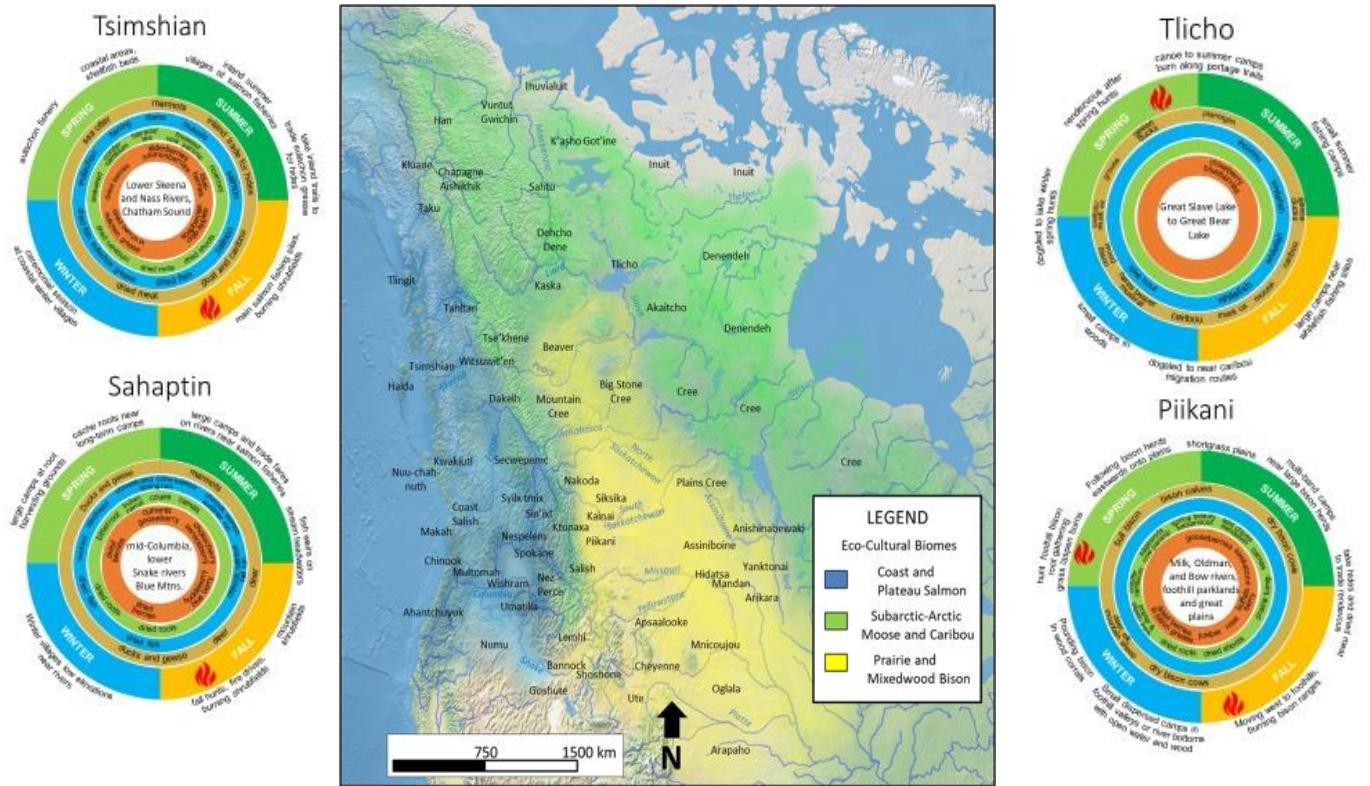


BIOMES TO ANTHROMES IN AMERICA'S NORTHWEST

Human's Keystone Ecological Role



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 Clifford A. White
 CW and Associates
 Canmore, Alberta
cliffawhite@gmail.com

ABSTRACT

Indigenous peoples hypothetically have long-influenced broad regional ecosystems through 1) niche construction by fire to create habitat for resources (plants, animals, and fish) and 2) optimal foraging that alters resource abundance, particularly for favored prey species. This hypothesis can be termed “habitat mediated optimal foraging” (HMOF). The northwest region (NW) of North America provides an excellent study area to evaluate changes in these potential human influences due to the relatively recent colonization by Eurasians. This study reviews indigenous people’s seasonal rounds for eco-cultural biomes and describes current ecoregion mapping. Databases of fire frequency studies and historical journal accounts compiled at the ecoregion scale are then used to provide evidence that humans, through hunting, gathering, and culturing, were the keystone species that structured the food webs of eco-cultural biomes. Recent global-scale human population and technological growth are causing a rapid transition of these long-term biomes to “anthromes”, a set of globally-standard land use types of various levels of urbanization, agriculture, and forestry. These altered human ecosystem management practices are resulting in major changes in fire regimes and species abundance. However, broad areas of the Pacific Northwest remain in relatively “natural” condition and may be managed for ecosystem conservation. Indigenous people’s potential long-term keystone role should be understood, and possibly maintained or restored to conserve these landscapes.

Acknowledgements:

Many thanks to Charles Kay, Ted Binnema and others who have sent me references to historical journals over the years. Marie-Pierre Rogeau, Mark Heathcott, Mark Hebblewhite and Jonathan Farr provided excellent comments on earlier drafts of this report. Val Geist was always a great supporter of this kind of interdisciplinary work, and I, like many, miss his scholarship and cheery encouragement.

Data Sources:

- Ecoregions visible online at: <https://ecoregions.appspot.com/>
- Wildlife and plant resources observed in historical journals currently at:
<https://lensoftimenorthwest.com/themes/lens-northwest-files/google-earth-map-journal-wildlife-observations/>
- After c. 2025, back-up digital databases will be archived with various global biodiversity data centers (hopefully) and at very least, at the Whyte Museum Archives, Banff, Alberta Clifford A. White fonds: <https://www.whYTE.org/digitalvault/categories/archives-library>

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1. INTRODUCTION

Humans have had the most widespread and diverse influence on Earth's species. We can alter the abundance and behavior of other biological beings in two basic ways. First, we can modify our environment to create niches by use of fire, aquaculture, horticulture, and agriculture. Secondly, as the planet's dominant omnivore, and with our ability to store resources, we can optimally forage a broad range of species in various locations and seasons to maintain evolutionary fitness. What makes both these attributes significant in humans is our ability to modify, and pass these behaviors through generations by social learning (Winterhalder and Smith 2000, Smith 2011, Berkes 2012). For most of the Holocene, human niche creation and optimal foraging generally occurred at a relatively local level. Hunter-gatherers exploited and consumed resources within the same or immediately adjacent ecoregions, and local feedback mechanisms within ecoregions would regulate human densities and behavioral patterns. However, the scale of these activities has now reached an intensity where our modern geological epoch can be termed the "Anthropocene". Global trade and technology allow humans to create large areas of specialized land use categories such as urbanization and croplands or "anthromes" (Ellis et al. 2010). Biodiversity and ecosystem processes within intensely developed land use categories may have more in common with similar land use types on other continents than within their local region.

However, here I consider that even past hunter-gatherer cultures could influence ecosystem development and maintenance across broad regions and long periods (Ellis et al. 2021). This paper combines an understanding of human niche construction and optimal foraging to consider long-term human influences on the northwest (NW) ecosystems of North America during the Holocene to Anthropocene transition. In this biologically productive region, terrain, biology, and humans all interact to create a diversity of ecosystems and cultures, that can be grouped into three regionally broad "cultural and natural areas" (Kroeber 1947), herein termed "eco-cultural biomes": the west coast-plateau salmon biome associated with rivers draining to the Pacific Ocean, the bison biome associated with the prairies and northern mixed wood of the Great Plains, and the boreal moose and caribou biomes associated with the northern taiga (Figure 1). These long-evolved ecosystems (Pielou 1991) were rapidly changed by direct and indirect influences from arrival in the northwest of the European industrial culture in ~1800 CE. This new human impact was profound. For example, on the Great Plains, an ecosystem of nomadic peoples supported by millions of migrating bison (Binnema 2004) collapsed within a century (Hornaday 1889, Daschuk 2019). The Columbia River, a vector for thousands of people harvesting salmon for over 10,000 years (Campbell and Butler 2010) was dammed into a nearly salmon-free series of hydropower reservoirs within two centuries of European contact (Goble 1999).

Fortunately, from research in the disciplines of archaeology, anthropology, traditional knowledge, and history, we have strong knowledge of NW ecosystem conditions before European contact and during the transitional period (Helm 1981, Binnema 2004, Deur and Turner 2005). Moreover, through the fields of ecology, wildlife ecology, botany, and others, we know many NW ecological food webs and processes,

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and the impacts of modern human industrial cultures on long-term ecosystems (Krebs 1994, Freedman et al. 2015). In addition, most of the NW lands, waters, and associated flora and fauna remain legally protected as a public resource--federal, provincial, state, and territorial laws maintain or restore long-term species abundance, ecological assemblages, and resource productivity for the public good (Geist and McTaggart-Cowan 1998, Hessburg and Agee 2003). Finally, there is increasing political and legislative support to at least understand and respect, and in some cases, even restore the effects of long-term indigenous lifeways on ecosystems (Parks Canada Agency 2000, Nabokov and Loendorf 2004, Lake et al. 2017, Hessami et al. 2021)

This paper evaluates the hypothesis that humans are a keystone species that structure long-term NW regional ecosystems. I first describe general human annual rounds of resource and fire use in each of the biomes. To evaluate spatial variability, I then describe indicator species for ecoregions (Wiken et al. 2011, Dinerstein et al. 2017) that constitute the biomes. On this basis, the paper then provides a generalized food web and potential human trophic interactions. Using niche construction and optimal foraging theory I then formulate some basic hypotheses on the strength of these interactions. I test these hypotheses with two types of data: 1) a regional synthesis of dendrochronological or charcoal studies of long-term fire frequency and seasonality, and 2) first person-journal observations for the period CE 1691 to 1928 that describe historical wildlife and vegetation resources used by humans. I use these datasets to compare historic and current fire frequency and indicator species abundance in 42 ecoregions grouped into the 3 “eco-cultural biomes”. This provides a basis to discuss how these burning and foraging activities could have influenced long-term ecological patterns and processes in these biomes and ecoregions, and how this has changed as the land use changes into modern anthromes (Ellis et al. 2010). These transitions across space and time then allow a preliminary evaluation of human’s potential keystone role in structuring NW biomes, and to evaluate some options for maintaining or restoring some of these eco-cultural practices.

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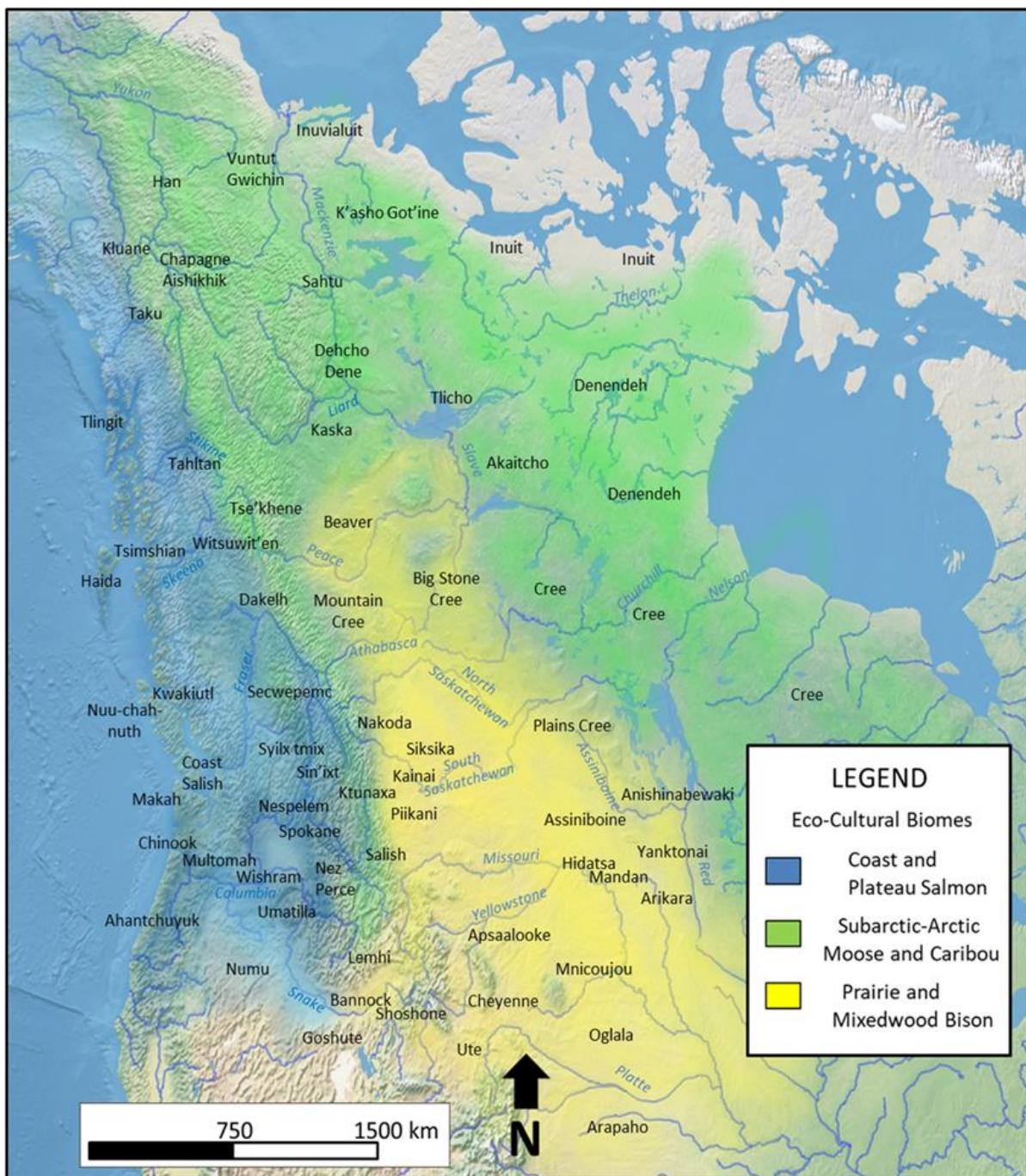


Figure 1: Eco-cultural biomes of the northwest region of North America (Kroeber 1947, Dickason and McNab 2009 p. 41) and general homelands for selected indigenous groups (<https://native-land.ca/>)

2. NORTHWEST STUDY AREA

The long-term ecology of North America's northwest can be described from the relatively coarse spatial patterns of eco-cultural biomes to increasingly finer-scale spatial descriptions of ecoregions, to the more detailed descriptions of the food web and trophic interactions of species within ecoregions. Scientific names for species described here are listed in Appendix A.

2.1 Northwest Eco-cultural Biomes

The NW region (Figure 1) centers on the western cordillera at the headwaters of watersheds of streams bound for the Pacific (e.g., Columbia, Fraser, Skeena, Stikine, Yukon), Atlantic (e.g., Saskatchewan, Missouri), and Arctic oceans (e.g., Athabasca, Peace, Liard). From a biophysical perspective, North American regions are mapped as ecoregions and biomes according to dominant climatic, terrain, and vegetation cover (Wiken et al. 2011, Dinerstein et al. 2017). In contrast, cultural research describes broad regions characterized by long-term human occupation patterns that often have similar boundaries to biophysically based biomes, but also characterize past human densities and traditional resource uses (Kroeber 1947, Dickason and McNab 2009). For indigenous homelands within "eco-cultural" biomes, Kassam et al. (2021) observe that "seasonal rounds are deliberative articulations of a community's sociocultural relations with their ecological system." In this study, I evaluate seasonal rounds (Figure 2) and ecoregions (Figure 3) grouped into three "eco-cultural" biomes (Figure 1).

2.1.1 Northwest Plateau-Coast "Salmon Biome"

Before depopulation by infectious diseases introduced by Europeans (Boyd 1999a), the Northwest Plateau and Coastal Salmon biome (Figure 1) was relatively densely populated (Ubelaker 1988, Chaput et al. 2015) with numerous indigenous groups (Suttles 1990, Prentiss and Kuijt 2004). The mainstays of the economy were Pacific herring and several salmon and trout species (McKechnie and Moss 2016). Annual surges of salmon migrating from the Pacific Ocean up streams such as the Columbia, Fraser, and Skeena into the adjacent plateau and mountains were an important source of nutrients not just for people (Campbell and Butler 2010), but for food webs including grizzly bears and many other species (Schindler et al. 2003). Humans also cultured, hunted, and gathered numerous other biotic resources (Ames 2005, Lepofsky et al. 2005, Turner and Peacock 2005). Examples of seasonal rounds (Figures 2a,b) from indigenous knowledge and historical observations show that people's activities centered on rivers and coasts, but they also spent substantial periods in uplands. Sophisticated means to process and store foods were developed to tide people through times of scarcity, and surpluses fueled trade networks across the biome such as the "grease trails" used to move eulachon fat into the interior valleys (Marsden and Galois 1995, Patton et al. 2019). Where resources were super-abundant, such as at major salmon fisheries along rivers, annual congregations or "trade fairs" occurred to expedite trade (Hajda and Sobel 2013). Locations for these large summer trading meetings include the Dalles on the lower Columbia River (Hunn and Selam 1990), Kettle Falls on the mid-Columbia, and the Pavilion and Bridge rivers area on the Fraser (Prentiss and Kuijt 2014).

