



# Bottom-up versus top-down megafauna–vegetation interactions in ancient Beringia

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During the last glacial period, the Bering Land Bridge was inhabited by a diverse bestiary of large mammals, many now extinct (1), and covered by the steppe-tundra, a widespread, now largely vanished biome (2). Given the twinned losses of big animals and a major ecosystem during the last deglaciation, a central question is to understand whether and how these events were connected. Did bottom-up processes rule, in which changing climates led to changing habitats, which then triggered population declines and, ultimately, extinctions of Arctic megaherbivores? Did top-down processes govern, in which declining populations of megaherbivores, pressured by the regional arrival of humans by at least 32,000 y ago (3), led to altered nutrient cycling and reduced grazing strength, facilitating a widespread replacement of a grass–forb steppe-tundra (4) with a shrub tundra dominated by willow (*Salix*), birch (*Betula*), and alder (*Alnus*) (5)? Or, given that these are complex ecosystems governed by multiple interacting processes, were extinctions and ecosystem transformations all part of one larger positive feedback loop? In PNAS, Monteath et al. (6) shed light on these questions of top-down and bottom-up processes through a careful analysis of the temporal and spatial patterns of late Quaternary megafaunal extinctions and vegetation transformation in eastern Beringia, now known as Alaska.

Better answers to these questions have clear implications for contemporary global change ecology and conservation biology. For, if climate was the ultimate driver of Beringian ecosystem transformations and extinctions, then this adds urgency to today's efforts to conserve habitats and helping species adapt to climate change, for example, via the resist–accept–direct framework (7). Conversely, evidence that top-down trophic processes were decisive would add impetus to efforts to restore

ecosystem functioning through rewilding efforts (8), by either reintroducing extirpated species to their former range or functional analogs if the species are fully extinct. Evidence for strong top-down processes would also imply that early humans had a major indirect role in vegetation transformations at subcontinental scales, adding weight to arguments that the Anthropocene began millennia ago (9).

## Determining Causes of Species Extinctions in a Rapidly Changing World

The many large ecological and environmental changes during the last deglaciation make it one of the best geological model systems for the biospheric transformations currently underway, yet also challenge efforts to determine causality. Carbon dioxide concentrations rose by 50%, triggering a global warming of 6 °C to 7 °C (10, 11) and the melting of ice sheets worldwide, raising sea level by over 100 m. Populations of an evolutionarily novel species (humans) were expanding worldwide. Plant and animal ranges shifted individually by up to hundreds to thousands of kilometers in the midlatitudes and upper latitudes, leading to rapid rates of change (12) and mixtures of species with no modern analog. Globally, two-thirds of large terrestrial vertebrate species went extinct during the Late Quaternary (13), while fire regimes intensified (14). Paleoecologists frequently use temporal lead–lag relationships to empirically test causal hypotheses (i.e., if event B happens after (lags) event A, then B cannot have caused A). However, with all the many changes underway during the last deglaciation, combined with uncertainties in radiocarbon and other dating methods, confidently establishing lead–lag relationships and causality is nontrivial.

The synthetic analysis by Monteath et al. (6) combines 361 previously published directly dated bones

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from extinct or extirpated megafauna (woolly mammoth [*Mammuthus primigenius*], steppe bison [*Bison priscus*], and horse [*Equus* spp. and *Haringtonhippus francisci*]) and extant megafauna (moose [*Alces alces*] and wapiti [*Cervus canadensis*]), 169 directly dated shrub macrofossils, and 15 fossil pollen records, the latter from the Neotoma Paleoecology Database (<https://www.neotomadb.org>). All faunal records were screened to remove bones dated only by indirect stratigraphic association and those dated using older and less accurate methods. The age inferences for all fossil pollen records were recalculated using the latest age–depth modeling software [OxCal (15)] and radiocarbon calibration curve [IntCal20 (16)]. Fans of Scrat the Squirrel will be pleased to know that radiocarbon-dated ground squirrel nests provided additional information about the presence of steppe-tundra and deep active permafrost suitable for burrowing.

