

STRUCTURALLY NOVEL BIOMES: A RESPONSE TO PAST WARMING IN BERINGIA

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Abstract. At northern high latitudes, biosphere responses to and interactions with climate warming are expected to be significant during the 21st century. Most predictions of climate–biosphere interactions rely on experiments and observations in contemporary landscapes, e.g., modern distributions of vegetation types and their structural features are used to delimit potential biosphere–atmosphere feedbacks. Paleorecords look beyond the present to examine vegetation configurations under climatic regimes that approximate future scenarios. To enhance the knowledge of arctic and subarctic ecosystems under varying climatic conditions, we analyzed pollen and macrofossil data from Beringia (northeast Siberia, Alaska, and northwest Canada; 130° E to 130° W) over the past 21 000 years, with a focus on structural and functional features of the vegetation. During the early Holocene (~13 000–10 000 cal yr BP), shrub tundra ecosystems responded to climate warming through a shift from shrub tundra to deciduous forest or woodland. Early-Holocene vegetation was structurally, and hence functionally, novel compared with today's dominant vegetation types. "Modern" boreal forest developed in the mid-Holocene (~10 000–6000 cal yr BP), when evergreen conifers expanded in much of the region. The shift from tundra to deciduous forest could have happened rapidly and in situ as the result of individual (phenotypic) and/or population-scale responses to climate warming. Because the structural and functional properties of deciduous forest differ from those of evergreen coniferous forest and tundra, deciduous boreal forest should be included in the range of future scenarios used to assess the probable feedbacks of vegetation to the climatic system that result from global warming at northern high latitudes.

Key words: Beringia; boreal forest; climate change; Holocene; novel biomes; plant functional types.

INTRODUCTION

The effects of increasing global temperatures are already becoming clear in northern high latitudes, where sea ice and permafrost have begun to melt (SEARCH SSC 2001) and tree and/or shrub growth has increased at many locations (Chapin et al. 1995, Barber et al. 2000, Sturm et al. 2001, Lloyd 2005). Such changes potentially generate land-surface feedbacks to the global climate system (for example, changes in planetary albedo are predicted if boreal forest were to replace tundra over large areas; Bonan et al. 1992, Levis et al. 1999). Global change studies in arctoboreal regions usually focus on the responses of currently dominant plant taxa that affect ecosystem structure and function (e.g., Hobbie et al. 1999) and have strong feedbacks

with the atmosphere (e.g., Chapin et al. 2000, Eugster et al. 2000). The transition between evergreen boreal forest and tundra has received special attention (McGuire et al. 2003), because differences in surface properties such as albedo and fluxes of sensible heat and moisture may amplify climate warming if these forests expand northward (Foley et al. 1994). An expansion of evergreen forests is commonly proposed for North America and most of Eurasia, and the replacement of deciduous conifer forest by evergreen conifer forest has been predicted in northeast Siberia (Claussen 1996, Kaplan et al. 2003). The possibility of evergreen forest expansion has led to various modeling studies; for example, Betts (2000) modeled the carbon sink created by increased forest growth and extent and found this potential negative radiative forcing was offset by decreased albedo.

In contrast, some vegetation scenarios that consider moisture limitations suggest increased dominance by deciduous trees. Though global climate models generally simulate greater precipitation at high latitudes

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(see Walsh et al. 2002), precipitation estimates are highly uncertain. Even if precipitation increases, warmer temperatures may lead to greater evapotranspiration and drier conditions for plant growth, especially in rain-shadow regions such as interior Alaska (Barber et al. 2000). Under scenarios of decreased effective moisture, stand- and landscape-scale models have predicted future vegetation dominated by deciduous forest or even grassland for Alaska (Bonan et al. 1990, Starfield and Chapin 1996, Chapin and Starfield 1997). Once established, deciduous forest may persist for centuries within areas that currently support tundra, if the dispersal of conifers is slow (Rupp et al. 2001). Given differences in potential feedbacks to climate between evergreen coniferous forest and broadleaf deciduous forest (e.g., greater sensible heat flux from coniferous forest; Eugster et al. 2000), the existence of alternative scenarios of future vegetation has serious implications for understanding the consequences of climate warming. Thus there is an urgent need to evaluate the range of possible future responses, interactions, and feedbacks between the biosphere and other elements of the climate system in the far North.

