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Evaluating CO₂ and CH₄ dynamics of Alaskan ecosystems during the Holocene Thermal Maximum



QUATERNARY



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ABSTRACT

The Arctic has experienced much greater warming than the global average in recent decades due to polar amplification. Warming has induced ecological changes that have impacted climate carbon-cycle feedbacks, making it important to understand the climate and vegetation controls on carbon (C) dynamics. Here we used the Holocene Thermal Maximum (HTM, 11-9 ka BP, 1 ka BP = 1000 cal yr before present) in Alaska as a case study to examine how ecosystem Cdynamics responded to the past warming climate using an integrated approach of combining paleoecological reconstructions and ecosystem modeling. Our paleoecological synthesis showed expansion of deciduous broadleaf forest (dominated by Populus) into tundra and the establishment of boreal evergreen needleleaf and mixed forest during the second half of the HTM under a warmer- and wetter-than-before climate, coincident with the occurrence of the highest net primary productivity, cumulative net ecosystem productivity, soil C accumulation and CH₄ emissions. These series of ecological and biogeochemical shifts mirrored the solar insolation and subsequent temperature and precipitation patterns during HTM, indicating the importance of climate controls on C dynamics. Our simulated regional estimate of CH₄ emission rates from Alaska during the HTM ranged from 3.5 to 6.4 Tg CH_4 yr⁻¹ and highest annual NPP of 470 Tg C yr⁻¹, significantly higher than previously reported modern estimates. Our results show that the differences in static vegetation distribution maps used in simulations of different time slices have greater influence on modeled C dynamics than climatic fields within each time slice, highlighting the importance of incorporating vegetation community dynamics and their responses to climatic conditions in long-term biogeochemical modeling.

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1. Introduction

Northern high latitudes play a crucial role in the earth's climate system. Boreal and subarctic regions in the northern hemisphere are warming faster than low latitude areas (IPCC, 2007) due to changes in albedo resulting from shorter annual snow cover, reduced extent and duration of sea ice, and ecological shifts (Bonan et al., 1992; Overpeck et al., 1997; Serreze et al., 2000; Parry et al., 2007). The impact of warming on boreal ecosystems has been well-documented and expressed as altered phenology and range

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0277-3791/\$ - see front matter © 2013 Elsevier Ltd. All rights reserved. http://dx.doi.org/10.1016/j.quascirev.2013.12.019 shifts of species (Walther et al., 2002; Root et al., 2003; Parmesan, 2006; Callaghan et al., 2010). These observed ecological changes are closely linked to climate carbon-cycle feedbacks, which may have a large impact on CO₂ levels and climate (Cox et al., 2000; Jones et al., 2003; Friedlingstein et al., 2006; Heimann and Reichstein, 2008). For example, northward treeline advancement not only creates a positive feedback between ecosystem and the atmosphere via biophysical processes (increasing the radiative forcing of the land by reducing growing season albedo and increasing spring energy absorption, fluxes of sensible heat and moisture (Bonan et al., 1992; Foley et al., 1994; Chapin et al., 2000; Grace et al., 2002)), it also causes changes in the release or absorption of globally relevant greenhouse gases (e.g., CO₂ and CH₄) and soil carbon (C) storage whose liberation of C into the atmosphere would have a large impact on climate (Schuur et al., 2008, 2009). Therefore, it is

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important to understand the climate controls on vegetation community changes *and* the subsequent C dynamics, which later on can feed into bottom-up approaches (process-based ecosystem models or large scale up-scaling, contrasting to "top-down" approaches using atmospheric inversion) for climate predictions. Past pronounced warming events can be good examples to illustrate these controls via proxy-based reconstructions and ecosystem modeling.

A peak in Holocene warmth (Holocene Thermal Maximum, HTM) occurred transgressively between 11 and 5 ka BP across the northern high latitudes characterized by increasing summer solar insolation (Berger and Loutre, 1991; Kaufman et al., 2004; Wanner et al., 2008; Renssen et al., 2012). Climate proxy records suggest that both the timing and magnitude of the HTM varied across the globe because of complex forcings and feedbacks including ice sheet dynamics and the thermal inertia of the ocean (Kaufman et al., 2004; Renssen et al., 2009; Bartlein et al., 2011). In Alaska and northwestern Canada, the HTM peaked at 11-9 ka BP, coincident with the peak in orbitally-forced summer insolation (Kaufman et al., 2004; Renssen et al., 2012). The immediate response to the orbital forcing was largely possible, because most of Alaska was not glaciation during the Last Glacial Maximum (LGM). Pollen-based reconstructions and macrofossil evidence suggest that boreal deciduous broadleaf forest/woodlands with Populus spp. (poplar, aspen) extended beyond modern treeline in Alaska during the HTM (Anderson, 1988; Mann et al., 2002; Ager, 2003; Edwards et al., 2005; Anderson et al., 2006). Range expansions of Populus (aspen) and Betula (birch) trees extended into regions that are now herb and shrub tundra, including the northern Seward Peninsula and northern Alaska (Edwards et al., 2005). The presence of Picea (spruce) macrofossils on the Seward Peninsula in Alaska suggests that at least scattered Picea trees were also present at 10 ka BP, much earlier than previously thought (Wetterich et al., 2012). Furthermore, a recent pollen record from the southern Seward Peninsula shows a presence of both Picea and Larix spp. in the Lateglacial (Hunt et al., 2013). In addition to vegetation distribution reconstruction, proxy indicators also provide evidence on how climate and vegetation community structure may have synergistically impacted ecosystem C dynamics. Basal peat dates from across the boreal and subarctic region, including Alaska, indicate high rates of peatland initiation and development (MacDonald et al., 2006; Jones and Yu, 2010) and widespread thermokarst lake formation (Walter et al., 2007) in the lowlands during the HTM. Evidence from a few high-resolution peat records indicates that the highest rates of vertical C accumulation occurred in the early Holocene, suggesting relatively wet conditions on peatlands, as dry conditions would facilitate rapid decomposition of the accumulating peat (Jones and Yu, 2010). However, while site-level proxies data can generally produce well-represented vegetation community dynamics and provide implications to C dynamics, they cannot make quantitative estimates over various aspects of C dynamics that extend across large spatial domains. Therefore proxies alone are insufficient to provide a holistic view of the biogeochemical processes that may have occurred in the past.

Here we used an integrated approach of compiling available paleoecological records and ecosystem modeling to provide a synthesized picture of the climate, vegetation composition and C dynamics (vegetation productivity, CH_4 emissions, and subsequent biogeochemical processes) of Alaskan ecosystems during four time slices (15–13 ka BP, 11–10 ka BP, 10–9 ka BP, and 7–5 ka BP), encompassing the relatively cool Bølling-Allerød, the period of early Holocene warmth, and the mid-Holocene transition to nearmodern conditions. Through the markedly contrasting climatic boundary conditions across millennial scales, we explored the relative role of environmental and ecological controls on simulated regional C dynamics and the biogeophysical synergies between vegetation and the atmosphere. More specifically, we examined how changes in climate (combination of warming climate, changing precipitation patterns and radiation) may have affected ecosystem structure and functioning in the Arctic and boreal region. Better understanding of how high-latitude ecosystems respond to past warming has substantial implications for disentangling the relative controls of climate and vegetation on ecosystem C balance. We use the HTM in Alaska as a case study to try to understand the biotic and abiotic processes involved in generating the vegetation and ecosystem patterns observed in the paleorecords.