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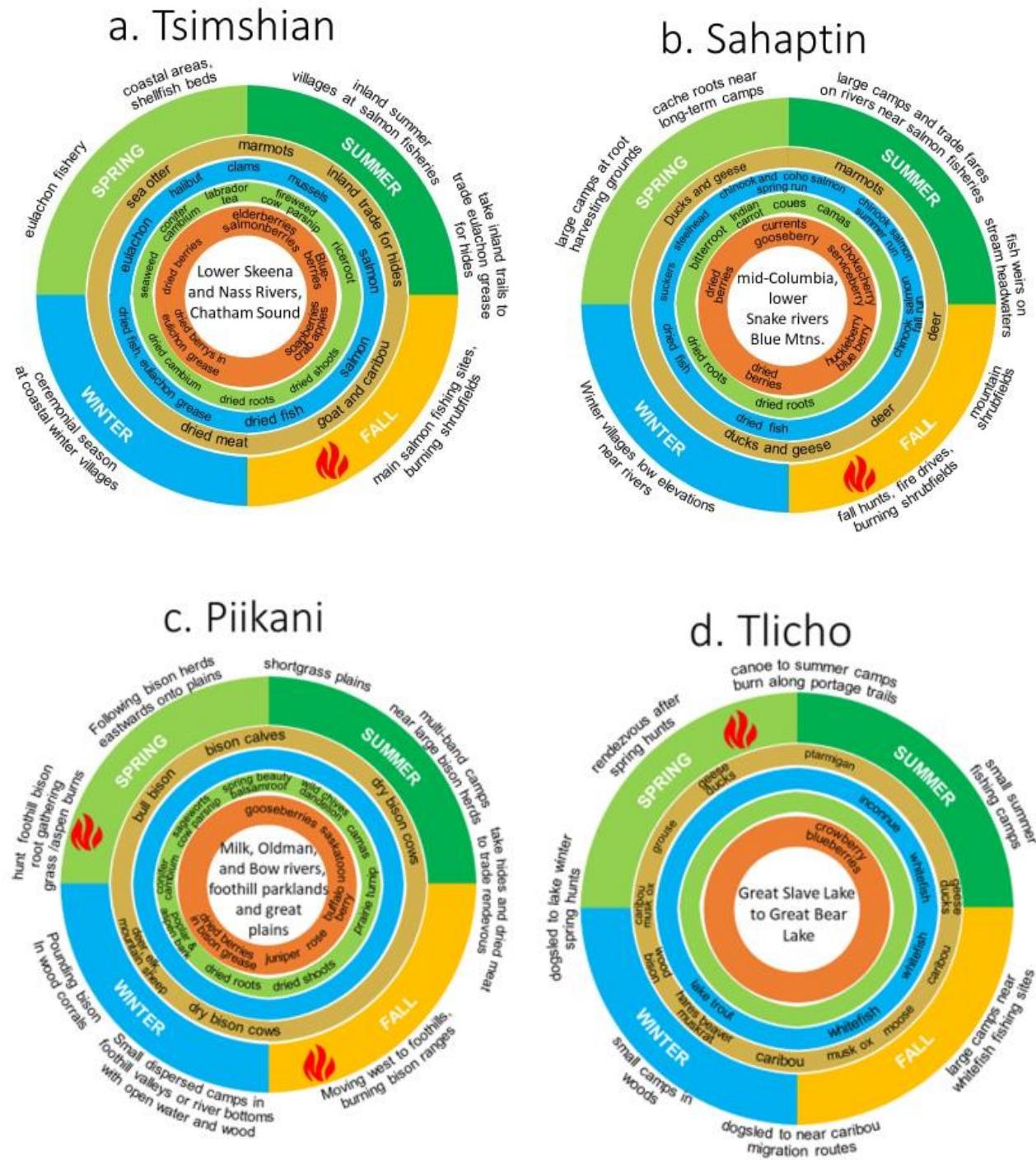


Figure 2. Examples of seasonal rounds showing periods of resource and fire use based upon indigenous knowledge and other research for: a. Tsimshian (Gottesfeld 1994, Marsden and Galois 1995, Galois 1998, Burton 2012, Patton et al. 2019); b. Sahaptin (Hunn and Selam 1990); c. Piikani (Peacock 1993, Reeves 2003, Brink 2008, Zedeño 2017, Roos et al. 2018), and d. Tlicho (Wheeler 1914, Helm 1981, 2004). Red flames indicate described periods of traditional fire use.

The use of fire by indigenous peoples of the northwest salmon biome is well-documented (Agee 1996, Boyd 1999b, Hessburg and Agee 2003). In mid-elevation forests, both the Tsimshian and the Sahaptin burned shrub fields to maintain berry production (Figure 2a, b). Burning typically occurred in the fall, when grasses and shrubs were cured (Hunn and Selam 1990 pp. 130–132, Gottesfeld 1994) before moving to winter villages. Other plant communities maintained by routine fall burning included camas fields, bunchgrass prairies, oak and ash savannahs, and beargrass patches (Beckwith 2004, Storm and Shebitz 2006, Pellatt and Gedalof 2014).

2.1.2 Western Subarctic “Moose and Caribou Biome”

The eco-cultural biome of boreal forest or taiga graduating into arctic tundra (Dickason and McNab 2009) is a vast area of historically low human density (Ubelaker 1988, Chaput et al. 2015), but still fully occupied by indigenous groups including the Cree, Chipewyan, Beaver, Dene, and Kaska (Figure 1). The ability of humans to survive the rigors of northern living is remarkable—the eco-cultural outcome of over 50,000 years of developing traditional technologies for clothing, shelter, and hunting, first in Eurasia and then in North America (Hoffecker 2005). The seasonal round of indigenous groups often included moving to locations to procure fish and plants (Figure 2d). Fish (whitefish, inconnu, lake trout) appear to have been frequently important across the subarctic and were harvested in all seasons. For example, along the Mackenzie River, whitefish were particularly important in late fall or winter when easily stored by freezing (Helm 2004). In spring and fall, migrating waterfowl provided significant fall. Similar to other subsistence cultures, numerous plant species provided nutrition, shelter, and medicinal needs (Marles et al. 2012). Human survival across the western subarctic is partially dependent on moose (Smith 1981) and caribou (Gordon 2003, 2005). The Sahtu recognize three ecotypes of caribou—barren-ground, woodland, and mountain (Polfus et al. 2016). Caribou and moose have varied strategies to co-exist with humans. Barren-ground caribou form large herds each spring as they migrate northwards onto the tundra where they are distant from most humans and other predators because firewood and other resources are scarce (Gordon 2005). In the mountains and boreal forest, moose and woodland caribou often had very low densities and were highly wary of humans. It took outstanding hunting skills for a historic hunter to locate and kill a moose (Thompson 2009 pp. 109–111), and scattered herds of caribou in the mountains and forests make periodic and difficult-to-predict movements (Polfus et al. 2016).

In northern mixed-woods and forests, dry and cured herbaceous vegetation is highly flammable immediately after snow-melt. The “Indian fires of spring” (Figure 2c) were lit to reduce subsequent wildfire danger around camps, clear travel routes, and maintain plant and wildlife habitats (Lewis 1980, Lewis and Ferguson 1988). The different habitats utilized by moose and caribou are well-understood. For example, while traveling with the Tlicho, Wheeler (1914) observed frequent spring burning along travel routes and as a result, the “old hunters speak of the moose range as expanding, of the caribou range as contracting.”

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2.1.3 Prairie, Mixed-wood, and Foothills “Bison Biome”

The great plains of North America stretch from Texas to Great Bear Lake (Figure 1). Vegetation ranges from dry short-grass prairies in the south to mixed-wood boreal forests in the north (Wiken et al. 2011). Bison is the biome’s characteristic species (Geist 1991, 1996). In the pre-industrial period, the plains ecotype numbered millions in the grasslands, and the woods type occurred in lower densities in northern woodlands (Allen 1876, Roe 1972, Gates et al. 2011). On the prairies, numerous indigenous cultures depended on bison including the Sioux, Blackfoot, Cheyenne, and Assiniboine to obtain a wide range of products including food, clothing, and shelter (DeMallie 2001, Calloway 2003). Plains indigenous people were highly mobile, and densities were moderately low (Kroeber 1947, Chaput et al. 2015). The complex inter-relationship between annual bison and human movements and habitat use on the plains is summarized by numerous authors (Moodie and Ray 1976, Epp 1988, 2004, Morgan 2020). Humans made long seasonal rounds (Figure 2d) out onto the plains in summer following the bison herds, but at the approach of winter, people left the open ground and made long-term encampments in woodlands or mountain foothills that provided wood for heat, a wider range of resources, and shelter from storms (Reeves 2003, Zedeño 2017). Numerous plant species were utilized in season across this broad range of habitats (Peacock 1993). In the range of the northern wood bison, humans exploited a broader range of resources (Figure 2c) including moose, elk, and fish (Burley et al. 1996), but made special trips to hunt bison (Helm 2004).

Human-caused fires have been extensively documented on the prairies (Nelson and England 1971, Moore 1972, Roos et al. 2018). People could ignite fires by mid-late summer once the grasses cured, throughout the winter in snow-free areas, and the spring until green herbaceous plants emerged (Moore 1972, Fidler 1991, Pyne 2007). Humans drove bison with fire during hunts, but more importantly, depending on the time of year, people lit fires to divert herd movements, or to stimulate new growth plant shoots to attract bison and other herbivores (Roe 1972 pp. 633–35, Allred et al. 2011). Morgan (2020) provides evidence that indigenous cultures from the drier areas of the Great Plains, such as the Blackfoot Nations and Gros Ventre, generally avoided killing beaver. These people recognized the role of the beaver in ponding water and maintaining riparian zones that provided numerous resources for people (e.g., habitat for many plant and animal species, fuel wood, shelter).

2.2 Ecoregions

Ecoregions are mapped at a finer spatial scale than biomes, providing moderately detailed landscape-level integrations of climate, terrain, and vegetation. Figure 3 shows ecoregions mapped for the northwest study area (Wiken et al. 2011, Dinerstein et al. 2017). Table 1 provides further information on select indicator communities and species for ecoregions evaluated in this study, grouped by eco-cultural biomes.



Figure 3. Northwest ecoregions map from Wiken et al. (2011). Ecoregions are coded to Table 1.

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Table 1: Pacific Northwest ecoregions evaluated in this study(Wiken et al. 2011, Dinerstein et al. 2017) grouped by eco-cultural biomes, with selected indicator species, and number of days (n) from historic journals with information on the abundance of wildlife, plant, or fish resources.

Biome	Code	Ecoregion	Select Indicator Communities and Species	n
Plateau-Coastal Salmon	6.2.1	Skeena-Omineca-Rocky Mtns.	aspen, lodgepole pine, spruce, salmon, moose, caribou, bear	201
	6.2.2	Chilcotin Ranges/Fraser Plateau	bunchgrasses, aspen, pine, spruce, salmon, deer, sheep	37
	6.2.3	Columbia Mtns/Northern Rockies	white pine, hemlock, cedar, fir, salmon, bear, caribou, elk, moose, goat	431
	6.2.7	Cascades (includes N. Cascades 6.2.5)	douglas-fir, hemlock, cedar, salmon, deer, elk	48
	6.2.8	Eastern Cascades and Foothills	sagebrush, ponderosa pine, salmon, deer, black bear	58
	6.2.9	Blue Mountains	wheatgrass, sagebrush, ponderosa pine, salmon, deer, elk	182
	6.2.11	Klamath Mountains	firs (douglas, white, oaks, pines (Jeffrey, ponderosa), salmon, deer, elk	61
	6.2.15	Idaho Batholith	firs (grand, douglas), pines (ponderosa, white), salmon, deer, black bear	128
	7.1.4	Pacific Coastal Mountains	tundra, hemlock (mtn, western), sitka spruce, otter, salmon, goat, bear	21
	7.1.5	West Coast Hemlock-Spruce	hemlock, red cedar, sitka spruce, Douglas fir, salmon, otter, shellfish, elk	193
	7.1.6	Pacific and Nass Ranges	hemlock, red cedar, douglas fir, salmon, eulachon, herring, deer	98
	7.1.7	Strait of Georgia/Puget Lowland	camas, oak, douglas fir, salmon, herring, black-tailed deer, elk, black bear	106
	7.1.8	Coast Range	sitka spruce, redwood, douglas fir, salmon, deer, elk	141
	7.1.9	Willamette Valley	oak savanna, douglas fir, salmon, black-tail deer	102
	10.1.1	Thompson-Okanogan Plateau	grasslands, douglas-fir, lodgepole pine, salmon, deer, bighorn sheep	47
	10.1.2	Columbia Plateau	grasslands, sagebrush, salmon, mule-deer, pronghorn	301
	10.1.3	Northern Basin and Range	grasslands, sagebrush, mule deer, pronghorn, coyotes	254
	10.1.8	Snake River Plain	dry grassland, sagebrush, salmon, mule deer, bison, bighorn sheep,	642
Subarctic-Arctic Moose-Caribou	2.1.5	Foxe Uplands	discontinuous tundra, sedges, caribou, muskox, polar bears, seals	23
	2.1.9	Banks Island and Amundsen Lowlands	moss, mixed low herbs, shrubs, caribou, muskox, polar bears, seals	38
	2.2.1	Arctic Coastal Plain	shrubby tundra, caribou, arctic fox, wolf, brown bear,	34
	2.2.2	Arctic Foothills	shrubby tundra, sedge tussocks, caribou, musk ox, wolf, brown bear	31
	2.3.1	Brooks Range Tundra	tundra, open woodlands, caribou, moose, Dall's sheep, caribou, grizzly	14
	2.4.1	Amundsen Plains	rock, shrub tundra, stunted spruce, caribou, musk ox, moose, grizzly bear	395
	2.4.2	Aberdeen Plains	shrub tundra, whales, geese, caribou, moose, lynx, wolf, grizzly bear	113
	2.4.4	Queen Maude Gulf Chantrey Lowlands	shrub tundra, geese, caribou, musk ox, grizzly bear, walrus, seal, whales	57
	3.1.1	Alaska Interior Lowlands-Uplands	spruce, tamarack, tundra, salmon, caribou, moose, bears, wolf	56
	3.1.3	Yukon Flats	wetlands, spruce, aspen, birch, salmon, geese, moose, bear, lynx	25
	3.2.1	Ogilvie Mountains	open spruce, birch, moss-lichen, moose, caribou, Dall's sheep, grizzly bear	19
	3.2.2	Mackenzie and Selwyn Mtns	tundra, open spruce, barren talus, caribou, moose, sheep, grizzly, wolf	82
	3.2.3	Peel River and Mackenzie Plateaus	tundra, open spruce-tamarack, caribou, moose, grizzly-black bear, wolf	48
	3.3.1	Great Bear Plains	open spruce-tamarack, trout, caribou, moose, grizzly-black bear, wolf	189
	3.4.1	Kazan River-Selwyn Lake Uplands	tundra-forest transition, caribou, black bear, arctic fox, wolf	276
	3.4.5	Coppermine River/Tazin Uplands	tundra-forest transition, caribou, moose, grizzly and black bear, wolf	362
	5.1.1	Athabasca Plain-Churchill Upland	boreal forest, black spruce, jack pine, caribou, moose, black bear	203
	5.1.5	Hayes River Upland-Big Trout Lake	boreal forest, black spruce, jack pine, moose, caribou, lynx, black bear	33
	6.1.1	Interior Highlands-Klondike Plateau	tundra, dwarf shrubs, spruce, caribou, Dall sheep, moose, caribou	41
	6.1.4	St. Elias Mtns. (merged with 6.1.5)	ice, rock, tundra, white spruce, Dall sheep, grizzly, moose, caribou	0
	6.1.5	Watson Highlands	tundra, birch-willow shrublands, spruce, moose, caribou, Dall sheep	313
	6.1.6	Yukon-Stikine Highlands/Boreal Mtns	tundra, birch-willow, spruce-fir, moose, caribou, stone sheep, grizzly	155
Plains-Prairie-Mixed-wood Bison	3.3.2	Hay and Slave River Lowlands	aspen, poplar, spruce, jack pine, whitefish, geese, bison, moose, caribou	479
	5.4.1	Boreal Uplands/Peace Lowlands	mixed conifer-deciduous, moose, white-tailed deer, black bear, wolf, bison	593
	5.4.2	Clear Hills and W. Alberta Uplands	conifer and deciduous forest, moose, deer, elk, caribou, black bear, wolf	211
	5.4.3	Mid-Boreal Lowland and Interlake Plain	spruce, balsam fir, jack pine, white-tail deer, moose, black bear	181
	6.2.4	Canadian Rockies	aspen, lodgepole pine, spruce, deer, elk, sheep, goat, bison (eastside)	420
	6.2.6	Cypress Uplands (merged with 9.2.1)	wheatgrass, aspen, lodgepole pine, deer, elk, bison	5
	6.2.10	Middle Rockies	douglas-fir, lodgepole pine, aspen, grasslands, deer, elk, sheep, goat, bison	891
	6.2.13	Wasatch-Uinta Mountains	sagebrush, aspen, lodgepole pine, juniper-pinyon, black bear, elk	45
	6.2.14	Southern Rockies	sagebrush, aspen, pinyon-juniper, spruce-fir, mule deer, elk, sheep, bison	216
	9.2.1	Aspen Parkland/Glaciated Plains	aspen and oak groves, fescue grasslands, waterfowl, deer, bison, moose	579
	9.3.1	Northwestern Glaciated Plains	grama and wheat grass, white-tail deer, pronghorn, bison, wolf	402
	9.3.3	Northwestern Great Plains	grama, wheat and needle grass, sagebrush, pronghorn, bison, deer	401
	9.3.4	Nebraska Sandhills (merged with 9.4.1)	bluestem, sandreed, grama grasses, bison pronghorn, bison, wolf	2
	9.4.1	High Plains	grama, buffalo, wheat grass, bison, pronghorn, wolf	329
	9.4.2	Central Great Plains	bluestem, grama, buffalo grasses, bison, pronghorn, wolf	406
	10.1.4	Wyoming Basin	arid grassland, sagebrush, mule deer, pronghorn	338

2.3 Food Webs, Ecological Processes, and Keystone Species

Figure 4a is an ecological food web model (Krebs 1994 pp. 545–551, Memmott 2009, Thompson et al. 2012) for select northwest species identified in seasonal rounds (Figure 2), and ecoregion descriptions (Table 1), adapted from historical (Richardson 1829) and current (Laliberte and Ripple 2004, Vynne et al. 2022) species range descriptions, and studies of ecosystems such as west coast kelp beds (Estes and Duggins 1995, Szpak et al. 2012), salmon-bearing streams (Schindler et al. 2003, Campbell and Butler 2010), boreal forests (Krebs and Boonstra 2001, Neufeld et al. 2021), the Rocky Mountains (White et al. 1998, Hebblewhite et al. 2005, Wagner 2006, Ripple and Beschta 2012), and Great Plains grasslands (Fox et al. 2012, Duchardt et al. 2021). Most food web indicator species have relatively broad habitat requirements and can potentially exist in appropriate habitats in a range of ecoregions and biomes (Table 1). For regional analysis, it is the potentially broad distribution, variability in abundance, and interactions of these species that make them important food web indicators at a landscape level. In Figure 4a, these species are displayed across a gradient from the plateau-salmon biome on the left to the boreal-caribou-moose salmon biome in the center, to the plains biome on the right. For food web analysis species are grouped by trophic level from primary producers (plants), then on to herbivores (e.g., deer, elk, moose), to predators (sea otter, cougar, wolf), and upwards through the food chain to omnivores consuming both plant and animal matter (e.g., bears and humans).