A major uncertainty in such evaluations is that future conditions will likely lie outside the bounds of current experience. A paleoecological approach contributes long-term records of vegetation response to climate change that extend the range of contemporary observations and experiments. It complements modeling studies by providing information about the nature of systems under climates greatly different from the present, providing a means to evaluate simulations of biotic responses to novel conditions. This paper highlights the value of paleodata through a synthesis of pollen and macrofossil records from Beringia (northeast Siberia, Alaska, and far northwest Canada) for a key period of interest: the early Holocene climate warming, ~13 000–10 000 cal yr BP. Results indicate that a deciduous forest biome, which lacks a widespread counterpart on the contemporary Beringian landscape, extended across the region for several millennia. With future climate warming, a similar deciduous biome has the potential to develop in extant tundra regions, conferring markedly different surface properties than would occur with the expansion of evergreen boreal forest typically predicted for the 21st century.

STUDY AREA

Beringia is defined here as the region between the Verkhoyansk Range of eastern Siberia and the western Yukon Territory, Canada, with the division between west and east Beringia falling along the Bering Strait. During glacial times when sea levels were as much as 125 m lower than present, Beringia was a vast subcontinent that included low-lying areas of the then exposed Bering, Chukchi, and East Siberian Seas (Fig. 1).

Beringia is currently dominated by cold, dry, air masses in winter (January means are typically around -20°C , January precipitation < 20 mm). The growing season is cool in coastal and mountainous regions (e.g., July mean at Kotzebue and Magadan is $\sim 12^{\circ}\text{C}$) but warm in continental interiors (July mean at Fairbanks and Seimchan is $\sim 15^{\circ}\text{C}$; Fig. 1). The majority of precipitation falls in summer, but the amount varies with location: continental interiors often experience water deficits due to warm temperatures and low precipitation (particularly in rain-shadow areas), whereas cooler coastal areas seldom experience water deficits.

The vegetation is dominated by boreal forest and low-to-high shrub tundra (height 0.25–2.0 m; Bigelow et al. 2003). Forests cover southern and interior regions, while tundra lies to the north and along the Bering Sea. In west Beringia, forests are comprised of the deciduous needleleaf tree, *Larix dahurica*, with broadleaf trees on disturbed valley bottoms (*Populus suaveolens*, *Chosenia arbutifolia*) and hillsides (*Betula platyphylla*, *B. lanata*). Forest shrubs include *Pinus pumila*, *Betula exilis* and *B. middendorffii*, *Salix* spp., and various heath species. A high-shrub tundra of *P. pumila* and *Duschekia fruticosa* (formerly classified as *Alnus fruticosa*) extends east and north of the *Larix* forest. Beyond this lies low-shrub tundra. Coastal areas are dominated by Poaceae–Cyperaceae–*Artemisia* tundra with prostrate *Salix* and occasional *Betula* shrubs. In east Beringia, the interior forests are dominated by the evergreen conifers *Picea mariana* and *P. glauca*, occasionally mixed with *Larix laricina*. Successional hardwoods are *Betula neoalaskana*, *B. papyrifera*, *Populus balsamifera*, and *P. tremuloides*. *Alnus crispa* shrubs, sometimes in dense thickets, occur beyond *Picea* tree line or on floodplains. Low- to high-shrub tundra of *Betula nana*, *B. glandulosa*, and *Salix* spp., often with a strong component of graminoid and heath species, covers coastal regions of the Beaufort, Chukchi, and Bering Seas. For further vegetation details, see Anderson and Lozhkin (2002) and Viereck et al. (1992).

