Model 3 variables are fenced and unfenced bison populations and the \log_{10} transformation for each. Model 4 variables are plains and wood bison and the \log_{10} transformation for each. Model 5 is a regression across time and space for all data points in \log_{10} transformation. Model 6 variables include the data points extracted that were either implicitly or explicitly stated in literature, the \log_{10} interaction was not significant so it was removed. Model 7 was a test of nullity.

AIC Best-Fit Model Analysis							
Model	K	AICc	ΔAIC	AIC Wt.	Cum Wt.	df	
1. Fence x subspecies	7	951.01	0.00	0.68	0.68	211	
2. Ecoregion	9	953.12	2.11	0.24	0.92	209	
3. Fence	5	955.36	4.35	0.08	1.0	213	
4. Subspecies	4	972.06	21.05	0.00	1.0	214	
5. Regression	3	995.27	44.26	0.00	1.0	215	
6. Explicit / implicit	4	996.82	45.81	0.00	1.0	214	
7. Null	2	1090.90	139.90	0.00	1.0	216	

Table 4: Pairwise comparisons based on the slope of lines for fenced plains bison, unfenced plains bison, and unfenced wood bison across the average \pm 1 standard deviation. The R^2 value for each slope is provided under its respective variable.

Pairwise Comparisons of Slopes					
Variable		Cross-Variable	Avg – 1stdev	Avg	Avg + 1stdev
Fenced Plains	x	Unfenced Plains	p = 0.86	p < 0.01	p < 0.01
$R^2 = 0.13$					
Unfenced Plains	x	Unfenced Wood	p = 0.12	p = 0.01	p = 0.09
$R^2 = 0.46$					
Unfenced Wood	x	Fenced Plains	p = 0.04	p < 0.01	p < 0.01
$R^2 = 0.72$					

CHAPTER III

SYNTHESIS AND RECOMMENDATIONS FOR THE FRAMEWORK OF SCALED ECOLOGY

Project review

To answer the question if total species ecology is scaled in time and space, I performed a systematic literature review of bison (*Bison bison*) ecology to identify individual ecological processes and their components as they occur spatiotemporally. Through AIC-best fit analysis, I isolated fencing and subspecies as the variables that best described variation to better understand bison ecology as it pertains to management and conservation efforts. I created a heuristic model of bison ecology over time and space to provide a visual representation of scaled ecology. I then highlighted areas that best describe the current management paradigm of bison conservation herds through the spatial limitations of most conservation herds, and the temporal management disruptions that are commonly associated with each. This methodology is useful to understand the convergence of where management is capturing bison ecology, and where it isn't, and to pose thoughtful insights of how bison conservation can improve for the future of the species.

Subspecies and fencing

Unfenced plains and unfenced wood bison showed almost identical slopes in their scaled ecology, with wood bison expressing their ecology at higher spatial scales. Embedded into the subspecies difference in the AIC-best fit model was ecoregion, as all populations found in the Taiga were of the wood subspecies, and almost all Great Plains and Northwestern Forest populations were of the plains' subspecies. This highlights the already well-established fact that ecoregional and subspecies differences have substantial effects on bison ecological expression (Bailey, 2009; Gates et al., 2010; Larter and Gates, 1994; Mekonnen et al., 2016). Wood bison change habitat selection seasonally as the best sources of energy change with them, such as forest

lichen in the transitional period between fall and winter, and wintertime sedge selection when water is frozen to provide access (Larter, 1988). In comparison, plains bison require less movement for the same nutritional gain unless impacted by elevational gradients like those found in YNP or HM (Gates et al., 2010; Geremia et al., 2019; Van Vuren, 1979). Additionally, these ecoregional differences underpin the differences we see in subspecies, as wood and plains bison have each adapted separately to their respective ecosystems (Bork et al., 1991; Gates et al., 2010; Larter and Gates, 1994). Therefore, subspecies and ecoregion differences need to be considered in management adaptations as they are more fine- scaled approaches than our study model.

Fencing was found to be an important factor in the expression of plains bison ecology. The spatiotemporal scaling of ecological processes was weak for this group, but it may not mean that fencing is inhibiting ecological expression entirely. From personal observations for example, the bison in the South unit of Theodore Roosevelt National Park (THRO) occupy roughly 185 km², and while they use the entirety of the park year-round, they also increase the time spent and remain for longer time periods in certain areas seasonally. This indicates to me, that even though the bison of THRO do not have the spatial availability to have clearly separate seasonal ranges, it is likely that their confinement has pressured the population to exhibit seasonal range use differently, rather than lose it entirely. It is also a possibility that the low association of scale in fenced herds is a result of scientific reporting, as this group had the most data points associated with small spatial, but large temporal scales.

Fencing has been and will continue to be a necessary and effective management tool for the restoration of the species (Coder, 1975; Egerton, 1964), but the reliance on fencing for all populations may not always be necessary (Babin et al., 2011; Callenbach, 2000; Zier-Vogel and Heuer, 2022). In Banff National Park, temporary fencing was used to encourage site fidelity, and some hazing efforts post removal of fencing resulted in the landscape use management hoped for

3+ years after reintroduction (Zier-Vogel and Heuer, 2022). The need for more investigative studies to map the full range of ecological consequences of wild bison herds is apparent (Fagre et al., 2022; Nickell et al., 2018; Risch et al., 2020). This research is just one step toward supporting this need. Unfortunately, there is an absence of plains bison in free-ranging states to understand the totality of bison ecology in the Great Plains region despite the native optimal habitat (White, 2023), increased resiliency and tolerance to climate change (Martin et al., 2021) and increased positive effects to grassland biodiversity (Ratajczak et al., 2022) compared to their domestic cattle counterparts. While information gathered from the few free-roaming herds in the U.S. such as YNP and the Henry Mountains is invaluable, many factors that act on the expressed ecology of bison are not present in Great Plains herds such as montane habitat, large elevational gradients, and associated precipitation and vegetation differences. An avenue of research that could potentially address this need is ecological research of bison herds within the commercial bison industry. Bison exist on a spectrum of wildness (Rogers, 2021) and though commercial bison ranching is often heavily removed from indicators of wildlife, some privately owned herds in this sector rival the spatial capacity many DOI herds are allotted (Gates et al., 2010). It could be useful to observe bison ecological processes in these herds to identify similarities and differences that could progress bison conservation efforts. However, the results of this research suggest that bison ecological processes are not expressed evenly between fenced and unfenced populations. This will be a crucial barrier to understanding ecological needs and parameters for rewilding plains bison across the lower latitudes of their historical range in the Great Plains. This void of confidence likely contributes greatly to the perceived risks and social fears from researchers, managers, and the public.

Fencing due to ownership boundaries for conservation herds that are adjacent to each other offer a unique opportunity, as shared stewardship of herds may provide for the removal of

internal fencing, providing an increase of spatial capacity for ecological expression without sacrificing protections against human-wildlife conflict (Symstad et al., 2019). This approach has been successful in small herds (Stone and Miller, 2013), and could similarly benefit large adjacent herds such as those in Wind Cave National Park and Custer State Park which are divided by an internal fence, and Badlands National Park and the Pine Ridge Reservation that share a fence line.

Historical bison conservation shaped current practices and perceptions

With the unique history of North American bison, the events that isolated bison conservation practices from those of other wildlife are apparent. Initial efforts to save bison from outright extinction in the early 1900's required high levels of oversight with captive breeding herds and translocation to fenced sanctuaries across America (Boyd 2003, Sanderson et al., 2008). Many who championed the return of successful bison populations were private ranchers, passionate with preserving the wild western frontier (Freese et al., 2007). While the success of bison today could not have been achieved without these individuals, they contributed to bison conservation in ways familiar to domestic cattle ranching (Boyd, 2003; Freese et al., 2007; Sanderson et al., 2008). With isolation, and ranching management techniques, priority efforts to maintain high allelic diversity among remaining bison resulted in high density fenced sanctuaries that incorporate regular total herd management that mirrors animal husbandry practices for population control (Bailey, 2013; Hartway et al., 2020). Genetic conservation priority and associated remnant cattle management strategies have persisted from the 1940's to today (Bailey, 2013; Boyd, 2003). An economic effect resulted from these practices and led to the creation of the commercial bison industry that holds over 90% of all bison in North America (Rogers, 2021). With the economic and agricultural regulations associated with commercial bison ranching, many states designated bison as livestock, since few "wild" populations were extant when commercial

herds were established (Boyd, 2003). The livestock designation is an unfortunate political barrier for progress toward increasing wild populations, as the regulations and laws governing livestock vary greatly from that of wildlife, which can make rewilding unfeasible in many cases (Pettorelli et al., 2018), and muddies the water of what bison conservation should look like (Barnard, 2020).