2. Methods

2.1. Overview

In this study, we examined the C dynamics during four time slices: a time slice encompassing a millennial-scale warming event during the last deglaciation known as the Bølling-Allerød, 15–13 ka BP; HTM during the early Holocene, 11–10 and 10–9 ka BP; and mid-Holocene, 7–5 ka BP. We compiled stratigraphic pollen data from Alaska to classify biomes based on plant functional types (PFTs), which were spatially interpolated to generate biome maps of Alaska corresponding to each of the four time slices. Climate data were downscaled and bias corrected from ECBilt-CLIO model output (Timm and Timmermann, 2007). The results of the gridded pollen biome outputs and downscaled climate were used to drive the Terrestrial Ecosystem Model (TEM) including the Methane Dynamic Module (MDM) (Zhuang et al., 2004) to conduct simulations for C cycling and CH₄ dynamics in Alaska.

2.2. Biome map generation

Available stratigraphic pollen data from Alaska with existing chronologies were compiled to generate biome maps for the four time slices. The data were compiled from the North American Pollen Database (NAPD) and the Paleoenvironmental Arctic Sciences (PARCS) database, in addition to published pollen records not included in the databases for which we were able to attain the raw pollen data (Fig. 1). Available calibrated radiocarbon chronologies for each record were used to bin the pollen data into 1000-year time slices. Because many records contained chronologies based on older bulk ¹⁴C dates instead of Accelerator Mass Spectrometry dates and some records contained only a few ages (Table SI1), the binning of the data into 1000-year time slices allowed for multiple samples from each site to be included in each bin, which helped account for potentially large dating uncertainties in some of the cores. In the biomization method, pollen taxa were converted to PFTs based on their distinctive traits and climatic requirements and the PFTs were used to generate affinity scores to fit each assemblage into biomes in the BIOMISE program (Prentice et al., 1996). The definitions of the PFTs and biomes used in this analysis follow Bigelow et al. (2003) and Kaplan et al. (2003). Modifications were made to the BIOMISE program to include plant taxa that could be characterized as wetland (peatland), including Sphagnum moss spores, and to compensate for low-pollen producing taxa such as Populus spp., which expanded its range into the Arctic during the warmer-than-present HTM. However, because it does not produce a lot of pollen and because the pollen degrades easily, early Holocene percentages are low (<5%). The goal was to account for these 'non-analog' vegetation biomes (Edwards et al., 2005) during the HTM in Alaska, and so *Populus* pollen was weighted (\times 2). Each location at each time slice was classified into a BIOMISE biome (Table 1), based on a calculated affinity score obtained from the pollen types present and their relative abundances. As a benchmark



Fig. 1. Map of Alaska showing pollen data sites and locations mentioned in the text.

for the use of the objective biomization method, we used the BIOMISE program to construct a modern vegetation map based on the North American Modern Pollen Database (Whitmore et al., 2005) for Alaska. The modern biomization results agreed favorably to other studies and observed modern biomes and validated our biomization method (Fig. SI1; Bigelow et al., 2003; Whitmore et al., 2005; Edwards et al., 2000).

BIOMISE codes were reclassified to be compatible with the TEM ecosystem types (Table 2). STEP and TEDE were consistently assigned low affinity scores (i.e., no samples were biomized to STEP and TEDE) thus were not included in reclassification to TEM categories. The TEM ecosystem types were then interpolated using nearest-neighbor approach across Alaska to obtain final biome map at $0.5^{\circ} \times 0.5^{\circ}$ grid resolution. To account for broad-scale topography in determining location of biomes, mountain ranges and large water bodies (bays and inlets) were delineated as 'Barren' and data could not be interpolated across them. It is worthy to note here that we acknowledge the limitation of nearest-neighbor approach on this relatively small and unevenly distributed dataset. In fact, we tried other methods such as indicator kriging (indicator kriging employs indicator transform at discrete intervals of each ecosystem type value and then applies ordinary kriging to produce mapped cumulative probability at each indicator interval). When we applied indicator kriging interpolation across Alaska the cumulative probability map showed very similar pattern to the nearest-neighbor result (Fig. SI2). However, indicator kriging needs empirical discretion to determine the probability threshold for assigning specific ecosystem type code to each grid (especially critical at the boundary of a particular ecosystem type and when probabilities of two ecosystem types are similar). In addition, the cumulative probabilities did not add up to 1 for some of the grids due to the discretization process. Therefore, without sufficient information to support decision-making, we chose to stick with the nearest-neighbor method. The spatial interpolation was performed in R statistical systems (http://www.r-project.org).

We derived two vegetation maps for the time slice encompassing the HTM in Alaska, 10,000–9000 ¹⁴C yr BP (~11,600–10,100 cal yr BP) and 9300–8500 ¹⁴C yr BP (~10,500–9500 cal yr BP). The pre- and post-HTM time slices each has a vegetation distribution map representing 12,500–11,500 ¹⁴C yr BP (~14,500–13,350 cal yr BP) and 5700–4750 ¹⁴C yr BP (~6500–5500 cal yr BP) respectively. Vegetation distribution was assumed to be static within the corresponding time slice.

2.3. Climate, wetland extent and other regional input data

We used the transient 21,000-year ECBilt-CLIO simulation (Timm and Timmermann, 2007; Timmermann et al., 2009; SIM2b) as the basis for the large-scale climate. Climate fields include precipitation, surface air temperature, net incoming solar radiation Tabla 1

Description of BIOMISE codes used	in biomization procedure.

BIOMISE code	Biome name in BIOMISE	Description (PFTs)
STEP	Temperate xerophytic shrubland	Grass, sedge, steppe forb
CUSH	Cushion-forb tundra	High arctic rosette or cushion forb, arctic forb, graminoid
DRYT	Graminoid and forb tundra	Arctic forb, graminoid, sedge, arctic evergreen broad-leaved prostrate shrub
PROS	Prostrate dwarf-shrub tundra	High arctic rosette or cushion forb, arctic forb, graminoid, arctic deciduous broad-leaved prostrate shrub
DWAR	Erect dwarf-shrub tundra	Graminoid, sedge, arctic deciduous broad-leaved prostrate shrub
SHRU	Low- and high-shrub tundra	Sedge, arctic evergreen broad-leaved prostrate shrub, arctic deciduous broad-leaved prostrate shrubs; arcto-boreal deciduous broad-leaved dwarf shrub, arcto-boreal evergreen needle-leafed low/high shrub;
CLDE	Cold deciduous forest	Arcto-boreal deciduous broad-leaved dwarf shrub, arcto-boreal evergreen broad-leaved dwarf shrub, arcto-boreal deciduous/evergreen broad-leafed/needle-leaved low/high shrub; boreal-evergreen needle-leaved tree; boreal deciduous broad-leaved tree, boreal evergreen/deciduous broad-leaved low/high shrub
TAIG	Cold evergreen needle-leaved forest	Arcto-boreal deciduous broad-leaved dwarf shrub, arcto-boreal evergreen broad-leaved dwarf shrub; boreal-evergreen needle-leaved tree; boreal deciduous broad-leaved tree, boreal deciduous broad-leaved low or high shrub
сосо	Cool evergreen needle-leaved forest	Eurythmic conifer, boreal evergreen needle-leaved tree, boreal deciduous broad-leaved tree, temperate evergreen needle-leaved tree, maritime evergreen needle-leaved tree, northern temperate deciduous broad-leaved tree
CLMX	Cool-temperate mixed forest	Eurythmic conifer, boreal deciduous broad-leaved tree, temperate evergreen needle-leaved tree, maritime evergreen needle-leaved tree, northern temperate deciduous broad-leaved tree
COMX	Cool mixed forest	Eurythmic conifer, boreal evergreen needle-leaved tree, boreal deciduous broad-leaved tree, temperate evergreen needle-leaved tree, (northern) temperate deciduous broad-leaved tree
TEDE	Temperate deciduous forest	Eurythmic conifer, boreal evergreen needle-leaved tree, boreal deciduous broad-leaved tree, maritime evergreen needle-leaved tree, northern/southern temperate deciduous broad-leaved tree, temperate evergreen broad-leaved woody plants

