



Human paleoecological integration in subarctic eastern Beringia



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ABSTRACT

We contribute to the understanding of megafauna extinction and human dispersal in subarctic eastern Beringia by focusing on changes in the trophic dynamics of the large mammal community as well as the ecological role of humans as a predator and competitor. We reconstruct habitat use by megafauna and humans throughout the Pleistocene–Holocene boundary based on zooarchaeological data and stable isotope ratios of collagen. Our results are consistent with habitat heterogeneity and availability being important factors in the changing abundance of large herbivores. We argue that an increase in herbivore diversity and biomass at the beginning of the Bølling–Allerød interstadial and a relative lack of competitors favored the initial human colonization of subarctic eastern Beringia. As herbivore resources dwindled later in the Late Glacial, people increasingly relied on bison and wapiti. By efficiently extracting some of the highest-ranked resources in the landscape, people are likely to have contributed to the trophic displacement or regional extirpation of other large predators. The ecological patterns that we observe in subarctic eastern Beringia are consistent with a mixture of both top-down and bottom-up controls over biotic turnover.

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1. Introduction

The fossil record of eastern Beringia at the Pleistocene–Holocene boundary has drawn much attention from archaeologists and paleoecologists for its relevance to questions central to both disciplines. The paleontological record of Beringia is one of the best-preserved examples of the Late Pleistocene mammalian megafauna¹ that disappeared at the onset of the Holocene. In parallel, its archaeological record documents one of the latest stages of modern human dispersal, with the earliest permanent settlement of latitudes above 60° north, as well as the earliest colonization of what would become North America. Questions related to megafauna extinction and human dispersal are at the core of both paleoecology and archaeology in that they bear strongly on our interpretative models of the functioning of past and present ecosystems and of the sustainable integration of hunter-gatherer populations within

communities of large mammals.

Processes and causes leading up to Ice-Age megafauna extinction and eventual replacement have been the subject of intense discussion for decades. Some have considered Pleistocene megafauna extinction to be the end-result of protracted population declines, in response to habitat degradation/reduction from climatic deterioration or instability throughout MIS 3–2 (e.g. Szpak et al., 2010; Rabanus-Wallace et al., 2017). Hypotheses emphasizing long-term climatic processes are supported by genetic evidence of population stress and decline among steppe bison (Shapiro et al., 2004), brown bear (Leonard et al., 2000; Barnes et al., 2002), lion (Barnett et al., 2009), mammoth (Debruyne et al., 2008), and, from bone measurements, horse (Guthrie, 2003). Climate-based hypotheses however rely for the most part on the coincidence between climate change and population decline and tend to overlook the specific processes by which megafauna would have gone extinct. Species' tolerances depend on a variety of physical conditions and pattern of coexistence, and few of these studies have discussed how complex ecological interactions may have contributed to population dynamics (for exceptions see Guthrie, 1984; Mann et al., 2013, 2015).

Hypotheses based on ecological interactions have been for the

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¹ Megafauna include herbivores >44 kg (Stuart, 1991) and carnivores > 21.5 kg (Carbone et al., 1999).

most part limited to models of extinction resulting from human predation. In eastern Beringia, these have centered on horse and mammoth, which are described by some as ecologically naïve prey that human hunters would have over-harvested, surpassing their natural population replacement rate (e.g. Surovell et al., 2016). In turn, the loss of these large ecosystem engineers and of their structural influence on soil formation and vegetation succession would have triggered a larger biome shift (Zimov et al., 1995). However, this “overkill hypothesis” is, also, based foremost on the temporal coincidence between human colonization and horse and mammoth extinction (Guthrie, 2003, 2006; Stuart et al., 2004; Solow et al., 2006; Buck and Bard, 2007; Nogués-Bravo et al., 2008; Haile et al., 2009; MacDonald et al., 2012; Bradshaw et al., 2012; Surovell et al., 2016). It overlooks the facts that (i) with the exception of insular ecosystems and post-industrial human societies, large herbivore populations tend to be regulated by bottom-up (habitat) rather than top-down (predation) processes (Sinclair, 2003; Sinclair et al., 2003; Owen-Smith and Mills, 2008; Hopcraft et al., 2010; Fritz et al., 2011); (ii) current archaeological data suggest that eastern Beringian hunters were mostly focusing on bison and wapiti (Table 2 further in text) even when and where horse were also available (Mann et al., 2001, 2013); and (iii) some species that are particularly vulnerable to human predation due to their behavior, such as the muskox, survived into the Late Holocene.

Rather than concentrating on a few selected herbivore species, human hunters may have had more impact on the structure of the predator guild² and the overall food web. Humans have a long history of competition and co-evolution with other large predators (Stiner, 1994, 2002, 2004, Brantingham, 1998a,b, Van Valkenburgh, 2001, Discamps et al., 2011, Rodríguez-Gómez et al., 2013, 2016). As such the ecological role and impact of people in the eastern Beringia megafauna communities may have depended on how resources were partitioned among human and non-human predators and the extent of competitive exclusion on the breadth of their respective niches. Humans as a species have a flexible diet, varying in recent times from a specialized foraging to broad omnivory (e.g. Stiner et al., 2000). This versatility generally allows humans to interact with other species at multiple trophic levels and spatial scales (Brose et al., 2005) and, depending on diet choice along a continuum of specialization to generalism, people may impact the whole trophic network of large mammals, or alternatively contribute to its stabilization.

