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Early-Holocene warming in Beringia and its mediation by sea-level and vegetation changes

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Abstract

Arctic land-cover changes (e.g., expansion of woody vegetation into tundra and effects of permafrost degradation) that have been induced by recent global climate change are expected to generate further feedbacks to the climate system. Past changes can be used to assess our understanding of feedback mechanisms through a combination of process modelling and paleo-observations. The sub-continental region of Beringia (Northeast Siberia, Alaska, and northwestern Canada) was largely ice-free at the peak of deglacial warming and experienced both major vegetation change and loss of permafrost when many arctic regions were still ice covered. The evolution of Beringian climate at this time was largely driven by global features, such as the amplified seasonal cycle of Northern Hemisphere insolation and changes in global ice volume and atmospheric composition, but changes in regional land-surface controls, such as the widespread development of thaw lakes, the replacement of tundra by deciduous forest or woodland, and the flooding of the Bering–Chukchi land bridge, were probably also important. We examined the sensitivity of Beringia's early Holocene climate to these regional-scale controls using a regional climate model (RegCM). Lateral and oceanic boundary conditions were provided by global climate simulations conducted using the GENESIS V2.01 atmospheric general circulation model (AGCM) with a mixed-layer ocean. We carried out two present day simulations of regional climate, one with modern and one with 11 ka geography, plus another simulation for 6 ka. In addition, we performed five ~ 11 ka climate simulations, each driven by the same global AGCM boundary conditions: (i) 11 ka “Control”, which represents conditions just prior to the major transitions (exposed land bridge, no thaw lakes or wetlands, widespread tundra vegetation), (ii) sea-level rise, which employed present day continental outlines, (iii) vegetation change, with deciduous needleleaf and deciduous broadleaf boreal vegetation types distributed as suggested by the paleoecological record, (iv) thaw lakes, which used the present day distribution of lakes and wetlands; and (v) post-11 ka “All”, incorporating all boundary conditions changed in experiments (ii)–(iv). We find that

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regional-scale controls strongly mediate the climate responses to changes in the large-scale controls, amplifying them in some cases, damping them in others, and, overall, generating considerable spatial heterogeneity in the simulated climate changes. The change from tundra to deciduous woodland produces additional widespread warming in spring and early summer over that induced by the 11 ka insolation regime alone and lakes and wetlands produce modest and localized cooling in summer and warming in winter. The greatest effect is the flooding of the land bridge and shelves, which produces generally cooler conditions in summer but warmer conditions in winter, and is most clearly manifest on the flooded shelves and in eastern Beringia. By 6 ka continued amplification of the seasonal cycle of insolation and loss of the Laurentide ice sheet produce temperatures similar to or higher than those at 11 ka plus a longer growing season.

1 Introduction

For the northern high latitudes, climate models simulate significant regional-scale changes that are consistent with presently observed changes in global climate (ACIA, 2004, p. 146; Serreze et al., 2007) and with projected future global climate changes (e.g., Collins et al., 2013). The distribution and physiological status of vegetation, combined with other features of the terrestrial surface, significantly influence energy, water, and carbon exchange between the land and the atmosphere (e.g., Bonan et al., 1995; Chase et al., 1996; Chapin et al., 2005). Such exchanges produce feedback to local, regional, and global climates, which, in turn, affect plant distribution and physiology (e.g., Thomas and Rowntree, 1992; Foley et al., 1994). Thus the potential exists for land-cover status to enhance or mitigate climatic change through either positive or negative feedbacks to energy, water, and carbon budgets (Oechel et al., 1993; Lynch et al., 1999; Chapin et al., 2005) and to generate significant feedbacks to the seasonal and annual climatology of much of the Northern Hemisphere.

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Large areas of the arctic and sub-arctic land surface are underlain by continuous or discontinuous permafrost that affects soil and drainage properties. At the landscape scale, land cover is a complex mosaic of tundra (tall shrub, mesic tussock, dry heath, fellfield and barrens, etc.), forest (evergreen conifer, deciduous conifer, and successional hardwoods), wetlands, surface standing water and lakes, and glaciers. Northern ecosystems have received considerable attention in the global budgets of carbon dioxide and methane, because soils, peatlands, and lakes are important sources and sinks of these gases and highly sensitive to changes in surface energy exchange (Oechel et al., 1993; Bonan et al., 1995; Zimov et al., 2006; Walter et al., 2006; Walter Anthony et al., 2014). Climatically induced changes in vegetation distribution, especially those involving replacement of tundra by forest, and changes in soil and permafrost properties will have a dramatic impact on these processes (Smith and Shugart, 1993; Smith et al., 2005). Further, biophysical land-atmosphere coupling via albedo, interactions between vegetation and snow, and modulation of sensible and latent heat fluxes have important climatic implications on seasonal-to-decadal time scales (Harvey, 1988; Thomas and Rowntree, 1992; Bonan et al., 1995; Sturm et al., 2005; Myers-Smith et al., 2011).

Currently observed changes linked to 20th-century warming in the Arctic and sub-Arctic include the expansion of large shrubs in northern Alaskan and Siberian tundra (Sturm et al., 2001, 2005; Forbes et al., 2010), negative trends in evergreen tree growth (Barber et al., 2000; McGuire et al., 2010), and rapidly thawing permafrost (Osterkamp and Romanovsky, 1999; Romanovsky et al., 2010). Vegetation competition-succession model simulations suggest the potential for more extreme shifts from evergreen forest to woody-deciduous and/or treeless biomes as a transient response to warming (Chapin and Starfield, 1997). Ultimately these changes and the land-surface interactions inherent within them must be modeled in a realistic way to project future change in the earth system. One approach for adding to our understanding of the earth system, and the models used to study it, is to use a set of “natural experiments” based on known past climate changes to evaluate the forcings and feedbacks associated

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with observed land-cover changes and thus assess climate-model sensitivity to such changes. Unglaci-ated regions of the Arctic warmed early in the Holocene (Kaufman et al., 2004) and experienced considerable terrestrial change over a few millennia; we use this period to conduct a series of sensitivity experiments with a regional climate model driven by a general circulation model (GCM) simulation for 11 ka.

Beringia (Northeast Siberia, Alaska, and northwestern Canada) is well-suited for such an exercise because a diverse range of paleoenvironmental records is available over the interval from 21 000 yr ago to present (21 to 0 ka BP). The early Holocene (ca. 12 to 10 ka BP) was a time of major climate warming, and paleoenvironmental data document shifts among tundra, woody-deciduous and woody-evergreen dominance (Edwards et al., 2005). We designed and conducted a series of regional climate-model simulations based on observed changes in vegetation, substrate, and sea level in Beringia during the period of major warming centered on the onset of the Holocene (ca. 11 ka BP). Our primary goal is to assess the sensitivity of the simulated climates to regional land-atmosphere interactions and feedbacks ca. 11 ka. We also simulated 6 ka conditions, which were climatically more stable but still warmer than present.

1.1 Study area

The regional climate-model domain (Fig. 1) is larger than the region typically defined as Beringia (Hopkins, 1982); it encompasses the Indigirka drainage eastward to Chukotka and Kamchatka in the western portion of the study domain, and Alaska, a considerable portion of northwest Canada and the adjacent seas in the eastern portion of the study domain. The regional topography is complex, including several mountain ranges, plateaus, low-lying tectonic basins and flat coastal plains. The easternmost parts of the study area lay under the Laurentide ice sheet during the last glaciation; other areas were affected only by local mountain glaciation (Kaufman et al., 2004; Elias and Brigham-Grette, 2007).

The modern climate of the study area has been described by Mock et al. (1998) and Edwards et al. (2001), from which the following description derives. In winter, the

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climate is influenced by the status of a mid-tropospheric trough-ridge system. An upper-level trough is centered on average to the east of China, and northward of the trough radiational cooling generates a strong surface high over Siberia. Consequent northwesterly winds block the incursion of maritime air into easternmost Asia and are linked to January temperatures as low as -40°C (Mock et al., 1998). High pressure over northwest Canada is associated with cold January temperatures of about -30°C . Conditions are somewhat warmer (-15°C) along the southern coast of Alaska (Mock et al., 1998; Edwards et al., 2001). Summer temperature is driven by high radiation receipts and the advection of warm air into both eastern and western portions of the study area via subtropical high pressure systems that develop to the south. Summer temperatures range from ~ 5 – 15°C across the study area (Steinhauser, 1979; World Meteorological Organization, 1981). Temperatures generally increase from north to south, except where there is local coastal cooling, and in interior basins of Alaska, which can experience July temperatures of 15°C or higher. In eastern Asia cooler temperatures inland relate to northerly flow due to the position of the East Asian trough over eastern Siberia.

Precipitation is low in winter; inland January total precipitation long-term means may be < 25 mm (Steinhauser, 1979; World Meteorological Organization, 1981), but southern regions of the study area receive abundant orographically enhanced precipitation of a meter per year or more. Typically, there is a late summer precipitation maximum related to mid-latitude cyclones that are steered across the region by the East Asian trough. July precipitation ranges from 50–100 mm; in eastern Asia precipitation levels increase southwards, while Alaskan interior basins are generally drier than western or coastal areas.

At a larger scale, the tendency for frequent cyclogenesis over Eurasia, Alaska, and Canada in summer is associated with the development of an Arctic frontal zone. The frequent association of the front with the boreal forest/tundra boundary appears to be related in part to moisture availability and albedo (Pielke and Vidale, 1995; Liess et al., 2012). The front appears most strongly in regions where significant topographic features are contiguous with the ecotone (Lynch et al., 2001). In the absence of large

changes in climate, the forest-tundra border may exert a stabilizing effect on regional climate as the relatively high-albedo tundra side of the border will remain cooler than the lower-albedo forest side of the border (Ritchie and Hare, 1971; TEMPO Members, 1996; Lynch et al., 2001). In contrast, when large, externally driven changes in regional climate occur, shifts in the location of the forest-tundra border may locally amplify the climatic change (Foley et al., 1994).

On a regional scale, the distribution of precipitation is strongly influenced by topography, particularly in coastal Alaska and Canada, but also in upland regions in the interior (e.g., the Brooks Range), where precipitation is greater than in lowland regions. The same is true in western Beringia, where precipitation is enhanced in the Chersky, Kolyma, Koryak, and Verkhoyansk mountain ranges and in coastal mountains in the Kamchatka Peninsula.