and vapor pressure $(2.5^{\circ} \times 2.5^{\circ})$. This earth system model of intermediate complexity uses a fully coupled 3-dimensional atmosphere, ocean and sea ice, which enables the simulation to capture the proper feedbacks between the atmosphere and ocean during the deglaciation. The changes in ocean circulation resulting from the deglaciation can only be captured using a transient simulation (Renssen et al., 2005a), and these ultimately affect the larger-scale atmospheric circulation. ECBilt-CLIO model had also been used in other HTM studies where the model reproduced the interaction between orbital-induced summer insolation and ice-sheet configuration that were reflected in proxy records (e.g., Renssen et al., 2009). We applied delta-ratio bias-correction with observed halfdegree data from the Climate Research Unit (CRU2.0) and inverse-square distance interpolation method, similar to the approach taken to downscale and bias-correct future climate scenarios (Hay et al., 2000), to correct the climate anomalies for the detailed topography and coastlines of Alaska at a resolution of $0.5^{\circ} \times 0.5^{\circ}$. To drive the TEM, we used the same time-dependent forcing atmospheric CO₂ concentration data as were used in ECBilt-CLIO transient simulations from the Taylor Dome (Timm and Timmermann, 2007).

Spatial wetland inundation data were extracted from the NASA/ GISS global natural wetland dataset (Matthews and Fung, 1987) with an original spatial resolution of $1^{\circ} \times 1^{\circ}$ and then resampled to $0.5^{\circ} \times 0.5^{\circ}$ for the TEM simulation. We postulate that given the same topography of Alaska during HTM and the similar vegetation distribution of 6 ka BP as of present, using modern wetland extent could be a reasonable approximation. The modern wetland extent was applied to simulations of all time slices. Spatially resolved soil–

Table 2

Assignment of biomized pollen data to the ecosystem types used in TEM.

TEM description (ecosystem types)	BIOMISE code			
Alpine tundra	CUSH	DRYT	PROS	
Moist wet tundra	DWAR	SHRU		
Boreal evergreen needleleaf and mixed	TAIG	COCO	CLMX	COMX
forest (including coastal western				
hemlock—Sitka spruce forest)				
Boreal deciduous broadleaf forest	CLDE			

water pH data were extracted from Carter and Scholes (2000). Elevation data were derived from the Shuttle Radar Topography Mission and were resampled to $0.5^{\circ} \times 0.5^{\circ}$ spatial resolution.

2.4. Description of the Terrestrial Ecosystem Model

The TEM is a process-based, monthly-step and global-scale ecosystem model. The core C and nitrogen dynamics module (CNDM) incorporates spatially explicit data pertaining to climate, vegetation, soil and elevation to estimate monthly pools and fluxes of C and nitrogen in the terrestrial biosphere. The incorporated methane dynamics module (MDM) explicitly considers the process of CH₄ production (methanogenesis), CH₄ oxidation (methanotrophy) and the transport of the CH₄ from the soil to the atmosphere (Zhuang et al., 2004). Net CH₄ fluxes at the soil/wateratmosphere boundary depend on the relative rates of CH₄ production and oxidation within the soil profile and the various CH₄ transport pathways across the surface of soils. Water movement across the atmosphere-vegetation-soil continuum, water table depth, moisture dynamics and soil temperature profile are simulated by the hydrological module (Zhuang et al., 2002) and soil thermal module (Zhuang et al., 2001), and are integrated with CNDM and MDM to simulate C and nitrogen cycling. In TEM, the net ecosystem production (NEP) is calculated as the difference between the uptake of atmospheric CO₂ associated with photosynthesis (i.e., gross primary production or GPP) and the release of CO₂ through autotrophic respiration associated with plant growth and maintenance respiration, and heterotrophic respiration associated with decomposition of organic matter. Net primary production (NPP) is calculated as the difference between GPP and autotrophic respiration. Net NEP accumulation is calculated as the long-term cumulative difference between NPP and ecosystem respiration.

2.5. Model parameterization and simulation protocol

The parameterization for upland vegetation types (except boreal evergreen needleleaf and mixed forest) used in CNDM is based on previous TEM publications (Zhuang et al., 2003). Note that the range of *Picea mariana* did not expand greatly until 8 ka BP

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(Anderson et al., 1990; Edwards and Barker, 1994). Therefore for boreal evergreen needleleaf and mixed forest we used the parameterization based on white spruce dominated boreal mixed forest which is composed of 50% white spruce, 35% black spruce and 15% mixed birch, aspen and poplar (He et al., 2013). We used a Bayesian inference framework (Tang and Zhuang, 2009) to calibrate the rate limiting parameters of the MDM module based on three peatland sites (CA-WP1, CA-Mer, and US-Ivo, Table 3). In the TEM wetland simulation, CA-WP1 is categorized as forested peatland, CA-Mer as moist tundra wetland and US-Ivo as alpine tundra wetland. A set of 500,000 Monte Carlo ensemble simulations was conducted for each site-level calibration. Parameters with the highest mode in posterior distribution were selected for the regional simulation.

We conducted four model simulations for four time slices, in which the HTM slice was separated into two contiguous periods (11–10 and 10–9 ka BP) and simulated separately for two vegetation-distribution maps. The final state of C and N pools of each ecosystem type in the first half of the HTM slice was used as an initial state for the corresponding ecosystem type in the second half of the HTM slice simulation to maintain consistency. For all simulations except the period of 10–9 ka BP, the transient simulation started after the model reached equilibrium followed by a 150-year spin up. The spin-up used the first 150 years of each individual simulation. The model spin-up was applied before the transient simulation starts in order to set up initial values of all state variables (e.g., C and nitrogen pool sizes) due to the lack of reference for initial values for the time frame in this study.