The authors (6) show that the shrub expansion in eastern Beringia mostly happened first, between 16,000 and 14,000 y ago, while the megafaunal declines and extinctions happened later, between 15,000 and 12,000 y ago. Moreover, shrub tundra expanded during a time of frequent bone occurrences for the now-extinct woolly mammoth and horse, suggesting that tundra shrub expansion was not hindered by these grazers. Willow expanded first, followed by birch, consistent with a higher climate tolerance of Arctic willow species for cold and dry conditions. Ground squirrel nests are reported between 14,200 and 13,000 y ago, suggesting at least a temporary coexistence of shrub tundra and steppe-tundra and a mosaic of habitats during the period of grazer megaherbivore extinction.

### Implications for Contemporary Biodiversity Management

Hence, Monteath et al. (6) convincingly demonstrate that, in eastern Beringia at least, the observed lead–lag relationships are inconsistent with the hypothesis of strong governance of vegetation–megafaunal dynamics by top-down trophic processes. Rather, shrub expansion appears to have been governed by changing climates in eastern Beringia toward warmer, wetter, and more highly seasonal climates during the late Pleistocene to Early Holocene (17). The expansion of moose populations, an obligate browser, at 14 ka surely must be linked to increased forage availability, while the declines and extinctions of grazers such as woolly mammoth, steppe bison, and horse appear to have been facilitated by habitat losses, with human activity likely also contributing. If so, this demonstrated sensitivity of high-latitude ecosystems to past climate change carries alarming implications: The Arctic today is one of the fastest-warming parts of the world, and widespread changes to Arctic ecosystems are already emerging in response to rising temperatures and intensified fire regimes (18). Which Arctic animals of today will be the woolly mammoths of tomorrow?

A few minor cautions to keep in mind when reading this paper (6). First, this is one study system, and evidence against top-down controls here is not evidence against their importance

elsewhere. For example, Groff et al. (19) recently showed that the expansion of tussock grasslands on the Falkland Islands was regulated by the establishment of seabird colonies that enhanced transfers of nutrients from marine to terrestrial ecosystems. Second, bone frequency may carry a complex relationship to megafaunal population abundance, given the vagaries of collection efforts and given that past environmental change may alter the likelihood of bone preservation. This study also does not leverage some of the newer proxies for megafaunal presence and function, including coprophilous fungal spore records (20) and ancient sedimentary DNA (21). Ancient DNA records hint at the persistence of at least small populations of mammoth and horse from the central Yukon as late as 6,000 y ago, long after the apparent disappearance of these animals from the bone record (21). These critiques are not serious—the Monteath et al. (6) paper makes a valuable contribution, and its conclusions are not dependent on exact timing of final extinction—but rather highlight that we can anticipate an ever-better understanding of the spatiotemporal dynamics of past species extinctions and ecosystem transformations as new ecosystem and biodiversity proxies such as ancient DNA emerge and are integrated with classic approaches. The time is ripe for further multiproxy primary data campaigns and data syntheses.

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Lastly, this work (6) demonstrates the longevity of paleontological data and the power of careful data analytics that employ open community curated data resources for insights into past ecosystem dynamics at broad spatiotemporal scales. Many of the primary records analyzed here were collected decades ago. Thanks to on-going primary data campaigns and their painstaking stewardship and curation in community databases (22), we have an ever-sharpening understanding of the past distribution and diversity of life and the underlying environmental and anthropogenic drivers. Yet big data, if analyzed incautiously, can add more noise than insight, particularly for studies of the late Quaternary megafaunal extinctions, where inaccurate age estimates can lead to major errors in estimates of extinction timing and lead–lag relationships (23). Monteath et al. did the work the right way, carefully gathering and reviewing records to exclude those that were less securely constrained by accurate radiocarbon dates. Hence, this paper offers an excellent example of how the rapidly growing field of conservation paleobiology (24), working carefully at broad spatiotemporal scales, can directly inform contemporary efforts to conserve biodiversity and help species adapt to the rapidly changing environments of the Anthropocene.

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