



Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia

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Abstract

To account for the vastness of the northern arid steppes during Glacial episodes, I propose the proximate key variable was simply frequent clear skies. This hitherto under-emphasized point is the hub which best explains many questions. Low maritime cloud cover best accounts for today's tundra, and in a related way, the cloudy Polar Front accounts for the whole of the taiga. Even during Glacial maxima, the proximity of the sea to the Bering isthmus created intermittent maritime cloud cover. This regional cloud cover produced an ecological interruption, or buckle, of the arid steppe belt. While this Beringian mesic buckle did not serve as an intercontinental ecological barrier to most steppe-adapted species, it does seem to have limited the distributions of woolly rhinos, camels, American kiangs, short-faced bears, badgers, and some others. At the beginning of the Holocene, this narrow refugium seems to have been a source of some mesic-adapted species which colonized westward into the now tundra vegetation of northern Asia and eastward into northern North America. This Holocene expansion from a limited and regional Pleistocene refugium created our present misconceptions about Beringia. The mid-strait mesic ecological conditions were the exception to the more extensive, arid-adapted, communities of the Mammoth Steppe. © 2000 Published by Elsevier Science Ltd. All rights reserved.

1. Introduction

Today, the north is primarily wetlands. Most northern soils are paludified, or waterlogged, lakes are common, and the summer air is alive with wetland insects. Today's boreal vegetation is predominantly wet and cold-adapted and it is mostly inedible to large mammalian herbivores. Yet physical and biotic evidence from the late Pleistocene portrays a very different pattern of habitats that has no extensive analog in the far north, as we know it. We can only conclude from the fossil evidence that during the last full glacial (LGM), say 18,000 B.P., most of the north was unimaginably arid. Compared to today, there were virtually no standing lakes, trees or boglands, and only in rare spots were peats forming. Rivers were reduced to streams and low-sward herbaceous communities were widespread. These low-profile plants were apparently more deeply rooted than are today's tundra plants. We can conclude that loess sheets, sand seas, dune fields and wind were common features of this aridity; therefore, Pleistocene skies must have often been dusty. Winter winds would have caused drifting snow and the dirtying of those drifts from blown silt. For those of us accus-

tomed to many months of downy pristine snow-cover and frequent summer drizzles, swarms of insects, tussocks, thick humus mats, cushiony forest floors, tea-colored ponds, impenetrable alder and willow thickets, this emerging image of intense aridity in boreal environments during the late Pleistocene is sometimes difficult to credit.

I propose that we have made a series of mistakes in our pursuit of Pleistocene paleoecology of the north. Not very long ago, it was assumed that the Pleistocene unglaciated north was much like today, except colder. Because cold is such a critical variable today it was the obvious feature we could use to explain things like the elimination of trees. And acceptance of the Milankovich insolation cycles made it easy to derive more cold by ratcheting-up these extra-terrestrial forces. That simplistic assumption was a mistake.

As new fossil data began to show no-analog differences with the present, the next variable identified, in addition to cold, was aridity. Instead of looking closely at the various potential forces for aridity we assumed the most obvious, simply reduced precipitation. This bias also got us off on another inappropriate route. That was our second mistake.

Hultén (1937) described Beringia, a special Pleistocene floristic refugium for mesic-adapted tundra plants. This

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floristic refugium was a radical idea, and neatly accounted for the conspecific distribution on opposite sides of the now flooded strait. Geologists and paleoecologists have leaned hard on the idea of a 'Beringia' and have transformed Hultén's suggestion into a comprehensive vegetational concept, assuming that Hultén's floristic connections were the key to reconstructing the big picture of northern paleoecology. Focusing on the Russian northeast and northwestern Alaska as if it were the 'type-site' of the LGM has delayed our realization that conditions in this region were not the norm throughout the north. In actuality, neither the Pleistocene biotic geography nor the pattern of Pleistocene aridity corresponded to the area defined as Beringia; they were much larger.

2. A new paradigm

Recent publications of Anderson and Brubaker (1994), Hamilton et al. (1993) and Elias et al. (1996) have changed my views about the pattern of northern paleoecology in the Bering Strait area. Their new data have sharpened patterns which they and others have suggested for years, but these patterns directly contradicted conclusions from my data (and data of many other people working in more continental regions). I now acknowledge that their data reflect reality. So how do we explain the two contradictory data sets? I think we can do this by looking at the overall picture in a different way, and by so doing a new paradigm jumps out at us; there was a more mesic buckle in the arid steppic belt. This new paradigm links four themes: (1) The global-scale causes of aridity and steppe. (2) The local-scale proximate forces of aridity and steppe. (3) The explanation of the more mesic Beringian Buckle, geographic refugium and barrier. (4) Grazer biology and the productivity paradox.

I. Megacontinental aridity. Evidence for an intense aridity is clear during Glacials (Hopkins et al., 1982; Vrba et al., 1995), though its causes on such a megacontinental scale have been clouded in ambiguity. In the far north, aridity would have favored plants which today persist only in the most limited habitats, such as south-facing steep slopes, or other local, especially arid locations. We need to imagine a late Pleistocene environment in which the tables were turned, with mesic-adapted biota found only in uniquely damp situations and arid-adapted species dominant and wide-spread. However, the picture emerging is not just a matter of proportional changes from mesic to arid, but one so extreme that many mesic-adapted forest, forest succession, and forest floor animals and plants were driven to regional extinction throughout the north (Hopkins et al., 1982; Anderson and Brubaker, 1994). The northern perimeters of the distributions of many of these plant and animal species, which are domi-

nant northern species today, were, in the late Pleistocene, thousands of kilometers to the south. This phenomenon is true across Europe, Asia, and northeastern North America.

II. Forces producing aridity. We have treated too lightly the specific causes of this cold-arid northern environment during Glacial times, attributing them in a direct way to periglacial effects and the changing earth-sun geometry of Milankovich insolation cycles (Hopkins et al., 1982; Bartlein et al., 1991). But proximate causes were a combination of features; of these, there is an unrecognized, proximate key element that I propose was crucial – a much higher frequency of clear skies than seen today. This enhanced evapotranspiration in summer (aridity) and radiation deficit to the black night sky in winter (cold).

III. Beringian buckle. We have been trying to fit an upside down idea of Beringia onto our data. Evidence developed over several decades makes it clear that the Pleistocene floristic refugium Hultén called Beringia was a comparatively small zone and not at all representative of the area now delineated as Beringia nor of the more extensive Mammoth Steppe. Because of its exposure to low cloud cover of maritime origin, this more mesic zone lying along what is now the flooded strait was a unique buckle in the giant belt of the Mammoth Steppe.

IV. Grazing ecology, productivity paradox and megaherbivore keystones. The diet of these Pleistocene herbivorous mammals follows their adaptive norms – the grazers were primarily eating xerophilous sedges and grasses. Combining that certainty with the reconstructed ecology of cold steppes we can resolve the productivity paradox. Though large mammals themselves may have had important effects on the steppe vegetation, they probably were not the key in producing and maintaining it.

2.1. Megacontinental aridity – the mammoth steppe

There are many questions to be answered. How could such an arid habitat extend over such a vast area? What was its unifying woof? Why is there no extensive modern biotic analog? Why is its greater biotic kinship with steppe rather than with tundra?

2.1.1. The role of "periglacial effects."

What caused this special cold-arid boreal belt which almost encircled the globe? Historically, our understanding of this habitat began in Europe (see review by Ballantyne and Harris, 1994). In northwestern Europe, the landscape effects of cold (widespread cryogenic geological features, elimination of even cold-tolerant woody plants, expansion of the 'woolly' mammals, and so on) were directly linked to the proximity of glaciers. In England, one can easily imagine that the local ice-wedge casts and soil cryoturbation logically resulted from the enormous Devensian ice mass not many kilometers to the

north of Cambridge. But this very proximity seems to have created a general misconception about ‘periglacial’ matters. The cold-arid character and extent of the Mammoth Steppe is more complex than simple glacial proximity. Vast areas of Asia many hundreds or even thousands of kilometers from significant glacial proximity still exhibit features similar to ‘periglacial’ landscapes.

I suspect this idea of *periglaciality* was compounded in the United States by early researchers who also saw Pleistocene evidence of glaciers right next to the cryogenic landscapes in the Northeast (see Flint, 1971). There, in New England and along the Hudson, glacial effects are everywhere and one can credit this periglacial image. The word ‘*peri*’ implies adjacency, like standing next to an open refrigerator door. Although the large ice masses certainly had a profound effect on weather tracts and moisture depletion, attributing the Mammoth Steppe simply to ‘periglacial effects’ does not let us understand the complexity of large scale forces which were responsible. ‘Periglacial’ could be used appropriately in certain situations where it may actually apply, but on the whole it is an outdated concept built on a misconception and we are better off without it. Certainly, it is of little help to us here.

2.1.2. *Origins of the Megacontinental Mammoth Steppe*

The ultimate forcing agents of Pleistocene changes are hotly debated, centering around CO₂ atmospheric concentrations, solar input, oceanic current directions, and many other elements, all of which seem to change in synchrony with the climatic shifts. In the minds of many Quaternary climatologists (Partridge et al., 1995), tectonism seem however to be the main front-runner theory in this controversy (Manabe and Terpstra, 1974). Mountain uplift occurred in many continents during the Quaternary, but nowhere was this more pronounced than in Central Asia, which also concerns us here as it seems to have been responsible for much of the aridity of the Mammoth Steppe. Throughout the Tertiary the Indian Plate was driving into southern Asia, creating the largest mountain range in the world. Apparently, the rate of uplift increased during the last 2.5 million years, and especially during the last million (DeMenocal and Rind, 1993). As a result, the mountains of the Tibetan Plateau reached their greatest height, and produced their greatest climatic repercussions in blocking atmospheric flow from the monsoons of southeast Asia (Ruddiman and Kutzbach, 1989). This orography was responsible for maintaining both the Siberian–Mongolian high pressure and Aleutian low-pressure systems in their present locations (Manabe and Terpstra, 1974; Ding et al., 1992). A core of extreme aridity developed in the blocked monsoonal shadow.

From Western China and Mongolia this core of aridity now extends far to the West and East. However, during the Pleistocene this steppe at times extended

much further and it apparently expanded and contracted in synchrony with the Milankovich cycle. A strong winter monsoon is needed to intensify the Siberian–Mongolian high-pressure system; winter monsoons seem linked to intensification of clear skies and cold in the far north (An et al., 1995). It is also likely that the intensity of the Siberian–Mongolian high is strongly associated with northern hemisphere ice cover (DeMenocal and Rind, 1993; Chen et al., 1997). During the Milankovich-predicted low-insolation times, when aridity in Northern Asia intensified (Chen et al., 1997) and extended west into Europe, and eastward into northeastern Asia, the landscape took on a quite different character. It became a cold steppe, underlain with permafrost, and dominated mainly by cold-tolerant and arid-adapted species, including mixes of lion, horse, antelope, and rhino combining with collared lemming, arctic fox, reindeer, and muskoxen (Guthrie, 1990). Invertebrate fossils also exhibit unusual mixes of species (Berman and Alfimov, 1997).

Paleoclimatic reconstructions of atmospheric flow (see discussion in Soffer and Gamble, 1990) point to a latitudinally stable westward flow of the winter (January) storm track across Europe at about 47°N latitude between the Scandinavian ice sheet and that of the Alps, continuing on that latitude directly across Asia just north of the Tibetan Plateau. This runs down the West–East bore of the Mammoth Steppe. All the data of direction of loess deposition agrees with this (Porter and An, 1995).

So several geographic features (Fig. 1) seem to have worked in a complementary way to exaggerate the periodic spread of the cold steppes out of central Asia, during Milankovich low-insolation times both by limiting moisture and by promoting clear skies: (1) The driving force for the core Asian steppe was an enormous and stable high-pressure system north of the Tibetan Plateau. (2) Deflection of the larger portion of the Gulf Stream southward, past southern Spain onto the coast of Africa, reduced temperatures (hence moisture and cloud cover) that the Atlantic current brings to Western Europe. (3) Growth of the Scandinavian ice sheet created a barrier to North Atlantic moisture. (4) Likewise, the icing over of the North Atlantic sea surface with reduced flow of moisture from the east. (5) The winter (January) storm track seems to have swept across Eurasia on this axis. (6) Lowered sea levels exposed a large continental shelf to the north and east producing a vast northern plain which increased continentality to the north. (7) In the very far east, North American glaciers shielded interior Alaska and the Yukon Territory from moisture flow.

These physical barriers to moisture flow created a vast arid basin or protected ‘inner court’ spanning parts of three continents. Undoubtedly innumerable local effects would have shaped local conditions and created special situations, but the coherence of the Mammoth Steppe was much greater than local influences, particularly the local effects of ice sheets.

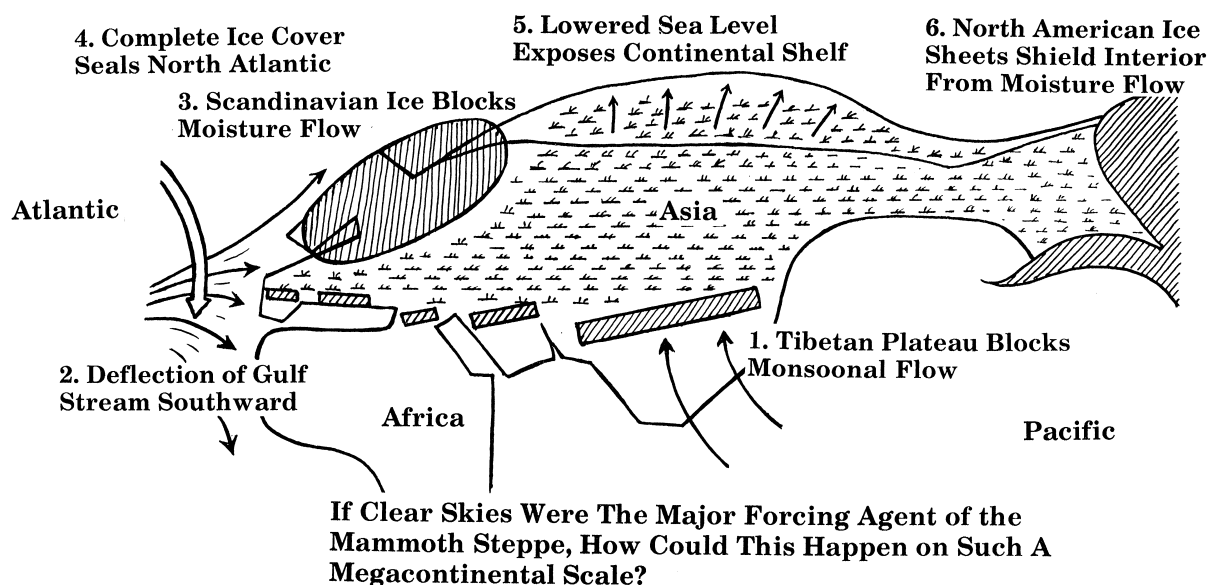


Fig. 1. A schematic map of Eurasia and northeastern North America. During Glacial times the interior of Asia, most of Europe and parts of Alaska and northeastern Canada were part of a giant interior court or 'basin,' protected from moisture flow on all sides. This allowed predominantly clear skies throughout the year, allowing the steppic biota to spread over this vast area from its homeland in central Asia.