This distinction between bison and wildlife has had lasting effects on the perception of bison across research, management, and the public. In research, Laskin et al. (2020) provides such an example as their article “Designing a fence that enables free passage of wildlife while containing reintroduced bison: a multispecies approach” clearly excludes bison as members of the wildlife group and highlights the exclusionary practices and intense management other wildlife species are not subject to. Even considering that the bison in question later acquire a more free-roaming status (Zier-Vogel and Heuer, 2022), the way we speak, write, and subconsciously perceive bison in research still creates a separation from that of other wildlife species. Within management, the common annual gathers needed for fenced populations often mimic domestic cattle roundups for sale, which is known to contribute to domestication (Bailey, 2013). It has only been in recent years where low-stress animal handling techniques have been employed in various management areas to alleviate animal exposure to intensive management, where bison are treated more like wildlife than their domestic cousins (Found and DeMoor, 2020; McCann and Moynahan, 2020).

Social fear

The lack of reliable historical accounts of free roaming bison landscape use has supported maintained captivity, and by default has normalized social acceptance thresholds for wild bison primarily existing behind fences (Bailey, 2013). Fear for commercial cattle operations by the potential transmission of diseases and competition for resources fuels much of public pushback as

well (Bruczyńska et al., 2022; Ranglack et al., 2015; Turner, 2020). Subsequent fear and perceived risk of free-roaming bison herds associated with human-wildlife conflict has resulted from these decades-long management approaches (Freese et al., 2007; Pejchar et al., 2021; Sanderson et al., 2008). Additionally, some research on free-roaming bison contributes to this narrative as well. The social fear of free-roaming bison is perpetuated by resurfacing accounts of post-reintroduction site fidelity failure before managers better understood the mechanisms that encourage site fidelity (Merkle et al., 2014; Watt and Heuer, 2020). For example, Jung (2017), Jung & Larter (2017) and Laskin et al. (2020), highlight a few adult male individuals moving outside expected areas rather than focusing on most of the adult female and juvenile population that remains in expected reintroduction locations. While the dispersal possibilities of bison are indeed important to consider, articles such as these push a greater concern for the minority dispersal rather than the majority site fidelity, which may adversely affect science-based management approaches.

Cultural significance

Although social fear persists, cultural and social value does too (Pejchar et al., 2021; Rogers 2021). Bison have a strong conservation legacy (Rogers, 2021) and many fondly support the ideals of the return of free-roaming bison to the Great Plains but are at a loss for how to accomplish it beyond these social and political barriers (Pejchar et al., 2021; Redford et al., 2016). Conserving bison is not only a measure of saving a native North American species, but preserving a way of life, ancestral heritage, and even family members for many plains tribes (Schneider, 2022). Rewilding bison and exploring more avenues for tribal ownership is a step toward regaining cultural autonomy and food sovereignty (Pietrorazio, 2021, Ruelle et al., 2022; Shamon et al., 2022). The U.S. federal government is making change toward facilitating these necessary remedies through long-term efforts such as the DOI Bison Conservation Initiative, and

short-term efforts such as a recent pledge of \$25 million for more bison on federal lands, transfer of bison to tribal ownership, and co-stewardship efforts (Department of Interior, 2023).

National culture effects bison conservation as well, where individualistic values often collide, but recognizing and managing bison as a staple of community growth and connectivity can bring competing ideologies to common ground (Picketts, 2017). Bison conservation has avenues for growth through cultural connectivity by hunting in a way that provides indigenous peoples with access to a pre-colonized way of life, and the U.S. with economic opportunities, as almost 14 million American hunters produce roughly \$40 billion dollars in non-commercial hunting expenses annually (Arnett and Southwick, 2015). This opportunity is likely greatest in rural areas of the Great Plains where depopulation has become a considerable occurrence and will likely continue (Johnson and Lichter, 2019), potentially opening conservation connectivity sites with minimal human-wildlife conflict risks.

The future of bison conservation

Despite the many challenges that face modern bison conservation, efforts to restore North America's largest land mammal across its historical range persists. Bison hold intrinsic value as a conservation beacon of success and hope (Reford et al., 2016) which maintains traction for the possibility and social support of more free-roaming herds even when faced with complex consequences (Faselt, 2022; Pejchar et al., 2021; Sanderson et al., 2008; Zier-Vogel and Heuer, 2022). The plethora of values bison represent provide new and dynamic approaches to conserve and restore the species into the future that combats sentiments of reaching the threshold of possibility (Huggins and Morales, 2023; Redford et al., 2016). Even if ecological restoration likely cannot be achieved for such an iconic species (Sanderson et al., 2008), we can still pursue a reality as close to it as possible.

Plains and wood bison seem to express their ecology similarly over scales of time and space, which provides increased confidence in the effect the current management paradigm has on wild bison populations. The ability for management to identify where it is conserving bison ecological processes, and where it is perhaps forcing adaptive change of these processes may now be attainable. This increase in clarity will likely provide avenues to which managers can adapt to better conserve bison and their ecology into the future, such as spatial expansions where feasible, and changes that allow better expression of ecology within spatial boundaries where expansion is not feasible.

Mapping the totality of bison ecology across scales of time and space will be an important tool in the future of bison conservation. Incorporating this approach through research that closes the gap between studies on large- and small-scale herds will provide a better picture of bison ecology overall. Additionally, increasing research on fenced bison herds and the ways in which fencing pressures adaptations to ecology underpins conserving bison as wildlife. Addressing the ways in which science perpetuates the distinction between bison and wildlife, while also incorporating research of commercial herds to supplement knowledge of ecology on large scales where available will be important in providing the necessary foundations to move restoration and rewilding projects forward.

Advances in quality of genetic conservation have moved mountains regarding population stability, perseverance, and preparation for inevitable challenges in disease and disaster (Hartway et al., 2020). However, it is possible that hyper-focusing in this area removes our attention from arguably foundational aspects of rewilding projects. Bison are unique in that the way we approach their conservation contradicts common practices for most wildlife species (Sanderson et al., 2008). Conserving bison into the future requires an array of conservation techniques, ideally those that remove domestication practices in wildlife management (Bailey, 2013), and giving

more attention to the ecological needs of bison (Sanderson et al., 2008; White and Wallen, 2012). With meta-population management strategies (Giglio et al., 2018; Hartway et al., 2020), stocking bison at maximum densities behind fences may no longer need to be the primary conservation approach. Adjusting population sizes to allow a more comprehensive expression of ecological processes and incorporating dynamic conservation areas within and between permanent conservation areas (D'Aloia et al., 2019) brings us one step closer to realizing wild bison restoration despite modern challenges. Incorporating bison ecology as it occurs across time and space provides an avenue of exploration to reduce this disparity.

Tribal ownership of bison is on the rise and has the potential to make large steps forward in the conservation of the species (Rogers, 2021), but requires dynamic shifts in management to better support tribal autonomy (Schneider, 2022), build trust for shared stewardship approaches (Symstad et al., 2019), and amplify landscape connectivity previously championed by native communities (Brown, 2022). Actively working toward deconstructing animal husbandry techniques from wild bison management (Bailey, 2013; Found and DeMoor, 2021; McCann and Moynahan, 2020; Redford et al., 2016) and addressing the socio-political barriers that have stunted progress (Faselt, 2022; Pejchar et al., 2021; Pettorelli et al., 2018; Redford et al., 2016) will be pertinent in the next chapter of bison conservation across their historic range.

Wildlife applications

This approach to scaled wildlife ecology is an important step in the future of wildlife conservation globally (Peters et al., 2011). Approaching wildlife and biodiversity conservation through the spatiotemporal lens is increasing in research and providing scientists and managers with better tools to comprehensively map the needs of various species (D'Aloia et al., 2019; Gilbert et al., 2022; Killion et al., 2018). This is particularly important for range-restricted

herbivorous mammals as the future of many of these species is uncertain (Atwood et al., 2020; Bucholtz et al., 2019; Fortin et al., 2020) and even more-so for migratory species (Albers et al., 2023) and those restricted by fences as we now understand this effect to be underestimated (O'Neill et al., 2022; Laurance and Oosterzee, 2019; McInturff et al., 2020; Wilkinson et al., 2021).

Beyond fencing as an inclusionary wildlife management tool as exists with bison, private exclusionary fencing is a known inhibitor of large mammal grazing and migration patterns, both of which have landscape and ecosystem consequences (Cushman et al., 2016; Osipova et al., 2018; Xu et al., 2021). While fences are a prominent tool for livestock and landowners, the consequences on species that are non-targets for exclusion are often not considered (Smith et al., 2020), despite the strong evidence and concern for their negative effects in the conservation community (Jakes, et al., 2018; Xu et al., 2021). Recent efforts to explore virtual fencing techniques that employ audio and electrical stimulus is promoted as a possible solution to physical fencing consequences (Campbell et al., 2019), but the ethical concerns of this method are still under debate (Grumett and Butterworth, 2022; Lee and Campbell 2021). Fencing is a global wildlife concern, and it has expansive effects on wildlife that are inclusionary or exclusionary by design (Jakes et al., 2018; Smith et al., 2020; Xu et al., 2018). Conservation of large mammals will continue to require increased attention to mitigating or removing fencing effects for both inclusionary, exclusionary, and non-target species globally to better facilitate the scaling and totality of species ecology (Jones et al., 2019; Smith et al., 2020; Xu et al., 2018; Zhang et al., 2021). For some species that are often not spatially restricted even in the presence of fencing such as deer (*Odocoileus spp.*) (Macdonald et al., 2022), or species where fencing heavily influences behavioral ecology as a non-target consequence such as American pronghorn (*Antilocarpa americana*) (DeVoe et al., 2022), research on their total scaled ecology would be a

useful comparison in mapping large mammal scaled ecology as it pertains to conservation efforts and the various effects of fencing. A heuristic model of scaled ecology may identify other areas particular to ecological needs for these species as well.