Land-surface properties also influence local precipitation. For example, the summer precipitation maximum in the Mackenzie Basin is associated with a minimum in large-scale vapor-flux convergence (Walsh et al., 1994), suggesting that substantial summer precipitation is derived from within-basin recycling of water vapor via evapotranspiration from the tundra and boreal forest. The numerous Alaskan lakes have a strong effect on surface fluxes and heat storage (Oncley et al., 1997; Rivers and Lynch, 2004), and it is possible that widespread fields of lakes that characterize some parts of the region may be an important source of feedback at the regional level (Subin et al., 2012).

Modern vegetation is a mosaic of forest and tundra communities. The northern Siberian coastlands, western and northern Alaska, Banks Island and the Canadian Beaufort Sea coastlands are characterized by tundra. Shrubs of varying stature dominate in many areas, but grasses and sedges characterize wet coastal zones. Alpine tundra occurs above boreal forest treeline at altitudes over 500–800 m. Forests in the Asian portion of the study region are dominated by the deciduous conifer *Larix gmelinii* (larch). River valleys also support gallery forests of *Populus suaveolens* (poplar) and *Chosenia macrolepsis* (willow), with various species of tree *Betula* occurring on slopes in southern areas. The shrubby stone-pine, *Pinus pumila*, forms areas of shrub tundra

in Northeast Siberia and is a common understory component of larch forests. The evergreen conifers, *Picea glauca* and *P. mariana* (white and black spruce) dominate forests in Alaska and northern Canada; here, hardwoods such as *Populus tremuloides* and *P. balsamifera* (aspen, balsam poplar) and *Betula neoalaskana* and *B. papyrifera* (paper birch) form seral stands after disturbances such as fire. Permafrost is continuous in the north and discontinuous to the south of the region (Rekacewicz, 1998). Extensive wetlands occur across the region related to topography and permafrost-impeded drainage. The southeastern part of the study area includes grassland and shrubland of the Columbia Plateau and interior Canada.

1.2 Key changes in land-cover features during deglacial warming

At the last glacial maximum (LGM: 25–18 ka BP) global sea level was lowered by ~ 120–135 m (Fairbanks, 1989; Yokoyama et al., 2000). The shelves of the Bering and Chukchi Seas and Arctic Ocean were exposed, and Alaska and Siberia formed a continuous land mass. The Laurentide and Cordilleran ice sheets (LIS, CIS) lay to the east and southeast of Beringia, and mountain glaciations occurred in the Brooks, Chersky, Kolyma, Koryak, and Verkhoyansk mountain ranges and other upland regions. Considerable eolian deposition occurred in lowland areas, particularly the northern coastal plain of Siberia, the Anadyr lowlands, and interior basins and the northern coastal plains of Alaska and Canada (Hopkins, 1982).

By 11 ka BP, rapidly melting continental ice sheets (and the large-scale atmospheric circulation changes associated with them), rising sea level, and increasing summer insolation generated a series of terrestrial changes in Beringia (Kaufman et al., 2004). Sea level rose rapidly during deglaciation (Fairbanks, 1989); estimates suggest the Bering Strait formed about 11 ka BP, but several millennia passed before the remaining expanses of exposed continental shelf were completely inundated (Manley, 2002; Keigwin et al., 2006). Beginning 15–14 ka BP, rates of thermokarst erosion increased, creating thaw lakes in low-lying regions underlain by frozen, unconsolidated substrates, such as exposed shelves, large floodplains, and loess-blanketed regions (Hopkins, 1949;

Williams and Yeend, 1979; Burn, 1997; Romanovskii et al., 2000; Walter et al., 2007). This period also marked the inception of wetlands and peat growth, which developed further in subsequent millennia (Jones and Yu, 2010). Thaw-lake formation accelerated in the early Holocene after 11 ka BP, but decreased subsequently (Walter et al., 2007; 5 Walter Anthony et al., 2014). It is likely that the current proportion of land occupied by lakes (for example 5–40% on the Arctic Coastal Plain) was attained during the early Holocene (Walter et al., 2007).

Over the period from ca. 15–8 ka BP, a sequence of changes in zonal vegetation occurred in Beringia. Across the region, graminoid-forb tundra that typified the LGM 10 was replaced around 15–14 ka BP by *Salix*- and *Betula*-dominated shrub tundra, generally interpreted to be initially of low stature (Anderson et al., 2004; Edwards et al., 2005). Over the next few millennia much of the region became dominated by woody taxa, although the species composition differed between the Asian and North American sectors. Between ca. 13–10 ka BP, lower-elevation regions of unglaciated Alaska and 15 Canada saw the expansion of deciduous tall-shrub and woodland vegetation; in Asia at this time vegetation cover at lower elevations included deciduous shrubs, hardwood trees such as *Betula platyphylla* (Asian birch) with *Larix* in the western portion of the region (Edwards et al., 2005). Between ca. 11–10 ka BP evergreen conifer forest developed in the eastern sector. The evergreen *Pinus pumila* spread across the western 20 sector, within and beyond the *Larix* forest limits. Shrub tundra remained dominant north of treeline across the whole region, except in the far north, where dwarf-shrub or herb-dominated tundra occurred. These general vegetation features persist to the present day, although there have been subtle changes in tree limits and forest composition (Anderson et al., 2004).

25 We focused on three features of 11 ka land-cover change for our model experiments: (i) the change in paleogeography caused by the flooding of the Bering land bridge and continental shelves, (ii) the change in vegetation represented by a shift from low-stature shrub tundra typical of early deglaciation to deciduous tall-shrub and woodland vegetation, (iii) the development of wetlands and fields of thaw lakes across low-lying

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terrain. We additionally examined the output from a simulation for 6 ka, a time when insolation patterns were still markedly different from present (Fig. 2) but land cover and continental outlines were similar to present.

2 Methods

5 2.1 Climate models

We used a hierarchical modeling procedure that involves running an atmospheric general circulation model (AGCM) to simulate global climate and provide continuous (every 6 h) time series of sea-surface temperature (SST), sea ice, and lateral boundary conditions (vertical profiles of temperature, wind, humidity) for the regional climate model 10 (RCM) simulations. In previous studies, this hierarchy of models has been demonstrated to reproduce present day climate and simulate regional-scale responses to changes in the large-scale controls that compare favourably with reconstructions of those responses from paleoenvironmental data (Hostetler and Bartlein, 1999; Hostetler et al., 1994, 2000). This method of coupling GCMs with RCMs to downscale climate is 15 now widely used in climate assessments (e.g., Mearns et al., 2012).

The AGCM is version 2.01 of the GENESIS climate model (Thompson and Pollard, 1995). Version 2.01 and later versions of GENESIS have been used extensively for paleoclimate simulations (Pollard and Thompson, 1997; Jousssaume et al., 1999; Pinot et al., 1999; Ruddiman et al., 2005; Tabor et al., 2014; Alder and Hostetler, 2014). 20 The atmospheric component of GENESIS is coupled with the Land Surface eXchange model, LSX (Thompson and Pollard, 1995), to simulate surface processes and to account for the exchange of energy, mass and momentum between the land surface and the atmospheric boundary layer. We used model resolutions of T31 (~ 3.7° in latitude and longitude) and 2° × 2° in latitude and longitude for the atmosphere and surface, 25 respectively. The model was run using a coupled mixed layer ocean (50 m in depth), which produces SSTs in radiative balance with global boundary conditions. We ran

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a number of sensitivity experiments in which we varied sea-ice parameters to optimize the simulation of present day sea ice. The boundary conditions for the RegCM simulations span the last 10 yr of 65 yr long GENESIS simulations.

5 The RCM is version two of the RegCM regional climate model (RegCM2; Giorgi et al., 1993a, b). Newer versions of RegCM now exist that offer more options and improved computational performance (Pal et al., 2007), but the atmospheric core of the model has remained essentially the same as RegCM2. Our version of RegCM2 is coupled with the LSX surface-physics package used in GENESIS. We employed a model
10 grid-resolution of 60 km (roughly 0.5°) for the simulations (Fig. 1a and b). To optimize our sensitivity tests we modified RegCM2 to include orbitally determined insolation, a lake model (Hostetler and Bartlein, 1990) to simulate lake temperature and ice and their feedbacks with the boundary layer, and we modified aerodynamic (e.g., roughness height) and biophysical (e.g., leaf area index) vegetation parameters in LSX to be consistent with the properties of the reconstructed Beringia vegetation. For the lake
15 sensitivity tests, we represented the spatial distribution of shallow thaw lakes by specifying time-appropriate (i.e., 0, 6 and 11 ka) model grid points as water. For all lakes, we specified a depth of 4 m and moderately high turbidity, which is sufficient to realistically capture the seasonal cycle of lake-atmosphere feedbacks in our experiments. The vegetation and lake implementations are discussed in more detail below. Each
20 RegCM2 simulation was run for 10 yr and the first 2 yr are excluded from our analysis to allow soil-moisture fields to equilibrate. Ten-year simulations with 8 yr averages are sufficient to allow for model spin up and to isolate mean climate responses associated with our array of prescribed changes in paleogeography, which, in most cases, represent substantial perturbations between and among experiments. In contrast to GCMs
25 where time-slice simulations may take 10s to 100s of years to reach equilibrium, RCM simulations reach equilibrium rapidly under the strong external forcing of the GCM.

2.2 Experimental design

We designed our experiments to isolate and quantify the potential controls of the early Holocene climate of Beringia. Our experiments thus include a set of varied atmospheric boundary conditions and surface changes that we describe and summarize below.

5 2.2.1 Present-day, 6 ka and 11 ka boundary conditions

The AGCM and RCM each require the specification of insolation, surface boundary conditions (including 11 ka continental outlines and land-surface and ice-sheet topography), atmospheric greenhouse gas composition, land-cover (vegetation and soils), and lake and wetland distribution (Table 1). Insolation for present, 6 ka and 11 ka
10 was specified following Berger (1978) (Fig. 2). Atmospheric composition (e.g., CO_2) was set to pre-industrial values (i.e., 280 ppm) for the Present-Day and 6 ka simulations, and to 265 ppm (Monnin et al., 2001) for the 11 ka simulations.