2.1.3. The problem of modern analogs on such a megacontinental scale

Plants are limited in the polar extremes by the short cold summer. Cwynar and Ritchie (1980) and Colinvaux and West (1984) were certainly right in saying that a barren and unproductive polar desert could not support a complex large mammal community, such as was described for the Mammoth Steppe. This led them into the wrong horn of a dilemma – if it were a polar desert then there were no large mammals. But the large mammals were there, it was not polar desert. The evidence for the over-all character of the biota of the Mammoth Steppe is remarkably different than that of polar deserts.

This misconception points out the mistake of trying to reconstruct northern paleoecology in the late Pleistocene by simply making it colder. Of course, cold is important in our reconstruction; yet summer LGM Milankovich insolation values are only a little different from modern values (Berger, 1978). I will discuss evidence that it was colder, colder from many different ways and degrees throughout this vast area. Exactly why it was cold is an interesting problem, but the answer to that problem may not alone explain the aridity.

Throughout the 1970s and 1980s there was a revolution in paleobiologists' thinking. Data began to show that past communities, even from the recent past, were often composed of species not found in association today. We came to realize that biomes were not reacting to climatic change as units but as individual species. Response to climatic changes was surprisingly individualistic with unexpected species by species differences. Our faunal and floral evidence revealed species mixes for

which we could find few or no modern analogs (e.g., for plants see Davis, 1981; Wessner and Armbruster, 1991; Anderson and Brubaker, 1994, for animals see Matthews, 1982, Guthrie, 1984b; Graham, 1987).

Obviously, these 'no-analog' associations can be overemphasized and misunderstood. In part, it is a metaphor for saying that biomes do not move around lock-step through time. This concept does not mean to suggest that there are never any valid analogs between the present and past, we would be nowhere without them; the past coexistence of reindeer (*Rangifer*) and saiga (*Saiga*) is informative to our imagination because of the information we can draw from them individually in the present, despite their non-overlap today (Sher, 1968; Guthrie et al., in press). There are patches of steppic communities in north-central Asia, some quite expansive, which are scattered into boreal habitats, which do provide some rough analogs to the Mammoth Steppe. And in North America there are rare, but similar situations, particularly on steep south-facing slopes. These steppic islands in the ocean of tundra/boreal forest help researchers better understand the tension of forces that produce particular biotic associations and physiognomies (Wessner and Armbruster, 1991). Taking the extreme no-analog position is a little too close to "Geological Postmodernism." It is certainly a truism that the covariance of many species' responses to varying climates is high, and some species pairs are their own interdependent variables – forest floor species are obviously dependent on the special environment that forest species create. These co-covariant clusters mean that biomes are real coherent entities, in degree. But it is this 'degree' aspect which gives us caution and perhaps insights.

The vast Pleistocene steppe seems to have had a high degree of unusual associations, not only in terms of species composition but also novel assemblages above the level of the community. Pleistocene biomes were different and some apparently had an overall physiognomic character unlike any today. It is one thing to reconstruct a past comprised entirely of species that are extinct, a Jurassic Parkland, for example, but it is almost an even greater stretch for the imagination to reconstruct a past environment which includes extant species but in peculiar associations and habitats. Try to imagine your favorite comedians playing serious or tragic roles. Can you conceive of a performance in which reindeer, cheetah, muskoxen, rhino, hyena, leopard, rhino, horse, ibex, sheep, arctic fox, and arctic lemming are on stage together? It sounds a farce or a comedy, but it is historical non-fiction.

2.1.4. Is it fair to place such a vast area under one biotic designation?

The concept of a biome is very useful even if, as an abstraction, it is technically fuzzy. Generally, plant communities do come in widely distributed physiognomically recognizable units. This is despite the fact that the species behave individualistically and thus specific composition within these biomes vary from place to place, and time to time. But, to repeat, just occasionally there are total biomes without modern analog.

The taxonomic difficulty with pollen from northern treeless landscapes makes it almost impossible to use *transfer function* concepts so common elsewhere. This transfer function process assumes that the correlation of modern pollen rain percentages with characteristic vegetation patterns can be transferred directly to the past. A crucial assumption of transfer functions is (1) proper identification at species level, (2) close association between a habitat and a particular species. Although these assumptions sometime work with arboreal pollen, they do not work with groups like grasses, sedges, or sages, because these are indistinguishable at lower taxonomic levels. Within a genus, sage (*Artemisia*) or the grass family, for example, the species vary all over the map in ecological specificity. So arguing that Pleistocene pollen percentages from the far north look like modern pollen rain from the Arctic Coastal Plain (Anderson and Brubaker, 1994) does not mean that the Pleistocene circumpolar northern vegetation (France, Russian Plain, Caucasus, Yenesi, Yakutsk, Fairbanks, etc.) can all be equated with modern Point Barrow, Alaska. In fact, these same Pleistocene pollen percentages are also very similar to those in the heartland of today's steppes.

2.1.5. What kind of megacontinental aridity must we explain?

First, some generalizations about this vast Mammoth Steppe: though it undoubtedly had many local variants,

and microclimates, the overall pollen record, and macrofossils, seem to indicate a low sward of herbaceous plants, with grasses, sedges, forbs and sages predominating. The fossil evidence shows that this kind of vegetation virtually eliminated browsing specialists (Guthrie, in prep.) like moose, *Alces*, and that a community of large mammal grazers were dominated in biomass by the “big three” – bison (*Bison*), horse (*Equus*) and woolly mammoth (*Mammuthus*), etc.

But these are not just hardy southern species that wander up into the north on occasion (Colinvaux and West, 1984). Over 2.5 Myr this steppe became the homeland for large grazers, their center of evolution and dispersal (Sher, 1986). So, it should be emphasized that this northern cold-arid landscape formed a special biogeographic province, which became the center for the evolution of several faunal and floral radiations – the most obvious of which was the Pleistocene diverse woolly fauna.

The substrate on which these steppe large mammals walked was generally firm. Paleosol evidence suggests that a humic soil mat was thin or non-existent. Widely occurring and persistent evidence of yearly erosion and redeposition of thin sheets of silt in the valley “muck” suggests that some bare ground would have frequently been exposed in between plants. Where fossil soils are preserved, we find that the fine root mass runs deeper than in most of today's boreal forest or tundra soils (Guthrie, 1990; Höfle, 1995). As indicated by paleosols, Pleistocene soils were more basic – some even showing carbonate and salt accretion (Tomirdiario, 1982; Walker and Everett, 1997). This contrasts with the acidity of most northern tundra and forest soils today. Basic soils in turn indicate a different plant community and a more arid situation. Basic paleosols and other features combined suggest a greater nutrient-carbon turn-over in the upper soil horizons. (See reviews in Guthrie, 1990; Schweger, 1990; Höfle, 1995).

There is evidence that soils thawed deeper in the LGM summer and yet geological features, such as deep permafrost and extreme ice wedges point to more winter withdrawal of heat from soil. This produces the paradox – of top soils warmer than those of today in summer yet colder than those of today in winter. How do we build a model which accounts for all these features, of which aridity was central?

To emphasize the large-scale shift in aridity, please imagine the tremendous geographic variation today across the north in precipitation and soil moisture. We are looking for agent(s) that was/were ubiquitous and comparatively encompassing in affecting all variations of this moisture gradient. For example, we know that aridity was wide-spread enough to eliminate virtually all tree species from the far north: alder (*Alnus*), spruce (*Picea*), larch (*Larix*), pine (*Pinus*), and perhaps tree birch (*Betula*), and probably several large willow species (*Salix*) – these

latter two genera are difficult to distinguish because of pollen similarities with dwarf species. This total, or virtually total elimination, is an theoretical demand which is difficult to meet with even major changes in temperature, precipitation, wind patterns, maritime influences, direct Milankovich insolation shifts, heightened loess deposition, fire, grazing intensity, etc.

While there is evidence of massive water erosion during warmer-wetter oscillations (Péwé, 1975; Péwé et al., 1997), water erosion appears to have been limited during full Glacial conditions (Péwé et al., 1997). There is geological evidence of some seasonal sheet wash during the LGM, probably associated with a more exposed surface than now. Wind seems to have been as important a direct force on the landscape as water during Glacial episodes. The common occurrence of Pleistocene dunes fields (e.g., Carter, 1981, 1984; Lea, 1989; Lea and Waythomas, 1990) and long-range eolian silt transport (Péwé, 1975) suggest more wind and more exposed soil surfaces than at present.

Although winter winds would not have moved frozen dunes, they would have rearranged snow cover causing drifts and increasing sublimation. Some soil surfaces would have been denuded of snow cover. Winter winds could then carry silt particles from these bare ground surfaces onto the drifted snow, as they do today in outwash deltas of Alaska Range passes.

I think this is a significant point because drifted snow has a lower albedo than a blanket of clean snow and this would have affected spring breakup causing a much more rapid spring melt and a more intense runoff with accompanying erosion. Textbook figures portray general reflectances of 80–85% for fresh snow in contrast to only 10–30% for dirty snow (Duff, 1993). Dirty snow surfaces also increase sublimation rates under the bright spring sun and of course the exposed ground between snow drifts would have thawed more quickly than now. The combined effects of these factors would have significantly changed soil temperatures and depth of thaw. Bare ground can absorb about 8 times more radiation than can clean snow (Duff, 1993). The very high albedo of the pristine snow blanket now typical of the far north usually means that it takes a full month of above freezing temperatures just to melt the snow cover before soil can ever begin to thaw (pers. observ.). Thus, undrifted, clean snow significantly limits the depth of thaw in summer. However, the other side of today's blanket of snow is that it protects the soil from extreme lows of winter air temperatures. It is easy to see how cryogenic features could have been exaggerated by Pleistocene winter winds that exposed some soil surfaces and generally redistributed and drifted snow cover. Mammoth Steppe soil temperatures at shallow depths were probably warmer in summer, while they were colder at greater depths in winter than today (Guthrie, 1990; Höfle, 1995). Deeper thaw would also have removed moisture from the surface by increas-

ing downward percolation, but this same moisture would have been available to deep-rooted water-stressed plants later in the season.

Thus, wind was certainly a critical force in creating and maintaining the Mammoth Steppe. But wind alone was not sufficient. Winds are infamous in the cool Aleutian Islands and yet the Aleutians are not arid nor is their treeless vegetation something we would call steppic. Other forces were active in the Mammoth Steppe, for example, frequent loess rain and retransport. Erosion would have kept nutrients stirred and available. But these factors are all spokes in the story. The hub of this story revolves around the explanatory power of clear skies. They explain the unique scale of both cold and aridity.

2.2. *Searching and finding the principal cause – clear skies*

Reduced cloud cover is only one factor among many that can result in aridification. How do we separate it from such potential factors as:

1. Increased temperature from atmospheric changes
2. Changes in sun angle and distance
3. More rapid run-off, sublimation, or percolation
4. Wind dehydration and snow redistribution
5. Selective grazing and trampling by large herbivores
6. Frequent removal of phytomass by wildfire
7. Radically decreased precipitation
8. Decreased cloud cover and its effect on evapotranspiration

The first option is unlikely, because so much of our evidence points to cooler summer air temperatures and certainly colder winters (reviewed in Guthrie, 1990). Similarly, number two, changes in sun angle and distance, a la Milankovich insolation curves, would, if anything, have had the direct effects of making things only slightly more arid and colder. Evidence regarding vegetation and soils does favor increased run-off, sublimation, and percolation. But it is more likely that these were important contributors to aridification, not the driving forces. Likewise with number four, wind. Again there is evidence of more wind (Lea, 1981; Lea and Waythomas, 1990), so winds were important, but a contributor, not the lynch pin. I will discuss item five, the keystone megaherbivore hypothesis, in detail later. I think it unlikely as a key causative agent of the Mammoth Steppe. Item six, wildfire, seems important in the maintenance of modern steppes, because it both kills woody plant seedlings and reduces insulative litter. But we have lots of fire now and it does not turn the taiga/tundra landscape into a steppe (Van Cleave et al., 1983, 1991). We must ultimately ask what were the agents that allowed fire to have these effects then and not now. If we can find that answer then we will have the principle component we are looking for.

Item number seven looks more likely, as many forces were in place to cause a decreased rainfall. But even today rainfall is very low in northeastern Asia and the high arctic of America. Certainly reduced moisture input was important in the production of aridity, but it may not have been the most important agent in the creation of the Mammoth Steppe. I propose that decreased cloud cover, and its effect on evapotranspiration, is one of the most unappreciated agents, and if there is a principle component of the Mammoth Steppe, I suggest it would be clear northern skies. I will, however, be continually suggesting interacting feedback links of several of the above factors in this story. But I hypothesize that, driven by the Siberian–Mongolian high-pressure system, clear skies uniquely activated and energized the other agents. One of the key features that characterizes steppes is that they fall below a negative balance in the net moisture input-loss equation, primarily through evapotranspiration.

Thus, in the far north the hub of all these complex interacting forces that torque the tension between tundra/boreal forest at one extreme and steppe at the other, is the degree and kind of cloud cover. Clear skies in the cold north are the under-emphasized cause of the Mammoth Steppe's steppe-ness. Paradoxically, this will also let us understand the true uniqueness of the exception – the buckle which became Beringia.

The increase of clear summer weather on the Mammoth Steppe would have increased the temperature of exposed soil through the greater absorption of solar energy (even while the air 2 m above the ground may be cool), accelerating evaporation from soil and plant surfaces. Clear skies explain the conflicting evidence from the proxy data – the general evidence such as sea ice and glaciers indicate colder summers (Rind, 1987) while the evidence from soil invertebrates clearly shows warmer summers (Berman and Alfimov, 1997). Evapotranspiration from warm soils results in some pumping of soil moisture from below, increasing mineral transport upward, maintaining a modestly alkaline top soil. The increased surface soil warmth from a bright sun would have increased the depth of thaw, hence slightly better developed and deeper root systems.