2.6. Statistical analysis

We conducted multilinear regression on climatic fields and C dynamics to identify influential climatic factors in controlling the ecosystem C dynamics. We chose to apply stepwise regression to disentangle the mixed effect of those climatic fields that are identified to be important in regulating C dynamics due to the following reasons: 1) simple Pearson linear regression cannot account for interactions between predictors; 2) the simple correlation often involves the indirect correlation between the dependent variable and predictors that also influence the response but are not represented in the statistical model. The analyzed climatic fields included monthly average temperature, monthly total precipitation, and monthly average net incoming solar radiation. The response variables included NPP and net CH_4 emissions. All statistical analyses were performed using the Statistics Toolbox in MATLAB (MathWorks, R2012a).

Table 3					
FluxNet peatland	sites	used	in	calibratio	n.

3. Results

3.1. Simulated paleoclimate during 15-5 ka BP

The highest net incoming solar radiation occurred during 11-9 ka BP, with 10-9 ka BP slightly higher than the previous millennium, followed by mid-Holocene (7-5 ka BP) and 15-13 ka BP had the lowest (Fig. 2e). Mean annual temperature (MAT) paralleled the pattern in insolation with MAT at 10-9 ka BP around -4 ± 1.8 °C, 11–10 and 7–5 ka BP both around -5 ± 1.6 °C, and 15–13 ka BP the coldest with MAT around $-7 \pm 2 \degree C$ (Fig. 2a). The range here indicates the interannual variation in MAT across millennial scale. Mean annual precipitation (MAP) across the four slices generally mirrored the pattern in radiation as well, except that there was only negligible difference between the HTM and mid-Holocene (Fig. 2c). The seasonal patterns of climatic fields revealed several distinct differences among four time slices. As the model runs on a monthly time step, the linearly interpolated monthly average temperature (Fig. 2b) showed that the days of year with temperature above 0 °C was lengthened by about 3–5 days in the HTM. The period from 15 to 13 ka BP exhibited 5-10 mm less monthly precipitation than the HTM and the mid-Holocene, likely indicating a drier overall climate (Fig. 2d). The mid-Holocene showed slightly less summer precipitation than the HTM, which was compensated by a slight increase in winter precipitation; this induced a change in the ratio of summer/winter precipitation and may have influenced spring snowmelt and runoff. The orbitallyinduced insolation maximum during the HTM was well represented in the downscaled climate. The 11–9 ka BP time slice had the highest summer net incoming solar radiation, followed by the mid-Holocene, and the 15–13 ka BP time slice had the lowest (Fig. 2f). Winter radiation was generally the same for all time slices, indicating that enhanced climatic seasonality during the HTM was driven by summer radiation.

3.2. Vegetation reconstruction

Our biome reconstructions show that the vegetation composition changed dramatically during the four time slices (Fig. 3). During the 15–13 ka BP time-slice, tundra vegetation dominated the terrestrial ecosystem, with the northwest coast and eastern interior covered by moist tundra; and southwestern Alaska and the interior south of the Brooks Range dominated by alpine tundra. The biomization results show patches of boreal deciduous broadleaf forest and boreal evergreen needleleaf and mixed forest

Site	CA-WP1	CA-Mer	US-Ivo
Latitude	54.95	45.41	68.49
Longitude	-112.47	-75.52	-155.75
Elevation (m)	540	70	N/A
Climate	Boreal	Temperate	Arctic
Wetland type	Treed poor fen	Open bog	Arctic tundra
Dominant vegetation	Picea mariana, Larix	Chamaedaphne, calyculata,	E. vaginatum, Betula nana,
	laricina, Betula pumila,	Vaccinium myrtilloides,	Sphagnum spp.
	Sphagnum spp.	Sphagnum spp.	
Data type	Gap filled NEP	Gap filled NEP (umol $m^{-2} s^{-1}$),	Gap filled NEP (umol $m^{-2} s^{-1}$),
	$(\text{umol } \text{m}^{-2} \text{ s}^{-1}),$	GEP (umol m ⁻² s ⁻¹), precipitation (mm),	GEP (umol $m^{-2} s^{-1}$),
	GEP (umol m ^{-2} s ^{-1}),	air temperature (°C), downward short	precipitation (mm), air
	precipitation (mm),	wave radiation (W m ⁻²)	temperature (°C), downward
	air temperature (°C),		short wave radiation (W m ⁻²)
	downward short wave		
	radiation (W m ⁻²)		
Data period (YY.MM)	03.08-09.09	98.06-09.12	04.01-06.12
Citation	Syed et al., 2006	Roulet et al., 2007	Oechel et al., 2000



Fig. 2. Downscaled climate during the four time slices. Mean annual (a) air temperature (°C), (c) total precipitation (mm), (e) net incoming solar radiation (W m⁻²), and monthly average (b) air temperature (°C), (d) total precipitation (mm), (f) net incoming solar radiation (W m⁻²) during each time slice.

north of the Alaska Range (Fig. 3a), but these are likely misclassified, since abundant Betula and Salix pollen more likely were in prostrate shrub form (see Discussion 4.2). Abundant fern spores, in conjunction with *Betula*, *Salix*, and sparse *Picea*, in these pollen records may also have resulted into the classification of these sites as boreal evergreen needleleaf and mixed forest (some records showing Picea pollen during this time interval also could be from refugial populations that survived the LGM; poor dating control for some of the records may also be a culprit in attaining forest biome categories this early in the record. See Discussion 4.2). As climate became warmer and wetter (see our downscaled climate Fig. 2a,c) as glaciers and ice sheets began retreating (wetter than previous period, but may still drier than modern, see Discussion 4.1) during the HTM (\sim 12–9 ka BP), boreal deciduous broadleaf and boreal evergreen needleleaf and mixed forests expanded (Fig. 3b). Peaks in Populus pollen in cores throughout Alaska during this time can explain the classification of boreal deciduous forest, although an abundance of Betula, Salix, and ferns in some of these records likely resulted in a misclassification of some of these biomes as forest when they were actually shrub tundra. Low levels of Picea pollen are present in several of the cores around this time and may account for the boreal evergreen needleleaf and mixed forest classification. The coastal tundra biome (moist wet tundra) covered most of Alaska north of the Brooks Range from 11 to 10 ka BP (Fig. 3b). At 10–9 ka BP, boreal deciduous forest expanded to the north of the Brooks Range making forest the dominant biome in Alaska (Fig. 3c), indicating an even warmer climate than 11-10 ka BP. The site encompassing the Arctic Coastal Plain was biomized as moist wet tundra. As spruce began to migrate into boreal Alaska during the end of the early Holocene (10–9 ka), a mix of deciduous and evergreen boreal forest began expanding (Fig. 3c). Tundra, boreal evergreen needleleaf and mixed forest prevailed in western Alaska during the 10-9 ka BP time slice. This lies in contrast to the boreal evergreen needleleaf and mixed forest and deciduous woodland that existed 11-10 ka BP. During the cool mid-Holocene period, the terrestrial landscape generally resembled present-day ecosystems (Fig. 3d), which is in agreement with previous



Fig. 3. Vegetation distribution map reconstructed from pollen data during each time slice. The BIOMISE biomes (as shown in different markers at pollen site locations) were reassigned to be consistent with TEM PFT category (colored patches). The barren grids were manually inserted as physical barriers, over which biomes could not be interpolated.

biomization efforts in Alaska (Bigelow et al., 2003). Boreal evergreen needleleaf and mixed forest, likely attributable to the establishment of *Picea glauca*, prevailed in southern and Interior Alaska, and tundra expanded to the north of the Brooks Range and western Alaska, including the Seward Peninsula and the Yukon-Kuskokwim Delta. The expansion of *Picea* spp. and the return of tundra on the Seward Peninsula likely indicates cooler climate than HTM, in line with the decreased summer insolation and MAT reported in our downscaled climate (Fig. 2a,f).