To further conceptualize the potential central role of human influence and integrate seasonal round activities (Figure 2) within food webs, the next step is to specifically describe ecological processes linking humans to various species as done in Figure 4b. People could directly reduce wildlife numbers by hunting, fishing, or destructive means of gathering plants. Alternately, people could enhance species numbers or habitat (Smith 2011). For example, on the northwest coast, there is strong evidence that indigenous peoples transplanted fish (Haggan et al. 2006) or plants (Peacock and Turner 2000) into new or depleted locations, and enhanced habitat and populations by creating shellfish beds (Lepofsky et al. 2015), burning vegetation (Gottesfeld 1994), or limiting the take of resources such as rules at fishing sites (Johnsen 2009, Campbell and Butler 2010). This model recognizes that animal behavioral responses to humans may also be important. This is particularly important for animals that have a long evolutionary relationship with humans. These species have evolved ways to detect, learn, and react to human actions such as hunting or habitat change in ways that enhance survival (Lima 1998).

A food web approach is necessary to evaluate the hypothesis that humans could be a long-term keystone species in one or more northwest biomes. The term was coined by Paine (1969), and is defined by Krebs (1994 p. 554) as a food web where:

A role may be occupied by a single species, and the presence of that role may be critical to the community. Such important species are called keystone species because their activities determine community structure (Paine 1969). Keystone species are most easily identified by removal experiments.

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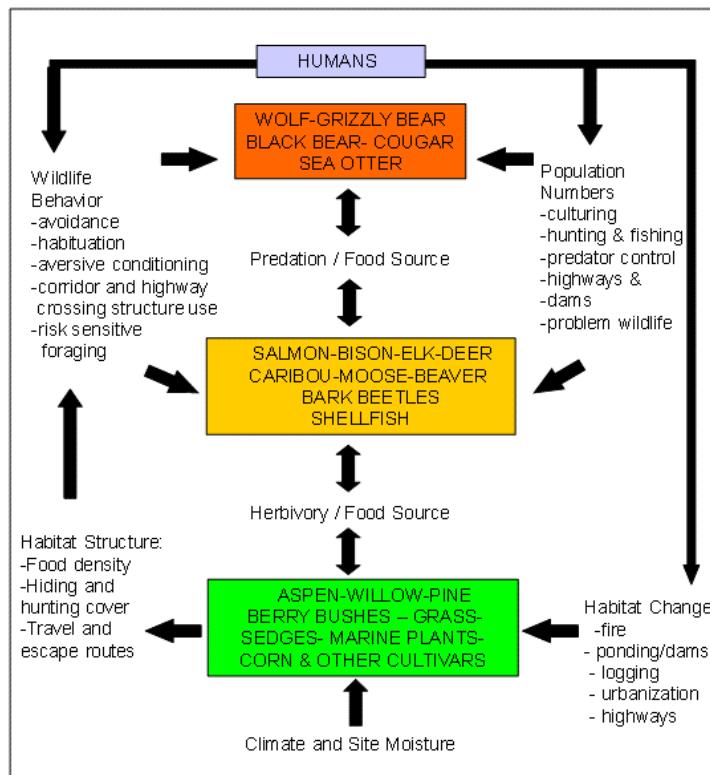
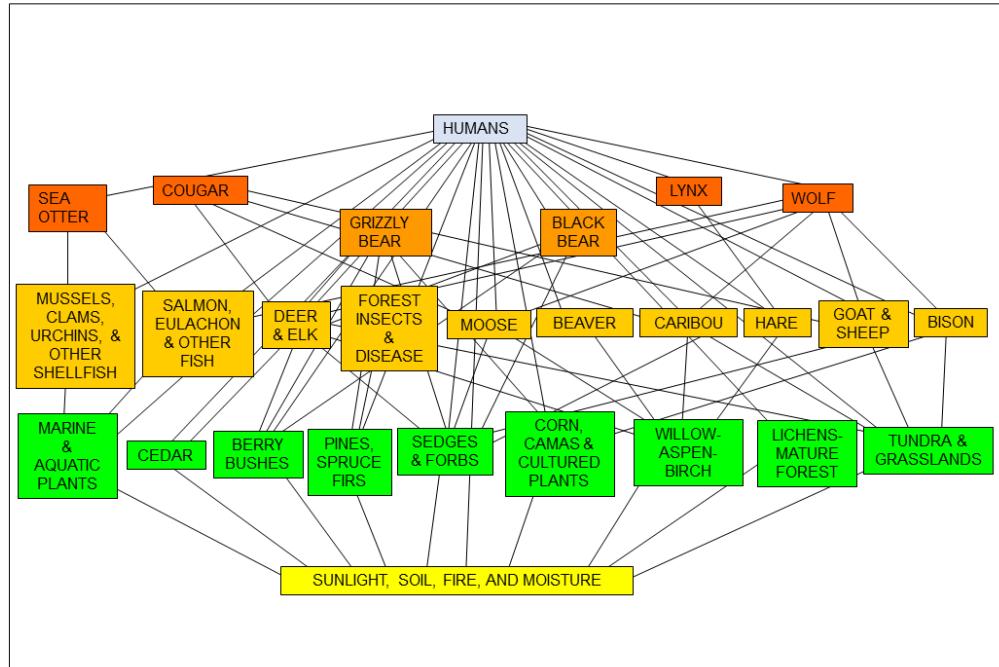


Figure 4: a. Food web model for select species in the Pacific Northwest ecoregions; b. Potential ecological interactions between species. See text for sources.

2.4 Modern-day Anthromes

Native land use practices were greatly altered after European contact by a host of causes including depopulation by disease, land dispossession, criminalization of various resources or fire use, and integration into globalized economic and food supply systems (Nabokov and Loendorf 2004, Binnema and Niemi 2006, Daschuk 2019, Carothers et al. 2021). Ellis et al. (2010) provide a global map for what they have termed as anthromes—a standard set of land uses that characterize human land use change over the last 300 years. Figure 5 shows anthromes mapped for northwestern North America as of 2000 CE. Contrasting this map with the eco-cultural biome's perspective (Figure 1), note first the disappearance of First Nation homelands and its replacement with the modern state, provincial and territorial boundaries of the United States and Canada. Secondly, anthromes on the “Used” end of the spectrum (settlements, villages, croplands) currently constitute only a small portion of the NW study area. Most of the area is mapped as relatively “Wild” (rangelands, semi-natural woodlands, and wildlands). However, for purposes of future discussion in this paper, this characterization does not necessarily mean that historic indigenous homelands (Figure 1), seasonal rounds (Figure 2), or natural ecoregions, food webs, and processes (Figures 3 and 4) still occur in many of these areas. For example, many resources used by humans in modern anthromes are provided by a globalized supply network. In contrast, in historic indigenous subsistence economies, resources were obtained from local ecoregions. As shown in Figure 4b, the human actions that influenced resources had short feedback loops to local people’s welfare (Berkes 2012, Polfus et al. 2016, Carothers et al. 2021, Hessami et al. 2021).

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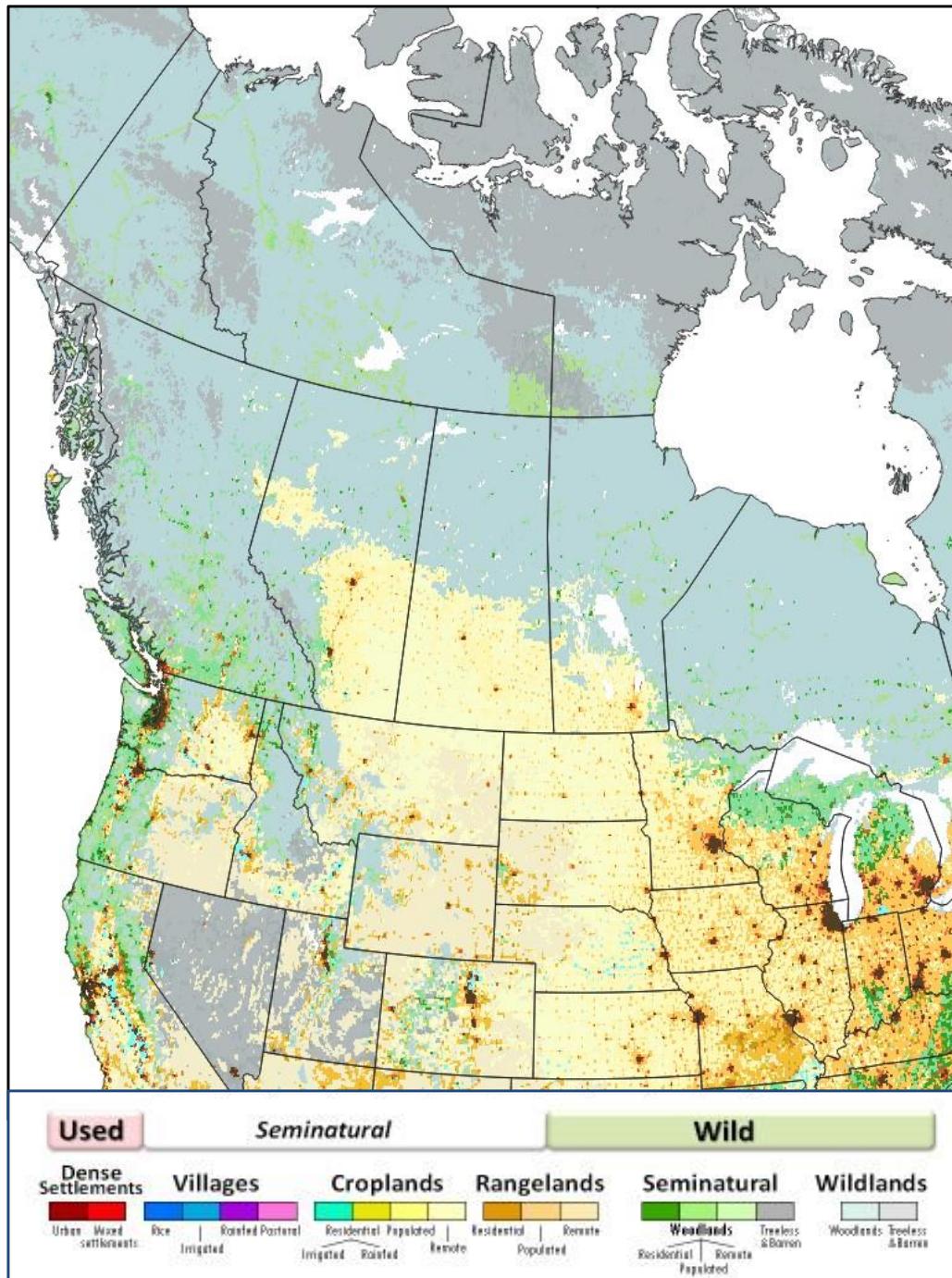


Figure 5: Anthromes mapped for northwest North America for the year CE 2000 mapped by Ellis et al. (2010) showing current state, provincial and territorial boundaries.

3. THEORETICAL CONSIDERATIONS

As adapted to humans, two partially complementary bodies of theory, niche construction (NCT), and optimal foraging (OFT) provide a conceptualization of human resource management and use (Zeder 2016, Ready and Price 2021). From the ecoregion-scale perspective of this paper, NCT helps explain more intensive human and resource interactions in localized core activity areas of seasonal rounds (Figure 2), with OFT having regional application moving from the core towards the edge of an indigenous group's territory.

3.1 Niche Construction Theory (NCT)

NCT posits that species that modify environmental conditions to be more favorable for survival will increase their fitness with evolutionary consequences for themselves and associated species. Classic examples are dam-building by beavers and the domestication of milk cows by humans (Odling-Smee et al. 2013). Theoretical conditions favoring localized niche construction or resource management by small-scale human societies include (Smith and Wishnie 2000, Berkes 2012 pp. 126–127): a) the resource is not super-abundant across the landscape; b) access to the resource is controlled, usually in a localized area; c) the resource rapidly or easily responds to cultural management; d) the resource has relatively low unit value (minimizing raiding or hoarding); and e) human group size is small stable allowing monitoring and adaptive management. Smith (2011) elaborates further that the basic tenet of NCT is that indigenous societies routinely modified their environment to increase the accessibility, abundance, and reliability of plant and animal resources by activities such as altering vegetation by burning, broadcast sowing annuals, transplanting, and in-place encouragement of perennials providing important fruits, shoots, or roots, and landscape-level creation of habitat by burning to increase animal prey. Although humans applied these techniques broadly across western North America, they are best documented in the salmon biome (Figure 1) where productive fisheries and vegetation supported dense human populations, long-term villages, and localized niche construction practices described above (Section 2.3).

NCT provides perspective on human's ancient and most powerful ecosystem management tool- the use of fire. Indigenous peoples universally lit fires for warmth, cooking, food preservation, hide treatment, signaling, wildlife and plant habitat, herding wildlife, clearing travel routes, warfare, and other uses (Lewis 1980, Pyne 1995, 2001, Stewart 2009, Huffman 2013). Although humans ignite fires at chosen times and locations, the further spread of flames is a physical process driven by terrain, fuel, and the vagaries of weather (Scott et al. 2014). Under certain conditions, any fire, independent of its ignition source, can spread to vast areas (Van Wagner 1985). However, in contrast to lightning ignitions in the Pacific Northwest that require summer convective conditions, human ignitions could occur during cooler and wetter conditions in the fall as soon as grasses senesce, during the winter where there is no snow cover, and during the spring before green-up. Thus, many areas could be burnt early in the northwest's annual cycle of spring biomass growth and late summer senescence. This burning reduces fuels before drier conditions that occur in summer the following year. A large-area "burn early-burn often" human-

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ignition pattern could yield several positive outcomes for indigenous NW cultures: 1) early, partial removal of biomass typically stimulates an earlier “green up” in the following late fall, spring, or early summer periods, stimulating roots and shoot production, and high-quality wildlife habitat, favoring resources all valuable to humans; 2) early partial removal of fuels during moister and cooler conditions protects habitats valuable to humans by reducing the possibility of intense fires in hot and dry periods that would kill many plants and require long recovery times; 3) the timing of burning can be altered to compensate for climatic and weather fluctuations. For example, people would simply burn later in a dry fall, and earlier during a dry spring; 4) light burning typically maintains a diverse range of tree ages and sizes. For example, older trees often persist in moist areas near streams. These trees eventually fall and their large woody debris provides habitat for numerous organisms including several species of salmon (Harmon et al. 2004), and 5) light burning typically removes some canopy trees, and favors herbaceous plants and shrubs that in turn are more apt to burn during low to moderately dry conditions. This positive feedback loop in which cultural fires create and maintain the herbaceous fine fuels that in turn facilitate future early senescence-period fire use, even during moderate fire danger, is theoretically a key ecological relationship between people, plants, weather, and fire frequency (Lewis 1980, Pyne 1995 pp. 132–134, White et al. 2011).

3.2 Optimal Foraging Theory (OFT)

Optimal foraging theory predicts that organisms develop behaviors to harvest resources with maximum efficiency to maintain high genetic fitness (Schoener 1971). As applied to humans, OFT provides a group of models evaluating resource selection, time allocation, and habitat patch choice. Model evaluation generally requires a goal (e.g., optimize acquisition rate), a currency (e.g., energy spent versus energy acquired), a set of constraints reflecting cultural and environmental conditions, and a range of feasible alternative actions (Winterhalder and Smith 2000). OFT models rank diet items in terms of their nutritional return in terms of procurement or culturing effort (Smith 1981). Researchers generally rate large mammals as the highest-ranked items, followed by smaller mammals, fish, and plant resources (Ames 2005, Tremayne and Winterhalder 2017).