In Beringia, plant structure may vary significantly within a species (Viereck and Little 1972; Table 1). For example, *Betula glandulosa* can be a low-growing (< 50 cm) shrub or a robust multi-stemmed individual nearly 2 m high, and hybrids with tree *Betula* (*B. neoalaskana*) typically reach several meters in height (Edwards et al. 1991). *Alnus crispa* and *Duschekia fruticosa* occur as low shrubs in tundra but can be 3–4 m tall in boreal forest or high-shrub tundra. *Salix alaxensis* is found as a 6–9 m tall tree, an erect shrub of variable stature, and in prostrate form (Viereck and Little 1972). The evergreen needleleaf shrub, *P. pumila*, is also morphologically variable, being < 0.5 m high at its northern limit, but up to 4 m in the southern tundra of Chukotka (Kozhevnikov 1978, 1988).

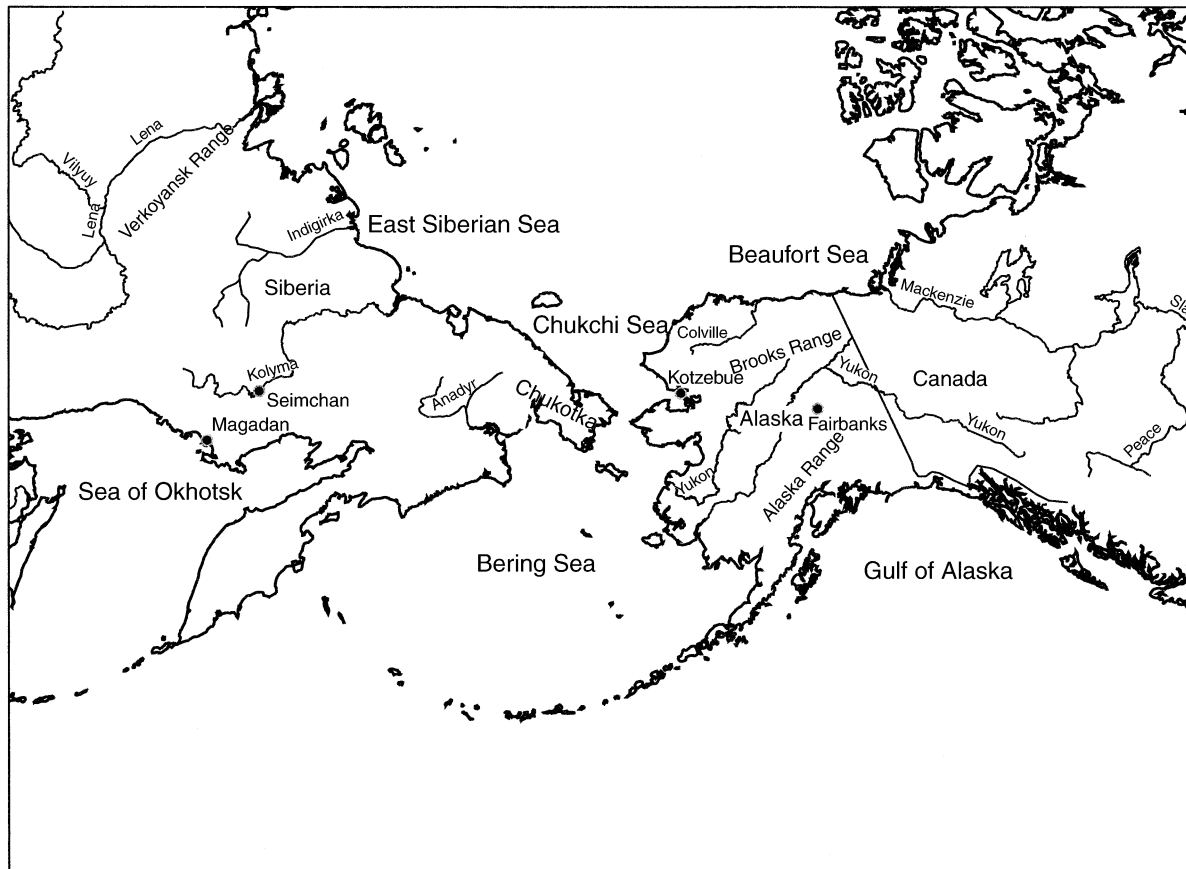


FIG. 1. Map of Beringia showing locations mentioned in the text.