Overall conclusions

This research is likely the first to address and support total species scaled ecology. Specifically, the scaling of bison ecology is affected by the physical boundaries of most management areas. Total ecological restoration as described by Sanderson et al. (2008) is a goal to continue striving for, and interim phases of this development undoubtedly include the ability for bison to be bison, in every way that can be achieved. Through collaborative efforts of federal, state, tribal, and private organizations, bison conservation is entering an age of new growth; one that provides opportunities for bison to fill their ecological and cultural roles. This scaled ecology approach is a new tool, which will inevitably require improvements. Even still, it shows great promise as a method to loosen the grip on the 1940's hold on bison as "terrestrial castaways" (Ritson, 2019) and bring them into the 21st century as the wild, and culturally significant entities they are.

This new approach to assessing the spatiotemporal ecology of a species has the potential to have far reaches in associated science and management, as heuristic models like the one presented here have the potential to isolate areas of research and management that require more attention. Additionally, the application of this approach provides new and dynamic methodologies to tackle the ever-increasing complexity of wildlife conservation efforts.

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APPENDIX A.

List of literature records included in analysis after systematic review. The number of data points (#DP) contributed by the record are accompanied by letters to identify if they were Spatial (S), Temporal (T), or Spatiotemporal (ST). The origin of the record whether from the BSG pre-compiled list (BSG) or database search (DB) is provided.

Literature Record	# DP			Origin
	S	T	ST	
Allred, B. W., Fuhlendorf, S. D., Engle, D. M., & Elmore, R. D. (2011). Ungulate preference for burned patches reveals strength of fire-grazing interaction. <i>Ecology and Evolution</i> , 1(2), 132–144. https://doi.org/10.1002/ece3.12			1	DB
Amick, D. S. (1996). Regional patterns of Folsom mobility and land use in the American Southwest. <i>World Archaeology</i> , 27(3), 411–426. https://doi.org/10.1080/00438243.1996.9980317			1	BSG
Augustine, D. J., & Frank, D. A. (2001). Effects of Migratory Grazers on Spatial Heterogeneity of Soil Nitrogen Properties in a Grassland Ecosystem. <i>Ecology</i> , 82(11), 3149–3162. https://doi.org/10.1890/0012-9658(2001)082[3149:eomgos]2.0.co;2	1			BSG
Aune, K., Roffe, T., Rhyen, J., Mack, J., & Clark, W. (1998). Preliminary results on home range movements, reproduction, and behavior of female bison in northern Yellowstone National Park. In <i>International symposium on bison ecology and management in North America. Montana State University, Bozeman, USA</i> (pp. 61-70).			2	BSG
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Gogan, P. J., Podruzny, K. M., Olexa, E. M., Pac, H. I., & Frey, K. L. (2005). Yellowstone bison fetal development and phenology of parturition. <i>The Journal of Wildlife Management</i> , 69(4), 1716-1730. https://doi.org/10.2193/0022-541X(2005)69[1716:YBFDAP]2.0.CO;2		6		BSG
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Green, W. C. (1992). The development of independence in bison: pre-weaning spatial relations between mothers and calves. <i>Animal behaviour</i> , 43(5), 759-773. https://doi.org/10.1016/S0003-3472(05)80199-X			1	BSG
Gross, J. E., & Wang, G. (2005). Effects of population control strategies on retention of genetic diversity in National Park Service bison (<i>Bison bison</i>) herds. <i>Final Report, Yellowstone Research Group, USGS-BRD. United State Geological Survey, Bozeman, Montana</i> .		2		BSG
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Halbert, N. D., Raudsepp, T., Chowdhary, B. P., & Derr, J. N. (2004). Conservation genetic analysis of the Texas state bison herd. <i>Journal of Mammalogy</i> , 85(5), 924-931. https://doi.org/10.1644/BER-029		2		BSG
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Halloran, A. F. (1968). Bison (Bovidae) productivity on the Wichita Mountains Wildlife Refuge, Oklahoma. <i>The Southwestern Naturalist</i> , 23-26. https://doi.org/10.2307/3668811		1		BSG
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Hartnett, D. C., Hickman, K. R., & Walter, L. E. (1996). Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. <i>Rangeland Ecology & Management/Journal of Range Management Archives</i> , 49(5), 413-420.		1		BSG
Hawkins, J. H., & Zeglin, L. H. (2022). Microbial Dispersal, Including Bison Dung Vectored Dispersal, Increases Soil Microbial Diversity in a Grassland Ecosystem. <i>Frontiers in Microbiology</i> , 13.			1	DB
Hecker, L. (2022). Influence of nutrition on the habitat selection of the Ronald Lake wood bison (<i>Bison bison athabasca</i>) herd. https://doi.org/10.7939/r3-p712-mg97			3	DB
Hein, F. J., & Preston, C. R. (1998). Summer nocturnal movements and habitat selection by <i>Bison bison</i> in Colorado. In <i>International Symposium on Bison Ecology and Management in North America</i> (pp. 96-106).		1		BSG
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Jung, T. S. (2011). Gray wolf (<i>Canis lupus</i>) predation and scavenging of reintroduced American bison (<i>Bison bison</i>) in southwestern Yukon. <i>Northwestern Naturalist</i> , 92(2), 126-130. https://www.jstor.org/stable/41300892			3	DB
Jung, T. S., & Larter, N. C. (2017). Observations of long-distance post-release dispersal by reintroduced bison (<i>Bison bison</i>). <i>The Canadian Field-Naturalist</i> , 131(3), 221-224. https://doi.org/10.22621/cfn.v131i3.1825			1	DB
Jung, T. S. (2017). Extralimital movements of reintroduced bison (<i>Bison bison</i>): implications for potential range expansion and human-wildlife conflict. <i>European Journal of Wildlife Research</i> , 63(2), 35. https://doi.org/10.1007/s10344-017-1094-5			2	DB
Jung, T. S. (2020). Investigating local concerns regarding large mammal restoration: group size in a growing population of reintroduced bison (<i>Bison bison</i>). <i>Global Ecology and Conservation</i> , 24, e01303. https://doi.org/10.1016/j.gecco.2020.e01303		11		DB
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Kelliher, F. M., & Clark, H. (2010). Methane emissions from bison—An historic herd estimate for the North American Great Plains. <i>Agricultural and Forest Meteorology</i> , 150(3), 473-477. https://doi.org/10.1016/j.agrformet.2009.11.019			1	DB
Kirkpatrick, J. F., McCarthy, J. C., Guderhuth, D. F., Shideler, S. E., & Lasley, B. L. (1996). An assessment of the reproductive biology of Yellowstone bison (<i>Bison bison</i>) subpopulations using noncapture methods. <i>Canadian Journal of Zoology</i> , 74(1), 8-14. https://doi.org/10.1139/z96-002		6		BSG
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Komers, P. E., Messier, F., & Gates, C. C. (1992). Search or relax: the case of bachelor wood bison. <i>Behavioral Ecology and Sociobiology</i> , 31, 192-203. https://doi.org/10.1007/BF00168647			4	BSG
Komers, P. E., Messier, F., & Gates, C. C. (1993). Group structure in wood bison: nutritional and reproductive determinants. <i>Canadian Journal of Zoology</i> , 71(7), 1367-1371. https://doi.org/10.1139/z93-188			8	BSG