2.2.1. If steppe then, why tundra/taiga now?

So why tundra today? Young (1978) was the first to comment that tundra vegetation is distributionally dependent on the influence of a maritime climate and in no part of the world, he contended, is true tundra vegetation found at low elevation more than 300 km from the sea (Fig. 2). But how do we account for this association? It is not simply that tundras experience high rainfalls, some tundras have lots of rain, others hardly any. It is not just because tundras experience extreme cold, continental interiors have the coldest temperatures.

Tundras are wet and treeless mainly because of the cool-wet summers created by their customarily being cloaked in low stratus clouds. The summer landscape adjacent to polar seas is a land of strong and deep thermal-moisture contrasts (Geiger et al., 1995). Sea water has an albedo, reflected solar radiation, of only 6–10% while a dry land averages between 10 and 30. Albedo for dense clouds is on the order of 60–80% (Duff, 1993). These dense low stratus clouds along coastal plains (which often settle onto the land as fog) considerably reduce net insolation. In addition to temperature reduction, these clouds also characteristically produce frequent fine drizzle and, most significant of all, greatly inhibit evaporation (Fig. 3).

Dense low-lying cloud cover in the far north greatly reduces net insolation onto the ground surface much more than at lower latitudes because of the sun's lower intercept angle. In the far north, in-coming radiation must penetrate more cloud mass, hence less energy reaches the ground surface. This more oblique zenith angle means that more in-coming radiation is reflected back into space (Fig. 3b and b'). See Barry and Chorley (1992) and Geiger et al. (1995) for a discussion. The caveat for all this, of course, is that these low vs. high zenith reflectance differences in sun angle vary considerably for cloud variety, surface irregularity and density. Using a common baseline of surface water albedo we can compare reflectance differences due to the angle of sun intercept. An overhead sun has only 2–5% energy reflected back to space, while a low sun angle produces a reflectance in the order of 50–80% (Barry and Chorley, 1992; Duff, 1993). Cloud reflectance varies from this in complex detail but not in principle. So we might approximate the difference of net energy reaching the ground through low lying clouds in the north as in the range of 10–20%, while at southern latitudes it is more in the range of 60–80%. Common experience with camera light-meters makes this dramatically familiar. Unfortunately, most of the field work on cloud-radiation interactions has been done in the tropical and temperate latitudes where most of the concerns lie with global weather patterns. Though the major dynamics are agreed upon, there is considerable controversy over cloud-radiation interactions, primarily because of all the complex variables with regard to cloud absorption (Kerr, 1995; Cess et al., 1995; Ramanathan et al., 1995; Pilewskie and Valero, 1995; Stephens, 1996 and responses). Clouds seem to absorb more energy than was predicted by models, and will considerably affect future Paleoclimatic modeling (Kerr, 1995).

There is a related phenomenon to consider. A 50% spatial cover of clouds with some altitudinal depth may mean that the characteristic low-angle sun of northern summers does not penetrate the openings directly but is backscattered and diffused mainly by the lateral cloud surfaces (Fig. 4). The modeling of all this is complex for

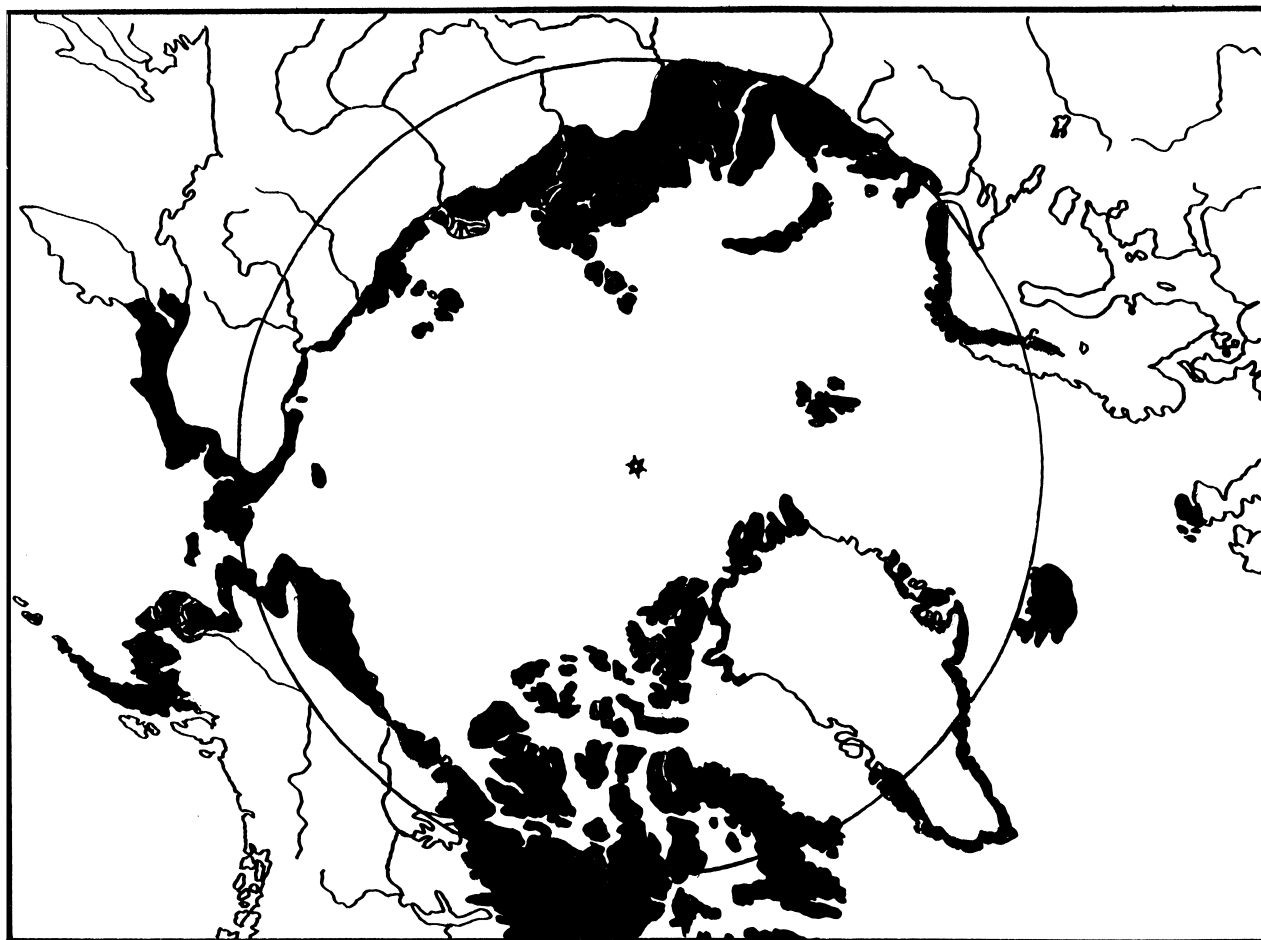


Fig. 2. Lowland tundra (shaded) seems to be mainly a product of maritime stratus (nimbostratus) cloud cover. Frequent low clouds reduce radiation reaching the soil surface, decreasing evapo-transpiration and lowering temperatures. Even with little rainfall, this shade-cooling and its low net evaporation produces characteristic paludified soils and standing water, selecting against tree growth. It is quite likely that treeless tundra landscape is not a good analog for the widespread continental Mammoth Steppe.

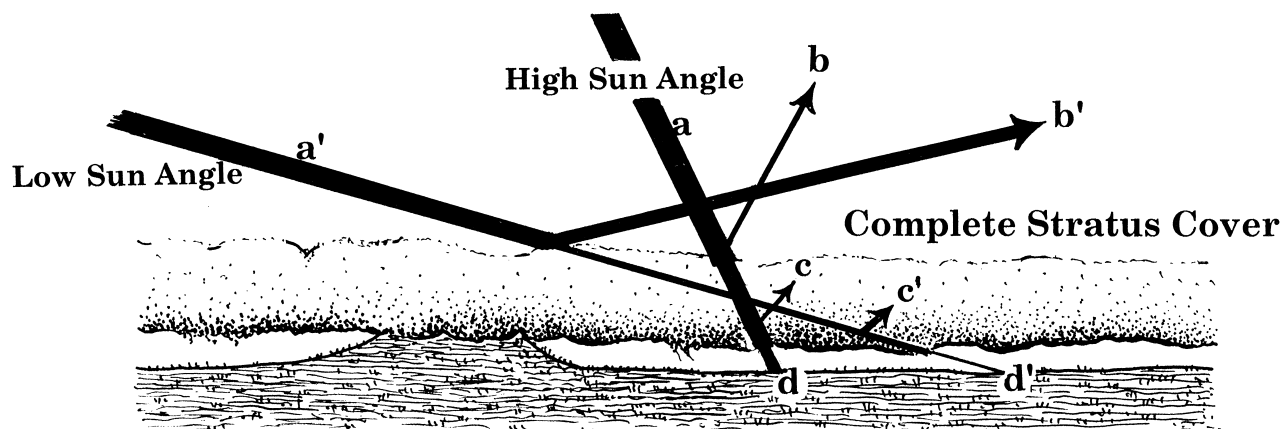


Fig. 3. The effect of low-lying stratus cloud cover is greatly exaggerated at high latitudes because zenith sun angle is low. The upper drawing of complete stratus cover shows that a high sun angle (a) produces less net reflection (b) than does a low sun angle (a') which produces a high albedo (b'). Incoming radiation from low sun must traverse a greater cloud mass resulting in more reflectance (c') compared to a high sun angle. Sun angle is thus critical in the amount of energy at the soil surface (d vs. d').

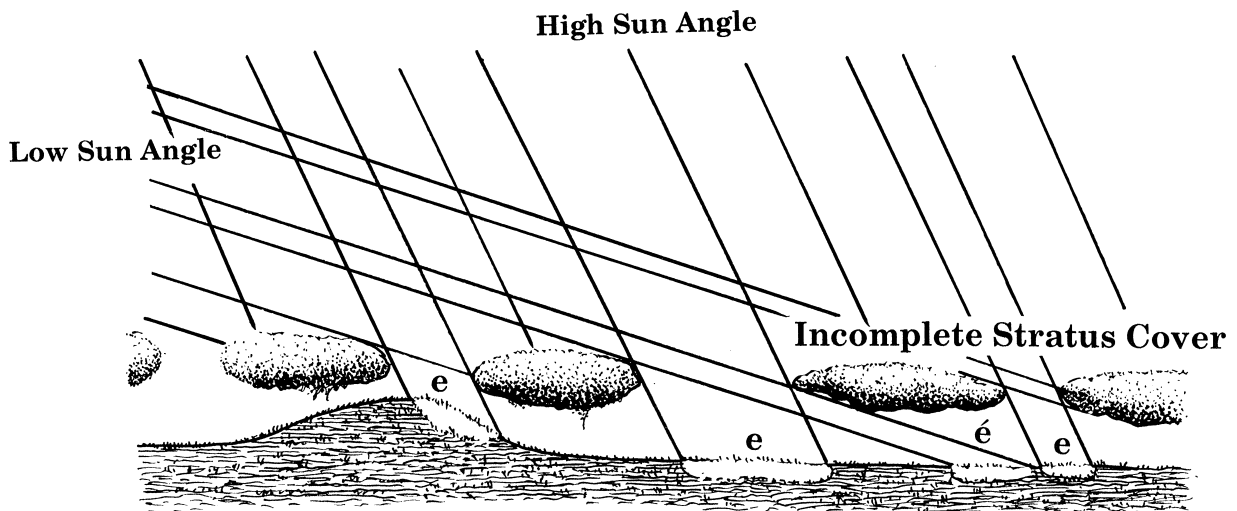


Fig. 4. The effect of incomplete cloud cover is also magnified by low sun angle at high latitudes. One can visualize a greater reflectance and reduced energy with a low sun angle ($\acute{e}$) than with a high sun angle (e). Sunny spots are more scattered and smaller.

different habitats, conditions, and cloud characteristics but the first-hand evidence from “ground-proofing” is clear. In the north, the effect of even incomplete low clouds with low angle mid-day sun is experienced on the ground as a much darker ambiance and a greater damp-chill than the same cloud cover further south with its mid-day sun.

Low-lying stratus cloud cover significantly impacts surface energy budgets and physical processes of soil evaporation, snow and ice melt, as well as biotic evapotranspiration. The upper surfaces of low stratus clouds reflect solar radiation back into space, and the cloud body absorbs considerable radiation, thus cooling ground surfaces, opposite to relatively high cirrus clouds that exhibit a high counterradiation hence magnifying warming (Kiehl, 1993). Modest cloud cover reduces the downward long wave radiation on a scale several times that produced by low insolation values of Milankovich curves, and 20 times that of a CO_2 doubling (Berger, 1978; Olsson et al., 1996). At northern latitudes, it is difficult to equal the degree of low cloud cover as a potent climatic agent.

Clear summer skies were the proximate trigger for Mammoth Steppe formation; they would have dried out the tundra/taiga landscape, increasing the fire risk, subjecting conifers and cryptogams (that is most tundra-taiga plants) which have little below-ground biomass to intolerable water stress, year-after-year favoring competition from steppic species. As the tundra landscape slid toward aridity the treeless low-sward vegetation with its incomplete ground cover, it would have resulted in more thermal contrasts: imagine dust in the air, fire running for kilometers, and drifting snow.