The impact of the variations in the obliquity (tilt) and climatic-precession (time-of-year of perihelion) elements of the Earth's orbit can be seen in the anomalies of insolation and the lengths of the different months and seasons (Berger, 1978; Kutzbach and Gallimore, 1988; Fig. 2). At 11 ka, perihelion was in late June, the tilt of the Earth's axis
15 was 24.2° , and the eccentricity was about 0.019 (as compared to the present values of early January, 23.4° , and 0.017). Consequently, June insolation was about 50 W m^{-2} greater than present at 65° N . However, owing to its elliptical orbit, the Earth moves faster near the time of perihelion (Kepler's law of equal areas), and at 11 ka June and July were about 2.0 days shorter than present (assuming a 360-day year and 30-day
20 months; Kutzbach and Gallimore, 1988). At 6 ka, perihelion was in September, the tilt was 24.1° , and eccentricity was about the same as at 11 ka. The maximum insolation anomaly consequently occurred later, in July, and was about 30 W m^{-2} greater than present at 65° N . Owing to the later time of year of perihelion at 6 ka than at 11 ka, August was the shortest month (1.65 days shorter than present). From Fig. 2 it can be seen that in February and August, both insolation and month-length anomalies for
25

11 and 6 ka were similar. Overall, the early-Holocene boreal summer and the mid-Holocene late summer could be described as shorter and “hotter” than at present.

Figure 1 shows the 0 ka (present) and 11 ka topography, ice and continental outlines, respectively. Ice-sheet elevations for the 11 ka AGCM simulation were derived from Peltier (1994), and for the 11 ka RCM simulations from Hostetler et al. (2000). Land-surface elevations (and hence the continental outlines), were specified for each model at 11 ka by interpolating Peltier (1994) ICE-4G topographic anomalies (i.e., 11 ka minus 0 ka differences) and applying these to the present day grid point elevation in the model. In the RCM at 11 ka, this procedure yields a land mask with an extensive land bridge between North America and Asia (Fig. 1b). We constructed a second set of land elevations to depict the flooded land bridge by superimposing the present day land mask over the 11 ka elevations, and setting all values outside of the present day shoreline mask to sea level (0.0 m; Fig. 1a). Because the topography in the region consists of either broad coastal plains with low slopes or rather steep terrain in coastal mountain regions, we did not need to “taper” the coastal elevations when creating this elevation data set.

Land-cover characteristics were expressed in both models as Dorman–Sellers “biome” types (Dorman and Sellers, 1989), which implicitly include the specification of soil characteristics associated with the vegetation. For the AGCM simulation these biomes closely followed Lynch et al. (2003). For the RCM simulations, present day land-cover characteristics (including wetlands) were derived from the Global Land Cover Characteristics data base (http://edc2.usgs.gov/glcc/globdoc2_0.php). The spatial pattern of the land-cover types was simplified to create general patterns at the same spatial resolution of information available from paleorecords for describing the 11 ka land-cover type patterns, including wetlands (Figs. 3 and 4). We further specified the distribution of shallow thaw lakes, and, to represent the short-stature deciduous tall-shrub/woodland vegetation in the early Holocene (“Deciduous Broadleaf Woodland”; Fig. 3), we defined an additional land-cover type for which we specified appropriate

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vegetation-type parameter values in LSX (e.g., leaf-area index, canopy structure and height, etc.).

2.2.2 Present-day, 6 ka and 11 ka surface characteristics

Surface characteristics describing land cover, sea level and the distribution of lakes and wetlands were defined for the present day, 6 ka and 11 ka RCM simulations. For the 11 ka RCM simulations, we used five separate sets of surface characteristics (land mask, topography, and land-cover type) that are described in detail below. The first set represents conditions prior to 11 ka, and represents the “point of departure” for the 11 ka experiments (and hence is referred to here as the “11 ka Control”). A second set represents conditions after the 11 ka changes (referred to here as “11 ka All”). Three other sets were defined to examine the individual effects of land-bridge flooding (“11 ka Sea Level”), vegetation change from tundra to deciduous tall shrub/woodland (“11 ka Vegetation”), and thaw-lake/wetland development (“11 ka Lakes”; Fig. 4b–f; Table 1). In each case, paleoenvironmental data indicate that full development of the sea level, vegetation, and thaw-lake/wetland changes took centuries to millennia, the marine transgression being the most long-lived. However, as our study features an equilibrium sensitivity experiment, we created just two steady-states of 11 ka land cover, representing conditions close to the onset of changes (11 ka Control) and conditions when all the changes were fully expressed (11 ka All). We also defined two sets of surface characteristics for the present day, in order to separate the effects of land bridge flooding from the other boundary-condition changes.

2.2.3 Present-Day simulation

The Present-Day (0 ka) simulation land cover included modern vegetation (Fig. 4a) defined as a mosaic of tundra and needleleaf forest (as described in Sect. 1.1), with short grass and semi-desert vegetation in the extreme southeast of the study area. The modern distribution of lakes and wetlands was used, as were modern topography and

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continental outlines, which created a land mask with the modern Bering Strait between Asia and North America.

2.2.4 Present-day simulation with an 11 ka land mask

We defined a second set of present day boundary conditions by combining the modern
5 land-cover data with an 11 ka land mask including elevation data. This set of boundary
conditions is used to separate the simple effects of the land-bridge flooding from the
combined effects of all of the other “paleo” boundary conditions.

2.2.5 6 ka simulation

We also used modern land cover (Fig. 4a) for the 6 ka simulation. Lakes and wet-
10 lands were well established at 6 ka (Walter et al., 2007; Jones and Yu, 2010). Pollen-
based biomes for 6 ka defined by the BIOME 6000 project (Prentice et al., 2000; Ed-
wards et al., 2000a; Bigelow et al., 2003) were used as a guide to vegetation cover.
In Siberia, the modern land cover (Fig. 4a) closely approximates the 6 ka biome dis-
15 tribution (Fig. 3b), while in eastern Beringia the western evergreen needleleaf forest
limit is displaced eastwards. Almost all post-glacial sea-level rise had occurred by 6 ka
(Manley, 2002) and the continental outlines are only slightly different from modern (as
shown in Fig. 3b); we considered the vegetation and coastline differences not signifi-
cant enough to require a separate 6 ka land cover mask.

2.2.6 11 ka Control simulation

20 The late-glacial development of Beringian vegetation proceeded over several millennia
from herbaceous vegetation, through low shrubs to tall shrubs and deciduous wood-
land (see Sect. 1.2). We use the low-shrub tundra to represent the vegetation for the
11 ka Control simulation; its surface properties differ little from the preceding herba-
ceous tundra vegetation (not modelled here). We also included the 11 ka LIS, CIS,
25 and mountain glaciers and ice caps, but not lakes and wetlands (Fig. 4b). Topography

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was defined using Peltier (1994) 11 ka geography, and by adding the paleo topographic
anomalies to the present day elevations. The resultant RCM land mask features lower
sea level, with the Bering land bridge in place between Asia and North America (see
Sect. 2.2.1), and 11 ka land and ice topography.

5 2.2.7 Sea-Level simulation

The Sea-Level simulation was identical to the 11 ka Control simulation, but with topog-
raphy defined using Peltier (1994) 11 ka geography and modern sea level (Fig. 4b and
c; see Sect. 2.2.1). This combination created an RCM land mask with 11 ka topogra-
phy but a flooded land bridge (i.e., the modern Bering Strait) between Asia and North
10 America.

2.2.8 Vegetation simulation

The 11 ka Vegetation simulation was identical to the 11 ka Control simulation with the
exception of vegetation (Fig. 4d). To describe the changed vegetation for this simulation
we used an approach involving several steps: the “biomization” of pollen data (Prentice
15 and Webb, 1998; Bigelow et al., 2003), evidence from plant macrofossils (Edwards
et al., 2005; Binney et al., 2009) and expert knowledge. The latter was needed be-
cause the biomized pollen maps and macrofossil records (Fig. 3) indicate broad trends
in vegetation cover but hold too few data points to allow for quantitative spatial in-
terpolation. We used records from the PARCS (Paleoenvironmental Arctic Sciences)
20 database (<http://www.ncdc.noaa.gov/paleo/parcs/index.html>) falling nearest to 11.5 ka
in age to guide the placement of deciduous broadleaf woodland for the 11 ka Vege-
tation simulation. This time slice gave the strongest signal of deciduous woodland in
eastern Beringia, defining the deciduous broadleaf woodland biome at about half the
sites across the region. Deciduous needleleaf (*Larix*) forest is not identified in far north-
25 east Siberia at 11 ka by biomized pollen maps, likely due to low *Larix* pollen counts in
the data; not even enhancing *Larix* by a factor of 15 (see Bigelow et al., 2003) identifies

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deciduous needleleaf forest at this time. However, the macrofossil record indicates the presence of deciduous broadleaf trees in east and west Beringia and of *Larix* in Siberia (Edwards et al., 2005; Binney et al., 2009; Fig. 3). Based on these data, in east Beringia we specified 11 ka vegetation as a mosaic of low-stature shrub tundra and deciduous tall shrub/woodland, with the latter occupying lower elevations. In west Beringia we specified 11 ka vegetation as a mosaic of low-stature shrub tundra and mixed deciduous woodland, also determined by elevation. We designated the exposed shelf and land-bridge as low-stature shrub tundra, as in the 11 ka Control simulation, as little is known about past vegetation of the submerged land areas at ca. 11 ka; pollen and macrofossil data from sub-marine sediment cores taken from the Bering Sea suggest shrub tundra (e.g., Elias et al., 1997; Ager and Phillips, 2008; Lozhkin et al., 2011).

2.2.9 Lakes simulation

The 11 ka Lakes simulation was identical to the 11 ka Control simulation with the exception of lake and wetland cover. For the 11 ka Control simulation, no lakes or wetlands were present on the RCM land cover grid. For the 11 ka Lakes simulation, lakes and wetlands were represented by their modern distributions, placing lakes in regions where thaw lakes dominate the modern landscape (Fig. 4e). Lake and wetland distributions are derived from the Global Land Cover Characteristics data base described above. Thaw lakes probably extended onto Arctic Ocean shelves (Hill and Solomon, 1999; Romanovskii et al., 2000) that are now inundated, and they probably also formed on the land bridge, but, as there is no information on their areal extent, we omitted lakes from these areas. The estimated average percent cover of lakes in modern lake-dominated landscapes from topographic maps and air photos is 5–40 %. In the experiment we used 40 % in order to provide the maximum possibility for a response in the simulation. Although thaw lakes are typically < 1.0 to a few km in diameter, the structure of the RCM necessitated that lakes were assigned as whole grid cells according to the same proportions.

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2.3 Summary

Our strategy was to examine a set of RCM simulations for 11 ka (Table 1) that together illustrate the impact of changes in vegetation, flooding of the land bridge, and development of thaw lakes and wetlands. We compared these 11 ka simulations with the 11 ka Control simulation and with simulations of the present day and 6 ka, to generate a set of experiments (Table 2).