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Komers, P. E., Messier, F., Flood, P. F., & Gates, C. C. (1994). Reproductive behavior of male wood bison in relation to progesterone level in females. <i>Journal of mammalogy</i> , 75(3), 757-765. https://doi.org/10.2307/1382527			1	BSG
Larter, N. C. (1988). <i>Diet and habitat selection of an erupting wood bison population</i> (Doctoral dissertation, University of British Columbia).	2			BSG
Larter, N. C., & Gates, C. C. (1990). Home ranges of wood bison in an expanding population. <i>Journal of Mammalogy</i> , 71(4), 604-607. https://doi.org/10.2307/1381800			4	BSG
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Larter, N. C., Sinclair, A. R. E., Ellsworth, T., Nishi, J., & Gates, C. C. (2000, November). Dynamics of reintroduction in an indigenous large ungulate: the wood bison of northern Canada. In <i>Animal Conservation forum</i> (Vol. 3, No. 4, pp. 299-309). Cambridge University Press. https://doi.org/10.1111/j.1469-1795.2000.tb00115.x	1			DB
Larter, N. C., Nishi, J. S., Ellsworth, T., Johnson, D., More, G., & Allaire, D. G. (2003). Observations of wood bison swimming across the Liard River, Northwest Territories, Canada. <i>Arctic</i> , 408-412. https://www.jstor.org/stable/40513079	1			BSG
Larter, N. C., & Allaire, D. G. (2007). <i>History and current status of the Nahanni wood bison population</i> . Yellowknife, Northwest Territories, Canada: Department of Environment and Natural Resources, Government of the Northwest Territories.	1			DB
Laskin, D. N., Watt, D., Whittington, J., & Heuer, K. (2020). Designing a fence that enables free passage of wildlife while containing reintroduced bison: a multispecies evaluation. <i>Wildlife Biology</i> , 2020(4), 1-14. https://doi.org/10.2981/wlb.00751			1	DB
Lott, D. F. (1981). Sexual behavior and intersexual strategies in American bison. <i>Zeitschrift für Tierpsychologie</i> , 56(2), 97-114. https://doi.org/10.1111/j.1439-0310.1981.tb01289.x	1	1		BSG
Lott, D. F., & Minta, S. C. (1983). Random individual association and social group instability in American bison (<i>Bison bison</i>). <i>Zeitschrift für Tierpsychologie</i> , 61(2), 153-172. https://doi.org/10.1111/j.1439-0310.1983.tb01335.x			1	BSG
Lott, D. F., & Galland, J. C. (1987). Body mass as a factor influencing dominance status in American bison cows. <i>Journal of Mammalogy</i> , 68(3), 683-685. https://doi.org/10.2307/1381605	1			BSG
MacNulty, D. R., Mech, L. D., & Smith, D. W. (2007). A proposed ethogram of large-carnivore predatory behavior, exemplified by the	1			BSG

Literature Record	# DP			Origin
	S	T	ST	
wolf. <i>Journal of Mammalogy</i> , 88(3), 595-605. https://doi.org/10.1644/06-MAMM-A-119R1.1				
Maher, C. R., & Byers, J. A. (1987). Age-related changes in reproductive effort of male bison. <i>Behavioral Ecology and Sociobiology</i> , 21, 91-96. https://doi.org/10.1007/PL00020232			1	BSG
Martin, J. M., Mead, J. I., & Barboza, P. S. (2018). Bison body size and climate change. <i>Ecology and Evolution</i> , 8(9), 4564-4574. https://doi.org/10.1002/ece3.4019		1		DB
Matthews, S. B. (1991). An assessment of bison habitat in the Mills/Mink Lakes area, Northwest Territories, using LANDSAT thematic mapper data. <i>Arctic</i> , 75-80. https://www.jstor.org/stable/40510984			1	BSG
McHugh, T. (1958). Social behavior of the American buffalo (Bison bison bison). <i>Zoologica</i> , 43, 1-40.		1		BSG
McHugh, T. (1979). <i>The time of the buffalo</i> . U of Nebraska Press.		2	3	BSG
McMillan, B. R. (1999). <i>Bison wallowing and its influence on the soil environment and vegetation characteristics in tallgrass prairie</i> . Kansas State University.			1	BSG
McMillan, B. R., Pfeiffer, K. A., & Kaufman, D. W. (2011). Vegetation responses to an animal-generated disturbance (bison wallows) in tallgrass prairie. <i>The American Midland Naturalist</i> , 165(1), 60-73. https://doi.org/10.1674/0003-0031-165.1.60			2	DB
McMillan, N. A., Kunkel, K. E., Hagan, D. L., & Jachowski, D. S. (2019). Plant community responses to bison reintroduction on the Northern Great Plains, United States: a test of the keystone species concept. <i>Restoration Ecology</i> , 27(2), 379-388. https://doi.org/10.1111/rec.12856			1	DB
McMillan, N. A., Fuhlendorf, S. D., Luttbeg, B., Goodman, L. E., Davis, C. A., Allred, B. W., & Hamilton, R. G. (2021). Are bison movements dependent on season and time of day? Investigating movement across two complex grasslands. <i>Ecosphere</i> , 12(1), e03317. https://doi.org/10.1002/ecs2.3317			2	DB
Meagher, M. (1986). Bison bison. <i>Mammalian species</i> , (266), 1-8.	3	1	3	BSG
Meagher, M. (1989). Range expansion by bison of Yellowstone National Park. <i>Journal of Mammalogy</i> , 70(3), 670-675. https://doi.org/10.2307/1381449		24	1	BSG
Melton, D. A., Larter, N. C., Gates, C. C., & Virgl, J. A. (1989). Bisoniana 102. The influence of rut and environmental factors on the behaviour of wood bison. <i>Acta Theriologica</i> , 34(12), 179-193.		1	1	BSG
Merkle, J. A., Cherry, S. G., & Fortin, D. (2015). Bison distribution under conflicting foraging strategies: site fidelity vs. energy maximization. <i>Ecology</i> , 96(7), 1793-1801. https://doi.org/10.1890/14-0805.1			2	DB

Literature Record	# DP			Origin
	S	T	ST	
Moodie, D. W., & Ray, A. J. (1976). Buffalo migrations in the Canadian plains. <i>Plains Anthropologist</i> , 21(71), 45-52. https://doi.org/10.1080/2052546.1976.11908778		1	1	BSG
Mooring, M., & Samuel, W. (1998). Tick defense strategies in bison: the role of grooming and hair coat. <i>Behaviour</i> , 135(6), 693-718.		1		BSG
Moran, M. D. (2014). Bison grazing increases arthropod abundance and diversity in a tallgrass prairie. <i>Environmental Entomology</i> , 43(5), 1174-1184. https://doi.org/10.1603/EN14013			1	DB
Nellis, M. D., & Briggs, J. M. (1997). Modeling spatial dimensions of bison preferences on the Konza Prairie landscape ecology: an overview. <i>Transactions of the Kansas Academy of Science (1903)</i> , 3-9. https://doi.org/10.2307/3628434	1			BSG
Nickell, Z., Varriano, S., Plemmons, E., & Moran, M. D. (2018). Ecosystem engineering by bison (<i>Bison bison</i>) wallowing increases arthropod community heterogeneity in space and time. <i>Ecosphere</i> , 9(9), e02436. https://doi.org/10.1002/ecs2.2436			2	DB
Obermueller, H., Wilkins, K., & Pejchar, L. (2021). Activity and Overlap Among Birds and Mammals Scavenging A Bison Carcass in Shortgrass Prairie. <i>Rangeland Ecology & Management</i> , 76, 69-73. https://doi.org/10.1016/j.rama.2021.02.002			1	DB
Olexa, E. M., & Gogan, P. J. (2007). Spatial population structure of Yellowstone bison. <i>The Journal of wildlife management</i> , 71(5), 1531-1538. https://doi.org/10.2193/2005-735		1		BSG
Oosenbrug, S. M., & Carbyn, L. N. (1982). Winter predation on bison and activity patterns of a wolf pack in Wood Buffalo National Park [Alberta, <i>Canis lupus</i> , <i>Bison bison</i>].			3	BSG
Painter, L. E., & Ripple, W. J. (2012). Effects of bison on willow and cottonwood in northern Yellowstone National Park. <i>Forest Ecology and Management</i> , 264, 150-158. https://doi.org/10.1016/j.foreco.2011.10.010			2	DB
Park, E. D. (1969). world of the bison.	3	1	8	BSG
Pfannenstiel, R. S., & Ruder, M. G. (2015). Colonization of bison (<i>Bison bison</i>) wallows in a tallgrass prairie by <i>Culicoides</i> spp (Diptera: Ceratopogonidae). <i>Journal of Vector Ecology</i> , 40(1), 187-190. https://doi.org/10.1111/jvec.12150			2	DB
Plumb, G. E., White, P. J., Coughenour, M. B., & Wallen, R. L. (2009). Carrying capacity, migration, and dispersal in Yellowstone bison. <i>Biological Conservation</i> , 142(11), 2377-2387. https://doi.org/10.1016/j.biocon.2009.05.019	2			BSG
Polley, H. W., & Wallace, L. L. (1986). The relationship of plant species heterogeneity to soil variation in buffalo wallows. <i>The Southwestern Naturalist</i> , 493-501. https://doi.org/10.2307/3671703	1			BSG
Post, D. M., Armbrust, T. S., Horne, E. A., & Goheen, J. R. (2001). Sexual segregation results in differences in content and quality of bison (<i>Bos bison</i>) diets. <i>Journal of Mammalogy</i> , 82(2), 407-413.		1		BSG