To a lesser degree than tundra, cloud cover affects the moisture balance which creates the boreal coniferous

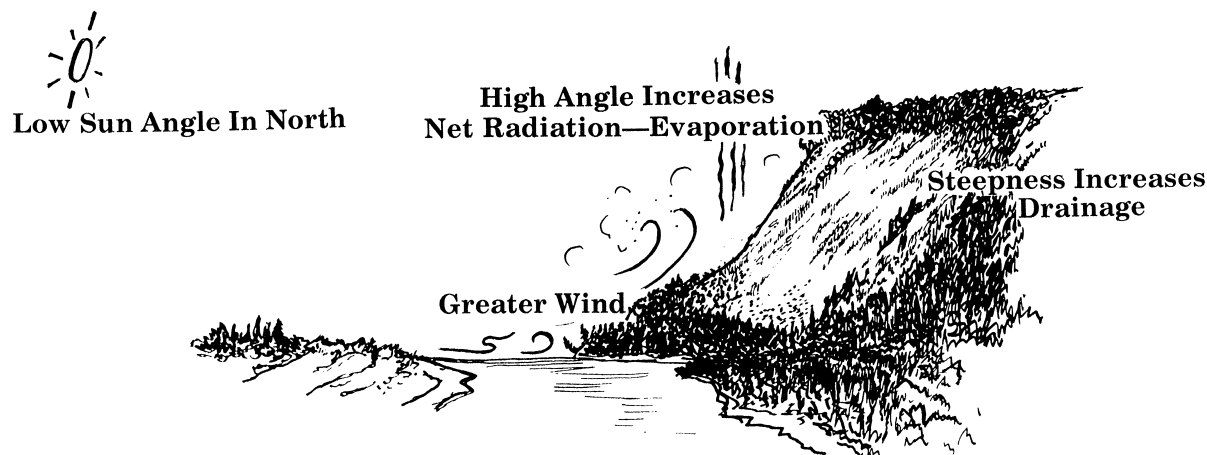
forests. Continental boreal forests, are often covered by low clouds in summer, and an accompanying fine drizzle, which greatly reduce evapotranspiration – part of their being located within the polar Front’s summer boundaries. For those of us who live within the boreal forest it is dramatically clear that an unusual run of clear sky and warm temperatures produces a great fire hazard – boreal forests are adapted to being damp. In contrast, arid-adapted steppic plants are highly fire-adapted, they have most of their biomass protected below ground. Occasional fires invigorate steppe graminoids, by removing built-up litter and recycling nutrients.

2.2.2. Implications of steppes on steep south-facing slopes within the boreal forests

Aridity can set the competitive-balance for the margin of, say, forest limits, as we see when conifers abut the steppes in Asia and in Alberta. In those areas, the boreal forest is pinched out by the combined forces of aridity and the competitive excellence of plants that are adapted to low moisture. It can not only be too cold to grow boreal forests, it can be too dry, as shown on the south-facing slopes in the boreal forests of central Alaska (Edwards and Armbruster, 1989). It is interesting that these south-facing slopes contain some characteristic tundra plants as well as arid-adapted species like *Agropyron spicatum* and *Artemesia frigida*. This is the confounding problem with reconstructing the paleoecology of the north – why it was not truly homologous with modern steppes, because it contained mixes of species that do not normally mix today. This strange heterogeneity is apparent across all taxa of both plants and animals.

Many south facing slopes today (Fig. 5) have exposed soil thinly cloaked with arid grasses and sedges, interspersed with flowering forbs, and sage (Yurtsev, 1974;

STEEP SOUTH SLOPES—A SPECIAL STEPPIC ENVIRONMENT IN TODAY'S FAR NORTH



Aridity Shifts Balance From Woodland to Steppes

Fig. 5. Today, the vegetation of steep south facing slopes in the far north is often very atypical of the surrounding landscape. This seems to be due to the greater aridity produced from better drainage and higher net radiation resulting in higher evapotranspiration. Comparatively speaking, these steep slopes are usually subject to more wind.

Young, 1976; Murray et al., 1983). These patches of steppic habitats can provide considerable ecological-physiological insights into the biotic tensions between steppes and more mesic facies. Whether these and other patches of steppic communities are true relicts of the Mammoth Steppe is problematic. The fossil evidence is yet unclear about relicts, but these treeless south slopes may merit the status of an analog. And calling an area a steppe is just a matter of scale I guess. As a reverse analogy, if boreal forests were now extinct, the discovery of a large isolated stand of spruce would be a major floristic discovery but calling it a boreal forest?

In any case these steppic bluffs are informative. Steep drainage causes rapid run-off and the more right-angle south-facing orientation to the summer sun increases evapotranspiration and warmth. Summer soil temperatures are warmer and thaw depth is greater. Armbruster and McGuire (1985), Wesser et al. (1988), and Edwards and Armbruster (1989), Wesser and Armbruster (1991) suggest that it is ultimately moisture that controls the lack of forest on such south facing bluffs in the far north, not temperature. Aspect and slope can radically change a landscape. Today tundra reaches far south on steep north-facing hill-sides.

So, facetiously, if we were simply to tilt the far north more vertically like these south-slopes, it would again return to steppe (Fig. 6). Or, the same thing could happen if the sun were higher in the sky, making its rays more direct. However, as a model (and I propose in reality) the same kind of aridity can be produced by simply increasing the amount of clear skies (Fig. 7). That is what must have happened during much of the Pleistocene.

It is noteworthy that today's steppe-like south-facing slopes are not present in any way because of large or small mammal herbivory. These steppe grasses and forbs go ungrazed by large mammals, unburned by fire, they receive little loess deposition, and they are not subject to special coldness, but experience the meteorological equivalent of clearer skies.

2.2.3. Unimpeded radiation to the black night sky

If clear skies produced decreased rainfall and enhanced evapotranspiration in summer what did they do in winter? In winter, the clear skies over the Mammoth Steppe enhanced radiation loss. The earth not only receives extra-terrestrial radiation it also loses it, mainly from surface radiation into space. Radiation loss is fortunately buffered by atmospheric gasses and high-altitude cloud cover that decrease the rate and degree of loss – the “green-house effect.”

While the clear skies of Mammoth Steppe summers would have lost more energy through radiation, this was more than compensated by the higher radiation received during the long sunny days. In winter, the balance was different. Net energy loss is particularly excessive under a cloudless night sky. This is acute during winter in northern latitudes when nights are inordinately long. Radiation input during the brief winter days is minimal. So, during winter, energy loss is cumulative from day-to-day, and can result in great energy deficits and unusually low temperatures. Today, in Alaska, the effects of this radiation loss are moderated by frequent winter cloud cover and insulative snow cover. But, the stable winter high pressure system over central Siberia results in

ONE WAY TO RETURN THE STEPPES TO THE FAR NORTH



If Alaska Were Tipped up at the Same Angle as South Facing Slopes it Would Dry Out From Increased Moisture Loss and the Resulting Arid Conditions Would Produce Steppe Vegetation

Fig. 6. It seems logical to imagine that if Alaska were somehow tipped to the angle of the steep south facing slopes, it too would experience a more arid, more steppe climate.

cloudless winter skies and produces allow major radiation loss to the dark night sky, producing some of the coldest recorded temperatures on earth. So we can expect, that during much of the Pleistocene, the clear winter skies throughout the Mammoth Steppe more efficiently withdrew energy from exposed soil surfaces produced by less snow fall and more wind-drifting. All the proxy evidence of increased permafrost depth, ice-wedge development, sea ice expansion, and other fossil cryogenic features supports this conclusion.

2.2.4. What would have caused such clear skies?

Paleocirculation patterns (CLIMAP, GCM's) are much debated, and attempts at a robust global paleocirculation model seem to improve every year. But these attempts must ultimately rely on proxy data and depend on "ground testing" for their validity. What we can say, as I suggested earlier, is that this special cold-arid northern grassland was like a monumental "inner court," surrounded on every side by moisture-blocking features: high mountains, frozen seas, and massive continental glaciers. These features kept rainfall low and maintained clear skies during much of the summer, creating the predominance of a stable high pressure systems. This was also true in winter.

2.2.5. Repercussions of cloud cover – nutrient vs. moisture limitations

Today, throughout most of the north, nutrients are in shorter supply than moisture, from both a physiological and ecological view we can say that nutrients are more limiting than moisture. Spreading standard garden fertilizer (Nitrogen, Phosphate and Potassium) in almost any northern landscape creates a startling effect (perhaps with the exception of a mature closed-canopy coniferous forest). This dose of nutrients changes the species, transforms plant growth, and greatly changes overall appearances of the site. The same is not true of moisture. Other than in a few rare summers and in some special conditions, going out with a garden hose and watering native northern vegetation every evening produces very little change. Van Cleve et al. (1983) found that, with some exceptions, nutrients and temperature controlled both the type and productivity of taiga forests, not moisture.

In a steppe environment the relative abundance of moisture and nutrients is reversed. Moisture, being very scant, is the most limiting factor. One can see the effect of water in a dry steppe by the very dramatic change in vegetation near a stream. Yet, in northern areas too, there is often special vegetation lining the creek banks which wind through tundra or boreal forest, but this

AN EASIER WAY TO RETURN STEPPES TO THE FAR NORTH IS TO REDUCE NET MOISTURE BY MORE DIRECT MEANS

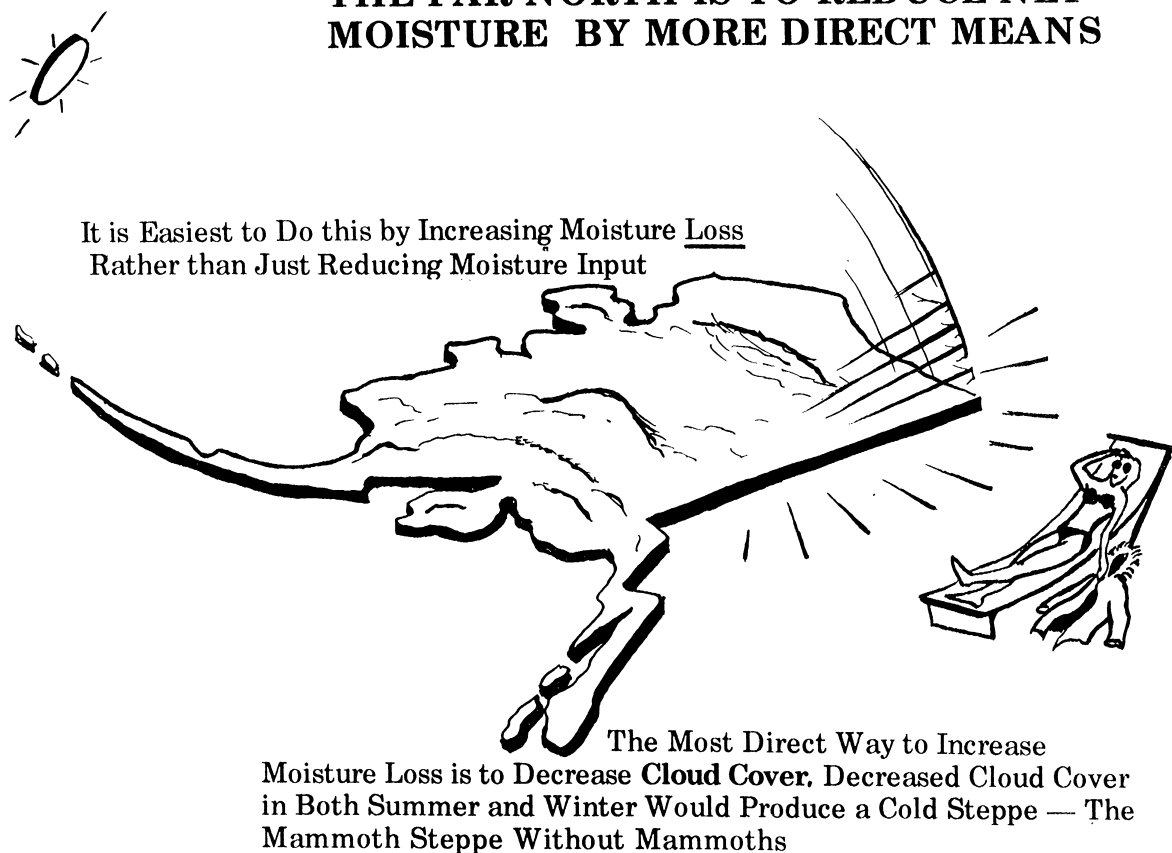


Fig. 7. We could, more easily, increase the amount of insolation by almost the same amount by decreasing cloud cover – producing steppes similar to those on today's south-slopes effect on a vast scale.

seems mostly the product of the comparative warmth of the flowing water and the nutrients it brings. Much of the character and community variants of steppes are due on a small scale to direct water gradients, and on a large scale to annual net moisture (and loss-retention ratios). The gradient across the American West and Midwest from Colorado to Indiana of short, mid, and tall grass is due to net moisture.

Wesser and Armbruster (1991) also found that, in addition to moisture, the steppe/forest transition was also affected by light intensity, that is, an experimental variable from shade to full-light (steppe plants being favored by full light and forest plants favored by shade). More on this momentarily with regard to the importance to the Mammoth Steppe of reduced cloud cover. In my mowed brome pasture in Fairbanks, Alaska, moss steadily accumulates in tree-shaded spots, but not in the open areas exposed to sun the whole day. Young trees spout up in partially shaded spots but not in the open pasture.

These respective limitations on nutrients and moisture result in different adaptive strategies between tundra (or boreal forest) and steppe plant species. Mammalian

foraging highlights these differences. Because they are not nutrient stressed, most steppe plants are not greatly damaged by modest grazing. Losing some of their plant tissue is not life-threatening to steppe plants (much of their biomass is below ground). With ample available nutrients, taking the risk of having to replace grazed plant tissue is less costly to the plant than using extensive biochemical defenses. Nutrient-limited tundra and boreal forest species in contrast have most of their biomass exposed above ground, and these tissues tend to be heavily defended against herbivores. Annual above-ground phytomass productivity alone is a quite incomplete guide to mammalian carrying capacity (reviewed by Guthrie, 1984a, b). All this is key in solving the productivity paradox, discussed later.

3. The Beringian buckle in the Mammoth Steppe

The maritime influence of the shallow, but mostly ice covered, Bering and Chukchi seas seem to have partially broken the continuity of the Mammoth Steppe during

the LGM. Young (1971) mentioned an aspect of this in his floristic zonation in Arctic regions. Both Young and Hopkins in the 1982 Beringian volume commented that geological evidence in Alaska shows a more mesic gradient: lowest in the east and increasing as it approaches the Seward Peninsula. Berman and Alfimov (1997) refer to Gorodkov and Mikkola et al., as having emphasized that many Asiatic steppic-adapted weevils and ground beetles range to the strait and stop, never having crossed into Alaska, during the Pleistocene. Murray (1995) also pointed to several plant species that are quite limited in distribution in the strait area but are only found on one side or the other. Anderson and Brubaker (1994) have repeatedly emphasized, from their work in Alaska, that during full Glacial times there is a significant gradient of moisture, again, driest in the east and more moist in the west. Likewise, Hamilton et al. (1993) stressed that while the interiors may have been quite arid during the LGM, regions near what is now the Bering Strait were more mesic with treeless tundra vegetation rather than arid steppe. They also proposed that this region may have been a refugium for tundra communities during the height of the last glaciation.