3.3. Vegetation productivity and regional C balance

Based on the vegetation distribution from the BIOMISE output and the downscaled climate data, the TEM simulation results show that the highest NPP occurred during the HTM (11–9 ka BP, Fig. 4a). The regional total NPP was the highest from 10 to 9 ka BP, resulting in an uptake of ~470 \pm 60 Tg C yr⁻¹, and the lowest between 15 and 13 ka BP, with an uptake of ~150 \pm 18 Tg C yr⁻¹. Cumulative NEP did not show much C sequestration during 15–13 ka BP (Fig. 4b). Significant C accumulation started from the HTM and reached its highest around 9.7 ka BP (Fig. 4b). This trend is probably due to increased temperature and precipitation from 10 to 9 ka BP coupled with the subsequent accelerated photosynthesis and a shift in the vegetation from shrub tundra to boreal deciduous broadleaf forest in northern Alaska, resulted in an increase in the soil C by about 3 Pg C from previous C storage (Fig. 4c). Terrestrial ecosystems of Alaska sequestered about 1.5 Pg C during the HTM and about 1 Pg C during 7–5 ka BP (Fig. 4b).

The seasonal variation of both NPP and NEP paralleled the general pattern of the climate (Fig. 5), where higher NPP and NEP coincided with warmer temperatures and enhanced precipitation during HTM compared to the 15–13 ka BP time slice. A prolonged growing season (NPP > 0) occurred between 10 and 9 ka BP (Fig. 5a), while 11–10 and 7–5 ka BP had the same growing season length. 15–13 ka BP showed a narrow window of positive net C assimilation, probably limited by cool temperatures (Fig. 5a). NEP



Fig. 4. Simulated regional total NPP (Tg C yr⁻¹), cumulative NEP (Tg C), and soil C (Pg C) across Alaska for each time slice. The red dotted line indicates 0 baseline. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

generally had a narrower window of positive net ecosystem C sequestration than NPP and fewer discrepancies among four time slices (Fig. 5b). 11–9 ka BP showed most enhanced seasonality in C dynamics as it has both summer peak as a C sink and winter bottom as a C source (Fig. 5b). The enhanced seasonal C dynamics may be associated with similarly enhanced climatic seasonality (warmer summer). The high respiration in winter during HTM may partly be attributed to the expanded forest coverage (boreal deciduous and evergreen mixed forest), which generally featured greater ecosystem productivity and respiration than tundra. During the growing season of the HTM, NEP reached about 50 g C m⁻² mon⁻¹ in Jun and –20 g C m⁻² mon⁻¹ in April, whereas during the 15–13 ka BP time slice, the highest monthly NEP was about 30 g C m⁻² mon⁻¹ and the lowest (–10 g C m⁻² mon⁻¹) in the winter (Fig. 5b).

3.4. CH₄ emissions

Regional annual net CH₄ emissions were highest during the HTM, averaging about 5 Tg CH₄ yr⁻¹ (Fig. 6). The 15–13 ka BP time

slice and mid-Holocene were both low with an average of about 3 Tg CH₄ yr⁻¹. Larger interannual CH₄ fluctuations were also found from 10 to 9 ka BP, during which the highest CH₄ net emission also occurred. Moist tundra in the Yukon-Kuskokwim Delta was the hotspot for CH₄ emission from 15 to 13 ka BP with an average of more than 10 g CH₄ m⁻² yr⁻¹ (Fig. 7a). Most of Alaska, except for the hotspot in the Yukon-Kuskokwim Delta, had CH4 emissions ranging from 0 to 4 g CH_4 m⁻² yr⁻¹ at that time. As the majority of moist tundra shifted into boreal deciduous and later boreal evergreen forest as climate became warmer and possibly more mesic in the HTM, the highest net CH₄ emissions occurred in coastal tundra in Alaska's North Slope and south of Yukon-Kuskokwim Delta where moist tundra of the low-lying area was prevalent (Fig. 7b,c). The coastal tundra in bottomland taiga emitted about 4-10 g CH_4 m⁻² yr⁻¹. Wetlands that were in the lowland of the taiga forest became the dominant high CH₄ source, emitting more than 10 g CH₄ m⁻² yr⁻¹ during the HTM (Fig. 7b,c). At the onset of the mid-Holocene, CH₄ emission levels dropped and close to that of the 15-13 ka BP with most of Alaska emitting less than 4 g CH_4 m⁻² yr⁻¹ (Fig. 7d).



Fig. 5. Simulated monthly averages of NPP (g C $m^{-2}\ mon^{-1})$ and NEP (g C $m^{-2}\ mon^{-1})$ during each time slice.

4. Discussion

4.1. Implications and limitations of climate data

Our downscaled climate results from the time slices studied showed that the coolest temperatures occurred at 15-13 ka BP, and the warmest climate occurred during the HTM, followed by a slightly cooler mid-Holocene (Fig. 2a,b), in line with the orbitallyinduced changes in summer insolation (Fig. 2e,f). This pattern suggests that orbital forcing is the primary control of temperatures in Alaska since deglaciation, without a significant regional-cooling effect of the Laurentide ice sheet, similar to what other studies concluded (e.g., Berger and Loutre, 1991; Renssen et al., 2009). In most parts of Alaska, the ECBilt-CLIO model estimates about 2 °C higher annual average temperature than present during the HTM (Fig. 2a, present temperature based on Stafford et al., 2000). The modeled mid-Holocene climate was also warmer than present but with a smaller magnitude of about 0.5 °C. The modeled climate at both periods compares favorably with estimates from other studies (Anderson and Brubaker, 1993; Kaufman et al., 2004). Several paleoclimate simulations (e.g. HadUM, González Trueba et al., 2008; GCM, Renssen et al., 2005b) showed wetter summer (in terms of precipitation, not necessarily effective moisture, defined as precipitation-evapotranspiration) and higher seasonality during the HTM than the pre- and post-HTM period throughout Alaska; these are generally consistent with our results. Our downscaled climate indicated a drier and cooler 15-13 ka BP period than the following HTM and mid-Holocene (Fig. 2a,c), corresponding to water-balance modeling and lake sediment cores which indicated low precipitation levels and cooler climate prior to 14 ka BP (12.5¹⁴C ka BP in Barber and Finney, 2000; Edwards et al., 2001). Barber and Finney (2000) estimated an increase in precipitation and lake levels from 14.5 ka BP to 6.5 ka BP ($12.5-6^{14}$ C ka BP), similar to the precipitation trend simulated in our climate scenarios. However, despite the increase in precipitation, their estimated absolute precipitation levels were all less than modern (25-45% less than modern at 10.5 ka BP (9¹⁴C ka BP) to 10–20% less than modern at 6.5 ka BP (6¹⁴C ka BP)), while our modeled paleoclimate data during four time slices were close to modern regional mean annual precipitation of Alaska of around 400 mm (based on Stafford et al., 2000). It is likely that our climate data have overestimated the precipitation. Precipitation is strongly influenced by local topography and has great spatial heterogeneity in Alaska, with 10 times less precipitation in northern Alaska than the precipitation high point in the southeast (Stafford et al., 2000), which large-scale earth system models usually fail to capture. However, reconstructed climatic anomalies (Bartlein et al., 2011) indicate that there may be less spatial heterogeneity in precipitation at 6 ka BP than present in Alaska (Fig. SI3). The slightly higher winter precipitation and the increased ratio of winter/summer precipitation in mid-Holocene shown in our results may help explain the high observed lake levels in the region at 6 ka BP (Barber and Finney, 2000), as spring melt with accompanying runoff has been identified as the single-most important source of water to arctic lakes (except severe storms) (Gieck and Kane, 1986; Barber and Finney, 2000). Along the same lines, the dry 15–13 ka BP period with low lake levels may also be attributed to the low winter precipitation and subsequent lower runoff from spring snow melt, especially as water remained locked in glaciers and remnant ice sheets.