The simulations (described above; Table 1) can be summarized as:

1. Present Day, a simulation of the present day (0 ka) with realistic land cover (including vegetation, shorelines, and thaw-lake distribution). This is the control simulation used to compare changes between 11 ka and present (Fig. 4a).
2. Present Day with 11 ka continental outlines, which used present climatology, vegetation and lakes/wetlands but the 11 ka continental outlines (i.e., Fig. 4a but with continental outlines as in Fig. 4b). This simulation is used to partition the effect of changed sea level from that of other key drivers, such as insolation.
3. 11 ka Control, a simulation of conditions that prevailed prior to the changes in vegetation, sea level, and thaw-lake distributions that are the focus of the study. This simulation functions as the control simulation against which the effects of these land-cover changes at 11 ka are assessed (Fig. 4b).
- 4.–6. Three simulations: 11 ka Sea Level, 11 ka Vegetation, and 11 ka Lakes, which address each land-cover change in isolation (Fig. 4c–e).
7. 11 ka All, a simulation with all three land-cover changes (i.e., sea level, vegetation, lakes) included (Fig. 4f), to illustrate the combined effects of these controls.
8. 6 ka, a simulation using 6 ka boundary conditions and modern land cover (Fig. 4a), to explore a climate with modern boundary conditions, except for an amplified annual cycle of insolation.

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The experiments (Table 2) were as follows:

1. Present Day minus Present Day (with 11 ka continental outlines), which assesses the effect of the Bering Strait and modern coastline on modern climatology.
- 5 2. 11 ka Control minus Present Day, which describes the full change in conditions from 11 ka (before land-cover transformation) to modern conditions (including the imposition of the Bering Strait).
3. 11 ka Control minus Present Day (with 11 ka continental outlines). This experiment reveals the effect of insolation on the 11 ka climatology, as the large impact of sea-level change in the fully modern (Present Day) simulation is removed by using the 11 ka continental outlines.
- 10 4.–7. Three experiments to examine the one-at-a-time changes in sea level, vegetation, and thaw lakes and one experiment to examine the effect of all three of the above changes. The control in each case is 11 ka Control.
8. 11 ka All minus Present Day, which describes the full change in conditions from 15 11 ka (after land-cover transformation and including the imposition of the Bering Strait) to modern conditions.
9. 6 ka minus Present Day, to examine the impact of mid-Holocene insolation anomalies.
10. 6 ka minus 11 ka All, to examine the climate change between 11 and 6 ka.
- 20 An experimental design that focuses on higher-order interactions among the controls would be theoretically possible but would require many more simulations. We elected to keep the experimental design relatively simple.

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3 Results

We present the modelling results in a series of figures that typically take the form of mapped monthly averages. Monthly averages are based on a 365-day year relative to the modern calendar (the effects of the “calendar bias” (Sect. 2.2.1) are of continental and hemispheric scale, and would not dominate the regional patterns of interest here; Timm et al., 2008). In some cases the complete annual cycle is shown, in others summer and winter months (e.g., January and July) that highlight the more interesting patterns that emerge from the simulations. Maps representing results of specific simulations show 8 yr climatologies; those showing the results of experiments display differences between experimental and control simulation long-term means (i.e., anomalies). Maps of all monthly values of key variables are available in the supporting online information (see Supplement).

3.1 Effect of the land-bridge flooding alone

The effect of the land-bridge flooding alone (i.e., with no other differences in boundary conditions between 11 ka and present) is assessed by the experiment that replaces the modern land mask and elevation with one appropriate for 11 ka. For reference, Fig. 5a shows simulated modern monthly average air temperature for the study area. Figure 5b shows the impact on modern climate of “restoring” the 11 ka continental outlines (and topography). The anomalies shown are the long-term mean differences of the Present-Day simulation (Supplement Fig. 1) minus the Present-Day (with 11 ka continental outlines) simulation (Supplement Fig. 2). The anomalies show the impact that flooding of the land bridge (and related topographical changes, like the collapse of the ice sheet) would have on the modern climate, if those paleogeographic changes occurred today (Supplement Fig. 3).

The prominent effect of shelf flooding is a reduction in the seasonality of 2 m air temperatures as a result of replacing land with ocean. Warm-season (May to October) temperature anomalies are strongly negative, particularly in those regions that are ocean

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with sea ice in the Present-Day simulation but which are land in the Present-Day (with 11 ka continental outlines) simulation (Fig. 5b). In the cool season (November through April) the temperature anomalies are strongly positive in the regions that are oceans in the Present-Day simulation but land in the Present-Day (with 11 ka continental outlines) simulation. (The impact of the decrease in elevation of the region that was ice-covered at 11 ka is visible as a small area of positive summer temperature anomalies in the northeastern corner of the model domain.)

The genesis of these temperature anomalies lies in changes in the surface energy balance related to large differences in the heat capacity and albedo of land and water in the two present day simulations (Supplement Fig. 3b). Net shortwave radiation anomalies are highly negative from May through August in the regions that change from land to ocean. This pattern shows the response to the large increase in albedo as dark land surfaces are replaced by ocean and permanent or seasonal sea ice. Positive net shortwave radiation anomalies occur over the region associated with the 11 ka ice sheet where elevation decreases. While present day land cover is used in both simulations, the higher elevations in the Present-Day (with 11 ka continental outlines) simulation results in a persistent snowpack in the northeastern part of the study area. Consequently, simulated net shortwave radiation is lower than present (thereby producing the positive anomalies). Net shortwave anomalies in the cool season (November through March) are close to zero, consistent with the low shortwave radiation inputs at that time of year.

Net longwave radiation anomalies in the warm season are positive where 2 m air temperatures are negative (Supplement Fig. 3b), indicating a smaller upward component of longwave radiation. From November to March, net longwave anomalies are strongly negative where 2 m air temperature anomalies are positive, indicating a greater upward component of longwave radiation. Net radiation anomalies follow those of net longwave radiation in the cool season, and form a mosaic of anomalies of different sign at other times during the year.

Among the non-radiative components, the anomalies of heat flux into or out of the substrate (i.e., into or out of storage) are most strongly expressed in the region where

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ocean replaces land. Strong positive anomalies prevail from June through August (Supplement Fig. 3b), as energy is stored in the soil during the warm season. Anomalies are strongly negative in the cool season (i.e., greater flow from the substrate to the surface). In the winter the formation of sea ice does not appreciably diminish the flow of energy out of storage. The anomalies of sensible and latent heat fluxes parallel one another throughout the year; they generally track both air temperature and surface skin temperature (not shown). The anomalies are negative from June through August, when the negative temperature anomalies are at their greatest and temperature and vapor-pressure gradients are likely also negative.

Feedbacks among the surface temperature and energy-balance anomalies are reflected to a limited extent by atmospheric circulation and moisture variables (Supplement Fig. 3a). In the region of negative warm-season temperature anomalies, 500 hPa surface height anomalies are also negative, and sea-level pressure anomalies are positive, consistent with the negative temperature anomalies. While spatially variable, precipitation anomalies are generally negative in the “flooded” region and positive in other regions.

3.2 The 11 ka Control simulation and differences with the present

The 11 ka Control simulation is intended to portray the regional climate just before land-bridge flooding, vegetation change and thaw-lake development occurred (Supplement Fig. 4). This simulation forms the basis for the calculation of “experiment-minus-control” anomalies at 11 ka. The 11 ka Control simulation also can be compared with present day simulations to separate and quantify the effect of the “global”, as opposed to Beringia-specific, changes in boundary conditions: the former being insolation, greenhouse gas, ice-sheet, and eustatic sea-level, the latter being the state of the ocean shelves, land bridge and land surface (Fig. 5c; Supplement Figs. 5 and 6).

In the 11 ka Control simulation, temperatures are generally lower than present during much of the year, reflecting the still-substantial Northern Hemisphere ice-sheets and slightly lower greenhouse gases relative to present (Fig. 5c). The radiative effects of the

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ice sheets and greenhouse gases are modulated by the greater amplitude of the annual cycle of insolation relative to present (Fig. 2). Overall, the amplitude of the annual cycle of temperature is greater than present. There is also a strong east–west gradient in temperature anomalies, which are strongly negative over and adjacent to the ice sheet.

5 The insolation forcing is greatest from May–September and is maximally expressed in the May-through-August temperatures, when the strongest positive anomalies over the emergent land bridge occur (Supplement Fig. 5a).

The combination of the annual forcing, attributed to the ice sheets, lowered sea level, lower greenhouse gas concentrations, and the seasonally varying insolation forcing, is registered by large spatial variations in the anomalies of the energy balance components. In general, the sign of the anomalies is opposite to those discussed in the land-bridge flooding section (Sect. 3.1) because the sense of the continental-outline changes is reversed in this experiment (i.e., here the anomalies are calculated as 11 ka Control with the 11 ka continental outline minus the Present-Day simulation whereas

15 in Sect. 3.1 the anomalies are calculated as Present-Day minus Present-Day with the 11 ka continental outline). Further contributions to the spatial patterns of the anomalies are attributed to the ice sheet, which, in summer, is characterized by strongly negative anomalies in net shortwave radiation, net radiation, and sensible and latent heat fluxes, and strongly positive anomalies in net longwave radiation and substrate heat flux (Supplement Fig. 5). Atmospheric circulation and the attendant moisture anomalies are determined mainly by the hemispheric circulation, which is influenced by the 11-ka ice sheet (Bartlein et al., 2014). Precipitation anomalies general follow those of temperature, and as a consequence, soil-moisture anomalies are generally negative, especially near the ice sheet from November through July (Supplement Fig. 5). Excep-

20 tions to this pattern occur in western Beringia and in the interior of eastern Beringia in summer.

Both the (exposed) land bridge and the 11 ka insolation enhance seasonality at 11 ka. Differencing the 11 ka Control and the Present-Day (with 11 ka continental outlines) simulations (Fig. 5d; Supplement Fig. 6) removes the effect of land bridge flood-

ing and highlights the effects of 11 ka insolation and the 11 ka ice sheet. The ice sheet exerts a general cooling effect year round, and during the short summer season, enhanced insolation results in air temperatures that are higher than those of present. Thus, at 11 ka, the presence of the land bridge amplifies the insolation forcing and is

5 an important driver of higher seasonality and relatively warm summers compared with present.