METHODS

Plant functional types (PFTs; Prentice et al. 1992, Chapin et al. 1996, Diaz and Cabido 1997) are widely used to study climate–vegetation interactions. They have the advantages of being transferable among ecosystems characterized by different floras and of reducing the complexity of community descriptions to a manageable suite of plant groups. Their bioclimatic responses and growth characteristics can be modeled and used to evaluate past climate–vegetation interactions. For this application, the PFT approach has the particular advantage of circumventing the interpretive problem posed by past vegetation that produced pollen assemblages with no modern counterparts (i.e., the “no-analogue” problem; Anderson et al. 1989, Williams et al. 2001). Knowledge of the constituent PFTs and the application of a fuzzy-logic algorithm (biomization, Prentice et al. 1996) allow reconstruction of the functional features of a biome from pollen data without need of modern analogues.

The biomization approach, however, cannot directly address functional implications of pollen assemblages that are ambiguous with respect to the structural properties of the vegetation they represent. In situations where a few key taxa dominate the pollen record and

each includes a broad range of plant morphologies, the taxa cannot be assigned to PFTs in a way that differentiates one biome from another. Early-Holocene pollen assemblages from Beringia are both no-analogue and structurally ambiguous, as the constituent taxa (see *Study area*) often occur in a wide range of sizes and morphologies. Furthermore, numerous species show large phenotypic responses to changes in growth environments (Callaway et al. 2003). Jackson et al. (1997) have demonstrated that information from plant macrofossils may greatly enhance the interpretation of fossil pollen data, and here we use a combination of pollen and plant macrofossil data to interpret the structure of early-Holocene vegetation. Table 1 lists the key taxa in this study, the range of growth-forms encompassed, and their PFT assignments.

The Beringian paleodata set

Our study is based on pollen records from 149 sites that span all or part of the period 21 000–1000 cal yr BP. We confine our data to 13 500–5500 cal yr BP (Fig. 2A), the period of early Holocene warmth and transition to near-modern conditions. Original data are archived in the Paleoenvironmental Arctic Sciences

TABLE 1. Plant functional type (PFT) assignments of major woody taxa in Beringia discussed in this study.

Taxon	Distribution and growth forms	PFT assignments used in this study
<i>Salix</i>	tundra and boreal forest; prostrate shrub, low-to-high erect shrub, and small tree to 9 m	deciduous broadleaf prostrate shrub, deciduous broadleaf low or high shrub, deciduous broadleaf tree
<i>Betula</i>	tundra and boreal forest; erect dwarf shrub, low-to-high erect shrub, and small to large tree	deciduous broadleaf erect dwarf shrub, deciduous broadleaf low or high shrub, deciduous broadleaf tree
<i>Alnus, Duschekia</i>	tundra and boreal forest; low-to-high erect shrub to small tree	deciduous broadleaf low or high shrub, deciduous broadleaf tree
<i>Chosenia</i>	boreal forest and occasionally in tundra beyond treeline; small to large tree	deciduous broadleaf tree
<i>Populus</i>	boreal forest and occasionally in tundra beyond treeline; small to large tree	deciduous broadleaf tree
<i>Larix</i>	boreal forest; deciduous coniferous tree	deciduous needleleaf tree
<i>Picea</i>	boreal forest; evergreen coniferous tree	evergreen needleleaf tree
<i>Pinus pumila</i>	tundra and boreal forest; low-to-high shrub (but reaching 4 m in some regions), stems decumbent in winter	evergreen needleleaf low or high shrub