Virtually all of the pollen cores taken from the bottom of extant lakes in interior Alaska and the Yukon Territory, reveal sediments which date not less than 15 ka (e.g., Ager, 1983, Anderson and Brubaker, 1994). Thus, if lakes did exist during the LGM, around 18 ka, they were probably rare. (I am excluding for now the special circumstance of “extinct” proglacial lakes, such as occurred in the Canadian Old Crow region or south of the Russian ice sheet and also the few scattered glacier-dammed lakes, like Lake Noatak in Alaska.) But the paleolake pattern in western Alaska is different. There a number of extant lakes that persisted during the driest peak of the LGM. For example, Colinvaux (1964) found that Imuruk Lake core extended through sediments from the LGM. Several of Anderson and Brubaker’s (1994) lakes in the region of northwestern Alaska also produced cores reaching into the LGM. Schweger in Hamilton et al. (1993) also proposed a more mesic situation in western Alaska, even finding some peat at full glacial, and a predominance of sedge pollen from LGM sediments. It should be noted however, that kobresia sedges (especially *Kobresia myosuroides* and *Kobresia simpliciuscula*) are quite xerophyllous and have left disjunct relict populations (Hultén, 1968) from what evidently was a continuous distribution across the Pleistocene Mammoth Steppe. I find thick masses of Kobresia seeds imbedded in frozen mammoth hair (Guthrie, in prep.), suggesting that this genus may have been adapted to using the long dense hanging hair of mammoth as a seed dispersal vehicle.

Goetches and Birk’s data in this volume shows mosses in among the arid forbs at full Glacial times on what is now the Seward Peninsula. Elias et al. (1992, 1996) and Elias, this issue, found more tundra adapted

insects to the west and more arid adapted insects to the east in Alaska. These data point to a different pattern – of moisture between eastern and western Alaska. What does this mean?

First, it is incomplete to see this phenomenon only as an Alaskan moisture gradient, because a mirror image of this maritime moisture existed on the other side of the strait (e.g., Lozhkin et al., 1993, Anderson and Lozhkin, this volume). That is, we cannot talk about this as a unidirectional moisture gradient. It is more completely viewed as a mesic crease separating the zones of maximal aridity, as a buckle in the Mammoth Steppe. There is animal and plant distributional evidence that suggests that there existed some north–south version of it throughout the cold-dry episodes during most of the late Pleistocene (Hamilton et al., 1993), and maybe the entire Pleistocene. The width of this buckle was probably internally ragged, its margins irregular over micro, meso, and macro spatial and time scales. Indirect biogeographic evidence I am about to discuss shows that this phenomenon retained an integrity through considerable time.

Like the Mammoth Steppe, this buckle was likely not vegetatively homogenous. Both Young (1971, 1976, 1978) and Yurtsev (1982) have argued, mainly on the basis of modern floristic evidence, that during the LGM there was a significant S–N gradient in this Strait region – the more southern region being more mesic. The exposed southern shelf was in the near proximity to the air flow from the North Pacific, which was closest to the main source of the moisture and cloud cover. I suspect some more mesic vegetation of the buckle may have been distributed northward to the Arctic Ocean, though probably more narrow in lateral extent and of a drier aspect. We can surmise this because biogeographic evidence from large mammals suggests certain species were blocked by this buckle and could have ranged around a mesic barrier if it were only in the south. Though much of the Bering Sea may have been ice covered for 9 months of the year (hence its source of moisture flow northward reduced) during LGM (Sanchetta and Robinson, 1983), the more open three months were the critical summer months. And the remaining pack ice would have had standing puddles on the surface and much evaporation–sublimation as a source of cloud moisture.

3.1. How ecologically significant was this break in the Mammoth Steppe aridity?

Though it may have been important for speciation in some plants, this mesic buckle was not a significant refugium or barrier for most terrestrial mammals (with the obvious exception of local insularity produced by rising–lowering sea levels). I will follow the conclusion here that while this was a significant break in the overall pattern, it was not a major one. It was not so tundra-like as to limit or prevent the characteristic arid-adapted

large mammals (saiga antelope, *Saiga*, woolly mammoth, *Mammuthus*, caballid horses, *Equus*, and most others) from exchanging back and forth. However, we have understood for a long time that there has been some kind of a biogeographic filter which prevented free exchange of some faunal elements across this specific zone. For example, an arid-adapted species from the west, woolly rhino, *Coelodonta*, reaches up to the head-waters of the Anadyr River, but fails to go further east. Likewise, the northwestern perimeter of North American camels, *Camelops*, and the American long-legged kiang-like equids, *Equus* (sp?) failed to extend across the strait. The short-faced bear (*Arctodus*), bonnet-horned muskoxen (*Bootherium*), and badger (*Taxus*) are found throughout the interior of Alaska and the Yukon Territory but apparently did not breach this western barrier (Fig. 8).

Another way of assessing the overall mesic degree of the landscape along this belt is to examine the Pleistocene large mammal fossil assemblages found within this buckle in Western Alaska. It is notable that assemblages from the river bars and mining districts of the Alaskan or Siberian interiors do not differ in any major way from those in the region of the mesic belt. Bison, horse, and mammoth predominate. The minor differ-

ences, of course, are the absence of the above species which did not transgress the purported barrier.

Recognition of this more mesic zone helps explain aspects of historical disagreements among Quaternary researchers. And it shows how the idea of a vast Beringian refugium prompted us to get the whole story inside out. Main dissenters against the steppe idea have worked primarily in this buckle or other special regions which could be expected to be slightly more mesic. Colinvaux (1964) took his Alaskan pollen cores from the heart of this buckle. Schweger, who has emphasized the mesic facies in the form of the “mosaic alternative” to the steppe began his work in Alaska by examining the pollen from this buckle for his doctoral thesis (Schweger, 1976), and he continued to work in this more mesic region (Schweger, 1982; Hamilton et al., 1993). Elias et al. (1996) have more recently examined peats, invertebrates, and pollen from cores in the Bering and Chukchi seas in the vicinity of the strait, and from this evidence have argued against a steppic interpretation for the entire mass of northern terrestrial landscapes. Anderson and Brubaker (1994) took most of their characteristically “mesic-mosaic” cores from the flanks of this buckle along north-eastern Alaska. These researchers concluded that the

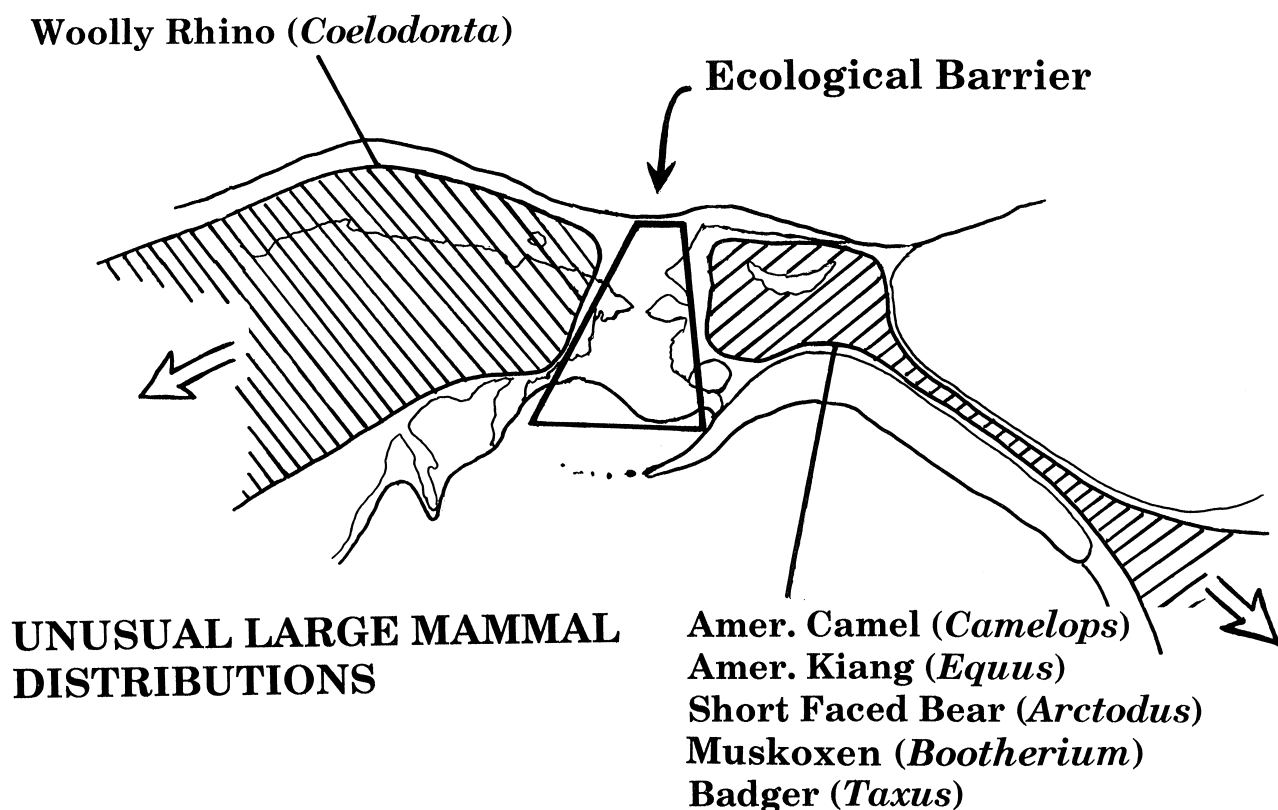


Fig. 8. Mammalogists have puzzled over the several Pleistocene species whose distribution approaches the Bering Strait then apparently ends. This pattern is not typical of most of northern species in the Pleistocene. There does appear to have been some kind of barrier in that region, but has received little speculation as to its nature. It is probable that this filter was related to the more mesic buckle.

vegetation of the far north was more of a mixed-tundra character than that reconstructed by paleoecologists working in other northern, more continental regions (Fig. 9).

3.2. Beringia – Getting it upside-down and inside-out

As noted, Hultén (1937) originally called attention to a special floristic zone across the Bering Strait because much of the cross-strait flora had an identifiable unity, and while the zone he delineated was modern, he imagined it was a major cross-strait glacial refugium. However, he was only thinking floristically, not in terms of

vegetation, and floristically he was correct. Other biogeographers (including myself) however, expanded his floristic idea into a giant Beringian refugium, including an entire vegetation within the boundaries from the Kolyma or Lena River on the west and the Yukon Territory in the east (Hopkins' *Beringia*, Yurtsev's *Mega-Beringia*, and Sher's *Beringida*).

Within the Beringian zone cross-strait endemism among current plants pertains to only a moderately small percent of the plant species. Most of the forbs have a more far-ranging intercontinental distribution, or are very closely related to wide-spread species on the other side of the strait. Also, most of the forest species and their

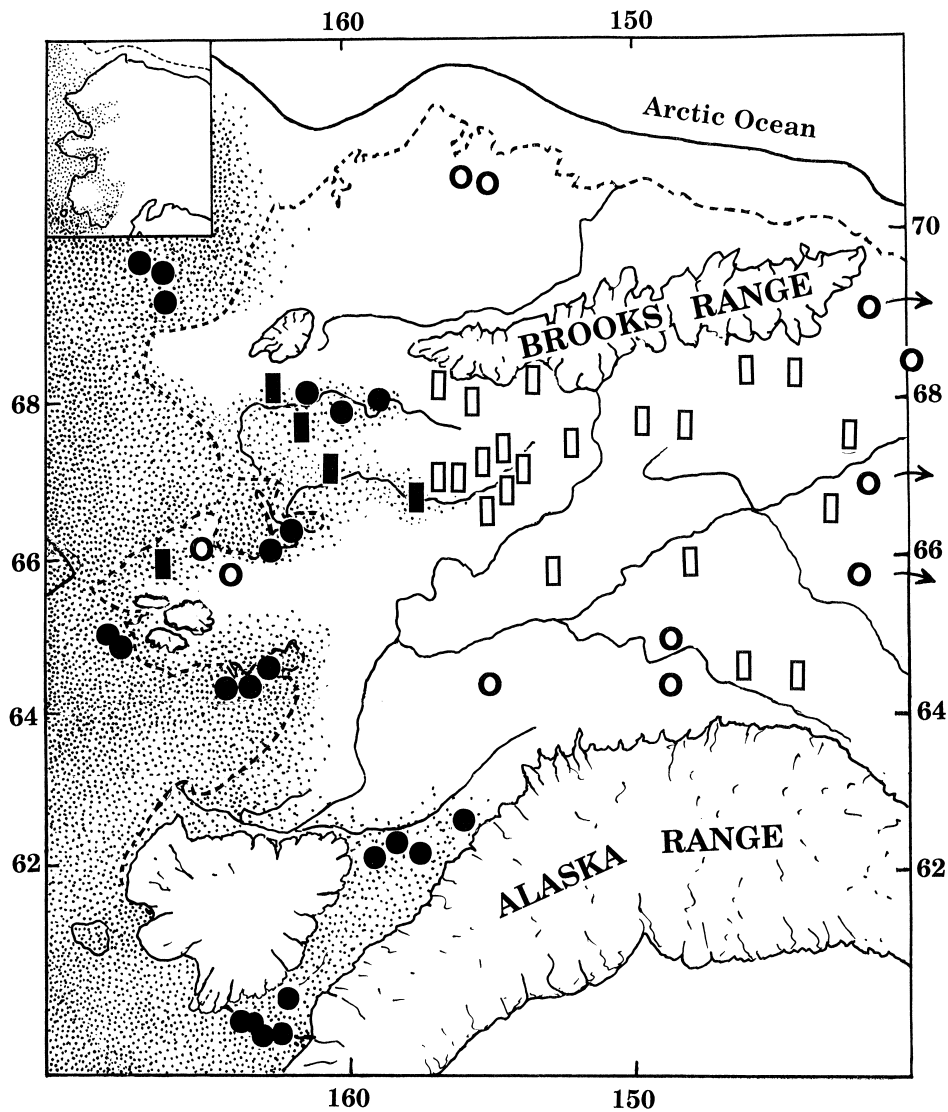


Fig. 9. The evidence for the more mesic buckle across the strait region comes from a number of sources. Elias (1997) has plotted the tundra beetles (black dots) vs. steppic beetles (open circles) from LGM sediments. I have combined this with a plot of Anderson and Brubaker's interesting (1994) pollen cores from a variety of lakes. Some cores penetrate the LGM sediments (black column), other cores bottom-out prior to the LGM (open column). (I have inserted an additional black column for Colinvaux's Imuruk Lake pollen core on the Seward Peninsula.). Note the overall pattern of these scatter points. Though there are some rare exceptions to this pattern from the many other Alaskan and Canadian LGM studies of beetles and pollen, most fit this same pattern.