3.3 The 11 ka experiments

3.3.1 Sea Level

The impact of land-bridge flooding at 11 ka is illustrated by the 11 ka Sea-Level simulation. Figure 6 shows the relationship between net radiation and temperature when the land bridge is flooded (January and July anomalies for contrast). The major influence on the energy balance comes from changing land to water, but the effects are not spatially uniform, as is the case for the present day land-bridge flooding experiment (Sect. 3.1). In Beringia, winter insolation is extremely low, and the January radiation balance is dominated by longwave radiation: incoming longwave radiation is relatively

15 constant but can be affected by circulation both within the RCM domain and through hemispheric circulation in the GCM, while outgoing longwave radiation is dependent upon surface properties and their respective temperatures, which here drive most of the observed variation. January net radiation anomalies show a strong dipole: positive north of Siberia (Laptev Sea) and negative over the land bridge (Fig. 6). This pattern results from changing the present day shelf north of Siberia from land to sea ice which consequently has low surface temperatures throughout the year. Examination of other simulated variables indicates that this change results in decreased upward longwave radiation but little change in downward longwave radiation, and hence the mean difference in net radiation is positive. In contrast, in the ocean directly north and south of the Bering Strait (Chukchi and Bering Seas), sea ice is present seasonally. In January the ice is not yet at its maximum thickness for the year so there is upward energy flux

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(greater upward longwave radiation). The difference in mean net radiation is negative, and thus surface temperature is relatively higher (see also Supplement Fig. 8b).

The net radiation dipole is absent in July (Fig. 6). While sea ice in the Chukchi and Bering Seas melts, the seasonal variation in temperature is strongly lagged. Even in July there is some sea ice present and temperatures are cooler than they would be otherwise owing to its relatively high albedo. The ocean warms in late summer and fall as the ice reaches minimum extent, leading to the warmer January conditions described above. Overall, summer temperatures in the vicinity of the flooded land bridge are cooler than when the land bridge is in place.

3.3.2 Vegetation

The effects of changing vegetation from low tundra to a tundra-woodland mosaic on both sides of the land bridge produces modest warming with the clearest effect in May (Fig. 7). While upward longwave radiation is relatively high, net downward shortwave radiation is greater, a response to the lowered albedo of the wooded land surface, which leads to a positive net radiation balance. In May, an air temperature increase of 1–2°C (relative to the 11 ka Control simulation) is simulated over wooded areas, reflecting increases in sensible and latent heat fluxes. Substrate heat flux is lower as the land-atmosphere temperature gradient is reduced (Supplement Fig. 10b).

In winter (January) net radiation anomalies due to changed vegetation are small (Fig. 7). In tundra areas winter temperatures are slightly but consistently colder reflecting less overall flow of heat to the ground and hence less upward longwave radiation in winter.

3.3.3 Lakes

Although the overall effect of placing lakes on the landscape is modest, it produces a clear pattern in summer (e.g., July: Fig. 8 top, Supplement Figs. 11 and 12) when grid cells occupied by lakes are cooler than surrounding areas or than in the 11 ka

Control simulation. For western Alaska, latent heat flux anomalies are positive in June and net radiation and sensible heat-flux anomalies are positive in June and July, and generally zero or negative the rest of the year (Fig. 8). For the entire study domain, the surface-temperature differences between the 11 ka Lakes simulation and the 11 ka Control simulation are substantial during April–August, and the accompanying changes in atmospheric circulation are consistent with these differences (Fig. 8, Supplement Fig. 12). Positive sea-level pressure or 500 hPa height anomalies (e.g., April) reflect greater heating at the surface and consequent displacement of the circulation whereas the negative anomalies (e.g., July) reflect atmospheric cooling and subsequently lower and displaced 500 hPa height-anomaly patterns, particularly over the south-central part of the land bridge where there are additional interactions with SSTs (Supplement Fig. 12). The overall impact of thaw-lake formation relative to that of vegetation is still small, however, and similar to that noted for “column-mode” simulations with an RCM under present day conditions (Rivers and Lynch, 2004).

3.3.4 All

The 11 ka All simulation shows the combined impact of all three land-cover changes (land-bridge flooding, vegetation change and thaw-lake formation). Figure 9 compares the monthly mean 2 m air temperature anomalies for changed vegetation, changed sea level and all land cover features changed together at 11 ka (see also Supplement Fig. 14). The vegetation change at 11 ka (Fig. 9a) acts to amplify the insolation effect, making the whole year warmer, especially in early spring and summer (April through June), when there is greater absorption of incoming shortwave radiation relative to other times of the year or to the same time of year in the 11 ka Control simulation. This increased absorption leads to more heat storage in late summer, which carries over and is released during the winter season, thereby increasing upward longwave radiation and causing a slight warming.

Changing sea level has the largest effect (Fig. 9b). In winter the temperature anomaly is largely controlled by land-bridge flooding. Because there is minimal incoming short-

5 wave radiation in winter (see above) the observed changes are modulated by albedo differences. The vegetation effect is overwhelmed by the sea-level effect through much of the year; it is only strongly expressed from April to June in the continental areas (Fig. 9c). The sea-level change acts to make winters warmer and summers cooler, countering the amplification of seasonality due to 11 ka insolation.

3.4 Principal responses other than temperature and energy-balance variables: 11 ka Control and 11 ka All vs. Present Day

10 During the interval from the LGM to present, the principal changes over the North Pacific and adjacent land areas in atmospheric circulation and variables that depend on circulation (i.e., clouds and precipitation) were governed largely by the retreat of the North American ice sheets, with secondary influences from land-ocean temperature contrasts induced by insolation variations and ocean heat transport (Bartlein et al., 2014). In particular, when large, the ice sheets in GENESIS perturbed the upper-level winds, generating a “wave-number-1” (one circumpolar ridge-and-trough) pattern that
 15 resulted in stronger-than-present southerly flow over Beringia, while at the surface, a strong glacial anticyclone developed. This circulation pattern results in the simulation of LGM near-surface air temperatures across much of the region that were as warm or warmer than present. By 11 ka, these effects had greatly attenuated, but large-scale effects on Northern Hemisphere circulation caused by the remnant ice sheet and greater
 20 land-ocean temperature contrasts in summer are apparent in the AGCM simulations that provide the lateral boundary conditions for the RCM. As a consequence, relatively modest regional-scale modifications of the large-scale circulation might be expected in the different 11 ka RCM experiments. However, given the topographic complexity of the region even small changes in circulation could have large consequences on clouds,
 25 precipitation and soil moisture (although soil moisture is also governed by surface water- and energy-balance variables; Edwards et al., 2001). In Beringia, at 11 ka as at present, below freezing cold season temperatures constrain intra-annual variations of soil moisture. As a consequence, January soil-moisture anomalies are related more

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to late-summer and early autumn atmospheric circulation and moisture conditions than they are to contemporaneous wintertime conditions.

5 The impact of larger-scale circulation anomalies represented in the GCM can be seen in RCM simulations for Beringia (Fig. 10, also see Supplement figures). The anomalies with respect to the present day differ little between the 11 ka Control and 11 ka All simulations (Fig. 10a and b), and consequently can be discussed together. The anomalies also indicate that effects of the land-cover changes on regional circulation were small. In the 11 ka simulations, January 500 hPa heights are generally
 10 lower than present across the North Pacific, and higher than present over the south-eastern part of the domain, while at the surface, negative sea-level pressure anomalies are centered over southwest Alaska and the Aleutian Islands. This pattern is somewhat analogous to the “January North-East Pacific Negative” pattern of Mock et al. (1998). As a consequence of the stronger-than-present southeasterly flow into eastern Beringia at both the surface and in the upper-atmosphere, cloudiness and precipitation are greater than present in southern Alaska, while in eastern Siberia, stronger
 15 than present offshore flow creates drier-than-present conditions. Soil moisture anomalies show a strong east (dry) to west (wet) pattern, which develops in October and persists through April.

20 In July, an east–west contrast in 500 hPa height anomalies exists (Fig. 10). Positive anomalies occur in the western part of the region, where at present the East Asian trough prevails, while negative anomalies occur over eastern Beringia, where at present a semi-permanent ridge develops. This anomaly pattern produces stronger-than-present zonal flow over the region that is consistent with the continued presence of negative (relative to present) 500 hPa height and sea-level pressure anomalies over the
 25 Arctic Basin upstream of the ice sheet and the developing enhancement of the North Pacific subtropical high (Bartlein et al., 2014). As a consequence of the stronger-than-present zonal flow, coastal areas in the southeastern quadrant of the region feature stronger-than-present onshore flow, and greater-than-present cloudiness and precipitation. In the interior of North America, precipitation is lower than present, which is

reflected by July soil-moisture anomalies. Soil moisture anomalies have a broad-scale pattern with generally positive values in western Beringia and negative values in eastern Beringia, a first order effect of a similar general pattern of precipitation anomalies (Supplement Figs. 5 and 15).

5 The 11 ka land-surface changes, which are dominated year-round by the land-bridge flooding and in spring in eastern Beringia by vegetation changes, have only a modest impact on atmospheric circulation and related variables, particularly in winter (Fig. 10c). In July, the large-negative temperature anomaly centered over the flooded region (Fig. 9c) is accompanied by a broad negative 500 hPa height anomaly (Fig. 10c). At
10 the surface a weak dipole prevails, with negative sea-level pressure anomalies over the Bering Sea contrasting with positive anomalies over the Arctic Basin. This pattern results in stronger-than-present upper-level flow into southwestern Alaska, wetter-than-present conditions, and positive soil-moisture anomalies, which appear in an arc from Kamchatka to southwestern Alaska. In the west, the circulation anomalies reinforce
15 a general pattern of greater-than-present soil moisture, while in southwest Alaska the moister conditions (Fig. 10c, Supplement Fig. 14) reverse the sign of negative 11 ka minus present anomalies. Overall, within-region changes in atmospheric circulation related to the various land-cover changes appear less important than changes in the surface energy balance and temperature in determining the nature of the early Holocene
20 climate.

3.5 Comparison of simulated temperatures for 11 ka Control, 11 ka All, 6 ka and Present Day

The general trends in the climate of Beringia over the Holocene can be described with the help of the 6 ka simulation, in which the only difference in boundary conditions
25 relative to present is the insolation forcing. Thus, the impact of insolation can be isolated, which is not feasible at 11 ka due to the amplifying or offsetting effects of the land-cover changes. Figure 11 shows monthly averages of simulated temperature for 11 ka prior to land-cover changes (11 ka Control), 11 ka with land-cover changes (11 ka All), 6 ka

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(with 6 ka insolation, no ice sheet and modern vegetation) and Present Day (0 ka). The changing pattern of yearly insolation (Fig. 2) can be seen in the longer period of above
freezing temperatures at 6 ka and present: the progressively later occurrence during the Holocene of the summer insolation-anomaly maximum gradually extends summer
5 into autumn.