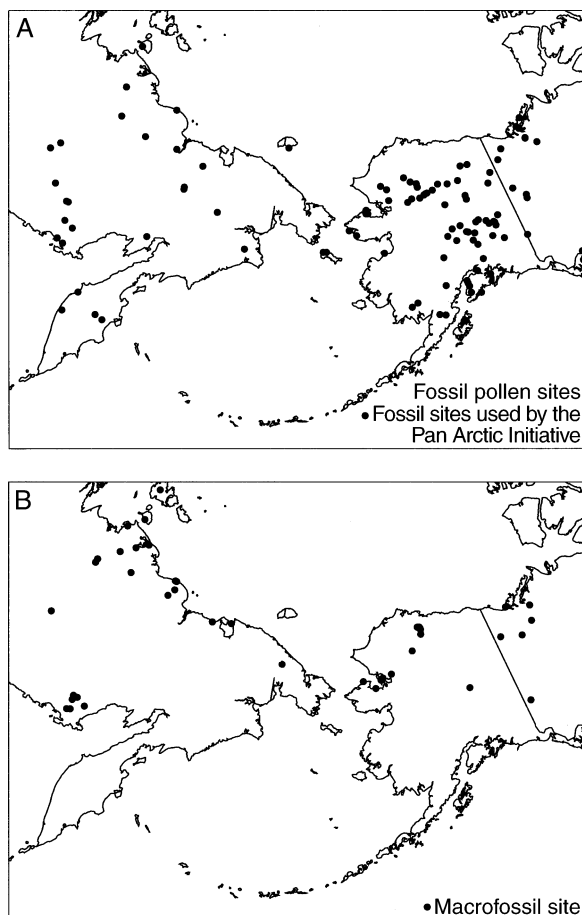


FIG. 2. (A) Location of sites in the Beringian pollen database, 21 000–1000 cal yr BP (149 sites, although there may appear to be fewer because dots overlap for nearby sites); (B) localities of tree-sized, dated, macrofossil finds, 13 000–10 000 cal yr BP (43 localities, although there may appear to be fewer because dots overlap for nearby sites).

(PARCS) database for Beringia (*available online*).⁷ Each of these records, representing lake sediments, buried peats, paleosols or alluvium, has been evaluated using standard quality controls (Edwards et al. 2000). Most site chronologies are based on calibrations of radiocarbon dates of bulk sediments, although recently published site chronologies typically use AMS radiocarbon ages obtained from preserved plant material. The median of the calibrated age probability distribution (Calib 4.0; Stuiver and Reimer 1993) is used for site age models, which take the form of a simple linear interpolation.

For each taxon, the pollen values at a site (expressed as percentages of total terrestrial pollen) are averaged for all samples in a 1000-cal yr period centered on a target time (e.g., data for 8000 cal yr BP are the average of all samples between 7500–8500 cal yr BP). We evaluate structural-functional aspects of the Beringian vegetation qualitatively by examining changes in dominant pollen taxa, defined by the following PFTs: deciduous needleleaf tree (*Larix*), evergreen needleleaf tree (*Picea*), deciduous broadleaf tree (*Betula*, *Populus*, *Salix*, *Alnus*, *Duschekia*), deciduous broadleaf shrub (*Betula*, *Alnus*, *Duschekia*, *Salix*), and needleleaf evergreen shrub (*P. pumila*). We tally the percentage of sites (note: the total site number increases from older to younger intervals) at which a pollen taxon reaches a threshold value that indicates the taxon was common in the surrounding vegetation. This threshold was determined from published studies of modern pollen-vegetation representation (for example, Ritchie 1974, Birks 1980, Anderson and Brubaker 1986, Lozhkin 2002).