As the earth’s top trophic level omnivore, humans have the highest capability to select, exploit, and culture a wide range of species. For the northwest, this is well-illustrated in seasonal rounds of indigenous peoples (Figure 2) and the regional food web (Figure 4). Moreover, humans also have the greatest capability to preserve and store resources during times of abundance (e.g., dried meat, fish, and plant products), and use them in later times (Kuijt 2009). Both these traits allow people to subsist on relatively low-ranked resources and then “prey-switch” to heavily exploit higher-ranked resources when intermittently available in the core of their territories or to use the preserved resources during travel to more distant areas to exploit these resources. Through specialization in processing some resources (e.g., hides, pemmican, and eulachon grease in the NW) humans can further extend the exploitation of resources by trade with adjacent indigenous groups. Trade networks between adjacent ecoregions with a different set of resources were a common characteristic of indigenous cultures (Wood 1972, Galm 1994) that have evolved into the globalized trade networks of today. As powerful consumers with a range of alternatives, people are therefore strong direct competitors with other

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predators, omnivores, and herbivores dependent on the same resources, and can even theoretically extirpate a competing consumer obligated to a depleted resource. When two potentially competitive species at the same trophic level are both used by humans (and/or other consumers), OFT predicts that the more numerous or resilient resource species will persist while its competitor's numbers may be strongly depressed—not through direct competition, but through “apparent competition” where humans (and other consumers), supported by a competing species or alternate resources, continue to consume the less resilient species (Holt 1977, DeCesare et al. 2010). Predator-prey theory predicts the extirpation of the less resilient species if it does not have refugia from this utilization (Sinclair et al. 2006 pp. 174–175), and negative population growth at low density could create a range limit for the species (Sexton et al. 2009). Intertribal buffer zones are potentially important refugia for highly ranked resources exploited by humans (Hickerson 1965, Kay 1994, 2007a, Martin and Szuter 1999). Bayham et al. (2017) integrate human foraging and group interaction theory to predict outcomes for prey in buffer zones with different scenarios of human cooperation and conflict.

3.3 Seasonal Rounds and Food Webs

For indigenous peoples in a central region of North America, Smith (2009) describes that long-term sustainability followed a general pattern of:

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

This may be the general pattern of resource exploitation and enhancement by small-scale human societies across a wide range of ecoregions and eco-cultural biomes in the pre-Anthrome period. Herein, this is termed “habitat mediated optimal foraging” (HMOF). For a given region, the long-term seasonal round (Figure 2) is potentially an optimal combination of activities such as hunting, gathering, and culturing that maintain sustainability (Kassam et al. 2021). Long-term stability in food web structure and productivity were achieved by using routine observations of local conditions as feedback to routinely modify these behaviors (e.g., travel patterns, time of burning, the intensity of hunting), and passing these adaptive behaviors through generations by social learning (Smith 2009, 2011, Berkes 2012 pp. 125–146). In regards to the role of keystone species described above (Paine 1969, Krebs 1994 p. 554), the transition from traditional seasonal rounds within the historical food webs of eco-cultural biomes to modern anthromes can be viewed as a massive “species removal experiment”—in this case removing the traditional role of indigenous humans—across the northwest. The ecological effects of local human seasonal rounds (Figure 2) have been largely removed and replaced by the anthromes (Figure 5) of a globalized system of exploitation and supply.

3.4 “HMOF” versus “DMAC”

One of the widest applications of ecological theory across much of the NW region are the current actions to recover endangered woodland and mountain caribou populations (Environment Canada 2011, 2014). The primary causal threat in caribou decline is hypothesized to be “disturbance-mediated apparent competition” (DMAC) where modern-day natural and anthropogenic disturbances have increased numbers of deciduous-browsing species such as moose, elk and deer. This in turn has increased the numbers of caribou’s predators (mainly wolves) and this increased predation is causing caribou’s demise across a broad regions of the southern NW (Seip 1992, Wittmer et al. 2007, 2013).

The DMAC hypothesis is relatively silent on the long-term role of humans in NW ecosystem (Figures 2, 4) and how this may have been altered in the ongoing biome to anthrome transition. The broader habitat mediated optimal foraging (HMOF) process described above considers that a wide diversity of plant, animal and fish species historically supported humans, other omnivores (Smith 2009, 2011). Moreover, indigenous peoples, through routine use of fire, or fisheries enhancement techniques could have maintained or restructured their habitat to maintain primary resources such as plants, fish and small mammals, but optimally foraged on larger animals whenever possible (Winterhalder 1981, Berkes 2012).

In essence, the HMOF hypothesis is just a broader temporal and ecological perspective of DMAC. Its testing requires data on longer term patterns of habitat disturbance, species abundance, and human land use patterns, and how these may have changed in the biome to anthrome transition.

4. METHODS

Three ecoregion-scale datasets are used to evaluate the effects of altered human burning and foraging activity during the biome to anthrome transition period (~1700 CE to present) in the northwest area.

4.1 Human Impacts on Northwest Ecoregions

Dinerstein et al. (2017) assessed current human impacts on the world's 846 terrestrial ecoregions, referencing Ellis et al.'s (2010) anthrome mapping system (Figure 5) for spatial analysis of types of human land use. The database from this study was used to map cumulative levels of current human impact for the 56 ecoregions in the NW study area. For each ecoregion, human impacts were rated at 4 levels: Very Low, Low, Moderate, and High.

4.2 Historic Wildland Fire Frequency

A simple model for interpreting the northwest historic fire regimes assumes that ignition and fuels were not limiting in most areas (Krawchuk et al. 2009). Lightning and human-caused fires were relatively common, and in past times, the resulting burn area was strongly related to annual weather fluctuating with decadal climate patterns (Kitzberger et al. 2007, Girardin 2007, Heyerdahl et al. 2008, Girardin et al. 2013). I extended a dataset of fire history studies for Canada (White et al. 2011) to include other northwest research compiled by Frost (1998), Hessberg and Agee (2003), Reilly et al. (2017), Hessberg et al. (2019) and the LANDFIRE mapping program (Rollins 2009) and categorized fire history studies by the general fire weather zones (Simard 1973) and ecoregion (Figure 3, Table 1). In most cases, fire history studies used dendrochronology to determine either the time-since-fire (in high-severity regimes) or fire intervals (in low-severity regimes). From this information, either the fire cycle (years required to burn an area equivalent to the area studied) or the mean fire interval (years) can be estimated. In landscapes with periodic random fire occurrence that is consistent over time and space, these estimates of fire frequency will be equivalent (Johnson and Wagner 1985). In cool-moist forests, fens, or grassland areas researchers may use soil charcoal evidence, for example, Hallett et al. (2003), to evaluate fire frequency. Where data is available, I describe fire frequency by historical period (years CE). For studies that describe fire cycles or intervals over multiple periods, the earliest period likely provides the best estimate of long-term conditions before alterations caused by contemporary cultural and land use change (White et al. 2011). Historic journal data (see below) provided further on the seasonality and cause of fires.

4.3 Historic Journal Observations

Historic humans, resources (wildlife, fish, fowl, and plant) and fire occurrence and abundance were indexed using the first-person, usually, daily, observations obtained from the journals of European mariners, fur traders, trappers, and government mappers for the period CE 1691-1860 in southern Canada and the United States, and CE 1770-1920 in northern Canada and eastern Alaska. Followed Kay's

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(2007a) method, three index measures quantify the observations of journalists for most resources. First, are resources seen. Where journalists reported old sign, that was assigned a value of one, fresh sign a two, and if they saw the resource, a three. Wildlife species categorized included bison, elk, white-tailed deer, mule deer, moose, caribou, pronghorn antelope, mountain sheep, grizzly bear, black bear, and grey wolf. The second index was quantity of resource obtained where either the exact number of animals, fish, or fowl killed is recorded, or where “some” or “a few” was recorded as 3, “several” as 7, and “many” as 10. The third index is herd size or resource abundance. Where journalists report sighting large numbers or abundant resources a value of 10 was assigned or 5 for moderate amounts.

Observations made by journalists at long-term camps, trading posts, or during periods of infrequent journal entries may be tallied by specified periods of 2 to 30 days with total kill numbers for the period. Resources seen, killed, and herd size/resource abundance were then added together for each species or resource type to obtain a measure of abundance. For humans, plants, cougars, and fire (larger than a campfire) observations, old sign was assigned a 1, fresh sign a 2, and if the journalists saw people, cougars, plants consumption, or fire spread, a 3, or a 10 if the group size was greater than ten, plant use was abundant, or fires covered large areas. The specific cause of the fire, if known, was recorded. Further, the quality of the journal observation was rated as “ND” or no data for day/period, or low, moderate, or high depending on the level of detail. The location was plotted for the nightly campsite, and again from low to high quality depending on the journalist’s description of the location. The databases for these observations and citations for journal sources (in a spreadsheet linked to Google Earth locations) are currently available at:

<https://lensoftimenorthwest.com/themes/lens-northwest-files/google-earth-map-journal-wildlife-observations/>

After c. 2025, back-up digital databases will be archived with various global biodiversity data centers (hopefully) and at very least, at the Whyte Museum Archives, Banff, Alberta: <https://www.whyte.org/digitalvault/categories/archives-library>

For the preliminary analysis described here, the index of historic resource and human abundance for observations are then averaged by resource (type or species) for ecoregions (Figure 3, Table 1). Where ecoregion boundaries extend beyond the study area, the mean resource index includes observations from across the ecoregion. Ecoregion means for select resources were then grouped by biomes, and graphically plotted by the value of the main biome resource (bison, caribou, fish) from highest to lowest on a gradient toward the nearest adjacent biome.

5. RESULTS AND DISCUSSION

5.1 Journal Observation Locations and Human Abundance/Impacts

Of the total historical journal database for the region ($n = 15,775$), 11,056 observations had wildlife or other resource use data of quality acceptable for use in this analysis (Table 1). Figure 6a shows the location of total observations overlaid on the mean index by ecoregion of humans encountered by these travelers. The locations of journal observations are biased towards, well-used low elevation travel routes (trails and rivers), trading post locations, and areas where early travelers might obtain resources (e.g., bison wintering grounds, dependable fisheries). Historical human abundance is highest along the west coast, and major river systems (e.g., Columbia, Fraser, Platte, Saskatchewan, and Mackenzie) with low human numbers in mountain ecoregions (e.g., Canadian Rockies) and northern arctic and subarctic areas. This is in concurrence with other assessments of historical human population densities (Kroeber 1947, Ubelaker 1988, Chaput et al. 2015). The transition to modern anthromes shows a similar pattern for current human impact at the ecoregion level (Figure 6b). In the south, coastal ecoregions and those along major river systems have the highest current human impacts, as well as those on the Great Plains that have been transformed by agriculture (Figure 5).

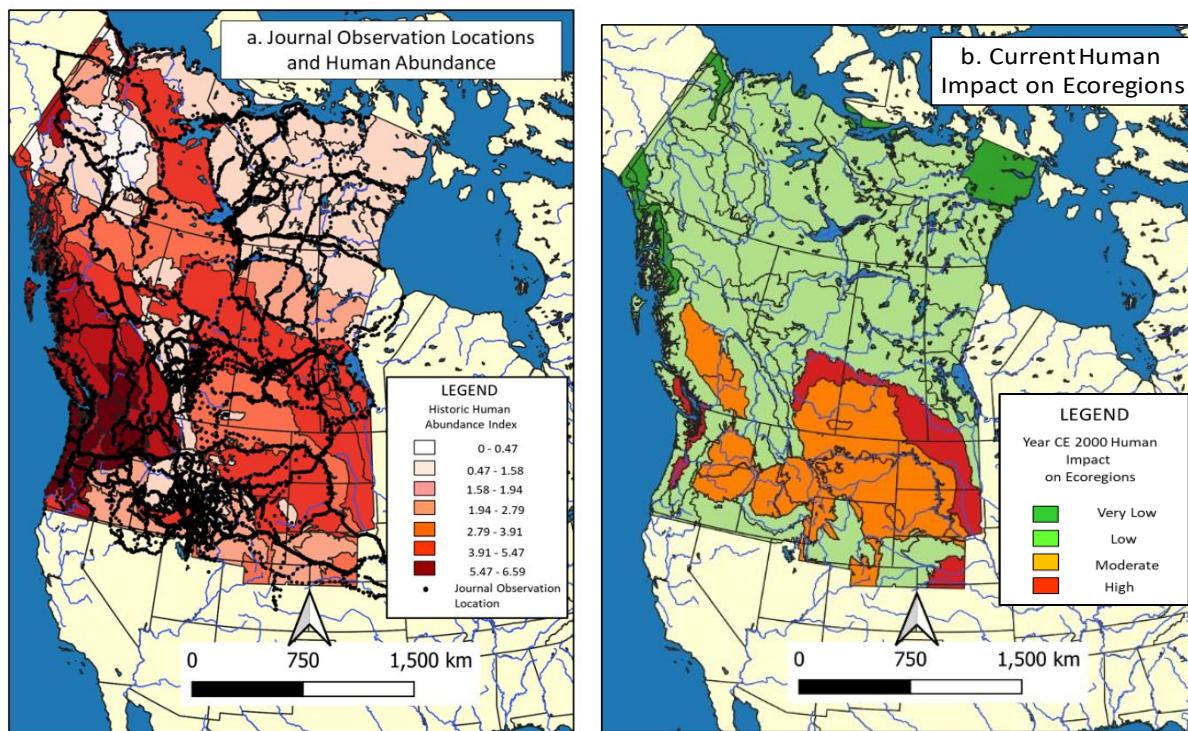


Figure 6: a. Locations for daily journal observations for the period 1691 (southern regions) to 1928 CE (northern regions) by historic travellers ($n = 15,775$ journal-days), and mean relative abundance index for the number of humans observed; b. Assessment of current (Year 2000 CE) human impacts on ecoregions adapted from Dinerstein et al. (2017).

Further north, Figure 6b shows many ecoregions as having low or very low human impacts. Ecoregion-scale studies (Dinerstein et al. 2017, Vynne et al. 2022) conclude that due to low human impact, nature and species conservation remains possible across much of this vast area.

5.2 Fire Cause, Seasonality, and Frequency

The historical journal database includes 259 observations (Table 2) of either ongoing or recent fires that had spread, or would likely spread beyond a campfire size, with causes assigned as follows: unclassified (34%), signaling (23%), unknown but likely caused by humans based upon time of year (14%), accidental fire escape (10%), hunting (10%), warfare (3%), habitat improvement (3%), other human purposes such as insect reduction or tree-felling (3%), and lightning (<.5%). Although 47% of burns were observed in the summer, 22% were observed in the fall, 18% in the winter, and 12% in the spring. This corresponds with the theoretical anthropogenic pattern of burning vegetation early as possible in the annual cycle of herbaceous growth (described in Section 3.1) where light-burning is possible as soon as plant growth cures in late summer and fall, continues into winter and spring when conditions are favorable, and may be subsidized by some lightning fires that occur mainly in summer.

Table 2. Historical journal observations of fire cause and season.

Cause	Fall	Season	Winter	Spring	Summer	Total
Unclassified	14		26	6	41	87
Human-signalling	11		0	7	42	60
Human- unknown reason	13		1	8	13	35
Human-accidental	4		3	5	13	25
Human-hunting	6		10	3	5	24
Human-warfare	1		4	2	1	8
Human-habitat	7		1	0	0	8
Human-other	2		1	1	7	11
Lightning	0		0	0	1	1
Total	58		46	32	123	259

The preponderance of historical human ignitions is documented for a wide range of northwest landscapes (Boyd 1999b, Pyne 2007, Stewart 2009), and specific regions including prairie grasslands (Nelson and England 1971, Moore 1972), boreal mixed wood (Lewis 1980), Rocky Mountains and foothills (Barrett and Arno 1999, White et al. 2002, Rogeau et al. 2016), and relatively dry western coastal mountains and lowlands (Storm and Shebitz 2006, Pellatt and Gedalof 2014). Anthropogenic fire was so common that many early European journalists were unaware that lightning could cause fires (Baker 2002). Given the many fires lit throughout the year by a region's residents for many varied purposes, only a few, by intent or accident, spread to large areas. However, the timing of their spread—often early in a drying period, and their location—near human travel routes and occupation areas either precluded lightning ignition or obscured evidence of its occurrence (Kay 2007b). Today, human ignitions

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(accidental and arson) remain common in rural and forested areas where industrial and recreational activities occur. However, in more remote regions, human ignitions have been greatly reduced through cultural change and prevention/education programs. In Canada for example, from 1959 through 1997, the burn area was dominated by large fires (>200 ha) started by lightning. Although these burns represented only 3% of the total number of fires, they burned 97% of the area (Stocks et al. 2002).

Fire frequency has also changed greatly through time across ecoregions. Results of select fire history studies from the NW area database are summarized by fire weather zone (Figure 7) and ecoregion (Figure 8a). Historically, fires were most frequent in warm dry ecoregions (extreme, very high, and high fire weather zones) with mean fire cycles or return intervals <50 years. Fire was less frequent in cooler and moister ecoregions in the low, very low, and minimal fire weather zones, with fire cycles exceeding 500 years. Fire frequency began to decline, particularly in the moderate to high fire danger ecoregions (Figure 7) by as early as 1750 CE (Johnson et al. 1990, Johnson and Larsen 1991, Van Wagner et al. 2006). Beginning in the early 1900s, and continuing recently, fire frequency had declined by over 90% across most southern ecoregions but has continued to occur moderately frequently in more northern regions (Figure 8b).

Although fire prevention, suppression actions, and land use change (e.g., agriculture) reduce current fire frequency (Hessburg and Agee 2003, Rogeau et al. 2016, Hessburg et al. 2019, Chavardès et al. 2021), the causes of the declines in fire activity in the pre-1900 CE period remain controversial (Wallenius et al. 2011). Historic climate change may have marginally reduced fire frequency (Johnson and Larsen 1991, Girardin et al. 2013), but the massive depopulation of indigenous people due to disease and starvation (Boyd 1999a, Daschuk 2019) and the disruption of seasonal rounds (Figure 2) by federal governments restraining the activity of native people (Nabokov and Loendorf 2004, Binnema and Niemi 2006) appear to be better correlated with the early timing and magnitude of reduced fire activity pre-1900 CE (White et al. 2011).