There are several limitations in the use of the climate model that compromise the explanation of the vegetation-climate coupled dynamics and the observed evident patterns in the paleoenvironmental data sets. These limitations mostly manifest themselves in the uncertainty associated with reconciling coarse resolution general circulation models (GCMs, a few degrees of longitude/ latitude degrees) and sparse, unevenly-spaced site-level pollen records with the local and regional physiography of Alaska (Mock and Bartlein, 1995). Large-scale climatic controls (e.g., insolation, CO₂, atmospheric circulation) are mediated by local-scale controls (e.g., topographic barriers and coastlines) and thus producing great heterogeneity in surface climatic responses on regional scales (Whitlock and Bartlein, 1993; Mock and Bartlein, 1995). Coarse resolution GCMs can produce large-scale "boundary conditions" (e.g., sea ice extent and height, insolation, etc.) of the climate system, but are too coarse to be able to simulate regional (or even local) ecological and hydrological conditions, especially for precipitation as it is strongly influenced by local topography (Edwards et al., 2001). Moreover, the insufficiencies within the climate models also impede matching paleoclimatic simulations to observations (Edwards et al., 2001; Bartlein and Hostetler, 2003). In this study, we recognize the uncertainty involved in the downscaled climate data and statistically interpolated vegetation distribution maps, we therefore aimed at constructing a largely wellrepresented picture of the C dynamics in Alaska during the early Holocene, and identifying the potential biotic and abiotic controls on C dynamics across four time slices of contrasting climatic boundary conditions.

4.2. Implications and limitations of vegetation reconstruction

Pollen and macrofossil data suggest that early-Holocene vegetation in Beringia was structurally and thus functionally novel compare with modern dominant vegetation types (Edwards et al., 2005). Between \sim 13.5 and 9.5 ka BP, deciduous broadleaf trees



Fig. 6. Simulated regional total net CH₄ emission (Tg CH₄ yr⁻¹) across Alaska during each time slice.

and shrubs (*Betula, Salix*) are prominent. Scattered tree-sized *Betula–Populus* woodlands are also reported in boreal regions of Alaska and Canada, as tree stumps and other macrofossils from tree-sized *Betula* and *Populus* species have been found beyond treeline in the Arctic (e.g., Kaufman et al., 2004). In many locations, their height may not have been full-sized and in many cases were probably "dwarf" or "low" forest, as concluded by other studies (e.g., Anderson and Brubaker, 1994; Bartlein et al., 1995). Despite a consistent presence of *Populus* pollen in existing pollen records in Alaska at that time, it is hard to determine how dense the stands were and whether any of the *Betula* pollen that is abundant in many records at that time existed in tree or shrub form. In our model, the vegetation biomass is parameterized according to present day

ecosystems, so our results may overestimate the magnitude of productivity and C pool sizes, the CH₄ emissions may also be overestimated due to overestimated substrate availability (productivity). However, the simulated seasonality of C dynamics should still be valid due to the primary control of climate on various biogeochemical processes (see Discussion 4.3). Another uncertainty involved in vegetation reconstruction is that our pollen data are not spatially uniform and sparse in some regions, such as much of west central Alaska (Fig. 3); such sampling bias is likely the primary cause for the blocky nature of our spatially interpolated vegetation distribution map, as various interpolation methods produced similar results. In addition, the position of each individual site relative to other sites reflect differences in topography and



Fig. 7. Spatial distribution of simulated net CH₄ emissions during each time slice.

microclimates driven by elevation and orography, which likely also contribute to the blocky nature of the reconstructed maps. Therefore, the ecosystem boundaries exhibited in our vegetation map contain spatial uncertainties.

The biome shift across the four time slices (Fig. 3) generally mirrored the orbitally induced insolation changes and associated climatic field variations. As climate became warmer and precipitation increased between 11 and 9 ka BP, cold deciduous forest expanded and replaced shrub tundra, ultimately leading to treeline advancement beyond its present range (Fig. 3b,c, Bartlein et al., 2011; Bigelow et al., 2003; Edwards et al., 2005; Williams et al., 2001). The treeline advancement likely induced a positive feedback between vegetation and the atmosphere through albedo feedback change, which is caused by the migration of dark boreal forests over snow-covered tundra. This positive feedback is consistent with other Holocene studies (Foley et al., 1994; TEMPO, 1996; Prentice and Jolly, 2000) as well as observations from today (Lloyd, 2005; McGuire et al., 2006, 2007). Pollen records suggest that deciduous trees replaced shrub tundra during the early Holocene in Alaska (e.g., range extension of Populus into northern and western Alaska), and evergreen forests did not expand in the region until the end of the HTM (Bartlein et al., 1995; Edwards et al., 2001, 2005). This inference supports the observed sequential changes in our vegetation reconstruction: the majority of tundra was replaced by deciduous forest during the 11-10 ka BP time slice when climate was warmer (Fig. 3b); as the climate cooled down at the end of HTM, the winter temperature fell within the limits for the growth of boreal evergreen conifers (Prentice et al., 1992), induced the replacement of coastal cold deciduous forest with boreal needleleaf and mixed forest (Fig. 3c). The early establishment of Populus-Betula-Salix woodland tundra during the HTM is supported by consistently present Populus in pollen records at this time, in addition to macrofossil evidence for Populus trees outside of modern treeline (Edwards et al., 2005; Mann et al., 2010). This is remarkable because of the poor preservation of Populus pollen and its low pollen rain, suggesting that Populus trees and perhaps forests occurred throughout much of Alaska during the HTM. Despite warmer-than-present temperatures, a lack of abundant spruce pollen in the records from 11 to 10 ka BP (no single site was biomized as taiga, Fig. 3b) resulted in the biome designation of cool mixed deciduous forest rather than taiga. Therefore, our use of the spruce-dominated model parameterization of boreal evergreen needleleaf and mixed forest may introduce uncertainty in the simulated C dynamics for that period. Specifically, the vegetation productivity may be underestimated (He et al., 2013). However, vegetation and soil C pool sizes may not result in large discrepancy based on previous model parameterization study in Alaska (He et al., 2013). The presence of small quantities of spruce pollen in our compiled dataset as early as 10-9 ka BP suggests Picea was beginning to establish in sparse stands in parts of Alaska, but its range was limited in the early part of the HTM possibly by relatively slow migration rates from refugial areas mostly outside of Alaska (absence of local refugia) following deglaciation (Anderson and Brubaker, 1994). Alternatively, small refugial populations may have survived the Last Glacial Maximum in Beringia (Brubaker et al., 2005), which was also later shown a pollen record from the Seward Peninsula that contained Picea pollen during the Bølling-Allerød (Hunt et al., 2013). These populations did not expand rapidly during the HTM because of a lack of an adequate climate or substrate. This lack of Picea during the first half of the HTM in Alaska contrasts with other regions of the western Arctic where Picea treeline expanded at that time (Ritchie and Hare, 1971; Ritchie et al., 1983; Spear, 1983).