Our macrofossil data set consists of 53 species records from 43 separate localities dated between 13 500 and 9500 cal yr BP, the period of no-analogue pollen spectra dominated by morphologically ambiguous taxa

⁷ (<http://www.ngdc.noaa.gov/paleo/parcs/bermapsearch.html>)

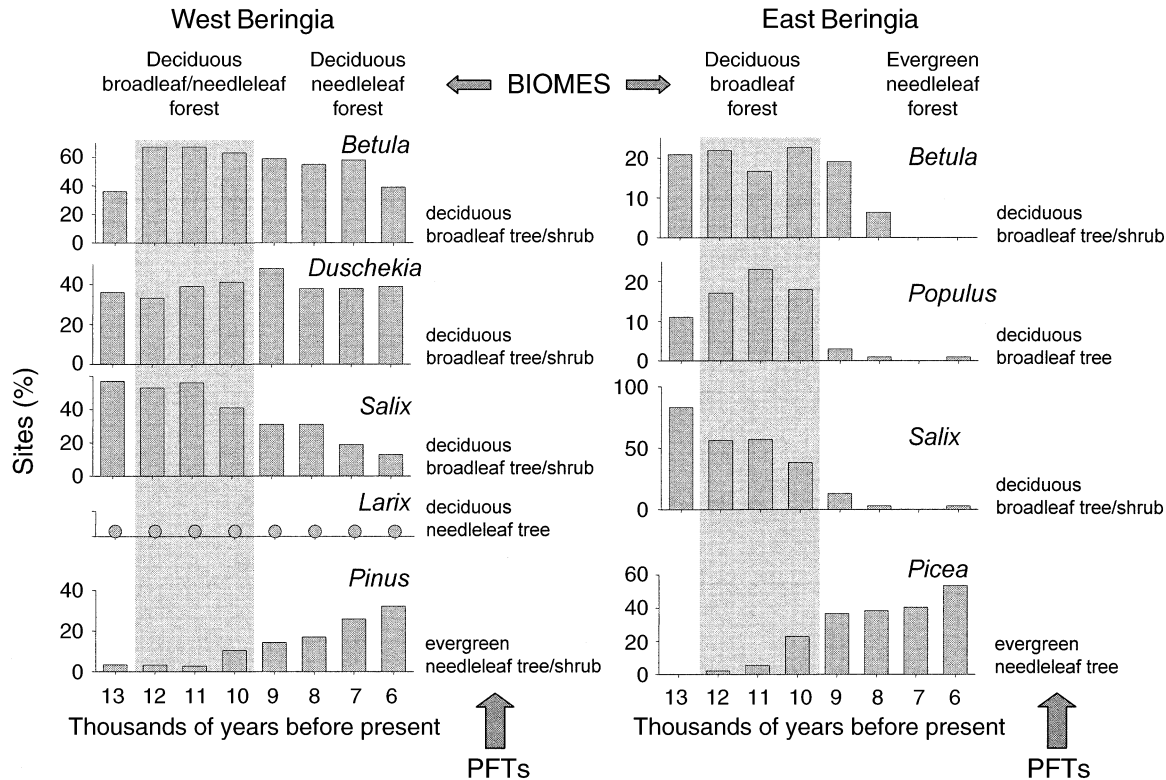


FIG. 3. Plant functional type (PFT) composition and biomes (vegetation types) for 13 000–6000 cal yr BP, shown separately for west and east Beringia. For key woody taxa in each region, the percentage of sites recording pollen values above an assigned threshold are plotted as vertical bars at 1000-yr intervals. To the right of each panel, the PFTs represented by each taxon are listed. The biomes across the top show the reconstructed vegetation types for 13 000–10 000 and 10 000–6000 cal yr BP.

(Fig. 2B). To qualify for inclusion, the macrofossil must be derived from an arboreal taxon (e.g., wood, leaf, cone, or fruit of *Larix* or *Populus*), or, in the case of morphologically ambiguous taxa, the wood fragment was large enough to indicate tree-sized stature (i.e., diameter of ≥ 10 cm). The appendix provides full details of the macrofossil records.

RESULTS

Pollen data

Between $\sim 13\,500$ and 9500 cal yr BP, deciduous tree and shrub taxa are prominent components of pollen spectra across Beringia (Fig. 3). In east Beringia, these taxa are exclusively broadleaf trees and shrubs, including *Betula*, *Salix*, and *Populus*. In west Beringia, the dominant pollen PFTs are deciduous broadleaf trees and shrubs (*Betula*, *Salix*, *Duschekia*) and the deciduous needleleaf conifer, *Larix*. In contrast to west Beringia, where *Duschekia* is an important component of the pollen flora, its sister taxon *Alnus* is extremely rare in east Beringia (and thus not included in Fig. 3).