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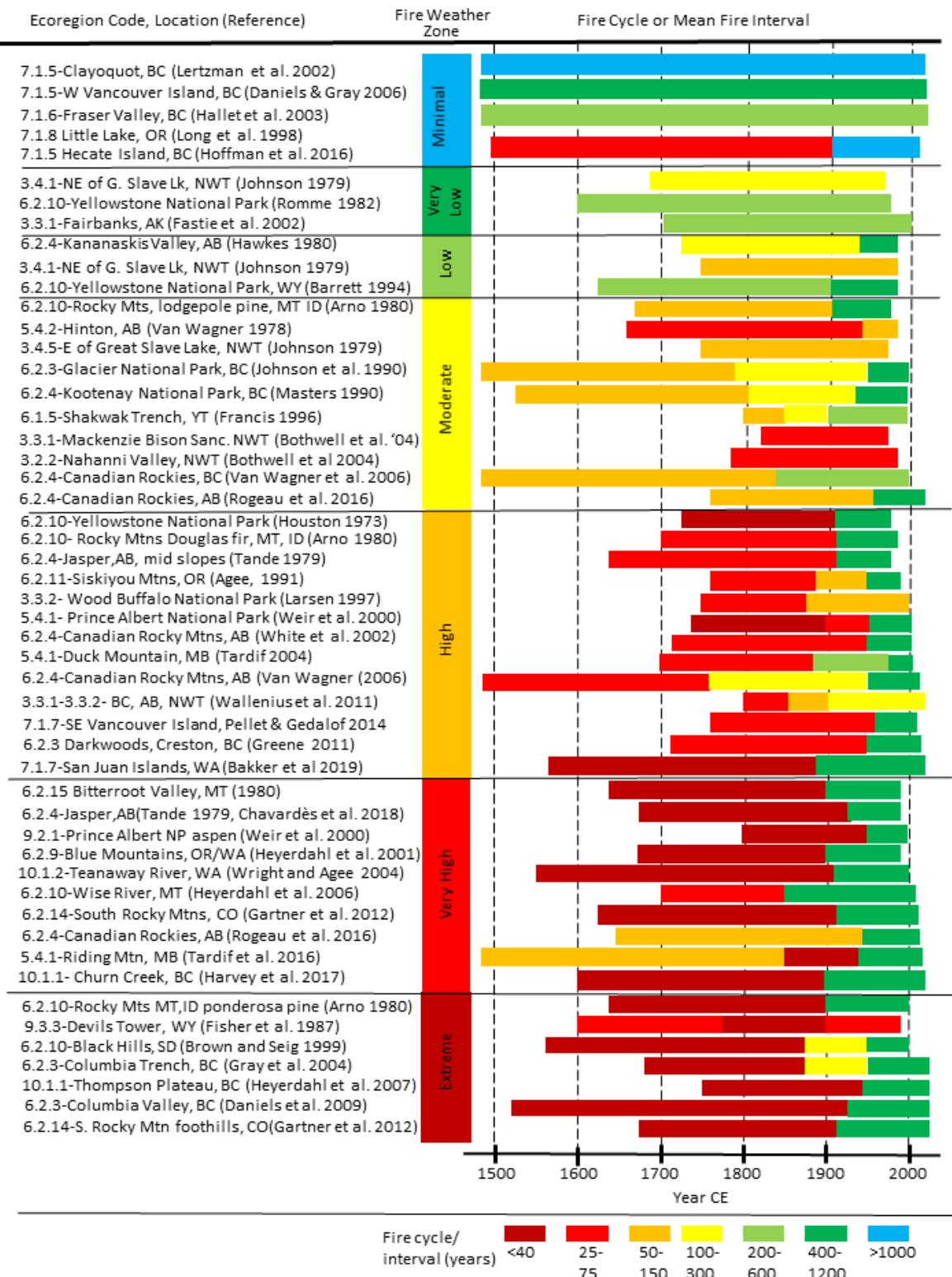


Figure 7. Results of select fire frequency studies for ecoregions (Figure 3, Table 1) grouped by fire weather zone (Simard 1973).

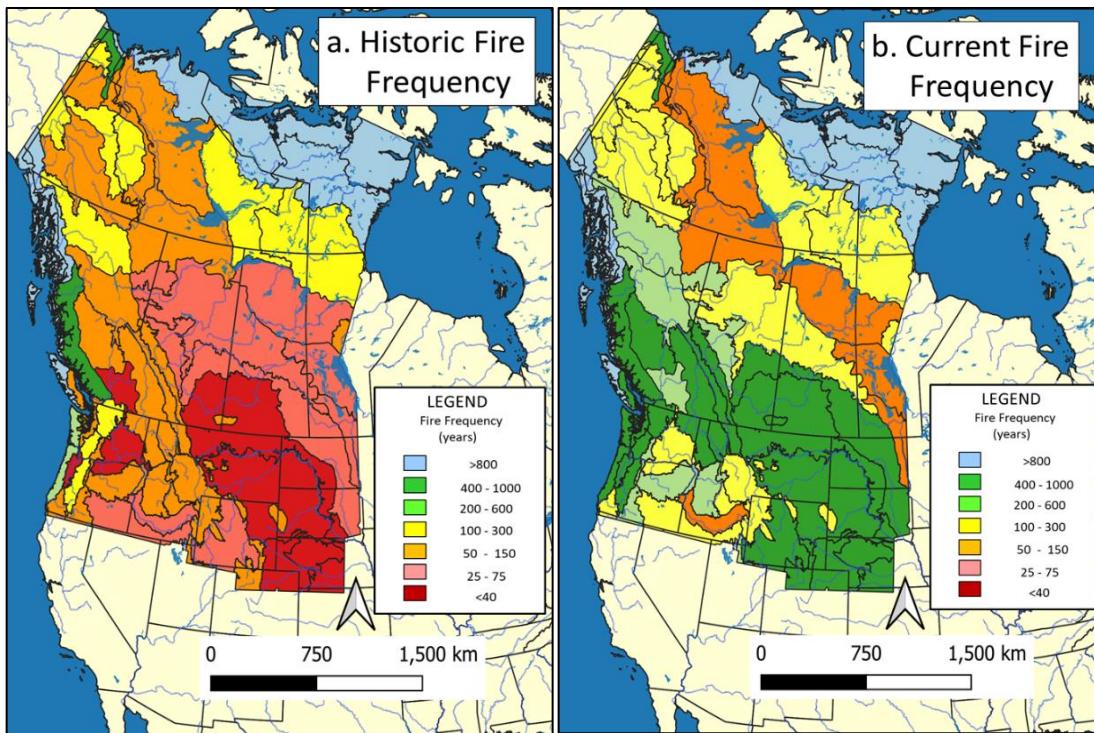


Figure 8: a. Historic (~1500 to ~1930 CE) fire frequency generalized for ecoregions. b. Current fire frequency generalized for ecoregions for the United States (1984-2012 CE) adapted from Parks et al. (2015) and for Canada (1952-2002 CE) from Stocks et al. (2002).

After several decades of fire suppression policies leading to very low fire activity in many southern ecoregions, or in areas near northern towns and villages, fire occurrence is now increasing due to warming climate, fuel accumulation, and a suite of ignitions from powerline failures, arson, lightning and other sources (Parks and Abatzoglou 2020, Parisien et al. 2020). These current-day fires differ from the historic, low and mixed-severity burns lit by humans during low to moderate burning conditions (Lewis and Ferguson 1988, Gottesfeld 1994, Lake et al. 2017). The new norm is large, relatively infrequent, high intensity conflagrations spreading due to extreme drought, wind, or fuel conditions, often during the driest and hottest days of the fire season (Hessburg et al. 2019, Chavardès et al. 2021). Unlike the historic burns that maintained long-term vegetation conditions, the new regime of large and intense conflagrations can radically change plant communities (Kolden et al. 2017, Hagmann et al. 2021).

5.3. Resource Abundance and Biome Transitions

Previous studies simply map historic species presence/absence for regions (Laliberte and Ripple 2004) or relative abundance for select areas (Kay 1994, 2007a, Kay et al. 2000), whereas this study provides the first quantification of relative species abundance across the vast area of three NW biomes. Mapping of mean abundance (Figures 9 and 10) suggests that several species/species groups (e.g., fish, caribou, and bison) historically had an “abundant center distribution” with core areas of high density surrounded by areas of declining density where, ultimately, negative population growth rates created range edges (Sagarin et al. 2006, Sexton et al. 2009). Figures 11 and 12 graph mean ecoregion resource abundance grouped by biome. Ecoregions on the vertical axes are plotted from the highest densities of bison and caribou towards the highest density of fish in the adjacent “salmon biome”. The results and discussion below describe potential “source” areas of high abundance for each species, then interactions between species in the transition zones between biomes.

5.3.1. Plants

Plant resource use is underestimated for several reasons including 1) Historical journalists rarely recorded the use of native plants for food, either by indigenous peoples or their expedition members—the quest for hides, meat, and fish was of greatest interest; 2) The resource use indexing method used for this study (Section 4.3) quantifies higher levels of plant use at about a 1/3 the numeric value applied to animal use observations; 3) High plant use likely occurred when journalists were at sustained stays at trading posts or native villages. These periods are only tallied at 5-10-day or longer intervals (e.g., the Lewis and Clark expedition at the Mandan villages). Thus, the data presented in Figures 9a and 10 is seriously underestimated compared to fish and mammals and includes only 333 observations of plant use (see Supplementary Data). The map of plant use shows relatively low human use of plants in northern moose-caribou ecoregions where many plants had medicinal value (Marles et al. 2012) but fish and mammals were most important for year-round subsistence (Gillespie 1981). Similarly, journalists recorded few occurrences of plant use on the Great Plains except berries in the fall season (primarily saskatoon) and corn along the middle Missouri River (Fenn 2015 pp. 229–243). However, on the Pacific western slope, there are numerous journal records of the use of plants, supported by traditional knowledge and other research (Deur and Turner 2005). Plants commonly used included camas (Beckwith 2004, Storm and Shebitz 2006), wapato (Darby 2005), and a wide range of other shoots, roots, and berries (Hunn and Selam 1990, Turner and Peacock 2005). Today, many habitats where these species were historically observed are urbanized, or managed for commercial food or forestry crops (Ellis et al. 2010).

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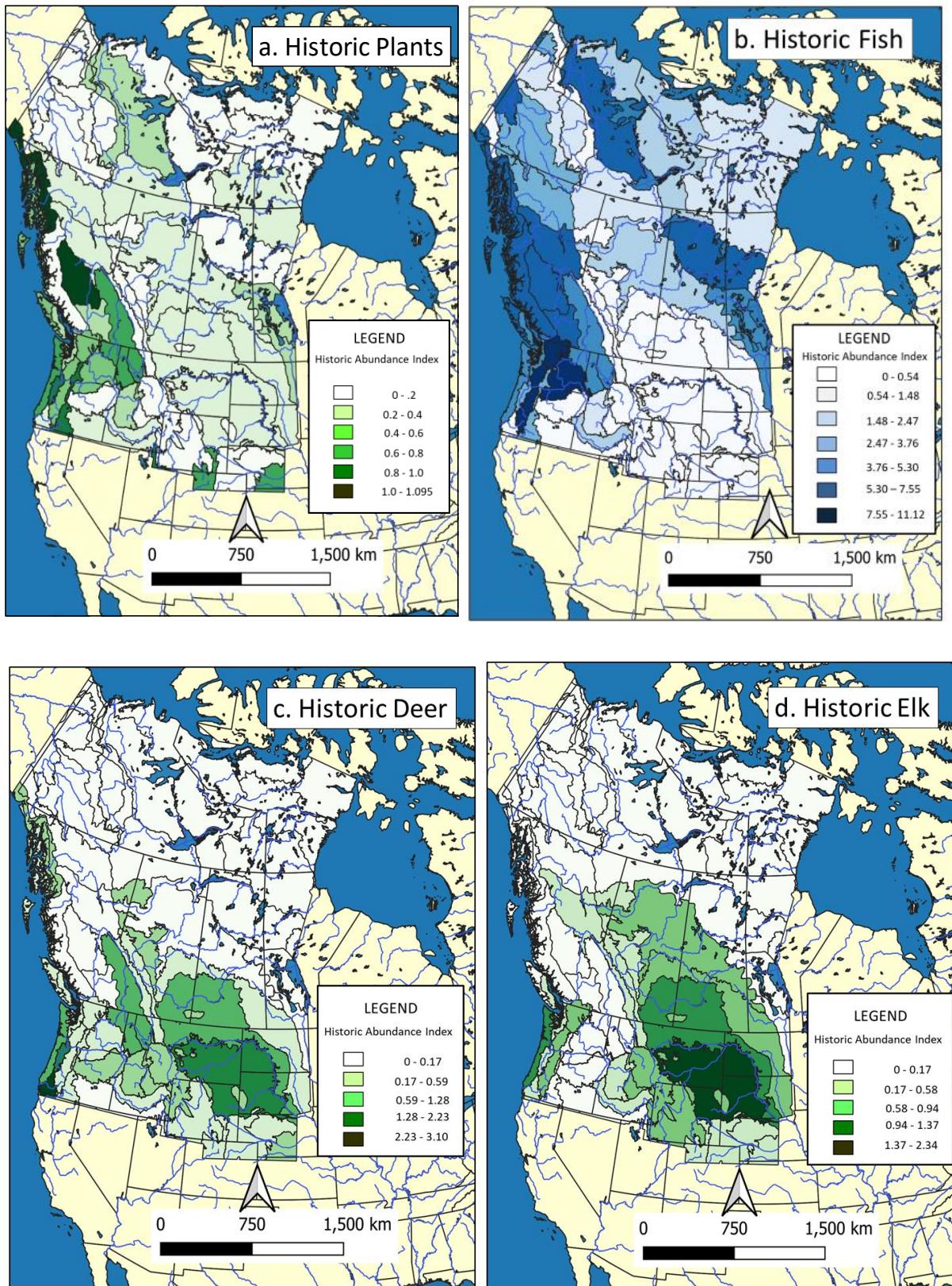


Figure 9. Abundance of selected resources observed by historical journalists by ecoregion. Current (2000 CE) mean moose abundance for ecoregions adapted from Jensen et al. (2018).

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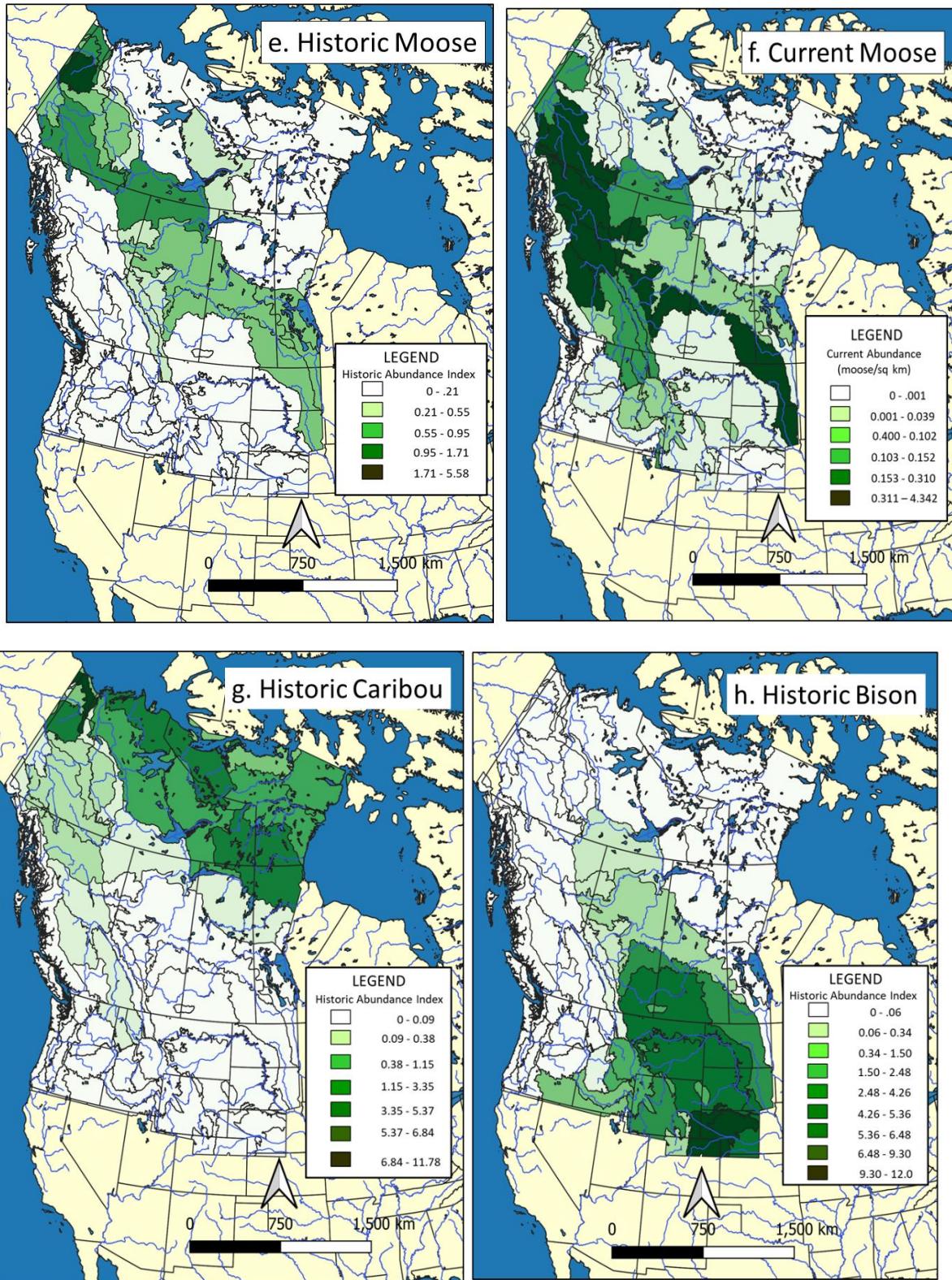


Figure 9 continued.