Literature Record	# DP			Origin
	S	T	ST	
Proffitt, K. M., White, P. J., & Garrott, R. A. (2010). Spatio-temporal overlap between Yellowstone bison and elk—implications of wolf restoration and other factors for brucellosis transmission risk. <i>Journal of Applied Ecology</i> , 47(2), 281-289.			1	DB
Ranglack, D. H., & Du Toit, J. T. (2015). Wild bison as ecological indicators of the effectiveness of management practices to increase forage quality on open rangeland. <i>Ecological Indicators</i> , 56, 145-151. https://doi.org/10.1016/j.ecolind.2015.04.009			2	DB
Ratajczak, Z., Collins, S. L., Blair, J. M., Koerner, S. E., Louthan, A. M., Smith, M. D., ... & Nippert, J. B. (2022). Reintroducing bison results in long-running and resilient increases in grassland diversity. <i>Proceedings of the National Academy of Sciences</i> , 119(36), e2210433119. https://doi.org/10.1073/pnas.2210433119			1	DB
Reed, D. H., O'Grady, J. J., Brook, B. W., Ballou, J. D., & Frankham, R. (2003). Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. <i>Biological conservation</i> , 113(1), 23-34. https://doi.org/10.1016/S0006-3207(02)00346-4		1		BSG
Reynolds, H. W., & Hawley, A. W. L. (1987). <i>Bison Ecology in relation to agricultural development in the Slave River Lowlands, NWT</i> . Canadian Wildlife Service.		12	4	BSG
Risch, A. C., Frossard, A., Schütz, M., Frey, B., Morris, A. W., & Bump, J. K. (2020). Effects of elk and bison carcasses on soil microbial communities and ecosystem functions in Yellowstone, USA. <i>Funct Ecol</i> , 34, 1933-1944.			1	DB
Ritson, R. J. (2019). <i>The Spatial Ecology of Bison (Bison Bison) in Multiple Conservation Herds across the American West</i> . University of Nebraska at Kearney.			15	DB
Roden, C., Hilde, V., & Guy, M. (2003). Reproductive success of bison bulls (Bison bison) in semi-natural conditions. <i>Animal Reproduction Science</i> , 79(1-2), 33-43. https://doi.org/10.1016/S0378-4320(03)00084-8			2	BSG
Roden, C., Vervaecke, H., & Van Elsacker, L. (2005). Dominance, age and weight in American bison males (Bison bison) during non-rut in semi-natural conditions. <i>Applied Animal Behaviour Science</i> , 92(1-2), 169-177. https://doi.org/10.1016/j.applanim.2004.10.005	1			BSG
Roden, C., Stevens, J. M., Vervaecke, H., & Van Elsacker, L. (2011). Reproductive effort of bison bulls (Bison bison) in semi-natural conditions. <i>Journal of ethology</i> , 29, 285-291. https://doi.org/10.1007/s10164-010-0256-7			2	DB
Rosas, C. A., Engle, D. M., Shaw, J. H., & Palmer, M. W. (2008). Seed dispersal by Bison bison in a tallgrass prairie. <i>Journal of Vegetation Science</i> , 19(6), 769-778. https://doi.org/10.3170/2008-8-18447			2	BSG
Rutberg, A. T. (1983). Factors influencing dominance status in American bison cows (Bison bison). <i>Zeitschrift für Tierpsychologie</i> , 63(2-3), 206-212. https://doi.org/10.1111/j.1439-0310.1983.tb00087.x	2		2	BSG

Literature Record	# DP			Origin
	S	T	ST	
Rutberg, A. T. (1984). Birth synchrony in American bison (Bison bison): response to predation or season?. <i>Journal of Mammalogy</i> , 65(3), 418-423. https://doi.org/10.2307/1381088			2	BSG
Schuler, K. L., Leslie Jr, D. M., Shaw, J. H., & Maichak, E. J. (2006). Temporal-spatial distribution of American bison (Bison bison) in a tallgrass prairie fire mosaic. <i>Journal of Mammalogy</i> , 87(3), 539-544. https://doi.org/10.1644/05-MAMM-A-115R2.1	2			BSG
Shaw, J. H., & Carter, T. S. (1990). Bison movements in relation to fire and seasonality. <i>Wildlife Society Bulletin (1973-2006)</i> , 18(4), 426-430. https://www.jstor.org/stable/3782742			2	BSG
Sheppard, A. H. C., Hecker, L. J., Edwards, M. A., & Nielsen, S. E. (2021). Determining the influence of snow and temperature on the movement rates of wood bison (Bison bison athabasca). <i>Canadian Journal of Zoology</i> , 99(6), 489-496. https://doi.org/10.1139/cjz-2020-0280		1	1	DB
Sigaud, M., Mason, T. H. E., Barnier, F., Cherry, S. G., & Fortin, D. (2020). Emerging conflict between conservation programmes: when a threatened vertebrate facilitates the dispersal of exotic species in a rare plant community. <i>Animal Conservation</i> , 23(6), 660-669. https://doi.org/10.1111/acv.12579	3		2	DB
Simon, R. N., Cherry, S. G., & Fortin, D. (2019). Complex tactics in a dynamic large herbivore-carnivore spatiotemporal game. <i>Oikos</i> , 128(9), 1318-1328. https://doi.org/10.1111/oik.06166	2			DB
Singer, F. J., & Norland, J. E. (1994). Niche relationships within a guild of ungulate species in Yellowstone National Park, Wyoming, following release from artificial controls. <i>Canadian Journal of Zoology</i> , 72(8), 1383-1394. https://doi.org/10.1139/z94-183			3	BSG
Smith, D. W., Mech, L. D., Meagher, M., Clark, W. E., Jaffe, R., Phillips, M. K., & Mack, J. A. (2000). Wolf-bison interactions in Yellowstone National Park. <i>Journal of Mammalogy</i> , 81(4), 1128-1135. <a href="https://doi.org/10.1644/1545-1542(2000)081<1128:WBIIYN>2.0.CO;2">https://doi.org/10.1644/1545-1542(2000)081<1128:WBIIYN>2.0.CO;2		1		BSG
Soper, J. D. (1941). History, range, and home life of the northern bison. <i>Ecological Monographs</i> , 11(4), 348-412. https://doi.org/10.2307/1943298			2	BSG
Taper, M. L., Meagher, M., & Jerde, C. L. (2000). The phenology of space: spatial aspects of bison density dependence in Yellowstone National Park. <i>taper</i> , 406, 994-2332.			11	BSG
Thomas, J. P., Larter, N. C., & Jung, T. S. (2022). Enabling safe passage: predicting river crossing hotspots for a threatened boreal ungulate susceptible to drowning. <i>Journal of Mammalogy</i> , 103(4), 932-944. https://doi.org/10.1093/jmammal/gyac011			1	DB
Towne, E. G. (2000). Prairie vegetation and soil nutrient responses to ungulate carcasses. <i>Oecologia</i> , 122, 232-239. https://doi.org/10.1007/PL00008851			1	BSG
Van Vuren, D. (1983). Group dynamics and summer home range of bison in southern Utah. <i>Journal of Mammalogy</i> , 64(2), 329-332. https://doi.org/10.2307/1380570			2	BSG

Literature Record	# DP			Origin
	S	T	ST	
Vervaecke, H., Roden, C., & de Vries, H. (2005). Dominance, fatness and fitness in female American bison, <i>Bison bison</i> . <i>Animal Behaviour</i> , 70(4), 763-770. https://doi.org/10.1016/j.anbehav.2004.12.018	1			BSG
Vinton, M. A., & Hartnett, D. C. (1992). Effects of bison grazing on <i>Andropogon gerardii</i> and <i>Panicum virgatum</i> in burned and unburned tallgrass prairie. <i>Oecologia</i> , 374-382. https://www.jstor.org/stable/4219987	1			BSG
Vinton, M. A., Hartnett, D. C., Finck, E. J., & Briggs, J. M. (1993). Interactive effects of fire, bison (<i>Bison bison</i>) grazing and plant community composition in tallgrass prairie. <i>American Midland Naturalist</i> , 10-18. https://doi.org/10.2307/2426430	8			BSG
Waggoner, V., & Hinkes, M. (1986). Summer and fall browse utilization by an Alaskan bison herd. <i>The Journal of wildlife management</i> , 322-324. https://doi.org/10.2307/3801921			1	BSG
Whicker, A. D., & Detling, J. K. (1988). Ecological consequences of prairie dog disturbances. <i>BioScience</i> , 38(11), 778-785.			1	BSG
White, P. J. (2022). <i>Bison and bighorns: assessing the potential impacts of reintroducing a large herbivore to a mountainous landscape</i> (Doctoral dissertation, University of British Columbia).			4	DB
Wilkins, K. D. (2018). <i>Ecological and Social Consequences of Collaborative Bison Reintroduction in the Western US</i> (Doctoral dissertation, Colorado State University).			1	DB
Winter, S. L., Allred, B. W., Hickman, K. R., & Fuhlendorf, S. D. (2015). Tallgrass prairie vegetation response to spring fires and bison grazing. <i>The Southwestern Naturalist</i> , 60(1), 30-35. https://doi.org/10.1894/FMO-19.1			2	DB
Wolff, J. O. (1998). Breeding strategies, mate choice, and reproductive success in American bison. <i>Oikos</i> , 529-544. https://doi.org/10.2307/3546680			1	BSG

APPENDIX B.