In this article we contribute to the paleoecological and archaeological issues related to megafauna turnover at the Pleistocene-Holocene boundary in subarctic eastern Beringia. In contrast to previous studies, we focus on community-level interactions and specifically consider the role of humans as both a predator and a competitor. Our results are consistent with people having a major ecological role in the megafauna turnover, but probably more as a competitor than as a predator.

2. Background

Prior to the Last Glacial Maximum (LGM; about 24,000–19,000 cal B.P.) eastern Beringia hosted a high biomass megafauna community which thrived in a dry, nutrient-rich vegetation landscape dominated by graminoids and high-protein forbs (Goetcheus and Birks, 2001; Zazula et al., 2003; Blinnikov et al., 2011; Zimov et al., 2012; Mann et al., 2013; Willerslev et al., 2014). This “mammoth-steppe” biome supported a range of sympatric species that do not co-exist today, and for this reason is often

considered to lack modern analogues (Guthrie, 2001; Goetcheus and Birks, 2001).

While the Mammoth Steppe ecosystem had remained essentially unchanged throughout much of the Late Pleistocene (MIS 5–2), it abruptly came to an end during the Late Glacial (about 19,000–11,700 cal B.P.). The dominant vegetation type in eastern Beringia shifted to shrub tundra with dwarf birch (*Betula nana*) by 16,000 to 14,000 cal. BP. In the subarctic, it then transitioned to a more closed environment by 13,000 to 10,000 cal. BP, including poplar (*Populus balsamifera* and *P. tremuloides*) and white spruce (*Picea glauca*) (Bigelow and Powers, 2001; Edwards et al., 2001; Anderson et al., 2004; Llyod et al., 2006; Viau et al., 2008), while at the same time tussock tundra became dominant in the Arctic (Mann et al., 2010; Oswald et al., 2014). In both regions vegetation change was accompanied by the spread of wetlands and peatlands and a general stabilization of the soils (Jones and Yu, 2010; Mann et al., 2010; Reuther, 2013). Changes in vegetation and soils appear synchronous with dramatic changes in the geographical ranges of up to a dozen species or genetically distinct populations of large mammals. Previously uncorded populations migrated from either western Beringia or North America while others got regionally extirpated, altering the composition of the megafauna community throughout the Late Glacial (Fig. 1).

In the subarctic up to six species or genetically distinct populations seemingly became extinct during a short interval ca. 15,000–14,000 cal B.P. The appearance of new migrants is not as well dated; nevertheless, up to seven species spread into eastern Beringia from either western Beringia or North America. Megafaunal diversity peaked at 15–18 species around 14,000 cal. BP forming a non-analogue community whose diversity was unmatched prior to and after that time.

3. Approach

Paleoecological studies are often based on isotopic data with carbon and nitrogen isotope values reflecting the range of habitats and resources used by the animal during its life - its Hutchinsonian niche (Newsome et al., 2007; Flaherty and Ben-David, 2010). Niche is constrained to some extent by an animal's morphology and is generally conserved through time in the fossil record (Martinez-Meyer et al., 2004); however, there is considerable flexibility in dietary and habitat use strategies among clades such as canids (Meachen et al., 2014; Pardi and Smith, 2015; Newsome et al., 2016), ursids (Milakovic and Parker, 2013; Bocherens, 2015), cervids (Drucker et al., 2011; Rivals and Semperebon, 2016) and bovids (Guthrie, 1980; Rivals and Semperebon, 2011), enabling members of a same guild to occupy significantly different niches (Kartzinel et al., 2015).

There is an apparent abundance of isotopic data from Beringian megafauna (Bocherens et al., 1996; Iacumin et al., 2000; Guthrie, 2001; Bocherens, 2003, 2015; Leonard et al., 2007; Fox-Dobbs et al., 2008; Rivals et al., 2010; Yeakel et al., 2013; Mann et al., 2013). However, these studies with the exceptions of Mann and colleagues' work in Arctic eastern Beringia (Mann et al., 2013; Mann et al., 2015) lack spatial and temporal resolution, sometimes retaining scales as large as the whole Mammoth Steppe (Iberia to the Yukon) and/or the entire Late Pleistocene. In contrast, we considered for this study a restricted region and period with a megafauna community formed of sympatric, co-extant species. We conducted additional isotopic sampling to obtain an adequate sample of specimens, increasing by more than three folds the existing dataset.

Data on human diets were derived from the archaeological literature and unpublished data from the authors, acknowledging that reconstructing diet from animal bones left at archaeological

² Defined here as the group of species that exploit similar resources (Simberloff and Dayan, 1991).

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