5.3.2 Fish

Historic journalists routinely reported on the availability of fresh or preserved fish as it was a primary source of food in numerous ecoregions with 1401 positive observations of actual fish use or abundance. Ecoregions containing salmon-bearing watersheds along the west coast had the highest fish abundance indexes (Figure 9b), and indigenous people's use of fish such as salmon and herring here is well-documented (Prentiss and Kuijt 2004, 2014, Campbell and Butler 2010, McKechnie et al. 2014). Harvesting fish species such as whitefish, trout, and inconnu also has long-term importance for human sustenance in northern ecoregions (Gillespie 1981, Helm 2004, Berkes 2012 pp. 147–166). Journalists crossing the Great Plains ecoregions only infrequently reported fish use, possibly due to few rivers and lakes, and an abundance of alternate prey such as bison, elk, and deer (see below). In the last century, large dam-building projects, particularly on the Churchill, Nelson, Peace, and Columbia rivers, have greatly altered historic fish abundance and migration patterns. Reservoirs now submerge indigenous salmon fishing sites along the Columbia River such as the Cascades, Dalles, and Kettle Falls (Goble 1999).

5.3.3 Deer and Elk

Three species of deer (mule, blacktail, whitetail) occur in the study area but are grouped here due to a lack of differentiation by many historical journalists. During the historical period, both deer and elk occupied a similar group of ecoregions (Figures 9 c,d) with the highest abundance along the west coast, the upper Columbia River watershed (for deer), and the central Great Plains (for both deer and elk). There were relatively low numbers of both elk and deer historically observed on the Columbia and Okanogan plateaus and adjacent ecoregions along the Columbia and Fraser rivers. This concurs with previous analyses of wildlife observations made by the Lewis and Clark Expedition (Martin and Szuter 1999, Lyman and Wolverton 2002, Laliberte and Ripple 2003, Kay 2007a), but provides further knowledge on the consistency and extent of this pattern from other early European travelers such as Alexander Mackenzie (2001) in the year 1793, Simon Fraser (2007) in 1805, David Thompson (1994) in the period 1807-14, and David Douglas (1914) in 1824-26. Today, elk populations have expanded into the interior of the Columbia and Okanogan plateaus (McCorquodale et al. 1988), and numerous other areas of the interior west (Sawyer et al. 2007). East of the Rocky Mountains, the historic distribution of deer and elk (Figure 9c,d) did not extend north of 55 degrees and 56-57 degrees latitude respectively (Richardson 1829 pp. 251–258). Today, whitetail deer are expanding northward from the plains into mixed-wood ecoregions (Fisher et al. 2020). Although recent climate and habitat change may be partially influencing these changes, a complementary explanation is that for long periods in the past elk and deer populations were depressed due to intense hunting by indigenous peoples sustained by alternate resources such as fish and plants (Kay 2007a), and in many areas, these species were further impacted by early European settlement that limited their range (Laliberte and Ripple 2004). However, the collapse of indigenous populations during the 1800s, predator control, modern hunting regulations, private property use restrictions and habitat enhancement by agriculture (Figure 5) are facilitating deer and elk increases both in numbers and extent across much of the northwest.

5.3.4 Moose

The range and relative population density of moose provide an even more illustrative case of potential long-term human influences, and recent change (Hatter 1950, Kay 1997). Historically, moose were very rare or did not occur in most of the salmon and southern bison ecoregions (Figure 9e). Core population areas appear to have been in the aspen parkland and boreal mixed-wood belt surrounding the northern prairies, and the northern interior mountainous areas of today's British Columbia, Yukon Territory, and Alaska. Indigenous people routinely attempted to hunt moose due to its large size and high-quality hide (Gillespie 1981, Winterhalder 1981, Helm 2004). However, in most regions moose were relatively rare, and finding and hunting them took great skill (Thompson 2009 pp. 109–110). Figure 9f shows that current moose distribution and density have increased greatly from the historic period (Jensen et al. 2018), especially in the northeast near Hudson's Bay, and towards the west coast. Moose numbers in central and northern British Columbia began to expand in the latter 1800s (Santomauro et al. 2012). This was decades before expansion of the timber harvesting industry into the area and coincides with declining fire frequency (Figure 7). Thus, habitat quality was decreasing as moose populations expanded. An explanation for this counter-intuitive trend is that a series of disease outbreaks in the 1800s greatly reduced indigenous populations (Boyd 1999a). This resulted in a release of moose numbers that had, over the long-term, been depressed by hunting from a high density of humans sustained by fisheries and other resources (Kay 1997) and who maintained trading networks to obtain hides that reached well into the interior from the coast (Marsden and Galois 1995, Galois 1998). Moose numbers could have similarly increased in other northwest ecoregions as indigenous people's numbers declined, and governments restricted traditional indigenous hunting.

5.3.5 Caribou

Historical journals provide numerous observations of North American caribou, but ecotypes (barren-ground, mountain, woodland) were rarely differentiated. Core caribou population ecoregions ran northwestwards across the arctic-taiga transition from Hudson's Bay, then arcing southwards down the western mountains, with caribou historically observed as far south as central Idaho (Figure 9g). Today, and historically, barren-ground caribou attain high densities by migrating northwards in spring into treeless areas that have no fuelwood, and have few alternate prey sources for humans and other predators (Kelsall 1968, Gordon 2003, Bergerud et al. 2008 pp. 432–444). In the past, this was a buffer zone between the Inuit and Inuvialuit peoples of the Arctic coast and the Dene peoples from the south (Wonders 1988) which further reduced human presence in caribou summer range.

Woodland and mountain caribou historically occurred at very low densities (Figure 9g) on the southern edge of their boreal forest range (Richardson 1829 pp. 250–251, Thompson 2009 pp. 114–115), or occupied upper elevations of the southern mountains (Bergerud and Elliot 1986). Caribou in these areas are now endangered (Environment Canada 2011, 2014). The current explanation for the decline in numbers of these caribou is that modern industrial land uses (logging and petroleum extraction) have created high-quality, early seral habitats for moose, deer, and elk. This in turn supports high predator numbers (e.g., wolves, bears, and cougar) that follow human-maintained access routes, particularly in

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winter, to hunt caribou (Wittmer et al. 2005, Serrouya et al. 2017). Researchers term this as the “disturbance-mediated apparent competition” (DMAC) hypothesis (DeMars et al. 2019). However, this explanation is not robust. Caribou numbers have declined in large protected areas (Hebblewhite et al. 2007, 2009, Arsenault and Manseau 2011) where industrial activity does not occur, winter human travel is limited, and current fire frequency is greatly reduced from historic times (Figures 5, 6b, 7, 8b). Researchers (Rettie and Messier 1998, Neufeld et al. 2021) also describe declining woodland caribou in remote boreal forests on the Canadian Shield with low industrial activity and relatively high long-term fire frequency (Figure 8).

A more complex hypothesis, consistent with indigenous people’s long-term burning and foraging patterns described above, and the broader “habitat mediated optimal foraging” (HMOF) hypothesis (Sections 3.3 and 3.4) is as follows:

- Historically frequent anthropogenic burning, often with low to moderate severity, maintained early seral habitats for moose, and in southern areas elk and deer, at lower elevations or near travel routes (Lewis and Ferguson 1988, Gottesfeld 1994), but retained older forests of caribou habitat at higher elevations and in areas more remote from high human use (Robinson et al. 2012, Konkolics et al. 2021). However, intense human hunting in mountain valley bottoms or near boreal streams kept populations of herbivores found in these areas in low or very low abundance (Sections 5.3.4, 5.3.5). This depressed food availability for wide-ranging wolves, bears, and cougars. Moreover, indigenous people hunted and trapped these predators. Caribou, found in areas more remote from humans thus had refuges of old growth habitat that had escaped fire, and relatively low predation.
- Declining indigenous populations and their hunting impacts, resulted in increasing distribution and numbers of moose, deer and elk as described above (e.g., moose: Figure 9e, 9f). This began to occur as early as the 1860s and occurred even in areas with potentially declining habitat quality due to decreasing fire frequency (Figure 8a,8b).
- From the 1860s to the 1960s, the Hudson’s Bay Company, followed by federal, state, provincial and territorial policies continued to maintain a vast network of fur bearer traplines across the northwest. Trappers, first mostly indigenous then joined by whites, often targeted large predators such as wolves, bears, and cougars. Poisons such strychnine were also used (Gunson 1991). This intense trapping, hunting, and poisoning maintained low predator numbers from the 1850s to 1970s. For example, in the contiguous United States wolves were extirpated (Mech 1970) and grizzly bears reduced to very low numbers (United States Fish and Wildlife Service 1982).
- As a result of low predator abundance many ungulate populations, including southern caribou maintained substantial numbers into the 1970s (Bergerud and Elliot 1986).
- After 1970, federal, state, territorial, and provincial governments reduced or eliminated predator control programs, or even restored predators. Outside of national parks, declines in the fur market reduced the take on traplines, and the number of active trappers. Regionally, wolf numbers began to increase (Gunson 1991, Bergerud and Elliott 1998, Bangs et al. 2001,

Hervieux et al. 2014). In national parks with high numbers of prey, wolves became super-abundant resulting in early declines or extirpation of caribou populations (Hebblewhite et al. 2009).

- After 1930, large areas of the NW impacted by increased road access, oil and gas extraction, and timber harvesting. This led researchers to conclude that habitat alteration or increased access routes were important factors in caribou decline (Rettie and Messier 1998, Wittmer et al. 2007, Hervieux et al. 2014). These factors likely contributed, but the loss of caribou also in large national parks or in areas with low industrial activity indicates that other underlying causes for increases in the numbers of alternate prey and hence high wolf numbers require further consideration (Hebblewhite et al. 2007, 2009, Neufeld et al. 2021, Superbie et al. 2022).

In summary, long-term patterns of human burning and hunting maintained southern boreal and mountain caribou habitat and populations prior to European contact. The disruption of these traditional indigenous practices by the 1860s allowed broad regional increases in elk, deer and moose populations (described above). However, wolf and other predator numbers were kept low by trapping and predator control up until the 1970s. After this time, predator numbers increased due to high regional prey abundance. This has been further aggravated by modern industrial and access patterns and has led to modern caribou population extirpations. If this eco-cultural hypothesis is valid, caribou recovery in some areas might require use of traditional knowledge to partially restore indigenous hunting and habitat management practices (e.g., Polfus (2016)).

5.3.6 Bison

American bison are recognized as one species with a “plains” ecotype in the south intergrading to a “wood” ecotype to the north (Allen 1876, Geist 1991, Gates et al. 2011). Historic observations (Figures 9h, 10) indicate bison numbers were highest in southern prairie ecoregions, gradually declining in abundance to the northwestern edge of the range in the boreal forest near Great Slave Lake. Due to high biomass and hide quality, bison were the favored prey for numerous indigenous peoples (Roe 1972, Geist 1996). In southern ecoregions, the species thrived by utilizing large grassland areas. For humans, these areas had little fuelwood, few alternate resources, and were often intertribal warfare zones (Binnema 2004, Kay 2007a, Bayham et al. 2017). Bison minimized human predation in these grasslands by forming large herds, remaining in buffer zones as much as possible, and when hunted, making long-distance and unpredictable movements (Binnema 2004, Brink 2008). In northern ecoregions, bison also persisted in intertribal warfare zones along the Peace and Slave rivers, and areas distant from well-used human travel routes (Tyrrell 1934, Mackenzie 2001, Fraser 2007).

The rugged terrain of the Rocky Mountains likely interacted with human hunting and trade patterns to define the western edge of bison range (Roe 1972, Bailey 2016, Farr and White 2022). Although high densities of bison were present in grasslands along the eastern slope of the mountains from the Platte River north to the Athabasca River, bison numbers rapidly declined moving westwards into the mountains. One explanation for this rapid decline in bison numbers is that all the valleys and passes through the mountains generally have narrow gaps, often less than 1 km wide as they pass into the

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mountains (White 2018). There are several historic accounts of indigenous hunters using this narrow mountainous terrain to channel and contain bison (Whealdon 2001 pp. 40–41, Merrill and Merrill 2012, Keigley 2019). Deep winter snows in this terrain would further favor human bison hunting, resulting in very few bison persisting in rugged mountain terrain (Kay 1994, White et al. 2001, Mosley et al. 2018). In contrast, on the headwaters of the Platte River, the South Pass across the Rocky Mountains is over 50 km wide and historically provided broad connectivity between the plains to the east and the upper Snake River to the west. It was traversed by great numbers of bison, with the western edge of bison range extending several hundred kilometers westwards across the Northern Basin and Range ecoregion towards the Pacific Ocean (Figure 9h).

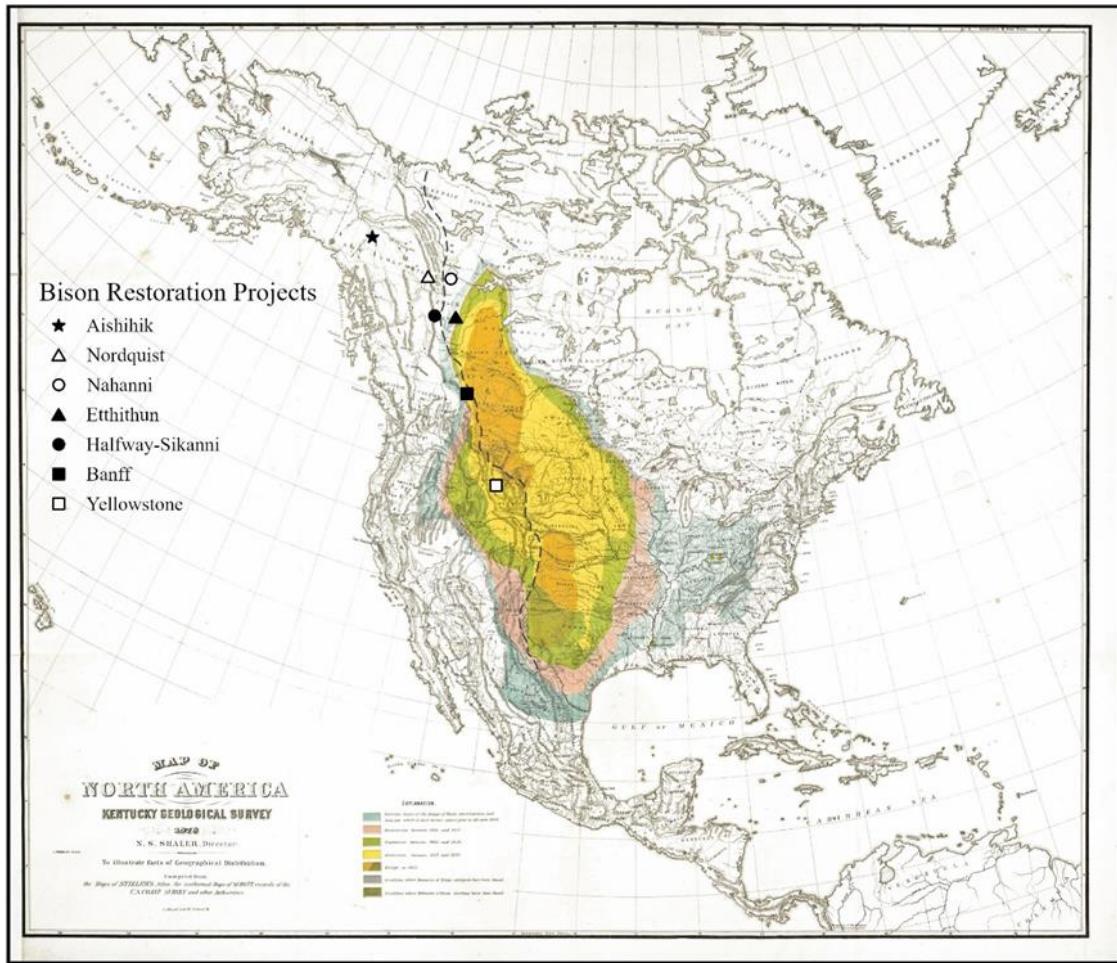


Figure 10: Range contractions of the American bison during the period from pre-1800 to 1875 as mapped by Joel Allen (1876) of the Kentucky Geological Survey showing the locations of select current bison restoration projects (Farr and White 2022). The figure shows the extreme edge of the historic bison range before 1800 (blue), the range contraction from 1800 to 1825 (pink), 1825 to 1850 (green), 1850 to 1875 (yellow), and the range in 1875 (orange). The dotted line delineates where the mountains of the Western Cordillera meet the Great Plains.

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By the mid-1850s, both indigenous and European hunters began to advance into the core refuges for bison in the center of the Great Plains (Allen 1876, Hornaday 1889, Isenberg 2000), and except some remote northern and mountain populations, bison were extirpated across most of their former range by 1880 (Figure 10). Today, large regions of what was formerly high-density bison range are agricultural production anthromes (Figures 5, 6b). However, in areas where bison populations are restored, and where human predation is limited, initial annual population growth rates can be high, even where a complete suite of non-human predators exists, or in areas outside of traditional bison range (Farr and White 2022). For example, bison population growth exceeds 10% in both the mountainous Yellowstone region where bison were historically only in low numbers (Kay 1994, Wagner 2006 pp. 155–157, Keigley 2019), and for an introduced population in the Yukon Territory (Jung and Egli 2016) where bison were not present in the historical record (Figure 9h, Figure 10). This indicates that it is not habitat quality, but predation by indigenous peoples in these areas that once limited bison numbers and distribution (Farr and White 2022). Further northwest, both bison and elk occurred in the Yukon into the mid-Holocene period (Zazula et al. 2017), and their prehistoric disappearance coincides with increasing human density in the region (Doering 2021).

5.3.7 Omnivores and Carnivores

Referencing the ecological food web and interactions models (Figure 4), indigenous peoples could influence the numbers of grizzly bears, black bears, wolves, and cougars by 1) killing them for food, hides, or their threat to people or their sources of food; 2) in the case of wolves, capturing them for domestication, 3) competing with them by depressing the resources these species depend on for food; or 4) through use of fire, increasing or decreasing habitat for plants or animals utilized by these species. Figure 12 graphs the mean historical abundance index by ecoregions for select omnivores and carnivores grouped into eco-cultural biomes. Immediately apparent is historical journalists only rarely recorded sign, sightings, or kills of these omnivores and carnivores. For example, a mean resource index value of .25 would indicate only sighting the species once every 3 months in the ecoregion. For a species such as grizzly bear that was of great interest to most early European travelers, this reflects low abundance near travel routes, campsites, and trading posts.