After 9500 cal yr BP, pollen of the evergreen needleleaf taxa *Picea* and *Pinus pumila* increases in east and west Beringia, respectively. *Populus* declines and is no longer a major pollen contributor in east Beringia

after ~ 9500 cal yr BP. In contrast, the pollen data show no declines of woody taxa in west Beringia. The expansion of *P. pumila* represents the addition of an evergreen needleleaf PFT to the deciduous forest elements already present.

Macrofossil data

Macrofossils of *Larix* and tree *Betula* dating to $11\,500$ – 9500 cal yr BP are widely dispersed in west Beringia, with some finds in areas that are currently covered by dwarf-shrub tundra. Other finds indicate that large-sized (e.g., >2 m high) *Duschekia* and *Salix* occurred at or slightly beyond modern tree line (Fig. 4). In east Beringia, reports of *Populus* logs and other macrofossils are numerous within current tundra as well as boreal regions. Tree-sized *Betula*-*Populus* (undifferentiated) is also reported in east Beringia.

DISCUSSION

Vegetation reconstruction

Pollen assemblages from $\sim 13\,500$ to 9500 cal yr BP have long posed a problem in vegetation reconstructions for east Beringia. Quantitative comparisons of pollen spectra from this period with an extensive modern pollen database from North America (Anderson et

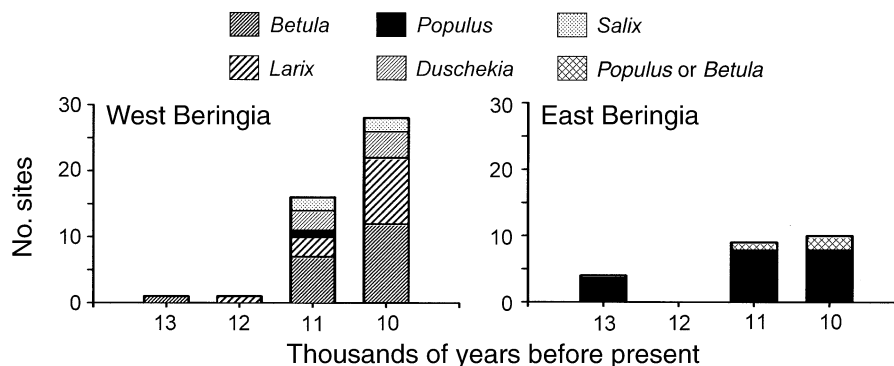


FIG. 4. Number of sites recording tree-sized macrofossils, differentiated by taxon, and dated between 13 500 and 9500 cal yr BP. West and east Beringia are shown separately in 1000-yr time slices.

al. 1989) revealed little similarity to modern spectra, suggesting that the vegetation differed substantially from any of the wide variety of forest and tundra types in current arctoboreal regions of Alaska and Canada. Despite the no analogue nature of past pollen assemblages, the prominent *Betula*–*Salix* component of the fossil spectra has usually been interpreted to indicate shrub tundra (see Ager and Brubaker 1985, Anderson et al. 1988). However, the widespread occurrence of *Populus* pollen has also led to the conclusion that scattered trees or woodlands were present in the early Holocene (e.g., Ritchie 1984, Ager and Brubaker 1985, Anderson et al. 1988, 1994, Bartlein et al. 1995).

The macrofossil data provide critical evidence for resolving the vegetation during this period. In west Beringia, where many records come from terrestrial sections with both pollen and macrofossils, the first widespread appearance of arboreal *Betula* and *Larix* macrofossils have led to the conclusion that an early shrub–tundra gave way to more forested conditions about 11 500 cal yr BP (Anderson and Lozhkin 2002). Macrofossils of tree-sized *Salix* and *Duschekia* also support the idea that large growth forms became common by this time (Fig. 4, Appendix). In east Beringia, the wood macrofossils confirm the widespread distribution of *Populus* (both *P. balsamifera* and *P. tremuloides* are reported) across the region by 11 500 cal yr BP.