List of literature records excluded from analysis after systematic review. The exclusion tier (E.T.) is numbered to indicate if it was removed prior to screening (1), Did not provide extractable spatial/temporal data from title and abstract review (2), or the record did not provide spatial/temporal data in a way that was extractable for the purposes of this study after reasonable effort (3). This tiered exclusion is also visually depicted (Figure 1). The origin of the record whether from the BSG pre-compiled list (BSG) or database search (DB) is provided. There were 105 duplicates from the BSG list and 68 duplicates from the DB search.

Literature Record	E.T.	Origin
Agabriel, J., Bony, J., & Petit, M. (1996). Quantities ingested and growth of young breeding bison: effect of the season. In <i>Annales de zootechnie</i> (Vol. 45, No. 4, pp. 319-325).	2	BSG
Agabriel, J., Bony, J., & Micol, D. (1998). Le bison d'Amérique: élevage, production et qualité de la viande. <i>Institut National de la Recherche Agronomique, Paris, France.</i> [In French.].	2	BSG
Aguirre, A. A., & Starkey, E. E. (1994). Wildlife disease in US National Parks: historical and coevolutionary perspectives. <i>Conservation Biology</i> , 8(3), 654-661. https://doi.org/10.1046/j.1523-1739.1994.08030654.x	3	BSG
Aguirre, A. A., Starkey, E. E., & Hansen, D. E. (1995). Wildlife diseases in national park ecosystems. <i>Wildlife Society Bulletin</i> , 415-419. https://www.jstor.org/stable/3782948	3	BSG
Allen, D. L. (1967). <i>The life of prairies and plains</i> .	2	BSG
Allen, J. A. (1876). <i>The American bisons, living and extinct</i> (Vol. 10). University Press, Welch, Bigelow.	2	BSG
Allenbrand, J. (2020). <i>Grassland soil microbial community composition and distribution response to grazing by Bison bison</i> (Doctoral dissertation).	2	DB
Allendorf, F. W. (1986). Heterozygosity and fitness in natural populations of animals. <i>Conservation biology: the science of scarcity and diversity</i> , 57-76.	2	BSG
Allendorf, F. W., Leary, R. F., Spruell, P., & Wenburg, J. K. (2001). The problems with hybrids: setting conservation guidelines. <i>Trends in ecology & evolution</i> , 16(11), 613-622. https://doi.org/10.1016/S0169-5347(01)02290-X	2	BSG
Allendorf, F. W., Luikart, G., & Aitken, S. N. (2007). Conservation and the genetics of populations. <i>Mammalia</i> , 2007(2007), 189-197. https://doi.org/10.1515/MAMM.2007.038	2	BSG
Allred, B. W., Fuhlendorf, S. D., & Hamilton, R. G. (2011). The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle. <i>Ecosphere</i> , 2(3), 1-17. https://doi.org/10.1890/ES10-00152.1	3	DB
Anderson, E., & Stebbins Jr, G. L. (1954). Hybridization as an evolutionary stimulus. <i>Evolution</i> , 378-388. https://doi.org/10.2307/2405784	2	BSG
Aniskowicz, B.T. (1990). Life or death? A case for the defense of Wood Buffalo National Park's bison. <i>Nature Canada Spring</i> : 35-38.	2	BSG

Literature Record	E.T.	Origin
Animal Plant and Food Risk Analysis Network (APFRAN). (1999). Risk assessment on bovine brucellosis and tuberculosis in Wood Buffalo National Park and area. Canadian Food Inspection Agency, Ottawa, Ontario.	2	BSG
APHIS, USDA (2003). Brucellosis Eradication: Uniform methods and rules, effective October 1, 2003. APHIS 91-45-013. Washington, D.C.	2	BSG
APHIS, USDA (2005). Bovine Tuberculosis eradication: Uniform methods and rules, effective January 1, 2005. APHIS 91-45-011. Washington, D.C.	2	BSG
APHIS, USDA (2006). Epizootiology and ecology of anthrax. USDA, Washington, D.C.	2	BSG
APHIS, USDA. (2007). United States animal health report 2007. Agriculture Information Bulletin No. 803. USDA, Animal Plant Health Inspection Service, Washington D.C.	2	BSG
Armbruster, P., & Reed, D. H. (2005). Inbreeding depression in benign and stressful environments. <i>Heredity</i> , 95(3), 235-242. https://doi.org/10.1038/sj.hdy.6800721	2	BSG
Artz, J.A. (1996). Cultural response or geological process? A comment on Sheehan. <i>Plains Anthropologist</i> 41(158):383-393. https://doi.org/10.1080/2052546.1996.11931814	2	BSG
Aune, K. and Linfield, T. (2005). Proposal to conduct a bison quarantine feasibility study. Proceedings of the 109th Annual Meeting of the United States Animal Health Association. Hershey, Pennsylvania.	2	BSG
Auttelet, K. L. (2015). <i>Yellowstone Bison: Conserving an American Icon in Modern Society</i> . Yellowstone Association.	2	DB
Avise, J. C. (1990). Principles of genealogical concordance in species concepts and biological taxonomy. <i>Oxford Surv. Evol. Biol.</i> , 7, 45-67.	2	BSG
Babin, J. S., Fortin, D., Wilmschurst, J. F., & Fortin, M. E. (2011). Energy gains predict the distribution of plains bison across populations and ecosystems. <i>Ecology</i> , 92(1), 240-252. https://doi.org/10.1890/10-0252.1	2	DB
Baccus, R., Ryman, N., Smith, M. H., Reuterwall, C., & Cameron, D. (1983). Genetic variability and differentiation of large grazing mammals. <i>Journal of Mammalogy</i> , 64(1), 109-120. https://doi.org/10.2307/1380756	2	BSG
Bailey, J. A. (2016). Historic distribution and abundance of bison in the Rocky Mountains of the United States. <i>Intermountain Journal of Sciences</i> , 22(1-3 September), 36-53.	3	BSG
Baker, R. J. (2003). Revised checklist of North American mammals north of Mexico, 2003.	2	BSG
Ballou, J. D. (1995). Identifying genetically important individuals for management of genetic variation in pedigreed populations. <i>Population management for survival and recovery</i> .	2	BSG
Balloux, F., & Lugon-Moulin, N. (2002). The estimation of population differentiation with microsatellite markers. <i>Molecular ecology</i> , 11(2), 155-165. https://doi.org/10.1046/j.0962-1083.2001.01436.x	2	BSG