The general pattern appears to be that cougar and coyotes were rarely observed across all ecoregions, and black bears were rare, but most observed in forested areas. The abundance of wolves and grizzly bears was greatest in a group of ecoregions where bison was most common (Figures 9h, 10, 11)—in the center of the bison eco-cultural biome. Travelers here periodically describe being attacked by grizzly bears, particularly in deciduous shrub thickets during berry season (Fowler 1898 pp. 41–44). In northern barren-ground ecoregions dominated by caribou, predators and omnivores were generally rare, possibly due to a low range of alternate available resources, and the long-distance migratory patterns of caribou (Kelsall 1968, Bergerud et al. 2008).

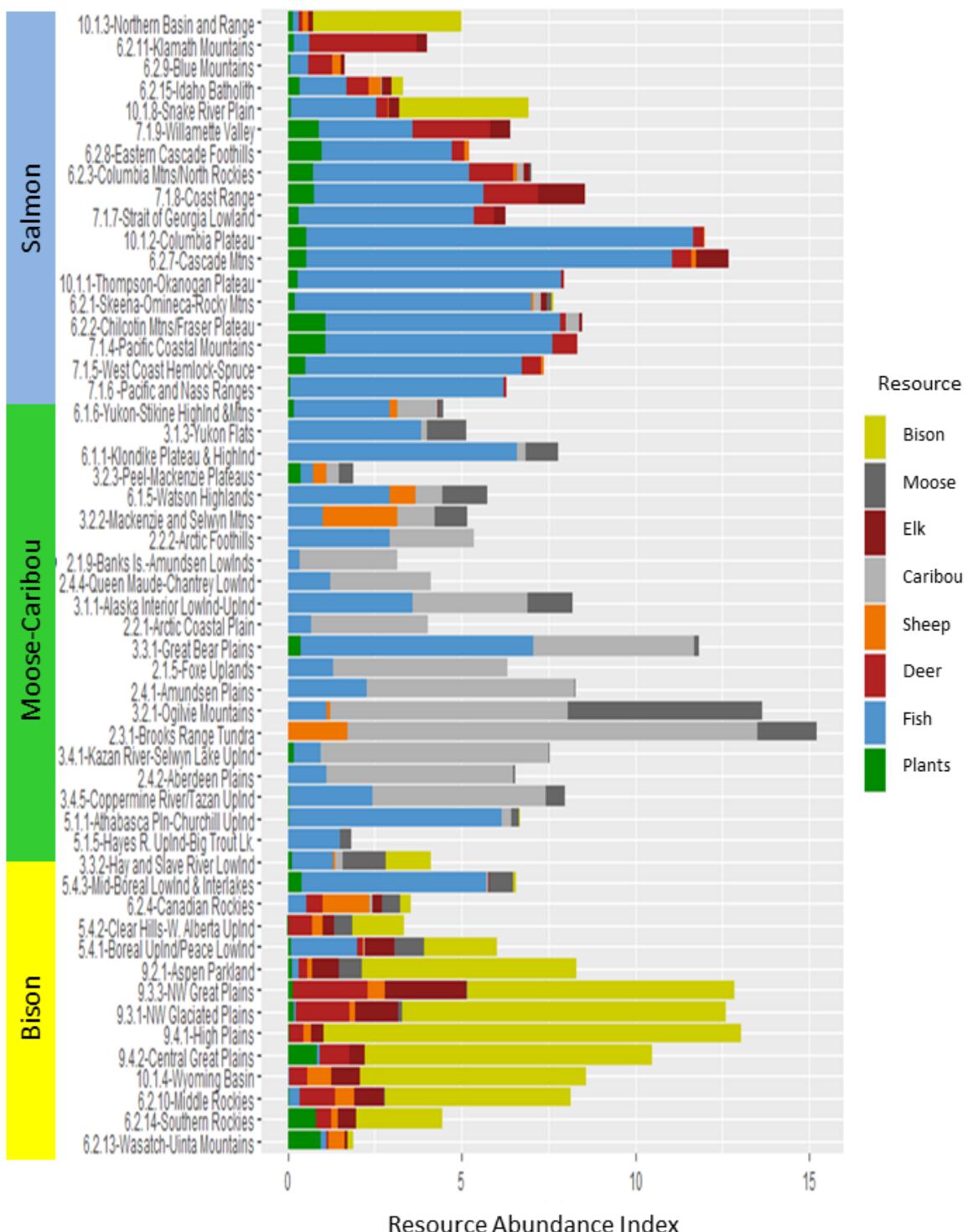


Figure 11: Mean historical resource abundance index values for ecoregions grouped into eco-cultural biomes.

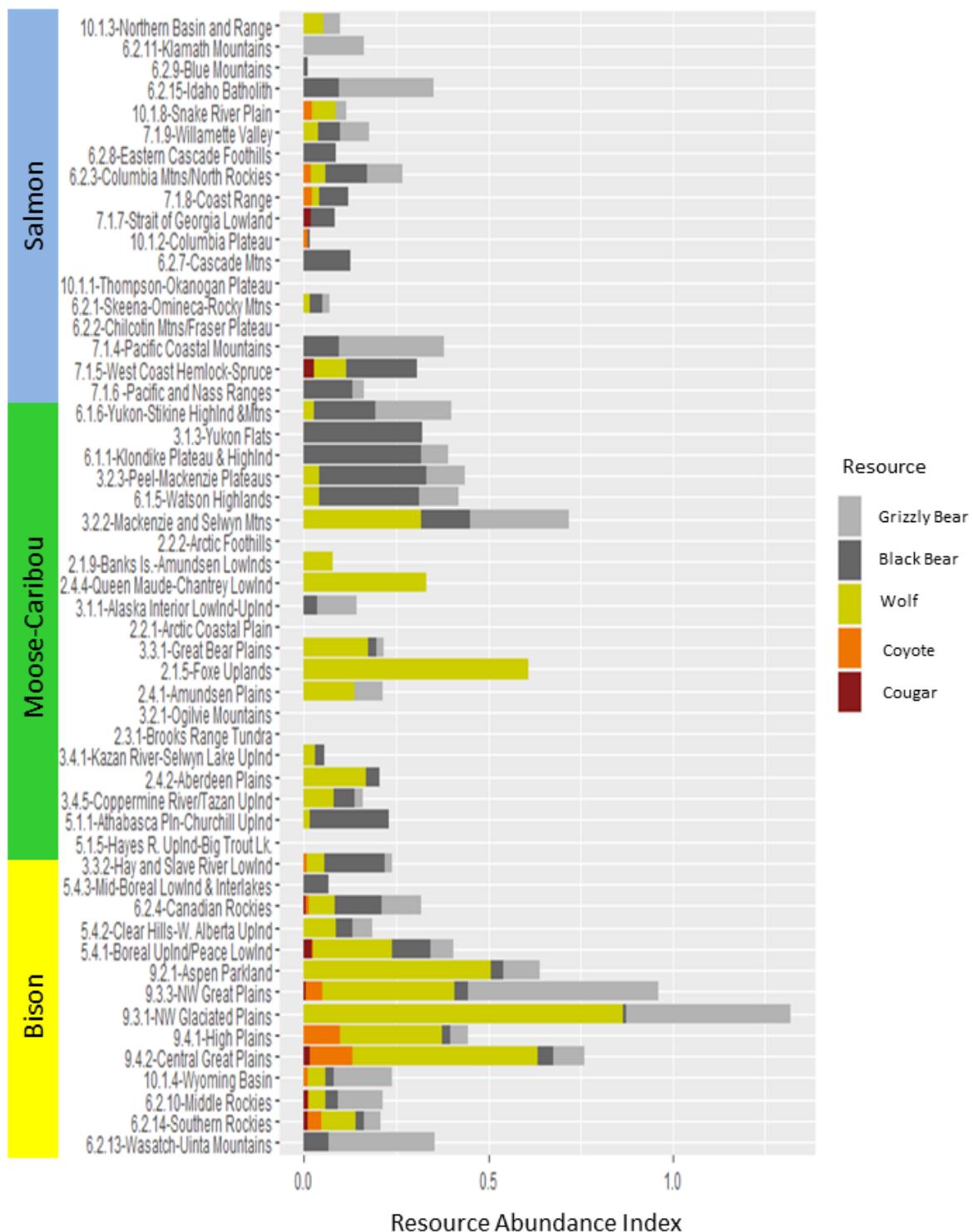


Figure 12: Mean historical abundance index values for select omnivores and carnivores for northwest ecoregions grouped into eco-cultural biomes.

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In the center ecoregions of the salmon biome (e.g., 10.1.2 Columbia Plateau), wolves and grizzly bears were historically very rare, likely due to high densities of humans, and low densities of prey such as moose, deer, and elk (Figures 9). Before the 1970s, intense hunting, predator control, and land use change (Laliberte and Ripple 2004, Vynne et al. 2022) caused range contractions of wolves and grizzly bears across ecoregions with moderate to high human impacts (Figure 6b), particularly those with dense settlements, croplands, or rangelands (Figure 5). Since the 1980s, the distribution and numbers of wolves and grizzly bears have increased across several southern mountainous ecoregions due to abundant prey populations (moose, elk, deer), reduced human-caused mortality, recolonizations, and reintroductions (Bangs et al. 2001, Hebblewhite et al. 2005, Eberhardt and Breiwick 2010). Increased numbers of these predators can extirpate caribou populations (see above), but may also reduce mountain sheep, goat, and other species that are secondary prey at higher elevations. In the long-term ecosystem, these species may have had less predation pressure due to indigenous hunting at lower elevations of both primary prey and their predators.

5.3.8 Transitions between Biomes

This section describes and evaluates the potential role of human optimal foraging and resource switching at the transition between biomes. Figure 11 graphs the mean ecoregion historic abundance index for select resources grouped by eco-cultural biome and plots the value of the main resource (bison, caribou, fish) from highest to lowest on a gradient towards the nearest adjacent biome. Core ecoregions in each biome historically had abundant levels of the key resource as described above.

Transition between Bison and Salmon Biomes- The boundary between bison and salmon-dominated biomes was relatively abrupt (top and bottom of Figure 11), occurring in central southern study area ecoregions including the Central and Southern Rocky Mountains (6.2.10, 6.2.14), Wasatch-Uinta Mountains (6.2.13), and Snake River Plain (10.1.8). Bison abundance steeply declines as fish abundance increases. Moreover, humans in most salmon biome ecoregions had access to relatively abundant edible plants, and in some areas, deer, and elk. This resulted in high densities of people along salmon-bearing streams (Figure 6a) primarily supported by fish and plant resources but also had extensive trade and hunting routes reaching eastwards to obtain highly-valued bison products such as hides, robes, and dried meat (Roe 1972, Anastasio 1985). Traditional, long-distance hunting expeditions to bison range are particularly well-documented for the annual rounds of the Nez Percé (Josephy 1997), the Flathead (Whealdon 2001), the K'tunaxa (Reeves 2003), and Bannock and Shoshone (Nabokov and Loendorf 2004). High numbers of human hunters encountering the low numbers of bison along the western edge of their range would likely limit range expansion westwards (Farr and White 2022). As Roe (1972 p. 259) explained:

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

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Transition between Bison and Caribou-Moose Biomes- These biomes blended across a broad arc of western North America's ecoregions (Figures 1 and 3) including the Canadian Rockies (6.2.4), Clear Hills, and West Alberta Upland (5.4.2), Hay and Slave River Lowlands (3.3.2), and Athabasca Plain and Churchill Uplands (5.1.1). In western mountainous areas, a range of alternate resources such as moose, elk, caribou, sheep, and deer were available to sustain people (Figure 12), but when encountered, bison were favored prey. Several northern indigenous groups extended their annual rounds eastward through the Canadian Rockies (Figure 1) specifically to hunt bison including the Secwepemc (Langemann 2002) and the Tse'Khene (Burley et al. 1996). The north and northeast edge of bison range was bounded by Great Slave Lake, then extending southeast along the edge of the Canadian Shield and tributaries and the well-used indigenous canoe-travel routes of the Athabasca, Clearwater, and Churchill rivers (Figure 9h). The Cree, partially sustained by fisheries, heavily hunted and trapped in this forested region (Smith 1981, Russell 1990, Meyer and Thistle 1995), and even moose were scarce (Thompson 2009 pp. 108–110). Except for indigenous buffer zones (see above), the few bison in this transition zone were preferred human-prey and heavily hunted (Tyrrell 1934, Simpson 1938). Possibly the low ecoregion density of bison and moose, and thus wolves (ecoregions 3.3.2 and 5.1.1 in Figures 9, 11, 12) created a niche for low densities of woodland caribou on the southern edge of the boreal forest (Neufeld et al. 2021, Superbie et al. 2022), even though fire frequency was high in the historical period (Figure 8a). Further south in the Boreal Upland-Peace Lowlands (ecoregion 5.4.1) historic fire frequency was even higher, reducing conifer habitats for caribou. Higher bison, moose, elk, and deer numbers (Figures 9 and 10) provided a diversity of resources for humans and other predators (Figure 11). Thus, by fire-use and prey-switching, humans would have contributed to the predator assemblage that historically created caribou's southern range in the northern mixed woods of the bison biome.

Transition between Caribou-Moose and Salmon Biomes- Historic caribou and moose habitat meshed with the west coast salmon biome in ecoregions extending from Idaho northwards to the Yukon River (Figure 1) including the Columbia Mountains-Northern Rockies (6.2.3), Chilcotin Mountains-Fraser Plateau (6.2.2), Skeena-Omineca-Rocky Mountains (6.2.1) in British Columbia, and Yukon-Stikine Mountains (6.1.6) and Yukon Flats (3.1.3) in the Yukon Territory (Figure 11). The role of alternative resources for humans is complex in this transition zone. In many ecoregions, abundant salmon resulted in high human numbers using valley bottoms (Figure 6a). Although sustained by fish and plants, people could prey-switch, and forage adjacent valley-sides to hunt elk, deer, and moose that provided not just protein, but fat, hides, and other products (Prentiss and Kuijt 2004, 2014). This predation limited these prey species to very low numbers, possibly extirpating them in some locations (Figure 9 c,d,e). Low densities of prey would in turn maintain only low numbers of wolf, bear, and cougars (Figure 12). Caribou, using higher elevations would have some refuge from predation. However, as described above, in current-day ecosystems, high deer, elk, and moose numbers provide prey for abundant wide-ranging wolves that endanger caribou that occur at higher elevations (Bergerud and Elliot 1986, Wittmer et al. 2005, Serrouya et al. 2017). This current predator-prey dynamic varies from historic conditions.

5.4 Future Research

The main hypothesis tested here is that throughout the Holocene, the NW ecosystems developed in concert with human hunting, gathering, and culturing patterns. As described by Smith (2009) in Section 3.3, this ultimately led to relatively stable and sustainable “eco-cultural biomes” for humans and their primary resource species. An approach to understanding these landscapes is to integrate the knowledge of human seasonal rounds (a socio-economic perspective) and food webs (an ecological perspective). Food webs can in turn be linked to species population models (Krebs 2015) to evaluate the potential effects of human niche-building and foraging activity. This ecological analysis can be in turn be synthesized with seasonal round information to form a consilience with the long-term traditional knowledge that sustained indigenous people’s cultures, homelands, and eco-cultural biomes (Kroeber 1947, Berkes 2012). This interdisciplinary understanding is necessary to fully grasp the potential implications of the ongoing modern transition of biomes to anthromes (Ellis et al. 2021).

Basic correlations with currently digitally-mapped habitat characteristics can illustrate patterns of historical species distribution and relative density such as for bison (Farr and White 2022), but better understanding requires applying theory (briefly described in Section 3) to quantify and model the potential processes involved. Here are some potential directions for research:

- **Human population-** Assessment of historical human population densities (Kroeber 1947, Ubelaker 1988, Chaput et al. 2015) are generally only available at a coarse scale. Traditional knowledge and seasonal round information may allow further resolution long-term human densities to the ecoregion level.
- **Fire weather, frequency, severity, and timing-** For this study, these fire regime variables were coarsely approximated to fire weather zone and ecoregion scales (Simard 1973, Stocks et al. 2002). However, historic and current fire weather can be spatially modelled at <4 km resolution, for example see <https://cwfis.cfs.nrcan.gc.ca/background/dsm/normal>. However, historic fire regime research requires fine-scale knowledge of human activity patterns to link ignition timing and locations into fire growth models, and ultimately a specific area’s fire frequency (Lewis and Ferguson 1988, Frost 1998, Hoffman et al. 2016). Historic and current fire frequency and intensity can be modelled to <1 km resolution (Rollins 2009). Working from seasonal round and historic journal observation types of information for ignition, researchers should be able to much more closely approximate anthropogenic fire frequency and timing patterns, and hence plant and wildlife habitat responses. Evidence of depopulation or cultural change should be visible in most dendrochronological fire history studies.
- **Human numeric and functional response to resource availability-** Applying predator-prey theory (Holling 1959, Holt 1977, Messier 1995, Holt and Barfield 2009) to human interactions with resources (Winterhalder and Smith 2000, Kay 2007a) is required to further understand species distribution and abundance, and eco-cultural biome properties. The density of humans (numeric response) should theoretically depend on the total resource availability in a region. From traditional knowledge and seasonal round information, researchers should be able to refine which resources are primary sources of sustenance, shelter, and other requirements for survival, and how this influences the abundance of humans at least the ecoregion scale. The

functional response might be modelled by distance functions for how far humans will travel to obtain various resources at various densities. For example, bison herds, caribou stream crossings, or salmon fisheries can attract humans from hundreds of kilometers away. The product of human's numeric and functional responses to resource/prey abundance counterbalanced with the resource's productivity (often determined by habitat quality) may ultimately determine where it can exist in abundance, and as the predation rate increases or productivity declines, the edges of its range. Figure 11 shows the ecoregion pattern for the primary species that define the WNA eco-cultural biomes: salmon, bison, and moose/caribou. Figure 12 indicates ecoregions where other predators (e.g., wolves, bears, cougar) could have also played an additive role. Researchers can test this basic model's application at finer scales across a wide variety of First Nation territories and varied landscapes.