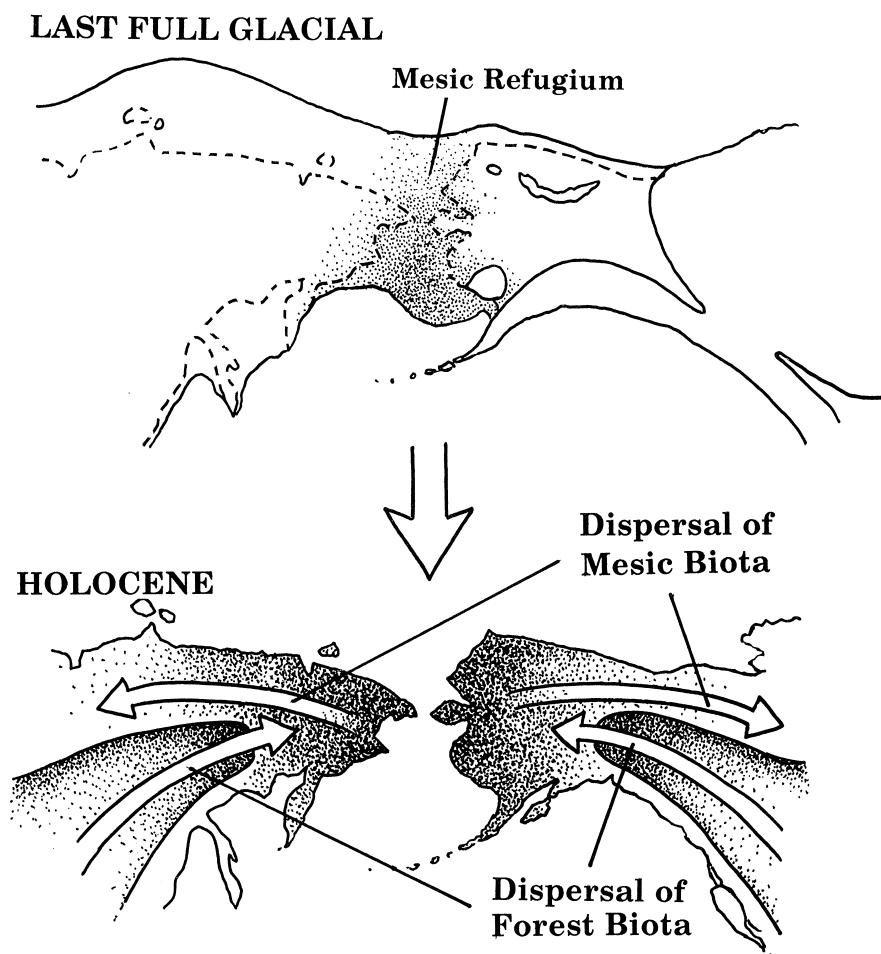


Fig. 10. Top Map. During the last full Glacial, around 18 ka, the predominant pattern across the far north seems to have been a belt of more arid landscape and steppic biota with a more mesic refugium in what is now the Bering Strait region. This mesic buckle was comparatively small in size and probably varied internally in climate and biotic composition on a N–S gradient. Bottom Map. During the Holocene, many mesic species spread both eastward and westward out of this refugium. At the same time, forest and associated species dispersed northward from their respective refugia far to the south. The more arid adapted species that had dominated the Pleistocene steppe were greatly reduced to minor habitats, underwent radical regional extinctions, or became totally extinct.

understory species have entered (re-entered for the most part, from being driven out during the LGM) this Beringian zone in the Early Holocene and are unique to their particular side of the strait (Fig. 10). In general, the more arid-adapted species have more circumpolar distributions.

So what produced the distributional pattern that resulted in the concept of a phytographic region, Beringia? I would hypothesize that some of the species that are now distributionally confined between the Kolyma to the Yukon Territory were once restricted to the narrow LGM mesic buckle, or at least the buckle was their distributional core. With the coming of the warm/wet Holocene most of these species expanded eastward and westward and a few others remained near the strait region.

In other words, the floristic biogeographic identity that Hult  n recognized as ‘Beringia’ is simply a modern affair, based neither on a vegetative pattern nor a pattern of a giant Pleistocene Beringian refugium, but on a few

key floral elements. And it is likely that these few key species were not dominant species during the LGM. *And what is especially important to note is that the mesic-adapted tundra species that now give this identity to today’s ‘Beringia’ were probably only a minor component even within that buckle.*

Even today the concept of ‘Beringia’ does not describe a good ecological zone, because many of the same kind of overall habitats, mammalian communities, flora, and vegetation patterns continue eastward across Canada and certainly westward, either across Central Asia or across Russia toward Scandinavia. It seems likely that stretching westward all the way from the mouth of the Yukon to the Bay of Biscay there were no significant barriers blocking the cold-arid adapted terrestrial communities during the LGM. That is certainly the case with the ‘mammoth fauna.’ Species do not abruptly stop at the Lena.

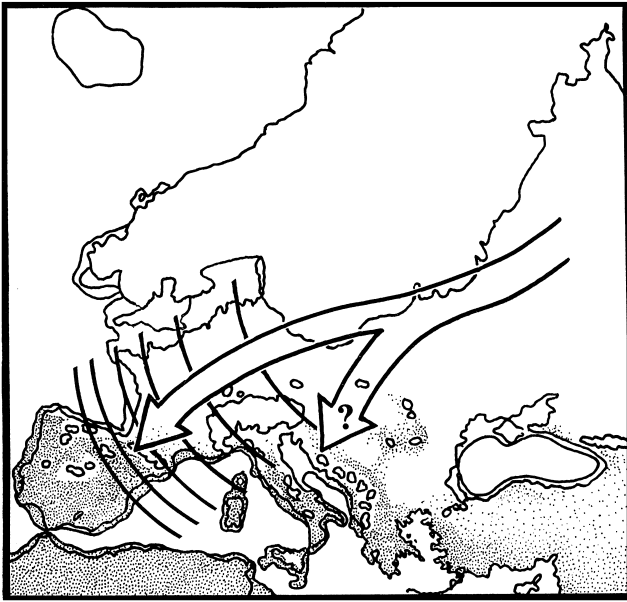


Fig. 11. On the western wing of the Mammoth Steppe certain biotic gradients also seem to correspond to an arid-mesic axis that runs roughly north and south. Nearing Iberia, horses (*Equus*) become more striped, reindeer (*Rangifer*) more spotted, and steppe bison (*Bison*) have more black-red contrast on the basis of Paleolithic art depictions. Ibex (*Capra*) and chamois (*Rupicapra*) also have more dramatic markings in the south. These gradients are discussed in detail elsewhere (Guthrie, in prep.).

Because Quaternary researchers were thinking of a Pleistocene tundra biota in Beringia, instead of a more steppic one, it was assumed that during the short episode of the LGM northern European ice sheet and the proglacial lakes that it backed-up (by blocking north-flowing rivers) were significant western physical obstacles to faunal and floral distributions. But that does not appear to be true. The steppic fauna and flora were distributed *around* these potential barriers. Most of the marked gradients in the character of the Mammoth Steppe belt run on a N-S gradient or at some related angle as (Fig. 11) in Europe (Guthrie, in press), not east and west. That is what makes the Beringian buckle an exception. A dense boreal forest did not exist as a southern restricting barrier as it does today. The cold steppes reached far south into Central Asia and Southern Europe. That the steppe biota were able to drop below these potential barriers of glacial ice and proglacial lakes is very clear in the vertebrate fossil evidence from Eastern Europe and Western Asia (see Kahlke, 1999 for maps). The only westward barrier to Pleistocene Beringia was the Atlantic. Also, the size of the north Eurasian ice sheet was rather small during isotope stage 3 and even relatively modest during isotope 4 (Van Andel and Tzedakis, 1996), so even if it had presented a biogeographic barrier it was only for a few thousand years during the peak of the LGM.

If “Beringia” was not a widespread natural unit in the Pleistocene and is not today, what causes us to focus on

this particular region as a place of special note? Because of its rich Quaternary geology. It is a place where Russian and Canadian-American Quaternary researchers have chosen to work. More importantly for others, it is the axis of intercontinental biotic exchange (or barriers to biotic exchange) between the hemispheres. And not the least, this was the route for human colonization north-eastward into North America. For these reasons, it will continue to be one of the most exciting areas of the world for Quaternary sciences.

3.3. In light of the Bering buckle paradigm, is the mosaic theory a red herring?

The new paradigm introduced here for picturing northern biota in the Late Pleistocene means we do not need the mosaic theory. The mosaic theory was a third theory, getting around the steppe vs. polar desert controversy that see-sawed back and forth over the last three decades (see Colinvaux and West, 1984; Cwynar and Ritchie, 1980; Guthrie, 1968, 1985, 1982, 1990; Schweger, 1990; Colinvaux, 1996; Elias et al., 1996 for but a few examples of this discussion).

Schweger and Habgood (1976), Anderson and Brubaker (1994), Elias (1997) rejected the polar-desert position, but seeing that there was evidence from the fossil record of exceptions to the arid-steppe generalization proposed a third view, that most of the unglaciated north consisted of a mosaic of several habitats, some more steppic, others more like modern tundra.

Certainly whatever it was it was a mosaic; all abstract supra-community designations come in some kinds of packages of mosaics. The American tall-grass prairie has (had) many mosaics (vast stands of hardwood groves, marshes of cat-tails and sedges, hill slopes of mid-grasses and cedar, and so on). Yet, it is legitimate to refer to this large region as a tall-grass prairie, and it would be short-sighted to deny that and call it a ‘too-complex-to-identify mosaic.’ I think the same is true of the northern Pleistocene cold steppes. They were steppes like none today, but different only in particular degrees, more than in physiognomic character. The use of the word *tundra* conjures up a scatter of modern images which are far off the mark of what the north was like during the LGM, even though there were many tundra species present. Likewise, I think dry tundra, steppe-tundra, or tundra-steppe are also misleading. It is curious that while Anderson and Brubaker (1994) were comfortable with calling all treeless landscapes tundra in the far north today, which covers dry felfields, tussock meadows, thick swards of arm-pit high grasses, coastal marshes, steep mountain meadows, muskegs and so on, yet these same authors specifically hold the designation of a vast northern Mammoth Steppe as implying one simple homogenous pattern (Anderson and Brubaker, 1994).

4. Grazers and their actual diet on the Mammoth Steppe: a basis for solving the productivity paradox

I think the new paradigm helps clean up the question of how a cold arid habitat could support significant numbers of large grazers. But let us be clear about what these mammals were really eating. Did the Pleistocene grazing fauna resort to eating uncharacteristic food, like dwarf willows or river-bar annual weeds (Colinvaux and West, 1984)?

Fossil mammals originally set up the image of northern steppes. I have discussed and reviewed the importance of large mammals as indicators of an arid grassland (Guthrie, 1968, 1982, 1990), and here will only reiterate several key points, and add a note about new evidence from paleodiet. The fossil evidence is clear about the predominance of horses, bison, and woolly mammoths, wherever the proper depositional conditions prevailed. Fossil remains of three key grazers are found all across the mammoth steppe and in all terrains, high-country, valley bottoms, flood-plains, etc. Were each of these three specialized Pleistocene grazers eating grass and other herbaceous plants or were they eating characteristic wet-

tundra or woody plants for their main diet? This point has been tested using the fossil record.

A close look at teeth in fossil skulls and jaws reveals fragments of plants preserved in the small enamel pits between the molar cusps (Guthrie, 1990). For the last two decades, commercial labs and range managers have worked together to develop histological plant fragment identifications of diets of rangeland species using fecal analysis. This same technique can be used with fossil dental samples. I collected approximately 10 samples of plant fragments from the teeth of museum specimens of each of the common Alaskan Pleistocene large mammal species. Histological analyses of these were conducted by the Colorado State University Histological Laboratory and are summarized in Fig. 12.

Plant fragments obtained from teeth of steppe bison and Siberian woolly rhino were overwhelmingly graminoids, particularly grasses. As woolly mammoth molars have no pits I used data from Russian studies that identified stomach contents of frozen mammoth mummies. Again, these consisted mainly of grasses. Muskoxen and caribou are mixed feeders and this is reflected well in the plant fragments from their respective molar samples (note the high percent of lichens from caribou, and of