Our biome distribution across Alaska around 6 ka BP was broadly similar to other estimates including the BIOME 6000 studies (Prentice et al., 1996; Edwards et al., 2000; Williams et al., 2001; Bigelow et al., 2003). Pollen data showed an eastward shift of Picea isochrones at 7 ka BP (Anderson and Brubaker, 1994), similar to the migration in tundra-conifer forest boundary between 9 and 7 ka BP in our reconstructed vegetation (Fig. 3c,d). This expansion of Picea likely reflects an increase in soil organic matter and waterlogged lowland soil conditions, which was also promoted by permafrost aggradation in the cooler mid-Holocene, providing substrate for lowland black spruce (P. mariana) expansion. Our spatial interpolation produced the western limit of taiga to the east of its modern limit (Fig. 3d) as suggested by other studies (Edwards et al., 2000; Bigelow et al., 2003). However, these estimates still involve uncertainties due to limitations of the interpolation method and insufficient data. The retreat of treeline on the Seward Peninsula in the cooler mid-Holocene as shown in our reconstruction likely reflects much shorter and cooler growing seasons, influenced by an expansion of sea ice in the Bering Sea (Crockford and Frederick, 2007) and the onset of the cooler Neoglacial climate.

An important feedback mechanism worth noting here is that changes in vegetation cover have been recognized as climate modifiers by altering the energy budget of the earth through changes in albedo and evapo-transpiration (ET) (Fischlin et al., 2007; Bonan, 2008). Broadleaf deciduous forest has higher transpiration rates as well as higher albedo than needleleaf evergreen forest (Chapin et al., 2000; Liu et al., 2005), which may have enable them to invade warming tundra more effectively (Edwards et al., 2005). Increased cover of deciduous broadleaf forest in the Arctic may eventually ramp up the hydrological cycle by increasing atmospheric moisture content and precipitation, contributing to further warmer climate with more precipitation. Swann et al. (2010) investigated the effects of expanding deciduous forest on relative forcing balance from albedo and ET (atmospheric water vapor) using a global climate model (CAM 3.0-CLM 3.5-CASA'). They found that the top-of-atmosphere radiative imbalance from enhanced transpiration can be up to 1.5 times larger than the forcing due to albedo change from the forest. This additional water vapor subsequently melts sea-ice and initiates a positive feedback. The expanded boreal deciduous broadleaf forest shown in our reconstructed vegetation map during the HTM with the corresponding warmer climate also potentially suggests this feedback mechanism existed between vegetation cover and climate. This hydrologic feedback may help explain how enough moisture was available during the HTM to aid rapid peatland expansion in Alaska (Jones and Yu, 2010).

4.3. Climatic and ecological controls on C dynamics

Simulated regional C dynamics did not vary much within each time slice. However, as different vegetation distributions were used for simulations at each time slice, there was a clear step change between time slices, indicating that vegetation composition is likely to be the primary control on modeled regional C dynamics between different time slices (Figs. 4 and 6). In the model, as key parameters controlling C dynamics (e.g., maximum rate of photosynthesis) are ecosystem type specific, vegetation distribution change has dominant effect on controlling regional productivity. Within each time slice, temperature, precipitation and net solar radiation were all identified as statistically significant controlling factors on NPP (p < 0.05 for all coefficients, Table 4). Such high correlation between climate and ecosystem C dynamics is probably the fundamental driver for vegetation composition change overtime (as shown in our reconstructed vegetation distribution), however, as our model does not incorporate dynamic vegetation, the chronological interaction between vegetation and climate is implicitly represented by the step change of C dynamics between

Table 4
Stepwise linear regression between C dynamics and climate variables.

Time slice	Response variable	Stepwise regression model ^a	Coefficient of each term in the model	Adjusted R ²
15–13 ka BP	NPP	$y \sim 1 + temp + prcp + nirr$	-31.6, 0.94, 0.30, 1.6	0.25
	CH ₄	$y \sim 1 + temp + prcp \times nirr$	1.98, 0.03, 0.0008	0.57
11–10 ka BP	NPP	$y \sim 1 + temp + prcp + nirr$	37.2, 2.6, 0.9, 2.0	0.38
	CH ₄	$y \sim 1 + temp \times prcp + nirr$	-1.2, 0.045, -0.002	0.66
10—9 ka BP	NPP	$y \sim 1 + temp + prcp + nirr$	14.4, 5.97, 0.6, 3.78	0.55
	CH ₄	$y \sim 1 + temp \times prcp + temp \times nirr$	-3.6, 0.004, 0.003	0.69
7—5 ka BP	NPP	$y \sim 1 + temp + prcp \times nirr$	23.0, 1.66, -0.04	0.32
	CH ₄	$y \sim 1 + temp + prcp \times nirr$	0.17, 0.024, 0.0006	0.81

^a All terms in the model have *p*-value <0.05. Here temperature (temp, °C) and net incoming solar radiation (nirr, W m⁻²) are monthly average, precipitation (prcp, mm) is monthly total.

time slices. Interactive effects among these climatic variables were identified to be more influential than each factor regulating CH₄ dynamics independently. CH₄ generally exhibited higher adjusted R^2 values than NPP, partly because in the model, CH₄ dynamics are mainly controlled by environmental factors, while NPP (and therefore autotrophic respiration) largely depends on ecosystem types and thus ecosystem-specific vegetation physiology. GPP generally had a much larger adjusted R^2 value (>0.8, results not shown) than NPP, corroborating the dominant plant physiological control on autotrophic respiration and thus weakening the climatic control on NPP variations.