Literature Record	E.T.	Origin
Barmore, W. J. (2003). <i>Ecology of ungulates and their winter range in northern Yellowstone National Park: research and synthesis, 1962-1970</i> . Yellowstone Center for Resources.	2	BSG
Bates, B., & Hersey, K. (2016). Lessons learned from bison restoration efforts in Utah on western rangelands. <i>Rangelands</i> , 38(5), 256-265. https://doi.org/10.1016/j.rala.2016.08.010	2	DB
Baumeister, T. R., Bedunah, D., & Olson, G. (1996). Implications of bison-grassland coevolution for management of elk on Montana's Rocky Mountain Front. <i>UNITED STATES DEPARTMENT OF AGRICULTURE FOREST SERVICE GENERAL TECHNICAL REPORT INT</i> , 25-31.	3	BSG
Beintema, J. J., Fitch, W. M., & Carsana, A. (1986). Molecular evolution of pancreatic-type ribonucleases. <i>Molecular biology and evolution</i> , 3(3), 262-275. https://doi.org/10.1093/oxfordjournals.molbev.a040393	2	BSG
Beissinger, S. R., & Westphal, M. I. (1998). On the use of demographic models of population viability in endangered species management. <i>The Journal of wildlife management</i> , 821-841. https://doi.org/10.2307/3802534	2	BSG
Belanger, R. J., Edwards, M. A., Carbyn, L. N., & Nielsen, S. E. (2020). Evaluating trade-offs between forage, biting flies, and footing on habitat selection by wood bison (<i>Bison bison athabasca</i>). <i>Canadian Journal of Zoology</i> , 98(4), 254-261. https://doi.org/10.1139/cjz-2019-0201	3	DB
Bell, D. E. (1992). The 1992 convention on biological diversity: the continuing significance of US objections at the Earth Summit. <i>Geo. Wash. J. Int'l L. & Econ.</i> , 26, 479.	2	BSG
Benedict, B. M., & Barboza, P. S. (2022). Adverse effects of Diptera flies on northern ungulates: Rangifer, Alces, and Bison. <i>Mammal Review</i> , 52(3), 425-437. https://doi.org/10.1111/mam.12287	2	DB
Bengis, R. G., Kock, R. A., & Fischer, J. (2002). Infectious animal diseases: the wildlife/livestock interface. <i>Revue scientifique et technique (International Office of Epizootics)</i> , 21(1), 53-65. 10.20506/rst.21.1.1322	2	BSG
Bercovich, Z. (1998). Maintenance of Brucella abortus-free herds: a review with emphasis on the epidemiology and the problems in diagnosing brucellosis in areas of low prevalence. <i>Veterinary Quarterly</i> , 20(3), 81-88.	3	BSG
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Hilborn, R. A., and Mangel, M. (1997). The Ecological Detective: Confronting Models with Data. <i>Monogr. Popul. Biol</i> , 28.	2	BSG
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Hobbs, N. T. (1996). Modification of ecosystems by ungulates. <i>The Journal of Wildlife Management</i> , 695-713.	3	BSG
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Hosler, S. C., Jones, H. P., Nelson, M., & Barber, N. A. (2021). Management actions shape dung beetle community structure and functional traits in restored tallgrass prairie. <i>Ecological Entomology</i> , 46(2), 175-186. https://doi.org/10.1111/een.12950	2	DB
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Hudson, R. J. (1998). From prairie to paddock: Shifting paradigms in Bison management. In <i>International Symposium on Bison Ecology and Management in North America</i> . Montana State Univ., Bozeman, MT (pp. 223-237).	2	BSG
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Johnson, L. C., & Matchett, J. R. (2001). Fire and grazing regulate belowground processes in tallgrass prairie. <i>Ecology</i> , 82(12), 3377-3389. https://doi.org/10.1890/0012-9658(2001)082[3377:FAGRBP]2.0.CO;2	3	BSG
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Kay, C. E., & White, C. A. (2001). Reintroduction of bison into the Rocky Mountain parks of Canada: historical and archaeological evidence. <i>Crossing Boundaries in Park Management</i> , 143-151.	2	BSG
Keery, L. (2019). <i>Evaluating the potential impacts of reintroduced plains bison (Bison bison bison) contained in a soft-release pasture in Banff National Park</i> (Doctoral dissertation, Royal Roads University (Canada)).	2	DB
Keigley, R. B. (2019). The prehistoric bison of Yellowstone National Park. <i>Rangelands</i> , 41(2), 107-120. https://doi.org/10.1016/j.rala.2018.11.004	2	DB
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Wilson, G. A. (2001). Population genetic studies of wood and plains bison populations.	3	BSG
Wilson, G. A., & Strobeck, C. (1998). Microsatellite analysis of genetic variation in Wood and Plains bison. In <i>International Symposium on Bison Ecology and Management in North America. Montana State Univ., Bozeman, MT</i> (pp. 180-191).	3	BSG
Wilson, G. A., & Strobeck, C. (1999). Genetic variation within and relatedness among wood and plains bison populations. <i>Genome, 42</i> (3), 483-496.	3	BSG
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Wilson, G. A., Olson, W., & Strobeck, C. (2002). Reproductive success in wood bison (<i>Bison bison athabasca</i>) established using molecular techniques. <i>Canadian Journal of Zoology, 80</i> (9), 1537-1548.	3	BSG

Literature Record	E.T.	Origin
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Wilson, M. C. (1996). Late quaternary vertebrates and the opening of the ice-free corridor, with special reference to the genus bison. <i>Quaternary International</i> , 32, 97-105.	2	BSG
Wilson, M. C., Hills, L. V., & Shapiro, B. (2008). Late Pleistocene northward-dispersing <i>Bison antiquus</i> from the Bighill Creek Formation, Gallelli gravel pit, Alberta, Canada, and the fate of <i>Bison occidentalis</i> . <i>Canadian Journal of Earth Sciences</i> , 45(7), 827-859.	2	BSG
Wilson, M. M. (2022). Remnants, Outlaws, and Wallows: Practices for Understanding Bison.	2	DB
Wilson, M. C. (1969). Problems in the speciation of American fossil bison. <i>Post-Pleistocene man and his environment on the Northern Plains</i> . Edited by RG Forbis, LB Davis, OA Christensen, and G. Fedirchuk. University of Calgary, Archaeological Association, Calgary, Alta, 178-199.	2	BSG
Winston, J. E. (1999). <i>Describing species: practical taxonomic procedure for biologists</i> . Columbia University Press.	2	BSG
Wissler, C. (1927). <i>North American Indians of the plains</i> (No. 1). New York:[sn.	2	BSG
Wobeser, G. (2002). Disease management strategies for wildlife. <i>Revue scientifique et technique (International Office of Epizootics)</i> , 21(1), 159-178.	2	BSG
Wobeser, G. A. (2013). <i>Investigation and management of disease in wild animals</i> . Springer Science & Business Media.	2	BSG
Wolfe, M. L., & Kimball, J. F. (1989). Comparison of bison population estimates with a total count. <i>The Journal of Wildlife Management</i> , 593-596.	2	BSG
Wolfe, M. L., Shipka, M. P., & Kimball, J. F. (1999). Reproductive ecology of bison on Antelope Island, Utah. <i>The Great Basin Naturalist</i> , 105-111.	3	BSG
Wołoszyn-Gałęza, A., Perzanowski, K., Januszczak, M., & Pagacz, S. (2016, April). Habitat preferences of a European bison (<i>Bison bonasus</i>) population in the Carpathian Mountains. In <i>Annales Zoologici Fennici</i> (Vol. 53, No. 1–2, pp. 1-18). Finnish Zoological and Botanical Publishing Board.	1	DB
Woodroffe, R. (1999). Managing disease threats to wild mammals. <i>Animal conservation</i> , 2(3), 185-193.	2	BSG
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Literature Record	E.T.	Origin
Wydeven, A. P., & Dahlgren, R. B. (1985). Ungulate habitat relationships in Wind Cave National Park. <i>The Journal of wildlife management</i> , 805-813.	3	BSG
Wyman, M. T., Pinter-Wollman, N., & Mooring, M. S. (2021). Trade-offs between fighting and breeding: a social network analysis of bison male interactions. <i>Journal of Mammalogy</i> , 102(2), 504-519.	3	BSG
Ying, K. L., & Peden, D. G. (1977). Chromosomal homology of wood bison and plains bison. <i>Canadian Journal of Zoology</i> , 55(10), 1759-1762.	3	BSG
Yoakum, J. D. (2004). Relationships with other herbivores. <i>Pronghorn Ecology and Management</i> , 501-538.	2	BSG
Yorks, T. P., Capels, K. M., & Irby, L. R. (1997, June). Preparing for the future: projecting herd sizes, market potentials, and the most effective management pathways. In <i>International Symposium on Bison Ecology and Management in North America</i> (pp. 384-395).	2	BSG
Yu, S. W. (2021). <i>American Bison Impacts on Riparian and Wallow Vegetation Communities</i> (Doctoral dissertation, Clemson University).	2	DB
Zarnke, R. L. (1992). <i>Alaska wildlife serologic survey, 1975-1992</i> . Alaska Department of Fish and Game.	2	BSG
Zaugg, J. L. (1986). Experimental anaplasmosis in American bison: persistence of infections of <i>Anaplasma marginale</i> and non-susceptibility to <i>A. ovis</i> . <i>Journal of Wildlife Diseases</i> , 22(2), 169-172.	3	BSG
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Zedeño, M. N. (2017). Bison hunters and the Rocky Mountains: An evolving partnership. <i>Quaternary International</i> , 461, 80-101.	2	DB
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Zeigenfuss, L. C., & Schoenecker, K. A. (2021). Effects of elk and bison herbivory on narrowleaf cottonwood. <i>Western North American Naturalist</i> , 81(1), 97-112.	2	DB
Zielke, L., Wrage-Mönnig, N., & Müller, J. (2017). Seasonal preferences in diet selection of semi-free ranging European bison (<i>Bison bonasus</i>). <i>European Bison Conservation Newsletter</i> , 10, 61-70.	1	DB
Zielke, L., Wrage-Mönnig, N., & Müller, J. (2018). Development and assessment of a body condition score scheme for European bison (<i>Bison bonasus</i>). <i>Animals</i> , 8(10), 163.	1	DB

Literature Record	E.T.	Origin
Zielke, L., Wrage-Mönnig, N., Müller, J., & Neumann, C. (2019). Implications of spatial habitat diversity on diet selection of European Bison and Przewalski's Horses in a Rewilding Area. <i>Diversity</i> , 11(4), 63.	1	DB
Zoch, P. A., Bement, L. C., & Carter, B. J. (1999). <i>Bison hunting at Cooper site: Where lightning bolts drew thundering herds</i> . University of Oklahoma Press.	2	BSG
Zontek, K. (2007). <i>Buffalo nation: American Indian efforts to restore the bison</i> . University of Nebraska Press.	3	BSG

APPENDIX C.

Checklist for “The PRISMA 2020 statement: an updated guideline for reporting systematic reviews” (Page et al., 2020). Includes the section, item number, checklist item, and location where the item is reported. Some item numbers were beyond the reach of this study and are listed as “Not Applicable” in the designated location section.