Both the 11 ka Control and 11 ka All simulations are affected by the presence of the LIS and CIS and their attendant zonal cooling effect, which counters the insolation and land-bridge effects. With no land-cover change (e.g., the 11 ka Control simulation;
Fig. 11a), the land bridge is relatively warm in summer. However, eastern Beringia,
10 which includes the western edge of the LIS, is cooler than Siberia, which has no ice sheet (see also Supplement Figs. 5 and 15). The coolest summer is seen in the 11 ka All simulation with land-cover changes (Fig. 11b), when the warming effect of the land bridge in summer is removed.

From 11 to 6 ka, all of the boundary conditions except insolation approached their
15 present day values. The insolation anomaly at 6 ka (Fig. 2) reached its maximum in July (vs. in June at 11 ka) and anomalies were slightly greater than those at 11 ka in late summer and autumn (August through October). Relative to the 11 ka All simulation, air temperatures were generally higher across the region at 6 ka, particularly in the area that was ice-covered at 11 ka.

20 In many respects 6 ka is similar to present, but the continental heating that reflects the positive summer insolation anomaly at 6 ka is obvious, particularly in eastern Beringia (Fig. 11c). August and September are warmer at 6 ka than at 11 ka and also than at 0 ka (Fig. 11d). The cooling effect of the flooded land bridge is evident in adjacent land areas; in continental interiors, the effect is less strong, and the widespread
25 presence of needleleaf forest may enhance summer warming via an albedo effect at both 6 and 0 ka (Fig. 4a).

The effect of other changes in boundary conditions other than insolation can be isolated by considering anomalies and differences in February and August. The nature of the insolation variations are such that anomalies in both insolation amount and

month length are nearly the same during those months at 11 and 6 ka (Fig. 2). Figure 12 shows the anomalies of net shortwave radiation, net radiation and temperature for February and August at 11 and 6 ka compared with present (Fig. 12a and c) and the change between 11 and 6 ka (Fig. 12b). As expected, the anomalies for shortwave radiation in February are small, owing to low inputs at the top of the atmosphere in winter. The anomalies of net radiation for the 11 ka All simulation are quite spatially variable for reasons discussed in Sect. 3.3, while those of temperature are almost uniformly negative across the region. From 11 to 6 ka, net shortwave radiation in August increased substantially. Because insolation at the top of the atmosphere was similar in August at 11 and 6 ka (Fig. 2), the net shortwave increase was likely generated by changes in albedo and a general reduction of cloudiness over the region related to expansion of the North Pacific Subtropical High in summer (Fig. 10d), both consequences of the generally warmer conditions at 6 ka relative to earlier. The general reversal in sign of the August net radiation and temperature anomalies between 11 and 6 ka (Fig. 12a vs. c) is thus related to boundary condition changes and mechanisms internal to the climate system, as distinct from changes in August insolation levels; these changes include an increase in greenhouse gas levels, the final disappearance of the ice sheet, and continued changes in land-surface cover.

4 Discussion

4.1 Major features of the 11-ka simulated climate

In the 11 ka All simulation the annual cycle of temperature in Beringia is highly seasonal, with warmer summers and colder winters than present (Supplement Fig. 15b). The summer and shoulder seasons are short and shifted earlier in the seasonal cycle, with warming limited to three months (May–July). Thaw lakes and wetlands produce modest and localized cooling in summer and warming in winter (Fig. 8). The vegetation change from tundra to deciduous tall shrub/woodland produces a widespread

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warming in spring and early summer greater than that induced by the 11 ka insolation regime (Fig. 7). In contrast, the land bridge flooding produces generally cooler conditions in summer but warmer conditions in winter that are manifested mainly on the flooded shelves and in eastern Beringia (Fig. 6). Precipitation anomalies are generally small and spatially heterogeneous, but precipitation in summer is generally lower than at present in eastern Beringia (Fig. 10b), as is soil moisture.

It is reasonable that the insolation anomaly at 11 ka had a major effect on summer temperature maxima and seasonality. Beringia was adjacent to the LIS, and while this likely had a moderating influence on temperature maxima, at least in regions proximal to the ice (Bartlein et al., 1991), a range of proxy records support a terrestrial thermal maximum in the earliest Holocene (e.g., Ritchie et al., 1983; Kaufman et al., 2004). In the 11 ka All simulation, positive net radiation anomalies are linked to positive summer temperature anomalies of 1.0 to $> 4.0^{\circ}\text{C}$ over much of the Beringian land mass in June and July, and much of Siberia is warmer in May (Supplement Fig. 15b). The summer, however, is short compared with today (Fig. 2), temperatures in August and September are cooler than present, and winters colder than present.

The simulations show lower summer precipitation and stronger summer heating (relative to present) and large negative soil-moisture anomalies in much of Beringia, particularly eastern Beringia. Low summer precipitation at 11 ka in the interior of Alaska and Yukon is also supported by observations of relatively low lake levels until ~ 10 ka (Abbott et al., 2000; Barber and Finney, 2000; Anderson et al., 2005; Finney et al., 2012). Stand modelling (Chapin and Starfield, 1997) and empirical observation (Barber et al., 2000) indicate that warm, dry conditions favour hardwoods and reduce growth of evergreen conifers. In addition, long, cold winters, short shoulder seasons and winter soil moisture deficits (resulting from late-summer and early autumn atmospheric and moisture conditions; see Sect. 3.4) may have combined to generate physiological drought going into spring, which would also favour the woody deciduous growth forms observed in the paleorecord (Fig. 3a).

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4.2 Key responses and feedbacks to 11-ka land-cover changes

The 11-ka set of experiments explores the sensitivity of the regional climate to land-surface changes brought about as a consequence of deglacial warming.

4.2.1 Flooding the land bridge

5 The land-bridge transgression is often cited as a key factor affecting early-Holocene Beringia (e.g., Burn, 1997; Abbott et al., 2000; Mann et al., 2001). In the 11 ka land-bridge flooding experiment (11 ka Sea Level) summer and autumn temperatures across Beringia are greatly reduced whereas winter temperatures increase (Fig. 6). This is the largest single response of regional climate to a land-cover change. The change works
10 in opposition to the insolation forcing, driving the system towards weaker seasonality and cooler summers. The changes are seen particularly in eastern Beringia, downwind of the land–sea reconfiguration. Our results emphasize the influence of the land-bridge transgression, but because we conducted a single sensitivity experiment, as opposed to a sequence of simulations, the results cannot clarify a more detailed temporal
15 pattern of change. However, the shift in seasonality and growing-season temperature and moisture may have promoted landscape-hydrologic changes such as paludification (Jones and Yu, 2010) and increasing lake levels (Abbott et al., 2000; Barber and Finney, 2000), particularly across eastern Beringia.

4.2.2 Vegetation feedbacks

20 The main response of replacing tundra with deciduous tall shrub/woodland is seen in the net radiation and temperature values for spring and early summer, when snow is still present (Fig. 7, Supplement Fig. 10b). The lower albedo of the woodland cover leads to stronger heating, particularly in the eastern region. A positive feedback is set up via the establishment of taller-stature vegetation, which contributes to a warmer
25 spring and works in opposition to the spring cooling (Fig. 5c) that is a result of the land-

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bridge flooding, plus the global controls of lower-than-present atmospheric greenhouse gas concentrations and SSTs.

4.2.3 Thaw lakes

Conversion of portions of the land-surface to shallow lakes via thermokarst processes
5 would be expected to influence surface energy dynamics. Rivers and Lynch (2004) demonstrated a moderate response in column model experiments for single locations in Beringia. In our study, the inclusion of thaw lakes shows a small local effect that becomes undetectable at larger spatial scales. These results align with those of studies examining lake effects on modern climate in a GCM (Subin et al., 2012). Regionally,
10 radiation and heat-flux anomalies are small (within inherent model variability) and spatially incoherent, suggesting that there is no regional impact of the lakes on climate via surface energy exchanges (Fig. 8). However, thaw lakes and peatlands are sources of greenhouse gas flux to the atmosphere (Walter et al., 2006; MacDonald et al., 2006; Walter Anthony et al., 2014), and their initiation and spread ca. 14–10 ka BP may have
15 had an impact on global climate through enhanced gas emissions.

4.2.4 All changes combined

Atmospheric circulation changes in Beringia related to the joint effect of the land-surface changes are small despite large changes in the surface energy balance and temperature (Fig. 10c). When the sea level, vegetation and lake changes are combined,
20 the vegetation effect, especially in eastern Beringia, opposes cooling brought about by the land-bridge transgression to make land temperatures slightly warmer in spring and early summer (Fig. 9c). However, the regional circulation is largely dominated by hemispheric-scale circulation changes. For example, at 11 ka, the larger-scale circulation leads to contrasts in precipitation and soil moisture between western (wetter than present) and eastern (drier than present) Beringia (Fig. 10b, Supplement Fig. 15).
25 This result may explain the late (ca. 13 ka) filling and low levels of shallow (i.e., < 15 m)

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lakes in the easternmost part of Beringia (Abbott et al., 2000; Barber and Finney, 2000) compared with similar lakes in western Alaska and Siberia, which were at least partially full before 13 ka and even during the last glacial maximum (Abbott et al., 2010; Ager, 2003; Lozhkin et al., 1993).

5 4.3 Comparison of 11 ka, 6 ka and present day

The simulated temperature patterns for the three time periods (Fig. 11) show the effect of the precession of the equinoxes in lengthening the summer season and in the progression to a later summer temperature maximum with time. Increased warmth in summer at 11 ka (Fig. 11a) is reduced with all land cover changes in place, particularly in the area of the land bridge (Fig. 11b). In interior continental regions, the absence of the ice sheet at 6 ka, combined with higher-than-present summer insolation and widespread cover of needleleaf forest, leads to temperatures as warm, or warmer than, those seen at 11 ka (Fig. 11c). Thus the 11 ka thermal maximum was manifest as a short, intense summer period with relatively low effective moisture, whereas summers warmer than present continued until at least 6 ka, with more moisture and a lengthening growing period. As these changes developed from 11 to 6 ka, they would have been major drivers of a range of terrestrial responses, such as further shifts towards evergreen forest dominance (Anderson et al., 2004), permafrost changes and the spread of paludification (Jones and Yu, 2010) and hydrological changes (e.g., increasing lake levels; Edwards et al., 2000b; Abbott et al., 2000).