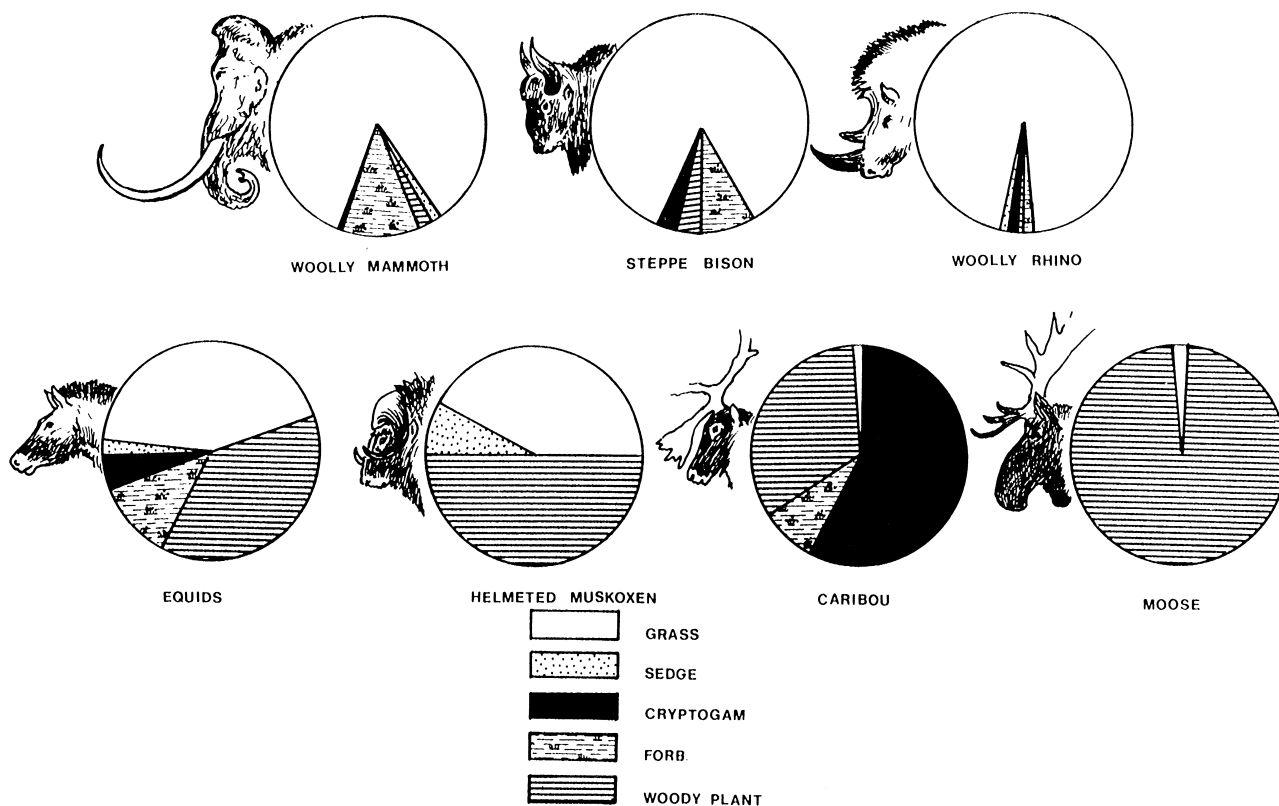


Fig. 12. Pie diagrams of percentage summaries based on plant tissue samples taken from molars of fossil steppe bison, woolly rhino, muskoxen, caribou, and moose; from fossil horse incisor pits; and from stomach contents of frozen woolly mammoths. Cuticle histological samples were ground and keyed microscopically. Mammoth and woolly rhino samples are from northeastern Asia. All others are from the Fairbanks, Alaska mining district. These represent combined samples of approximately 10 individuals each. A more extensive presentation of this data is to be made in another publication (Guthrie, in prep.).

willow from muskoxen diet). Moose dental samples (remember moose, *Alces alces*, are only present in the Holocene and were absent from the north during the LGM) reflected a diet mainly of browse which is consistent with what we know from modern studies. Thus, these fossil samples are quite similar to the adaptive target known for these species from anatomy and modern analogs. The notable exception occurred among dental samples from fossil Alaskan horses. Living equids are specialized grazers, yet over a third of the horse samples were from woody plants. This was puzzling. Were Alaskan Pleistocene horses deviating from the grazing pattern usual for horses?

As a check on correspondence with actual diets, I collected 10 samples each from extant African plains ungulate carcasses in the wild. The species sampled included a full spectrum of adaptive dietary ranges: from almost exclusive grazers, to mixed feeders, on to almost exclusive browsers (the dental samples from black rhinos were lost in the mail). Actual diet of each of the extant African species was well known, having been the subject of nu-

merous field studies, observation, and fecal analysis. Many of the studies had been conducted in the very areas where I took my samples (Kruger Park and Rooiport, the Cecil Rhodes Ranch at Kimberly, RSA). The rhino samples came from the Zimbabwe Natural History Museum in Bulwayo. With a single exception, plant matter from tooth samples matched the predicted diet of each species very well (Fig. 13). The exception was zebra. Actual diets of zebra are known to consist almost exclusively of grasses. Yet, my dental samples showed a high percentage of woody plants. Zebra diets do include minor components of forbs and woody plant leaves, but nowhere near the percentages shown in my samples.

There is, I believe, an explanation for this discrepancy that clarifies both the zebra and the fossil Alaskan horse data. Other than equids and mammoths, plant matter was obtained from molars of both extant African animals and fossil Alaskan species. Because the crowns of equid and mammoth molars are filled with cementum (as part of their extreme grazing specialty) there are no pits from which to obtain plant samples. So instead, the samples

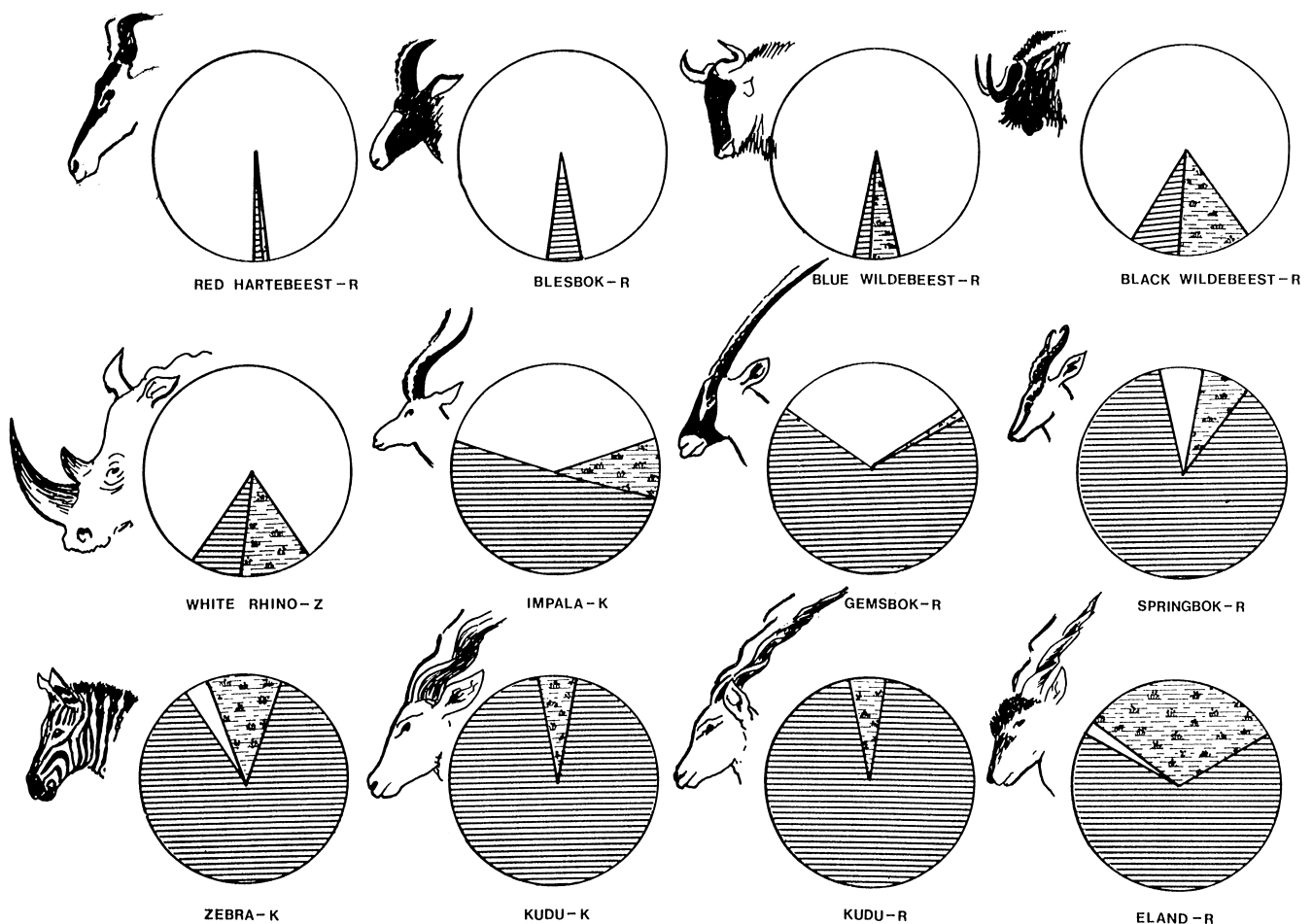


Fig. 13. Data summaries from African plains ungulates, for comparison. Same key as in Fig. 12. R designates samples from Rooiport, and K from Kruger, both in RSA, and Z from the Natural History Museum, Bulwayo, Zimbabwe. These represent sample summaries of approximately 10 individuals of each species.

from the Alaskan fossil horses and African zebra were taken from pits in the incisors. Equids primarily use their lips to feed on tender grass leaves and use their incisors to bite off more resistant material. Incisor pits contained woody plant material out of proportion to its presence in the total equid diet, but this probably is an accurate reflection of the selective use of incisors when eating woody plants. I think this reasonably explains the greater than predicted woody plant tissue for both zebra and Alaskan horse samples. Thus, this paleodiet study fully confirms the picture that grazing adapted species found as fossils in the LGM of Alaska were indeed using grasses as their dietary staple.

Large northern mammals which were specialized browsers, for example, moose, *Alces*, and mastodon, *Mammot*, occurred in Alaska only during the warmer-wetter Interglacial–Interstadial portions of the Milankovich cycle. Fossil remains of large browsers are totally absent during full Glacial cold and aridity. Even species which take a significant portion of their diet in woody plants were comparatively rare – species such as muskoxen, *Bootherium* and *Ovibos* (Guthrie, 1968). A similar patterning has been established in the European fossil record. For example, during the LGM European moose, *Alces*, which today live in the far north of Scandinavia, were driven toward the Mediterranean, to Spain and Italy. It is the combined presence of grazing specialists and the absence of browsing specialists which is so eloquent an argument for a grassland type of environment during full Glacial.

How abundant were these large grazers in this northern steppes? It is almost impossible to even guess. Fossil mammal assemblages do not let us approximate standing biomass or productivity. But, the high species diversity, large individual body size, wide distribution and ubiquity of these fossils all suggest that “mammoth fauna” was not extremely uncommon. Yet, the standing biomass and productivity in comparison to, say, an African or a mid-latitude American grassland, was most likely much lower.

4.1. The solution to the productivity paradox?

So we can confidently say that these grazers were eating the grasses to which they were adapted. But how could the Mammoth Steppes support a more complex large mammal community than today’s lush green northern landscape? Despite the moderately high standing biomass in the far north, little of today’s northern vegetation is edible for large mammals. This is because the kinds of plants which predominate are adapted to conservative nutrient use on cold soils which have low amounts of available nutrients. Some plants manage to thrive in these situations by using a relatively slow unproductive growth strategy and by devoting considerable resources to defense from herbivores. Thus, their low

above-ground productivity is ultimately due, not to a low standing biomass or even to inherently infertile soils, but to the low rate of nutrient turnover in the soil (Fig. 14). Cold soil paludification favors shallowly rooted plant species that contain large percentages of anti-herbivory compounds, which means that dead roots and leaf litter decompose so slowly (Bryant and Chapin, 1986) that they tend to produce a thick humus mat. These make “insulation-generating” soils, which at depth are unwarmed by summer sun, which in turn favor even more conservative plant species in a cyclic process. As a result, a reindeer walking through moist tundra or a moose through boreal forest, will find few edible plants or plant parts, and since the occurrence of edible plants is spotty, the large-mammal carrying capacity is low.

From what we can reconstruct, the standing biomass of the Pleistocene steppic vegetation had less leafy mass than is found on today’s northern landscapes, but it had a higher energy and nutrient turn-over. Paludification would have been prevented by clear skies. These same clear skies would have warmed the soil surface, increasing summer thaw levels and biotic and chemical activity in the more alkaline top soil. These conditions promoted deeper roots, longer growing season, early snow melt, and likely late snow arrival (Guthrie, 1982, 1984a). These, in turn, favored steppic plants with a quite different growth and anti-herbivory defense strategy, completely changing the equation for large mammals (Fig. 14). Unlike tundra–taiga, this steppic phytomass was in forms which large mammals could utilize. A herd of large grazers, like bison passing through, eat most of the standing steppic sward, as if it were mowed. That is not the way a large mammal approaches tundra–taiga vegetation.

A higher turnover of nutrients and carbon in the upper soil levels translates into a comparatively high productivity for the smaller amount of graminoid tissues. Since moisture loss is related to transpiration and transpiration is related to productivity, the rapid turnover of steppe plant tissues would have enhanced aridity (Field et al., 1992). But we are talking about *relative* turnover of a small standing steppe biomass, undoubtedly much smaller than the standing biomass of most tundra–taigas today. The high standing biomass gives many of today’s tundra–taigas the look of a vary productive landscape, but looks are deceptive.

Northern botanists and paleobotanists have repeatedly stressed the requirement for a moist soil to provide sufficient plant productivity to support large grazing Pleistocene mammals (Colinvaux and West, 1984; Colinvaux, 1986; Cwynar and Ritchie, 1980; Schweger, 1990; Zimov et al., 1995). It seems to be a botanist’s bias that water is inherently good, but that would not have been an Alaskan bison’s view. It is a problem of scale, good summer rains produce a bountiful steppe crop, but let summer dampness go for many years in succession and other less-edible vegetation takes over by out-competing

HOW CAN WE ACCOUNT FOR THE ACCUMULATION OF DEEP PERMAFROST COMBINED WITH A PRODUCTIVE STEPPE?

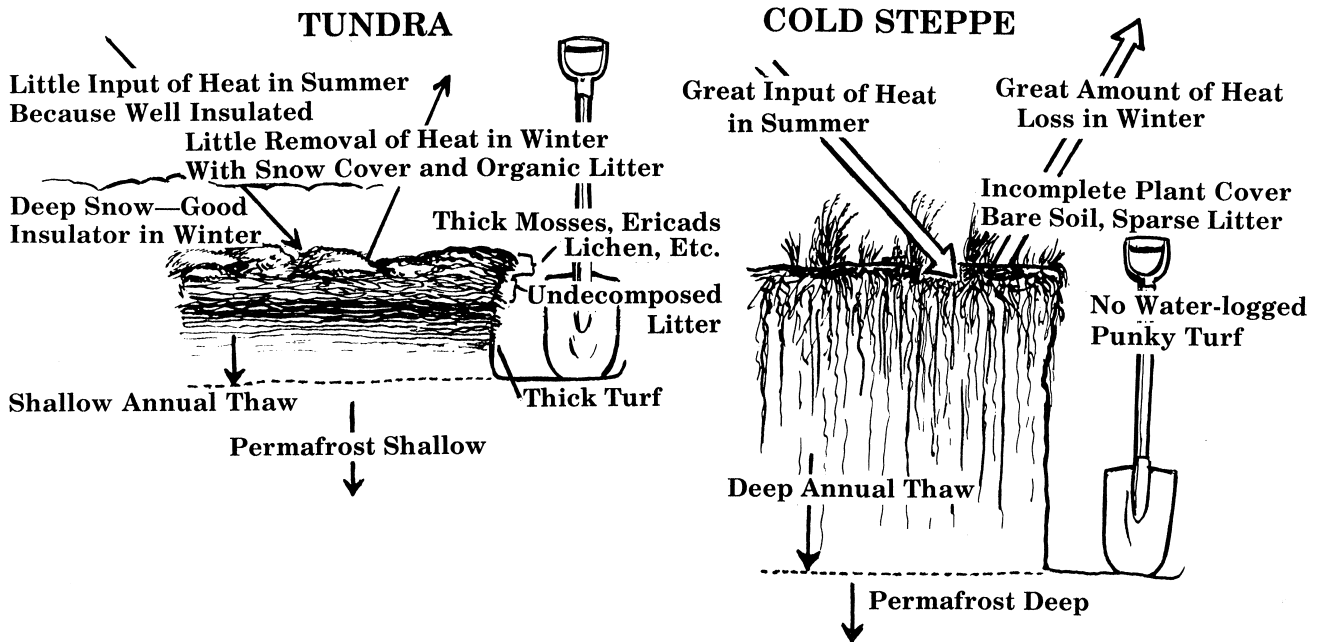


Fig. 14. Though each are quite diverse, characteristic tundras and characteristic steppes differ in fundamental ways.

steppe plants. There are significant trade-offs in being arid-adapted.