Given the insight into vegetation structure provided by the macrofossil data, Beringian vegetation appears to have been a structurally complex mosaic between 11 500 and 9500 cal yr BP. Shrub taxa reached tree sizes (>2 m), and, with arboreal taxa, formed open woodlands and deciduous forests. Broadleaf taxa dominated in east Beringia, whereas needleleaf *Larix* became increasingly important in west Beringia. Subsequently, evergreen needleleaf PFTs spread across much of east and west Beringia. In east Beringia, the deciduous biome was replaced by evergreen needleleaf forest dominated by *Picea*. The shift in dominant PFTs was less pronounced in west Beringia, where *Pinus pumila* expanded into *Larix*-dominated deciduous forest. This

change established the modern forest vegetation, a deciduous needleleaf forest with evergreen needleleaf understory. The absence of macrofossil evidence for trees prior to ~11 500 cal yr BP suggests that shrub tundra was the dominant vegetation cover of late-glacial landscapes.

The Beringian example illustrates the limitations of a taxonomic approach to reconstructing past vegetation (including conventional biomization). Although the pollen record alone does not discriminate between tree and shrub PFTs, the macrofossil record contributes evidence about structural characteristics of past vegetation. The combination of pollen and macrofossil evidence indicates that the structure, and hence function, of the early Holocene vegetation in both regions differed from any widespread modern biomes.

Implications of the paleorecord for future change

The early Holocene provides a unique opportunity to observe the response of a tundra system to climatic warming. A range of proxy data indicates that early-Holocene summer temperatures in Beringia were as warm or warmer than present (Kaufman et al. 2004), and conditions were relatively dry, at least in Alaska (Barber and Finney 2000). Thus, the Beringian pollen and macrofossil data imply that climatic warming at high northern latitudes may favor the development of deciduous forest biomes. This implication is consistent with the results of stand-based and landscape-scale simulations that show deciduous forests under warm, dry conditions (e.g., Starfield and Chapin 1996, Chapin and Starfield 1997, Rupp et al. 2001). Particularly in east Beringia, where *Picea* currently defines boreal forest limits, the rapid development of deciduous broadleaf forest within tundra—a “novel” ecosystem (Chapin and Starfield 1997)—would reduce the predicted positive temperature feedback to the atmosphere associated with a northward shift of evergreen forest (Chapin and Starfield 1997, Eugster et al. 2000).

Another implication of this study concerns modes of species responses to climate change. Over the past several decades, many studies have emphasized the im-

portance of species migration (e.g., Ritchie and MacDonald 1986, Hewitt 2000), but there is now a growing realization that several different responses are likely to be important. For example, Davis (Davis and Shaw 2001, Davis et al. 2005) has challenged both neo- and paleoecologists to consider the role of adaptive evolution, which may include selection of particular populations (ecotypes) or selection of genotypes within populations. Crawford et al. (1993) and Crawford and Abbott (1994) discuss changes in ecotype frequencies and changes related to phenotypic plasticity of individuals in arctic taxa. In the low Arctic and Subarctic, the vegetation across large regions is dominated by woody taxa with high growth-form variability that is in part related to phenotypic variation. The large growth-form responses of *Salix* and *Betula* species in controlled growth experiments (e.g., seasonal temperature and moisture availability; Bret-Harte et al. 2001, Xiao 2001; K. Schwaegerle, *personal communication*) illustrate the potential importance of phenotypic responses to future climatic warming. Thus, future warming may cause rapid in situ shifts of the dominant PFTs from low shrubs to high shrubs or trees. Similar structural responses to climate change may also occur at lower latitudes in regions where morphologically flexible shrubs are an important component of the vegetation.

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APPENDIX

A table showing radiocarbon dates of macrofossils from Beringia (13 500–9500 cal yr BP) is presented in ESA's Electronic Data Archive: *Ecological Archives* E086-091-A1.