As our model does not represent the dynamics of vegetation community change in response to environmental conditions, the use of static vegetation distribution map misses out the key link between ecosystem C dynamics and the atmosphere, especially on millennial scales. The step changes in our simulated productivity and CH₄ emissions between different time slices appear to demonstrate greater impact of vegetation distribution on simulated C dynamics than climatic fields alone within each time slice. Vegetation compositional changes usually occur during pronounced climate anomalies (e.g., range extension of Populus and Alnus in HTM, Bigelow and Edwards, 2001; Hu et al., 1993). Some remarkable vegetation community shifts can occur over a few hundred years (e.g., the *Betula* rise at 11 ka BP, Ager and Brubaker, 1985; Anderson, 1988; Anderson et al., 1990). Stand-replacing disturbances such as fire also has return interval over decadal to centurial time scales, causing major ecosystem structural shift (Harden et al., 2000; Lynch et al., 2004; Anderson et al., 2006). In light of the important role vegetation distribution plays in most ecosystem models (those without dynamic vegetation), it is crucial to explicitly represent vegetation community dynamics in longterm ecosystem modeling. Furthermore, the use of a modern-day vegetation parameterization ("no-analog" vegetation) and classification scheme to represent non-analog vegetation in the past is also likely to be a major source of uncertainty in paleoecological modeling studies. Future research should focus on better representation of paleo vegetation dynamics in biogeochemical models.

Our simulated monthly NPP showed a prolonged growing season during the HTM. However, due to the monthly time step model structure, simple linear interpolation between months can introduce uncertainty. A more appropriate inference may be growingdegree days (GDD) instead of growing season length, as a bioclimatic index of accumulated warmth during the growing season (Crucifix et al., 2002). GDD during HTM were likely to be the highest among all time slices and thus contributed to higher vegetation productivity, given that the HTM had the highest summer monthly average temperature. Our results showed that the warmer, wetterthan-before period from 10 to 9 ka BP resulted in both the highest ecosystem productivity and soil C with regional estimates of CH₄ emissions during the HTM (11–9 ka BP) ranging between 3.5 and 6.4 Tg CH₄ yr⁻¹; these results agree favorably with the trend in C accumulation rates estimated by Jones and Yu (2010, Fig. 2B) from peatland sites in Alaska and their conservative estimate of regional annual CH₄ emissions of 3-5 Tg yr⁻¹ from peatlands. Enhanced climate seasonality characterized by warmer summer, enhanced summer precipitation and possibly earlier snow melt during the HTM contributed to increased NPP in our modeling results, as summer temperature and growing season length (or GDD) are the primary controls of NPP, whereas respiration is mostly controlled by soil temperature and the degree of soil saturation, with the more efficient aerobic respiration occurring with decreased soil moisture and slower anaerobic respiration occurring with greater saturation (Hobbie et al., 2000). Such climatic effect on ecosystem productivity are consistent with modern studies (Tucker et al., 2001; Kimball et al., 2004; Linderholm, 2006). The period from 15 to 13 ka BP experienced lower winter snowfall than the HTM. based on our simulation result (Fig. 2c.d). The combination of decreased snowfall and low winter temperatures can result in deeper frost depth due to the decreased insulative effects of the snowpack, and thus decreasing decomposition and shortening the period for active photosynthetic C uptake, yielding overall low productivity (McGuire et al., 2000; Stieglitz et al., 2003).

Our estimate of net CH₄ emissions (~5 Tg CH₄ yr⁻¹) and NPP $(\sim 470 \text{ Tg C yr}^{-1})$ during the HTM was significantly higher than the modern estimate of Alaska by Zhuang et al. (2007), which gives a current net emissions of CH₄ from Alaskan soils of \sim 3 Tg CH₄ yr⁻¹ and ~194 Tg C yr⁻¹ of NPP (assuming average NPP of 130 g C m⁻² yr⁻¹ as shown in the study) from 1980 to 1996. Our modeled regional CH₄ emissions during the mid-Holocene were close to Zhuang et al.'s (2007) estimates as both climate and vegetation distribution in the mid-Holocene likely resembled that of today. Since we used the same wetland extent dataset in this study as was used in Zhuang et al. (2007), the combined effect of vegetation distribution (large extent of tundra and shrub land), enhanced summer solar insolation, precipitation, and temperature seasonality are likely to be the primary drivers causing the much higher regional CH₄ emissions during the HTM compared to modern emissions. Because our biomes are based on pollen data. and each site is interpolated over hundreds of miles and can only be prescribed one biome, the wetland extent may have been underestimated, as some grid cells would likely have been a combination of boreal evergreen forest and peatland, for example, during certain time slices. If the peat core data had more explicitly been prescribed into grids or subgrids in addition to the wetland extent data, potentially expanding the spatial area of peatlands in Alaska at that time, the HTM CH₄ emissions would likely be much higher. Also note that our assumption of the same wetland extent during HTM likely introduces overestimates of CH₄ emissions at the onset of HTM due to the low sea level at that time (~ 50 m below present, Bard et al., 1990; Alley et al., 2005; Keigwin et al., 2006).

One of the potential caveats in the modeled C dynamics is that the permafrost effect on soil C decomposition is not explicitly represented in the model. TEM5.0 simulates the down-regulating effect of permafrost on GPP and the presence of permafrost on water table depth and soil temperature profile (Zhuang et al., 2001, 2003), but it does not include the influence of frozen/unfrozen substrates and the altered microbial activity on soil C decomposition (Waldrop and Harden, 2008; Hicks Pries et al., 2012; Olefeldt et al., 2012; Knoblauch et al., 2013). Permafrost is typically associated with black spruce (Waldrop and Harden, 2008), and the expansion of *Picea* may be associated with climatic cooling that resulted in permafrost aggradation and cooling of the soil environment (and drying in terms of evapotranspiration). Furthermore, permafrost degradation was high during the HTM as evidenced by high rates of thermokarst lake initiation (Walter et al., 2007). Current field observations documented increased aerobic (CO₂) and anaerobic C (CH₄) release from biolabile C substrate that becomes available upon permafrost thaw (Hicks Pries et al., 2012; Vonk et al., 2013; Schuur et al., 2009). Thawing may also increase nutrient availability in the soil, which potentially enhances autotrophic and heterotrophic respiration (Keuper et al., 2012). We therefore suspect that our simulated CH₄ may have been underestimated by not considering permafrost dynamics.

5. Conclusion

Long-term climate changes over the course of the deglacial to mid-Holocene (15-5 ka BP) induced significant vegetation composition changes in Alaska. Enhanced insolation and subsequent changes in temperature and precipitation during 11-9 ka BP are the fundamental drivers for various vegetation community changes including range expansion, treeline displacement, and species migration. Our simulations showed peak NPP, CH₄ release and soil C accumulation during the HTM, likely attributable to (stepwise regression $R^2 \sim 0.4$ for NPP and $R^2 \sim 0.7$ for CH₄) greater solar insolation, warmer climate, and enhanced precipitation during the HTM. The regional estimate of CH₄ emissions during the HTM ranged from 3.5 to 6.4 Tg CH_4 yr⁻¹ and highest annual NPP of 470 Tg C yr⁻¹, significantly higher than modern estimates of CH₄ emissions and NPP in Alaska. The step changes in our simulated productivity and CH₄ emissions between different time slices demonstrate that the differences in the static vegetation distribution map used in simulations of the four time slices have greater influence on C dynamics than climatic fields within each time slice, highlighting the importance of incorporating vegetation community dynamics and their responses to climatic conditions in longterm biogeochemical modeling.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2013.12.019.

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