4.4 Broader implications

Our modeling experiments clearly demonstrate how the regional climate response to global forcing can be amplified, attenuated or reversed by the regional controls. Beringian climate was subject to a range of controls that waxed and waned, generating a series of unique climate states through the mid-Holocene. The subtlety and heterogeneity of response to forcing combinations may explain anomalous or conflict-

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ing paleodata. For example, the subtle (even absent) expression of the Younger Dryas event over much of the region (Kokorowski et al., 2008) is consistent with the initial dominance of insolation and subsequently the effect of the progressive land-bridge transgression (beginning at ~ 13 ka) on Beringian climate, both of which might have masked the Younger Dryas cooling. The spatial heterogeneity of summer warmth and its different seasonal expression through time argues against defining a single thermal maximum for the Holocene, even within Beringia (c.f. Kaufman et al., 2004), as this may unnecessarily constrain views of how Beringian climate evolved and over-emphasize the importance of the early Holocene as a period of extreme warmth.

Furthermore, the results of the model experiments have a range of implications not only for interpretations of past Beringian environments but also for the study of future climate change in northern regions through our identification of regionally relevant mechanisms and feedbacks. For example, attention is currently focused on potential effects of future climate change in arctic regions, including increased shrub size and the northward expansion of woody vegetation cover, both shrubs and boreal forest. Our results indicate that vegetation changes from low shrub tundra to tall shrubs or deciduous woodland can increase spring temperatures, in general agreement with other studies examining the effects of potential future vegetation change in the Arctic (e.g., Swann et al., 2010; Bonfils et al., 2012). The effect appears to be robust, even under markedly different conditions of insolation and seasonality.

The study of Earth-system responses to climate change both past and present, such as the modelling of carbon balance, hydrology, and permafrost dynamics, requires a foundation in adequate regional climate detail to produce coherent results. Our regional modelling study demonstrates the complexity of the interaction of hemispheric and regional controls and may serve as a basis for further investigations of key elements of Holocene ecosystem dynamics in Beringia.

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Table 1. Simulation boundary conditions and land cover.

Simulation Name	Insolation	CO ₂ (ppm)	Vegetation	Lakes	Continental Outlines	Topography and Ice	Supplement Figure
Present Day ¹	Modern	280	Modern	Modern	Modern	Modern	1
Present Day with 11 ka Continental Outlines ²	Modern	280	Modern	Modern	11 ka	11 ka Topography only	2
11 ka Control ³	11 ka	265	Shrub Tundra (~ 13 ka)	No Lakes	11 ka	11 ka	4
11 ka Sea Level ^{4,5}	11 ka	265	Shrub Tundra (~ 13 ka)	No Lakes	Modern	11 ka Modified	7
11 ka Vegetation ⁵	11 ka	265	Deciduous Shrub/Woodland (11 ka)	No Lakes	11 ka	11 ka	9
11 ka Lakes	11 ka	265	Shrub Tundra (~ 13 ka)	Modern	11 ka	11 ka	11
11 ka All ^{6,7}	11 ka	265	Deciduous Shrub/Woodland (11 ka)	Modern	Modern	11 ka Modified	13
6 ka	6 ka	280	Modern	Modern	Modern	Modern	16

¹ Vegetation is slightly simplified from the GLCC BATS values.

² Continental outlines and topography were adopted from the 11 ka Control simulation, along with land cover from the Present-Day simulation.

³ 11 ka "point of departure" for 11 ka vegetation, lakes, and shelf-flooding experiments. Shrub tundra represents vegetation prior to 11 ka (~ 13 ka).

⁴ Vegetation is from the 11 ka Control simulation. Modern continental outlines.

⁵ 11 ka modified topography is 11 ka topography (modern topography + Peltier anomalies), with gridpoints that would be ocean at the present day set equal to 0 m.

⁶ Vegetation includes large areas of deciduous tall shrub and woodland.

⁷ Effect of all three changes (in vegetation, lake distribution and sea level) from just before 11 ka (shrub tundra, no lakes, exposed shelf) to just after (deciduous shrub/woodland, lakes, flooded shelf).

Table 2. Experiments.

Experiment	Control	Description	Supplement Figure
Present Day	Present Day (with 11 ka continental outlines)	Impact of 11 ka land bridge and continental outlines at present	3
11 ka Control	Present Day	Impact of (pre) 11 ka continental outlines, vegetation, lakes and wetlands, and 11 ka ice, topography, insolation, and CO ₂ (relative to present)	5
11 ka Control	Present Day (with 11 ka continental outlines)	Impact as above except for continental outlines	6
11 ka Sea Level	11 ka Control	Impact of land bridge flooding at 11 ka	8
11 ka Vegetation	11 ka Control	Impact of change from shrub tundra to deciduous woodland at 11 ka	10
11 ka Lakes	11 ka Control	Impact of thaw-lake development at 11 ka	12
11 ka All	11 ka Control	Impact of sea level, vegetation and lake changes at 11 ka	14
11 ka All	Present Day	Impact of 11 ka continental outlines (flooded land bridge), vegetation, lakes and wetlands, ice, topography, insolation, and CO ₂ (relative to present)	15
6 ka	Present Day	Impact of 6 ka insolation (relative to present)	17
6 ka	11 ka All	Impact of changing insolation and CO ₂ between 11 and 6 ka	18

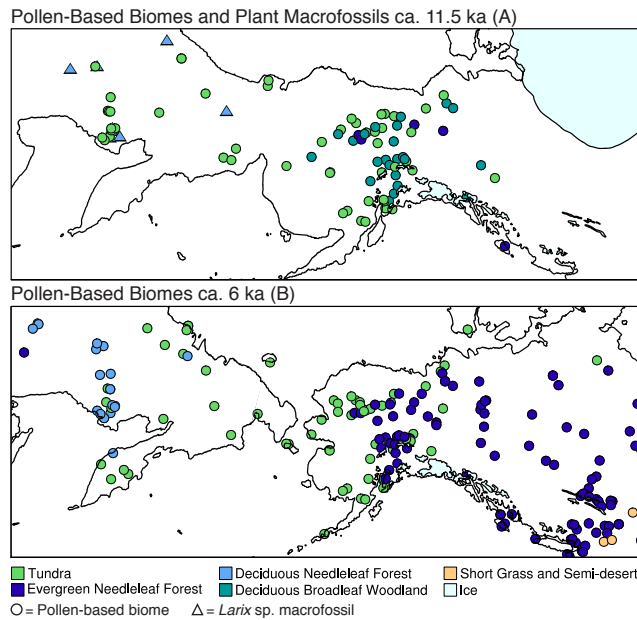


Figure 3. Pollen-based biomes for ca. 11.5 ka (**a**; this study) and ca. 6 ka (**b**; from Prentice et al., 2000; Bigelow et al., 2003). The 11.5-ka pollen patterns indicate deciduous broadleaf woodland in Alaska and Canada (**a**), but in Siberia this biome is identified from macrofossils only (not shown; see Sect. 2.2.8). At 6 ka deciduous needleleaf forest in Siberia is identified from widespread *Larix* pollen. The main difference between 6 ka and modern is the truncated distribution of evergreen needleleaf forest in western Alaska at 6 ka. Biome identities and colours map on to the RegCM land-cover PFTs in Fig. 4. Ice from Dyke et al. (2003) and coastline inferred from Peltier (1994) topographic anomalies.

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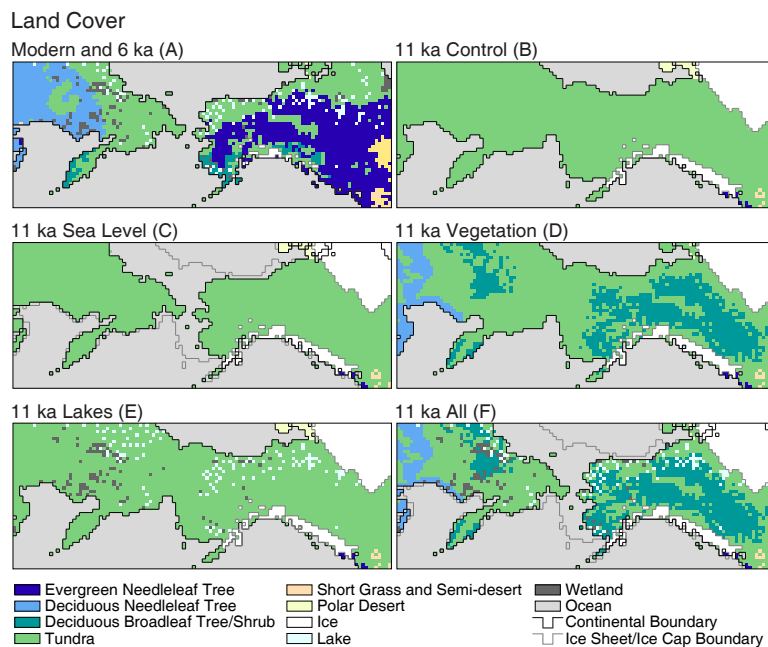


Figure 4. Land cover for RegCM climate simulations. Modern conditions are also used for the 6 ka simulation; there are minor differences in forest cover between modern and 6 ka (see Fig. 3). The vegetation cover in each simulation is represented by the set of RegCM plant functional types (PFTs); the PFT Deciduous Broadleaf Tree/Shrub was created to represent the characteristics of short-statured deciduous woodland and tall shrub communities. Land cover for 11 ka All (**f**) combines all three experimental land-cover changes. Each land-cover map is linked to a RegCM simulation; an additional simulation was made using modern land cover with 11-ka continental outlines (not shown).

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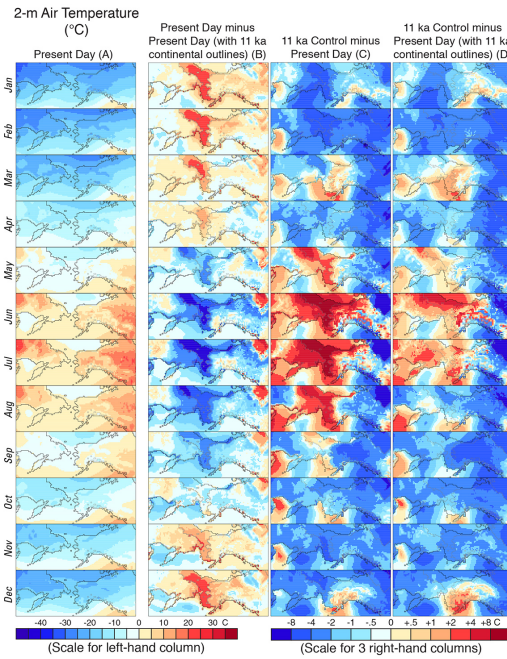


Figure 5. Simulated 2 m air temperature. **(a)** Present-Day (0 ka) simulation; **(b)** effect of land bridge flooding on present day climatology (Present Day minus Present Day with 11 ka continental outlines); **(c)** difference between 11 ka Control and present (11 ka Control minus Present Day); **(d)** difference between 11 ka Control and present as a result of insolation and boundary conditions other than sea level (11 ka Control minus Present Day with 11 ka continental outlines). Ice-sheet and coastal outlines as in Fig. 4.