Section and Topic	Item #	Checklist item	Location where item is reported
TITLE			
Title	1	Identify the report as a systematic review.	Page 14
ABSTRACT			
Abstract	2	See the PRISMA 2020 for Abstracts checklist.	Page v
INTRODUCTION			
Rationale	3	Describe the rationale for the review in the context of existing knowledge.	Page 15
Objectives	4	Provide an explicit statement of the objective(s) or question(s) the review addresses.	Page 17
METHODS			
Eligibility criteria	5	Specify the inclusion and exclusion criteria for the review and how studies were grouped for the syntheses.	Page 18/ Figure 1
Information sources	6	Specify all databases, registers, websites, organisations, reference lists and other sources searched or consulted to identify studies. Specify the date when each source was last searched or consulted.	Page 19
Search strategy	7	Present the full search strategies for all databases, registers and websites, including any filters and limits used.	Page 19
Selection process	8	Specify the methods used to decide whether a study met the inclusion criteria of the review, including how many reviewers screened each record and each report retrieved, whether they worked independently, and if applicable, details of automation tools used in the process.	Page 19/ Appendix A & B
Data collection process	9	Specify the methods used to collect data from reports, including how many reviewers collected data from each report, whether they worked independently, any processes for obtaining or confirming data from study investigators, and if applicable, details of automation tools used in the process.	Page 20
Data items	10a	List and define all outcomes for which data were sought. Specify whether all results that were compatible with each outcome domain in each study were sought (e.g. for all measures, time points, analyses), and if not, the methods used to decide which results to collect.	Not Applicable
	10b	List and define all other variables for which data were sought (e.g. participant and intervention characteristics,	Page 21

Section and Topic	Item #	Checklist item	Location where item is reported
		funding sources). Describe any assumptions made about any missing or unclear information.	
Study risk of bias assessment	11	Specify the methods used to assess risk of bias in the included studies, including details of the tool(s) used, how many reviewers assessed each study and whether they worked independently, and if applicable, details of automation tools used in the process.	Not Applicable
Effect measures	12	Specify for each outcome the effect measure(s) (e.g. risk ratio, mean difference) used in the synthesis or presentation of results.	Not Applicable
Synthesis methods	13a	Describe the processes used to decide which studies were eligible for each synthesis (e.g. tabulating the study intervention characteristics and comparing against the planned groups for each synthesis (item #5)).	Page 20 & 21
	13b	Describe any methods required to prepare the data for presentation or synthesis, such as handling of missing summary statistics, or data conversions.	Page 23
	13c	Describe any methods used to tabulate or visually display results of individual studies and syntheses.	Not Applicable
	13d	Describe any methods used to synthesize results and provide a rationale for the choice(s). If meta-analysis was performed, describe the model(s), method(s) to identify the presence and extent of statistical heterogeneity, and software package(s) used.	Page 22 & 23
	13e	Describe any methods used to explore possible causes of heterogeneity among study results (e.g. subgroup analysis, meta-regression).	Not Applicable
	13f	Describe any sensitivity analyses conducted to assess robustness of the synthesized results.	Not Applicable
Reporting bias assessment	14	Describe any methods used to assess risk of bias due to missing results in a synthesis (arising from reporting biases).	Not Applicable
Certainty assessment	15	Describe any methods used to assess certainty (or confidence) in the body of evidence for an outcome.	Page 22 & 23
RESULTS			
Study selection	16a	Describe the results of the search and selection process, from the number of records identified in the search to the number of studies included in the review, ideally using a flow diagram.	Page 23 & 24 / Figure 1
	16b	Cite studies that might appear to meet the inclusion criteria, but which were excluded, and explain why they were excluded.	Appendix B/ Figure 1

Section and Topic	Item #	Checklist item	Location where item is reported
Study characteristics	17	Cite each included study and present its characteristics.	Appendix A/ Figure 1
Risk of bias in studies	18	Present assessments of risk of bias for each included study.	Not Applicable
Results of individual studies	19	For all outcomes, present, for each study: (a) summary statistics for each group (where appropriate) and (b) an effect estimate and its precision (e.g. confidence/credible interval), ideally using structured tables or plots.	Not Applicable
Results of syntheses	20a	For each synthesis, briefly summarise the characteristics and risk of bias among contributing studies.	
	20b	Present results of all statistical syntheses conducted. If meta-analysis was done, present for each the summary estimate and its precision (e.g. confidence/credible interval) and measures of statistical heterogeneity. If comparing groups, describe the direction of the effect.	Page 25 & 26
	20c	Present results of all investigations of possible causes of heterogeneity among study results.	Not Applicable
	20d	Present results of all sensitivity analyses conducted to assess the robustness of the synthesized results.	Not Applicable
Reporting biases	21	Present assessments of risk of bias due to missing results (arising from reporting biases) for each synthesis assessed.	Not Applicable
Certainty of evidence	22	Present assessments of certainty (or confidence) in the body of evidence for each outcome assessed.	Page 25 & 26
DISCUSSION			
Discussion	23a	Provide a general interpretation of the results in the context of other evidence.	Page 26
	23b	Discuss any limitations of the evidence included in the review.	Page 27
	23c	Discuss any limitations of the review processes used.	Page 31 & 32
	23d	Discuss implications of the results for practice, policy, and future research.	Page 29 - 34
OTHER INFORMATION			
Registration and protocol	24a	Provide registration information for the review, including register name and registration number, or state that the review was not registered.	Not Applicable

Section and Topic	Item #	Checklist item	Location where item is reported
	24b	Indicate where the review protocol can be accessed, or state that a protocol was not prepared.	Not Applicable
	24c	Describe and explain any amendments to information provided at registration or in the protocol.	Not Applicable
Support	25	Describe sources of financial or non-financial support for the review, and the role of the funders or sponsors in the review.	Not Applicable
Competing interests	26	Declare any competing interests of review authors.	Not Applicable
Availability of data, code and other materials	27	Report which of the following are publicly available and where they can be found: template data collection forms; data extracted from included studies; data used for all analyses; analytic code; any other materials used in the review.	Not Applicable

From: Page MJ, McKenzie JE, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, et al. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. BMJ 2021;372:n71. doi: 10.1136/bmj.n71

For more information, visit: <http://www.prisma-statement.org/>

APPENDIX D.

Table containing identified key bison ecological components and some of their population and environmental associations

Ecological Components	Associations	References
Group size	habitat selection, predator interactions, movement frequency	Fortin et al., 2009; MacNulty et al., 2014; Van Vuren, 1979
Rut & Copulation tending	behavioral dynamics, sexual selection, spatial selection, soil compaction, temporal nutrient dump	Lott, 1981; Vervaecke & Schwarzenberger, 2006; Wyman et al., 2021
Parturition & birth synchrony	Predator mitigation, habitat selection, anthropogenic avoidance, environmental responses	Rutberg, 1984; Kaze et al., 2016; Gogan et al., 2013; Green & Rothstein, 1993
Hierarchical social dominance, social interaction, & intraspecific aggression	Group dynamics, herd demography, resource allocation, sexual selection, landscape use	Fortin et al., 2009; King et al., 2019; Green & Rothstein, 1993; Roden et al., 2005
Interspecific aggression & Flight	Landscape use, resource competition, predator avoidance, human-wildlife conflict	Simon et al., 2019; Ranglack et al., 2015; Fortin & Fortin, 2009;
Wallowing / Rubbing	Arthropod abundance and diversity, vegetative responses, amphibian utilization, forest encroachment maintenance, bird nests, water retention	Bailey, 2013; Bowyer et al., 1998, Nickell et al., Coppedge and Shaw, 1997;
Herbivory & Fire-based Herbivory	Grassland maintenance, heterogenous landscape use, grassland bird diversity, prairie dog habitat	Fagre et al., 2022; Fuhlendorf et al., 2009; Powell, 2006; Ratajczak et al., 2022;
Nutrient Distribution	Soil nutrient composition, vegetative responses, scavenger use of carcasses, disease mitigation	Risch et al., 2020; Szcodronski and Cross, 2021; Green, 1998
Movement within / between feeding patches	Patch-wide heterogeneity, soil microbial diversity, plant diversity, fire mitigation, nutrient cycling, plant dispersal	Geremia et al., 2019; Constible et al., 2005;
Movement within / between seasonal & within total ranges	Landscape heterogeneity, fire mitigation, nutrient cycling, plant dispersal, soil microbe diversity	Larter & Gates, 1994; Geremia et al., 2019;
Migration	Predator movement, landscape rest, nutrient distribution changes	Geremia et al., 2019;
Dispersal & range expansion	Landscape use, soil microbe diversity and expansion, density responses	Babin et al., 2011; Hawkins & Zeglin, 2022; Plumb et al., 2009; Meagher, 1989
Weather / Climate dependent movement	Habitat use and selection, bison-made trail-use in snow conditions, biodiversity in climate change, ecosystem responses	Sheppard et al., 2021; D'Aloia et al., 2019; McMillan et al., 2021, 2022;

Ecological Components	Associations	References
Population demography	Disease resilience, landscape use, dispersal effects	Hartway et al., 2020; Rosas et al., 2005
Gene flow / Introgression	Disease and climate change resilience, population sustainability	Halbert et al., 2012; Hartway et al., 2020; Giglio et al., 2018; Martin et al., 2018

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