Of course, what is ultimately at stake is not a simple matter of plant productivity because plant biomass does not directly translate to large mammal biomass. For a large mammal, the world is not equally 'green.' The chemical and physical defenses of plants means only some species and some plant parts are both nutritionally appropriate and palatably non-toxic. Among these, many are not accessible for much of the year, or access is very costly. As there is no indication from Pleistocene site records of species being limited to stream bottoms, uplands, or special situations we are challenged to explain what allowed bison, horse, and mammoth (the most common large mammal fossils) to prosper and be productive over a variety of landscapes. These three species would find most plants in today's northern vegetation inedible. And among the scattered edible ones, access in winter would be problematic. There are some rare exceptions to these generalizations across the north today, and they are quite informative. Bison and horse can manage in a few special situations (Guthrie, 1990), a few flood-plain sedge flats, extensive river bar systems and on the deltas where rivers emerge from windy mountain passes, and to some extent on the grassy succession from old forest fires.

Pleistocene horse, and mammoth were not species that foraged above the snow (Guthrie, 1990). They would

have benefited from the fact that, across the Mammoth Steppe, a large part of the forage would have been exposed in winter by winds and drifting snow, widening the most limiting ecological bottleneck – access to winter forage. All winter forage at these latitudes is still likely to be below maintenance levels – it is only a supplement to keep from using up fat reserves too quickly. Any difficulty imposed in obtaining winter forage is paid for in the expensive currency of a more rapid expenditure of body fat reserves.

We have reviewed ecological driving forces and outlined the character of the moisture-limited, nutrient-rich, steppe vegetation and its effect on forage quality for large grazers. But cause and effect are always difficult to sort out. This issue has been turned around by Zimov et al. (1995), proposing that instead of the Mammoth Steppe being maintained by climatic events it was driven internally by biotic forces.

4.2. Were megaherbivores the driving agent in creating and maintaining the Mammoth Steppe?

African researchers have recently developed awareness and documentation of plant–herbivore interactions in which the large mammal herbivores themselves maintain the vegetation in a special state of balance, uncharacteristic of what the interaction of climate and vegetation alone would produce. A review of the literature, showing

this phenomenon indeed does occur, is outside the scope of this paper (see McNaughton, 1979; Owen-Smith, 1987, 1988 for some of this discussion). Using recent African studies as a base, Zimov et al. (1995) and others (e.g., Putschkov, 1997) have proposed steppic vegetation in Pleistocene Beringia was less a consequence of macroclimate and more directly a product of trampling and grazing by large herbivores. Further they suggest that the late Pleistocene shift to modern tundra-taiga was the direct outcome of megafaunal extinctions due to “human overkill.” Finally, they propose that these northern steppes can be re-established by the re-introduction of large grazers, such as horses and bison, to the north. This is an exciting idea. But, the following are points I find problematic for the megaherbivore keystone hypothesis as the major agent in maintaining steppes in the far north, as opposed to climatic forces:

(1) Zimov et al. (1995) limit themselves to a discussion and modeling of mossy tundra vs. steppe. Yet, tundra is only a thin maritime border, especially in their primary study area on the lower Kolyma. Most of the area once occupied by the Mammoth Steppe is now forested by taiga vegetation. How could these grazing specialists convert boreal forest into steppe?

(2) We know from the fossil record that the major vegetational shifts prior to the LGM were acting in synchrony with the Milankovich climatic changes, such as during the last Interglacial, isotope stage 5e (e.g., Woillard, 1978; Péwé et al., 1997), when forests and tundra dominated in the far north, and steppes were rare. Who “overkilled” the grazers 125,000 years ago in the far north during 5e, and during the other previous Interglacials?

(3) Climatic change during marine isotope stage 3 (the Interstade saddle between the two major peaks of the last Glacial) was associated with the expansion of some boglands and peats. It also allowed trees and other mesic plants to recolonize Alaska. In Siberia and Alaska this was a time when steppic plants and more mesic vegetation apparently co-existed (Guthrie, 1990). There was a co-existence of a full array of large grazers like mammoth, horse, bison, wapiti, saiga, and camel with browsers like stag-moose and bonnet-horned muskoxen (Matthews, 1982; Guthrie, 1990). A similar co-existence is documented for that period in Northern Russia (Vereshchagin and Baryshnikov, 1982; Vasil'Chuk et al., 1997), and in Europe (Van Andel and Tzedakis, 1996). Why were these grazers successful in eliminating browse and browsers during isotope stage 2, the LGM, and not during the isotope stage 3 Interstade?

(4) All the large grazers did not become extinct at the beginning of the Holocene. For example, bison continued in Alaska and the Yukon Territory throughout the Holocene in small populations confined to marginal habitats, such as mountain passes and along open river flats,

almost until modern times, in fact some fossil bison have radiocarbon dates as late as a few hundred years old (Guthrie, 1990). In the 1930's bison from Montana were reintroduced into similar Alaskan habitats as occupied by the extinct Holocene bison. Yet, there is no evidence that the extinct Holocene or the reintroduced bison significantly transformed the vegetation where they lived, neither have the bison populations consistently expanded their ranges beyond these unique local habitats.

(5) Megaherbivore density and diet are very important to this keystone argument. Northern woolly mammoths and African elephants are quite different on both points. In Africa, the savanna elephants use grasses during the long growth seasons, but tend to browse during the dry season. African elephants occur in sufficiently high densities that this dry-season dependence on tree bark and leaves indeed can destroy enough trees to produce open grasslands. Elephants can cause this wholesale vegetation change because most trees and shrubs which turn green in the dry season are nutritious and edible. This quality dry-season forage during the dry-season allows high numbers of elephants to build-up without a seasonal bottleneck. Eventually, elephants do destroy most of the trees and the elephant population collapses. There is no arboreal parallel to this in vegetation across the far north. First of all, mammoth densities in the north were probably much lower than those of African savanna elephants. Also, most trees in the north (e.g., dwarf and shrub birches, larch, alder and spruce) are metabolically toxic and would have been avoided as a major food source by grazing mammoths. We can validate this with frozen stomach contents from isotope stage 3 (Guthrie, 1990).

(6) Unlike the African savanna, northern grasses and trees compete (Wesser and Armbruster, 1991) for shallow root space and for light during a brief summer. A mammoth's dietary avoidance of woody plants would, theoretically, have favored shrublands and woodlands, not the expansion of grasslands. Generally, when northern large herbivores browse it is on an intermediate succession stage. But this kind of use does not arrest, but rather speeds the succession processes (deToit et al., 1991; Pastor et al., 1988). For example, browsers on birch, willow, etc. hasten the development of mature spruce forests in the taiga zone, rather than retarding it as a grassland, shrubland or deciduous woodland stage (Bryant and Chapin, 1986).

(7) Zimov et al. (1995) must detail how large grazers convert a landscape of thick mosses, dwarf willow, muskeg bogs, and spruce woodlands into a graminoid dominated steppe through selective foraging. What do grazers eat in this habitat to transform it into grass? Zimov et al. imply the main agent of change is soil disturbance by large mammal trampling, but such disturbance would require corral-paddock densities. Indeed, these densities are what Zimov et al. have called for (i.e. 20–30 large grazers per km⁻²) in their proposed steppe

re-creation experiment using domestic horse and wild bison near the Chersky field station. But I think densities of one-tenth of this would have still been overstocking the Mammoth Steppe.

(8) Putschkov (1997) contends that the high densities of mammoths that used their tusks to break snow crusts to feed on grasses allowed the smaller animals, like saiga, access to winter resources. He proposes that this is one of the features that made mammoths the keystone herbivore, setting up a feeding succession for the rest of the ungulates. There are many problems with this idea (tusks are a social weapon and there is no physical evidence they were regularly used to sweep snow aside), but mainly it assumes snow disturbance on a scale which requires very high densities of mammoths, densities that would have been difficult to support on short-sward cold steppes.

(9) The counter proposal to nos. 7 and 8 (that high ungulate densities can cause trampling disturbance, and hence steppe) can be examined by natural experiments – we already have “trampers” in the north. Herds of hundreds of thousands of caribou across the north in regular migration routes (and there are many herds of domestic reindeer on the lower Kolyma, near Chersky) have not converted this wet-tundra landscape into a steppe. Reindeer can greatly change lichen stands (their traditional winter forage) across a wide landscape. And it is lichen that seems to be ultimately limiting to reindeer numbers. But this trampling makes the tundra even wetter.

(10) Zimov et al.'s. (1995) model assumes greater LGM summer rainfall and winter snow than today, and by implication greater cloud cover. In their opposition to the climate-vegetation model, they propose that grazers could have produced the steppes, and the steppes themselves could have produced the aridity by increasing both the evaporation and transpiration. But one must then ask, where is the fossil evidence of ponds and lakes from this increased rainfall, and why do we find large fossil dune fields down-wind from exposed river flats? The idea of extreme LGM aridity is not only based on fossil biota but also is grounded in extensive physical evidence, which this model ignores.

(11) While large mammal foraging is an important ecological factor and can especially influence woody plant succession (Bryant and Chapin, 1986), any model of steppe origins must produce forces which not only limit trees but *drive virtually all tree species like conifers out of the far north* without leaving behind as much as a single isolated stand. We know that in the Early Holocene most tree species had to recolonize from refugia thousands of kilometers to the south. And this phenomenon happened in such disparate places as Europe and Alaska-Yukon Territory. Grazers can influence vegetation, but can they do so at that level of thorough intensity on such a vast scale?

If the megaherbivore keystone hypothesis applies to the Mammoth Steppe, it seems to me that it must incorporate interactive climatic changes into its model, for without these its predictive powers are not robust.

5. Climatic-ecological variations in the Late Pleistocene and their implications for the Mammoth Steppe

Climatic proxy information from such sources as marine cores (e.g., Shackleton, 1987; Bond et al., 1993; Kotilainen and Shackleton, 1995), Greenland ice cores (e.g., GRIP, 1993), China loess chemistry (e.g., Porter and An, 1995; Chen et al., 1997), and others have shown larger fluctuations within isotope stages and across a number of different time scales than data had once portrayed, and our earlier models had projected. These variations are particularly significant for the Mammoth Steppe habitats, because trees invaded far northward in Siberia and Alaska during isotope stage 3 (Anderson and Lozhkin, this volume), yet in Europe most tree species were trapped beyond the southern mountains (Van Andel and Tzedakis, 1996). This did not mean that in stage 3 steppic Europe continued to experience peak LGM conditions. For example, during this Interstade (isotope stage 3) humans were able to penetrate far north toward the Baltic and they inhabited southern England (this is not true for isotope stages 4 and 2). Likewise, European large mammal faunas were more complex and species-rich during isotope stage 3 than during either isotope stages 2 or 4 (Stuart, 1982). This same pattern is seen in north-eastern Asia. In Alaska, during isotope stage 3, the mesic-arid adaptive spectrum was also very scrambled. As a diagrammatic example, radiocarbon dates from the extinct, mesic adapted, browsing stag-moose, *Alces latifrons*, are contemporaneous with dates from fossil of saiga, *Saiga tatarica*, a much more arid-adapted species, in the very same fossil localities (Guthrie et al., in prep.).

In a few rare places peats formed in the Alaskan valley bottoms (Guthrie, 1990) during isotope stage 3, and some tree species returned to Alaska (Matthews, 1974). It was a time of significant erosion, suggesting more moisture, yet not enough moisture to produce a complete ground cover of plants. Catchment basins show no overwhelming record of lakes or ponds, during this time. Overall it appears to have been a mix of riparian fingers of woods, but no forests, and uplands covered with a variety of arid communities, corroborating existing radiocarbon date patterns in the Asian far east (Vereshchagin and Baryshnikov, 1982; Sher, 1986, 1990; Vasil'chuk et al., 1997) and in the Yukon Territory and Alaska (Harrington, 1978; Matthews, 1982; Guthrie, 1990). New radiocarbon ages (Guthrie, in prep.) show the mammalian communities of grazers (horse, bison, mammoth, etc.) still predominated in isotope stage 3 while the more mesic-adapted browsers

reappeared. That is, these steppic species lived within a community enriched with mesic species. Again, we encounter a complex of ecological associations without extensive modern analog. But remember, the marine cores, the Greenland ice cores, and deep Chinese loess sections show tremendous climatic variations for the northern hemisphere in the Late Pleistocene – it was not a smooth pattern (see Chen et al., 1997 for a comparison). What all this variation meant on the ground is certainly not clear. Did species proportions fluctuate wildly from one century to the next?

Our new information highlights saw-tooth climatic switches at shorter time-interval scales, but we know that most biotic changes require some lag time (for example, several thousand years for trees to move northward). It is probable that extreme conditions during the short span (say, 100 years) of one sharp saw-tooth climatic episode may be sufficient to restart (back to zero) time-transgressive changes which would have required thousand(s) of years to complete. However, before that time another short saw-tooth episode may again set the clock back to zero. Thus, it would be possible to maintain a climatic mean of one condition and have many proxy species behave as if it were another. For example, in Europe, during stage 3, it may have been generally warm and wet enough for sylvan elements to recolonize from the south, but irregular and infrequent episodes of clear skies, and the aridity it produces, kept them out. This kind of phenomenon may have happened widely in the past.

I think this new emphasis on cloud cover and aridity gives us a new handle to think about some of the proximate forces driving these within-isotope-stage variations in northern environments.

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