- **Response of species post-contact-** Using the above approach, researchers should be able to interpret the response of several species such as salmon, deer, elk, moose, caribou, and bison after European contact. Changes such as human depopulation, increased/decreased hunting effectiveness, predator control etc. may be evident and the hypothesis of human's potential keystone role in maintaining long-term NW biomes more fully tested.
- **"Exceptions to the rule"-** The vagaries, innovations, and adaptiveness of human cultures provide numerous exceptions to basic patterns. In some situations, humans may enhance the abundance of resources, in others they may be more rapidly depleted. Examples are numerous. For bison, inter-tribal buffer zones between strongly antagonistic nations may have higher than expected bison abundance (Kay 2007a, Bayham et al. 2017). Movement corridors or valleys where bison are near the edge of a nation's territory may be heavily hunted (White 2018), or a movement corridor where one nation has exclusive control of territory might be used to move bison long distances towards trade centers (White 2020). For salmon, nursery lakes are often under one nations control, and a wide range of nurturing techniques can be applied to make these fisheries super-abundant (Johnsen 2009, Campbell and Butler 2010). For moose-caribou systems, as described above, exceptionally intensive indigenous harvesting of moose and other fur and hide bearers to supply hides for local people, and in trade for eulachan grease (Galois 1998, Santomauro et al. 2012) may have created the niche for western populations of mountain caribou. Similarly, for woodland caribou at the southern edge of their range on the Canadian Shield, heavy hunting by Woodland Cree (Figures 1, 13) of bison, moose, elk and deer, and their predators (wolves, bears) along well-used water travel ways (Smith 1981, Epp et al. 1993) could have contributed to the unique conditions required for caribou persistence in this area of high fire frequency and low primary productivity (Neufeld et al. 2021, Superbie et al. 2022). All these regionally specific historic situations provide opportunities for interdisciplinary research.
- **Active restoration-** At the ecoregion and biome scale, applied research for restoration purposes will likely not be possible for the plains bison biome where, due to modern agricultural land uses (Figure 5, 6b) wild bison population abundance (Figures 9g, 10, 11) cannot occur. However, large areas of most NW ecoregions in the salmon and moose-caribou biomes remain in relatively natural condition (Figure 5, 6b), and populations of most fish species, moose, caribou, and predator species are relatively abundant. In some areas fire regimes and resource availability

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may even approximate historic conditions (Figures 8-12). Here, the data presented in this report may provide enough evidence to suggest, that in some areas, restoration researchers, working with indigenous peoples could seek to maintain components of long-term eco-cultural biome, not current anthrome-created conditions. This research would likely require restoring some aspects of roles of indigenous peoples in the long-term fire regime and resource utilization.

- **Extend analysis of journal observations to southwest-** The WNA historical journal database includes >8,000 journal-days of observations for the southwest area of North America (see <https://lensoftimenorthwest.com/themes/lens-northwest-files/google-earth-map-journal-wildlife-observations/> or after c. 2025, back-up digital databases will be archived with various global biodiversity data centers (hopefully) and at very least, at the Whyte Museum Archives, Banff, Alberta: <https://www.whyte.org/digitalvault/categories/archives-library>. This historic data can be overlapped with the rich archaeological and traditional knowledge record for the southwest area to extend understanding of indigenous use of resources further into the past.

In summary, the way forward requires us to understand the potential keystone traditional human hunting, gathering, and culturing processes within ecoregions, and their finer scale patterns of habitat and seasonality (Smith 2009, 2011, Berkes 2012). Researchers aware of these patterns can better interpret the area-specific effects of humans on plants and animals (Deur and Turner 2005, Polfus et al. 2016, Hessami et al. 2021). Indigenous group trade, cooperation, and conflict also occur at varied scales that must be integrated in the to understanding of human foraging and food web patterns (Binnema 2004, Kay 2007a, Bayham et al. 2017). Documenting the Indigenous seasonal round for each region (Figure 2) is the first step in this process.



Figure 13: Woodland Cree camp in 1880 at Oxford House, Manitoba. (Robert Bell, Geological Survey of Canada, National Archives Canada).

6. CONCLUSION AND APPLICATIONS

This paper provides evidence supporting the hypothesis that the seasonal rounds of indigenous peoples, through niche construction, using fire, and optimal foraging for resources, influenced long-term ecological patterns and processes of northwest ecoregions and ultimately species ranges and eco-cultural biomes (Kroeber 1947, Kay 1994, McTaggart-Cowan 1995, Hessburg and Agee 2003, Deur and Turner 2005, Campbell and Butler 2010). Further, it provides an initial evaluation of how the relatively abrupt transition of these biomes after ~1750 years CE into anthromes (Ellis et al. 2010), and especially those anthromes with modern-day, globalized, high-intensity agricultural and industrial uses, disrupted these long-term burning and foraging processes. This may be a classic example demonstrating the outcome of removing a keystone species (Paine 1969)—in this case, indigenous humans. The ongoing ecosystem change in North America’s northwest region may provide an excellent case history to support Ellis et al.’s (2021) conclusion that “the primary cause of declining biodiversity, at least in recent times, is the appropriation, colonization, and intensifying use of lands already inhabited, used, and reshaped by current and prior societies.”

An obvious question is how could the relatively low-density human populations of most historic northwest regions play a keystone role in shaping whole biomes? Firstly, humans were an early post-glaciation occupant of the northwest, arriving with other early colonizing species over 12K years BP (Pielou 1991). Many other colonizing species likely had some adaptions to human hunting, gathering, and culturing practices. Indeed, several wildlife species such as grizzly bear, moose, elk, and white-tail deer may have crossed the Beringia land bridge from Eurasia with humans (Kurten and Andersen 1980, Martin 1984). Thus, for these species, possibly there was no human-caused depression of wildlife populations that increased over time, but instead a long-term pattern of species co-existence in varying densities and areas depending on habitat and other factors (Butler and Campbell 2004, Campbell and Butler 2010). Secondly, human activities occurred incrementally and adaptively each year over the millennium, with the general cultural objective to maintain or enhance habitats, not radically alter or destroy them. For example, humans would vary the times and locations of burning each year, guided by daily and seasonal weather observations. Periodically their ignitions did burn large areas, but this was often early in drying periods, not at the peak of drought. The annual pattern of hunting and foraging was similarly adjusted incrementally based upon observed wildlife abundance. Thirdly, humans with relatively stable populations in an ecoregion due to the above adaptions, could, through long-distance hunting forays or trade with neighboring peoples, limit the dispersal of highly valued wildlife resources in adjacent areas that might be at low densities at the edge of their range. This process was potentially significant in determining the historical range and abundance of several species including bison, elk, white-tail deer, mule deer, woodland caribou, and barren ground caribou. Again, the process was long-term, incremental, and adaptive (McTaggart-Cowan 1995). For example, Santomauro et al. (2012) document that indigenous people recall only harvesting a few moose each year along their western range edge in central BC during the 1800s. Could these just be the few animals that had dispersed that year from the higher density moose range to the east? Finally, species such as salmon in the ocean and large rivers, caribou on barren grounds, and bison on the Great Plains, developed high-density populations in regions where for various reasons-- technology, inhospitable habitat, inter-tribal warfare

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zones--humans could not intensively harvest them. These “source” populations could have sustained or repopulated “sink” areas at the edge of the range (White et al. 2001, Sinclair et al. 2006 pp. 97–99). If the source populations occurred in an intertribal buffer zone, it was this behavior pattern of humans that directly maintained their abundance (Kay 2007a, Bayham et al. 2017).

Assuming that indigenous people’s hunting, gathering, and culturing practices did play a keystone role in structuring NW ecosystems, we then need to assess the magnitude of potential ecological change as long-term eco-cultural biomes (Kroeber 1947) transition through time into modern anthromes. Our problem here is that even if we accept the premise of the keystone role for indigenous peoples, it is difficult to quantify this change over time and space. Anthrome mapping (Ellis et al. 2010) is based upon a Euro-centric conception of geographical presentation, land use and ownership, and computer technology (satellite imagery, geographic information systems). This simply cannot capture the intricate and varied pattern of indigenous seasonal rounds within a food web, so at best, these maps classify areas where more intense types of land use are digitally mapped. When this land classification is further extended to predict where “nature” has not been altered by modern land use (Figure 6b), but where the long-term role of indigenous peoples remains undefined (Dinerstein et al. 2017), this could result in a serious underestimation on the potential ecological impacts of altered indigenous occupancy and subsistence use. In addition to Ellis et al.’s (2021) recognition of “appropriation, colonizing, and intensifying” use of indigenous lands as causes of biodiversity decline, to fully understand northwest ecosystem change, even in “wild” areas will require a detailed understanding of the potential outcomes of changing the long-term human patterns of seasonal rounds, niche construction, and foraging. The ecoregion-scale mapping of fire history and resource availability presented in this paper is an early step in obtaining this knowledge.

North America’s northwest region is one of humankind’s planetary testing grounds for biodiversity conservation. Here are the world’s first national parks (Yellowstone and Banff), and immense areas of public lands and legislated wilderness. The conservation effort ironically proceeds with a massive ecological removal experiment. Over two centuries of disease, starvation, translocation by armed force, and cultural change have nearly eliminated the role of the region’s keystone species—indigenous humans (Farrell et al. 2021). The modern human culture then established national, provincial, state, and indigenous-controlled public lands. Today resources exploited from these hinterlands provide the basis for an extremely affluent and educated society. Fortunately, the enabling legislation for most of these various forms of public lands stipulates some level of species and ecosystem conservation. Societal wealth and values continue to provide support for this objective, and fund monitoring and research programs to evaluate outcomes (Crook et al. 2021). This ongoing research shows that ecosystem conservation may require restoration of some indigenous land use practices, and perspectives on public land management, policy and legislation are evolving accordingly (Berkes 2012 pp. 271–286, Clark et al. 2016, Lake et al. 2017, Hessami et al. 2021). For example, Canada’s 1990 National Parks Act requires that the first priority for national park managers is to maintain or restore “ecological integrity” (Woodley 2010), legally defined as *“a condition that is determined to be characteristic of its natural region and likely to persist, including abiotic components and the composition and abundance of native species and biological communities, rates of change and supporting processes”* and further policy clarification from

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Parks Canada (2000 pp. 7–2) recognizes that “*the influence of Aboriginal peoples is fully consistent with ... [the] definition of ecological integrity.... this traditional human role is an important element of the ecological integrity of the ecosystems that Parks Canada is mandated to preserve or restore.*”

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

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Appendix A: Common and Scientific Species Names

Common English name	Scientific (Latin) name
ash, Oregon	<i>Fraxinus latifolia</i>
aspen	<i>Populus tremuloides</i>
bear, black	<i>Ursus americanus</i>
bear, brown	<i>Ursus arctos</i>
bear, grizzly	<i>Ursus arctos</i>
bear, polar	<i>Ursus arctos</i>
beargrass	<i>Xerophyllum spp.</i>
beaver	<i>Castor canadensis</i>
birch	<i>Betula spp.</i>
birch, paper	<i>Betula papyrifera</i>
bison	<i>Bison spp.</i>
bitterroot	<i>Lewisia rediviva</i>
blueberry	<i>Vaccinium caespitosum</i>
buffaloberry	<i>Shepherdia canadensis</i>
bunchgrass (several species)	<i>Agropyron spicatum, Festuca scabrella</i>
camas	<i>Camassia quamash</i>
caribou, barrenground and woodland	<i>Rangifer tarandus</i>
carrot, Indian/wild	<i>Perideridia gairdneri</i>
cedar, western red	<i>Thuja plicata</i>
celery, Indian	<i>Lomatium grayi, L. salmoniflorum, L. dissectum</i>
chokecherry	<i>Prunus virginiana</i>
clams	several species
clams, butter	<i>Saxidomus gigantea</i>
clams, horse	<i>Tresus capax, T. nuttallii</i>
clams, littleneck	<i>Leukoma staminea</i>
corn	<i>Zea mays</i>
cougar	<i>Felis concolor</i>
cow parsnip	<i>Heracleum lanatum</i>
coyote	<i>Canis latrans</i>
crabapple, Pacific	<i>Malus fusca</i>
crowberry	<i>Empetrum nigrum</i>
currants	<i>Ribes aureum, R. cereum</i>
dandelion	<i>Taxacum officinale</i>
deer	<i>Odocoileus spp.</i>
deer, black-tail	<i>Odocoileus hemionus columbianus</i>
deer, mule	<i>Odocoileus hemionus hemionus</i>
deer, white-tail	<i>Odocoileus virginianus</i>
Douglas-fir	<i>Pseudotsuga menziesia</i>

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elderberries	<i>Sambucus racemose</i>
elk	<i>Cervus elaphus</i>
eulachon	<i>Thaleichthys pacificus</i>
fir	<i>Abies spp.</i>
fir, grand	<i>Abies grandis</i>
fir, subalpine	<i>Abies lasiocarpa</i>
fir, white	<i>Abies concolor</i>
fireweed	<i>Epilobium angustifolium</i>
forest insects and diseases	Numerous species
goat	<i>Oreamnos americanus</i>
goose, Canada	<i>Branta canadensis</i>
gooseberry	<i>Ribes aureum, R. cereum</i>
grass, buffalo	<i>Bouteloua dactyloides</i>
grouse, ruffed	<i>Bonasa umbellus</i>
grouse, spruce	<i>Falculipennis canadensis</i>
hare, snowshoe	<i>Lepus americanus</i>
hemlock	<i>Tsuga spp.</i>
hemlock, mountain	<i>Tsuga mertensiana</i>
hemlock, western	<i>Tsuga heterophylla</i>
herring, Pacific	<i>Clupea pallasii</i>
huckleberry	<i>Vaccinium caespitosum</i>
huckleberry, black	<i>Vaccinium membranaceum</i>
humans	<i>Homo sapiens</i>
inconnu	<i>Stenodus leucichthys</i>
juniper	<i>Juniperus spp.</i>
kelp	numerous macroalgae species
kelp, bull	<i>Nereocystis luetkeana</i>
kelp, ribbon	<i>Alaria marinata</i>
labrador tea	<i>Rhododendron groenlandicum</i>
lichen, black tree	<i>Bryoria fremontii</i>
lichen, lava (westcoast)	<i>Stereocaulon spp.</i>
lichen, reindeer	<i>Cladina</i>
lynx	<i>Lynx canadensis</i>
marmot, yellow-bellied	<i>Marmota flaviventris</i>
moose	<i>Alces alces</i>
musk-ox	<i>Ovis moschatus</i>
muskrat	<i>Ondatra zibethicus</i>
mussels	<i>Mytilus spp.</i>
oak, bur	<i>Quercus macrocarpa</i>
oak, Garry	<i>Quercus garryana</i>
otter, sea	<i>Enhydra lutris</i>

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parsnip, wild	<i>Lomatium triternatum</i>
pine, jack	<i>Pinus banksiana</i>
pine, Jeffrey	<i>Pinus jeffreyi</i>
pine, lodgepole	<i>Pinus contorta</i>
pine, pinyon	<i>Pinus edulis</i>
pine, ponderosa	<i>Pinus ponderosa</i>
pine, white	<i>Pinus monticola</i>
pine, whitebark	<i>Pinus albicaulis</i>
poplar	<i>Populus</i> spp.
prairie turnip	<i>Psoralea esculenta</i>
pronghorn antelope	<i>Antilocapra americana</i>
ptarmigan	<i>Lagopus</i> spp.
redwood	<i>Sequoia sempervirens</i>
riceroot, northern	<i>Fritillaria camschatcensis</i>
rose	<i>Rosa</i> spp.
sagebrush	<i>Artemisia</i> spp.
salmon	<i>Oncorhynchus</i> spp.
salmon, chinook	<i>Oncorhynchus tshawytscha</i>
salmonberry	<i>Rubus spectabilis</i>
saskatoon	<i>Amelanchier alnifolia</i>
seals	Phocidae family
seaweed	<i>Porphyra</i> spp, <i>Gracilaria lemaneiformis</i>
serviceberry	<i>Amelanchier alnifolia</i>
sheep	<i>Ovis</i> spp.
sheep, bighorn	<i>Ovis canadensis</i>
sheep, Dall's	<i>Ovis dalli</i>
shellfish	see mussels, clams, urchins
soapberry	<i>Sophora canadensis</i>
spring beauty	<i>Claytonia lanceolata</i>
spruce	<i>Picea</i> spp.
spruce, black	<i>Picea</i>
spruce, sitka	<i>Picea sitchensis</i>
spruce, white	<i>Picea glauca</i>
suckers	<i>Catostomus macrocheilus, C. columbianus</i>
tamarack	<i>Larix laricina</i>
trout, lake	<i>Salvelinus namaycush</i>
trout, steelhead	<i>Oncorhynchus mykiss</i>
urchins, sea	<i>Strongylocentrotus</i> spp.
walrus	<i>Odobenus rosmarus</i>
wapato	<i>Sagittaria latifolia</i>
whale, narwhal	<i>Monodon monoceros</i>

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whale, beluga	<i>Delphinapterus leucas</i>
wheatgrass	<i>Agropyron spicatum,</i>
whitefish	<i>Prosopium williamsoni</i>
wild chives	<i>Allium spp.</i>
willow	<i>Salix spp.</i>
wolf	<i>Canis lupus</i>