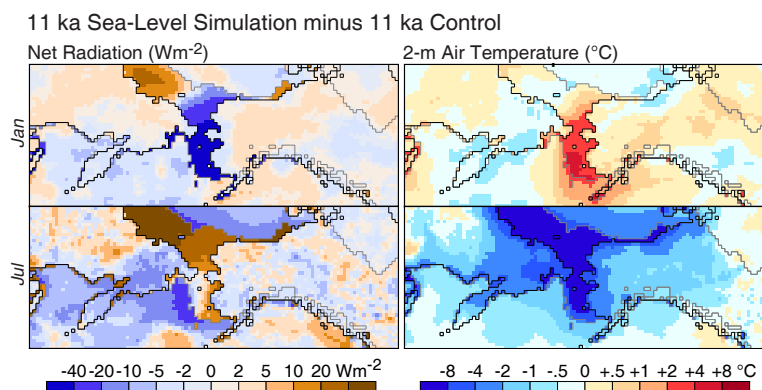


Figure 6. Results of 11 ka Sea Level experiment. Panels show the effect of flooding the land bridge at 11 ka (11 ka Sea Level minus 11 ka Control). Net radiation (left) and 2 m air temperature (right) for January (upper) and July (lower). Strong winter warming and summer cooling is seen over areas of flooded ocean shelf and adjacent land areas. Ice-sheet and coastal outlines as in Fig. 4.

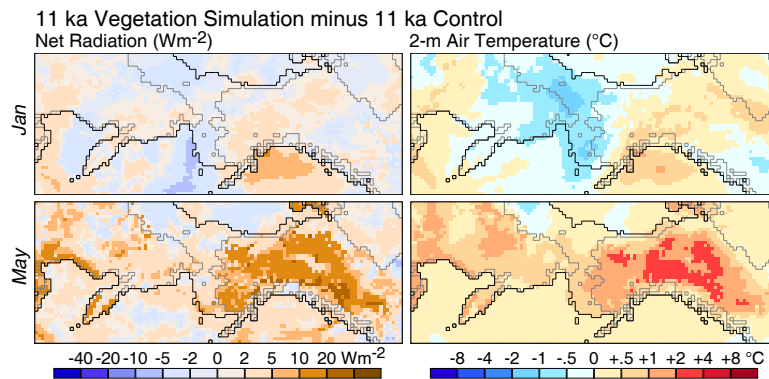


Figure 7. Results of 11 ka Vegetation experiment (11 ka Vegetation minus 11 ka Control). Panels show net radiation (left) and 2 m air temperature (right) for January (upper) and May (lower). The effect of taller, denser shrub/tree cover is seen most strongly in May, when 2 m air temperatures increase by 1–4 °C over the control values. Ice-sheet and coastal outlines as in Fig. 4.

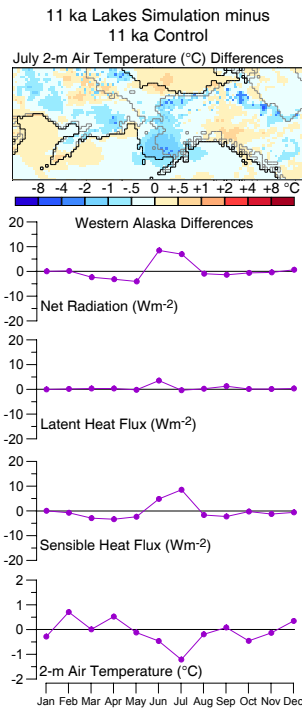


Figure 8. Results of 11 ka Lakes experiment. Top panel shows July 2 m air temperature differences (11 ka Lakes minus 11 ka Control). Lower panels show mean monthly differences for energy fluxes and temperature for RegCM grid cells in western Alaska (170–150° W longitude), where cooling is most pronounced. Ice-sheet and coastal outlines as in Fig. 4.

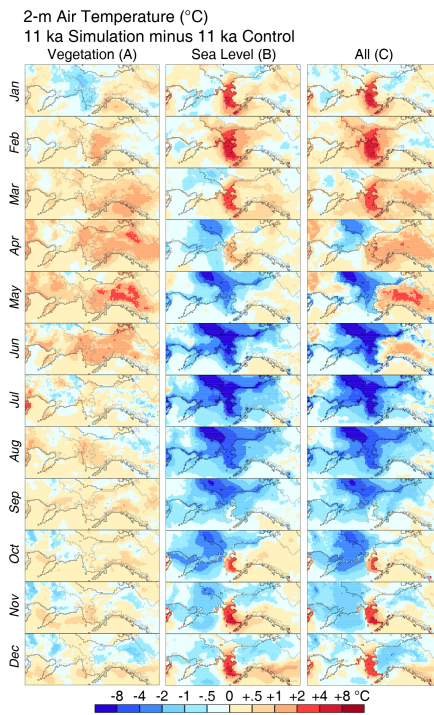


Figure 9. The effect on 2 m air temperature (°C) of changing vegetation (a), sea level (b) and all three land cover changes (vegetation, sea level and lakes; c) at 11 ka. Ice-sheet and coastal outlines as in Fig. 4.

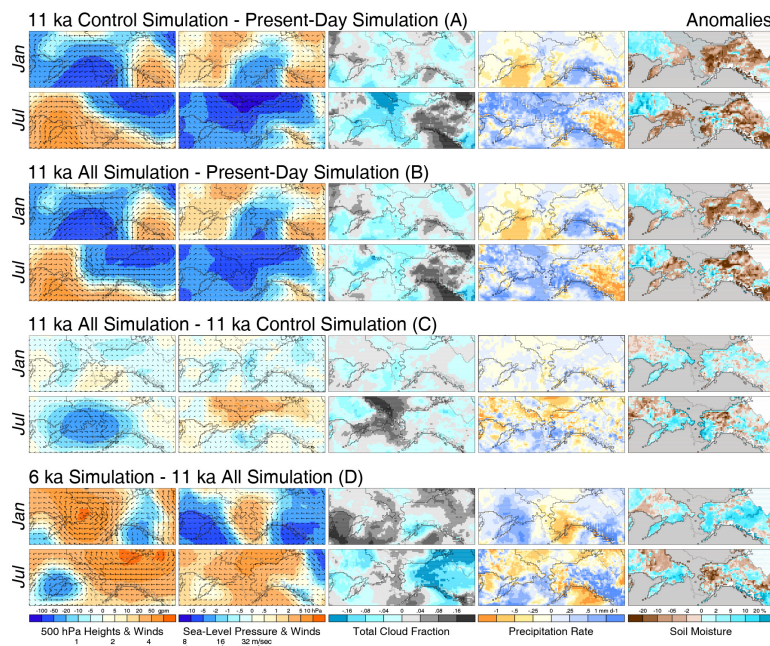


Figure 10. Atmospheric circulation (500 hPa heights and winds, sea-level pressure and surface winds), clouds, precipitation and soil-moisture anomalies. (a) 11 ka Control minus Present Day; (b) 11 ka All minus Present Day; (c) 11 ka All minus 11 ka Control; (d) 6 ka minus 11 ka All (showing the change between 11 and 6 ka). Ice-sheet and coastal outlines as in Fig. 4.

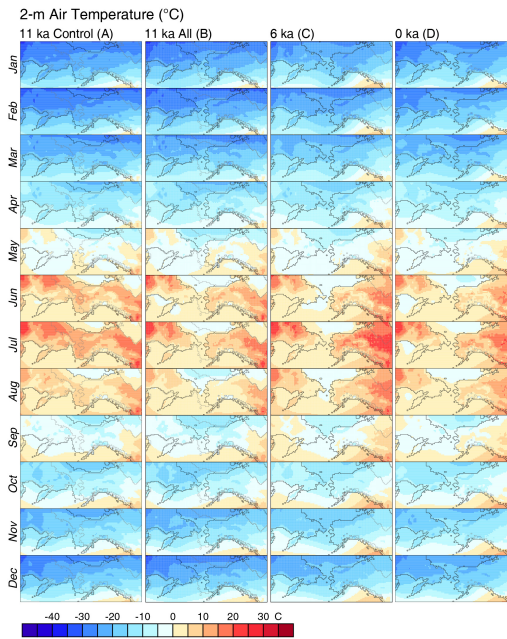


Figure 11. Monthly mean simulated temperature for 11 ka Control (**a**), 11 ka with changed surface properties (11 ka All; **b**), 6 ka (**c**), and present (0 ka; **d**). Ice-sheet and coastal outlines as in Fig. 4.

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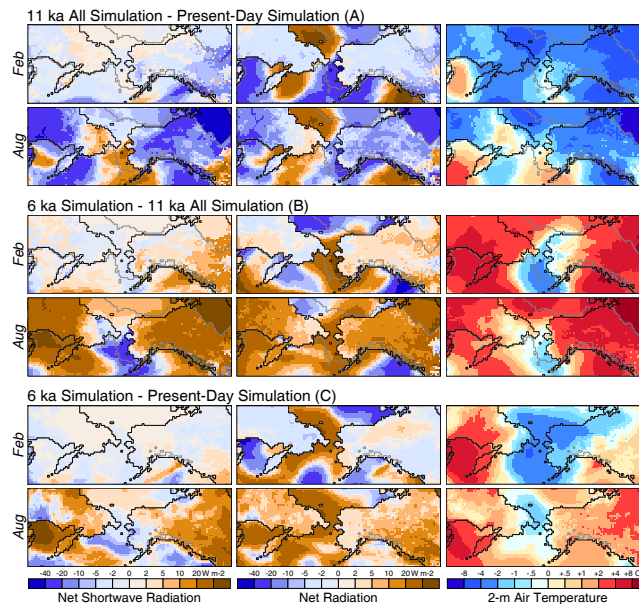


Figure 12. Net shortwave radiation (surface), net radiation and 2 m air temperature differences for February and August. **(a)** 11 ka All minus Present Day, illustrating the impact of 11 ka insolation (relative to that at present); **(b)** 6 ka minus 11 ka All, illustrating the impact of changes in boundary conditions other than concurrent insolation between 11 and 6 ka; **(c)** 6 ka minus Present Day, illustrating the impact of 6 ka insolation (relative to that at present). Ice-sheet and coastal outlines as in Fig. 4.

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