Global Change Biology

Global Change Biology (2011) **17**, 2567–2583, doi: 10.1111/j.1365-2486.2011.02446.x

Mechanisms influencing changes in lake area in Alaskan boreal forest

JENNIFER ROACH*, BRAD GRIFFITH†, DAVE VERBYLA‡ and JEREMY JONES*

*Department of Biology and Wildlife, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA, †US Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska Fairbanks, Fairbanks, AK 99775, USA, ‡Department of Forest Sciences, University of Alaska Fairbanks, Fairbanks, AK 99775, USA

Abstract

During the past ~50 years, the number and area of lakes have declined in several regions in boreal forests. However, there has been substantial finer-scale heterogeneity; some lakes decreased in area, some showed no trend, and others increased. The objective of this study was to identify the primary mechanisms underlying heterogeneous trends in closed-basin lake area. Eight lake characteristics (δ^{18}O, electrical conductivity, surface : volume index, bank slope, floating mat width, peat depth, thaw depth at shoreline, and thaw depth at the forest boundary) were compared for 15 lake pairs in Alaskan boreal forest where one lake had decreased in area since ~1950, and the other had not. Mean differences in characteristics between paired lakes were used to identify the most likely of nine mechanistic scenarios that combined three potential mechanisms for decreasing lake area (talik drainage, surface water evaporation, and terrestrialization) with three potential mechanisms for nondecreasing lake area (subpermafrost groundwater recharge through an open talik, stable permafrost, and thermokarst). *A priori* expectations of the direction of mean differences between decreasing and nondecreasing paired lakes were generated for each scenario. Decreasing lakes had significantly greater electrical conductivity, greater surface : volume indices, shallower bank slopes, wider floating mats, greater peat depths, and shallower thaw depths at the forest boundary. These results indicated that the most likely scenario was terrestrialization as the mechanism for lake area reduction combined with thermokarst as the mechanism for nondecreasing lake area. Terrestrialization and thermokarst may have been enhanced by recent warming which has both accelerated permafrost thawing and lengthened the growing season, thereby increasing plant growth, floating mat encroachment, transpiration rates, and the accumulation of organic matter in lake basins. The transition to peatlands associated with terrestrialization may provide a transient increase in carbon storage enhancing the role of northern ecosystems as major stores of global carbon.

Keywords: Alaska, boreal forest, carbon, climate change, drying, lakes, peat, permafrost, terrestrialization, wetlands

Received 5 October 2010; revised version received 17 January 2011 and accepted 22 March 2011

Introduction

Climate warming is pronounced in the Arctic and sub-Arctic (Serreze *et al*., 2000; Hassol, 2004; Hinzman *et al*., 2005; Kaufman *et al*., 2009) and has been associated with a net loss in the number (5–54%) and area (4–31%) of closed-basin lakes during the past ~50 years in the discontinuous permafrost regions of the Alaskan boreal forest (Riordan *et al*., 2006), in the permafrost-free regions of south-central Alaska (Klein *et al*., 2005), and both closed- and open-basin lakes in the discontinuous permafrost regions of Siberia (Smith *et al*., 2005). Within Alaskan boreal forest, lakes and wetlands are abundant on National Wildlife Refuges and serve as breeding grounds for millions of waterfowl and shorebirds that migrate annually from more southerly parts of North America, South America, Asia, and Australia. An understanding of the mechanisms responsible for losses in lake area is essential for robust projections of future landscape conditions and their subsequent implications for wildlife.

Correspondence: Jennifer Roach, tel. +1 907 474 5404, fax +1 907 474 7872, e-mail: jroach11@alaska.edu

Heterogeneous changes in lake area

An important clue to the mechanisms underlying losses in lake area is the presence of fine-scale (Wiens, 1989) (<2 km) spatial heterogeneity; some lakes remain stable or increase in area while neighboring lakes decrease substantially in size (Smith *et al*., 2005; Riordan *et al*., 2006) (Fig. 1). This fine-scale heterogeneity suggests that net loss in lake area at broader scales (e.g., study area) is not simply the result of a homogeneous phenomenon but rather represents disequilibrium between decreasing and nondecreasing lakes at fine scales. Thus, the mechanisms for overall loss in lake area at both coarse and fine scales may be associated with spatially heterogeneous characteristics that can vary between neighboring lakes. An improved understanding of what causes different trajectories of neighboring lakes could eluci-

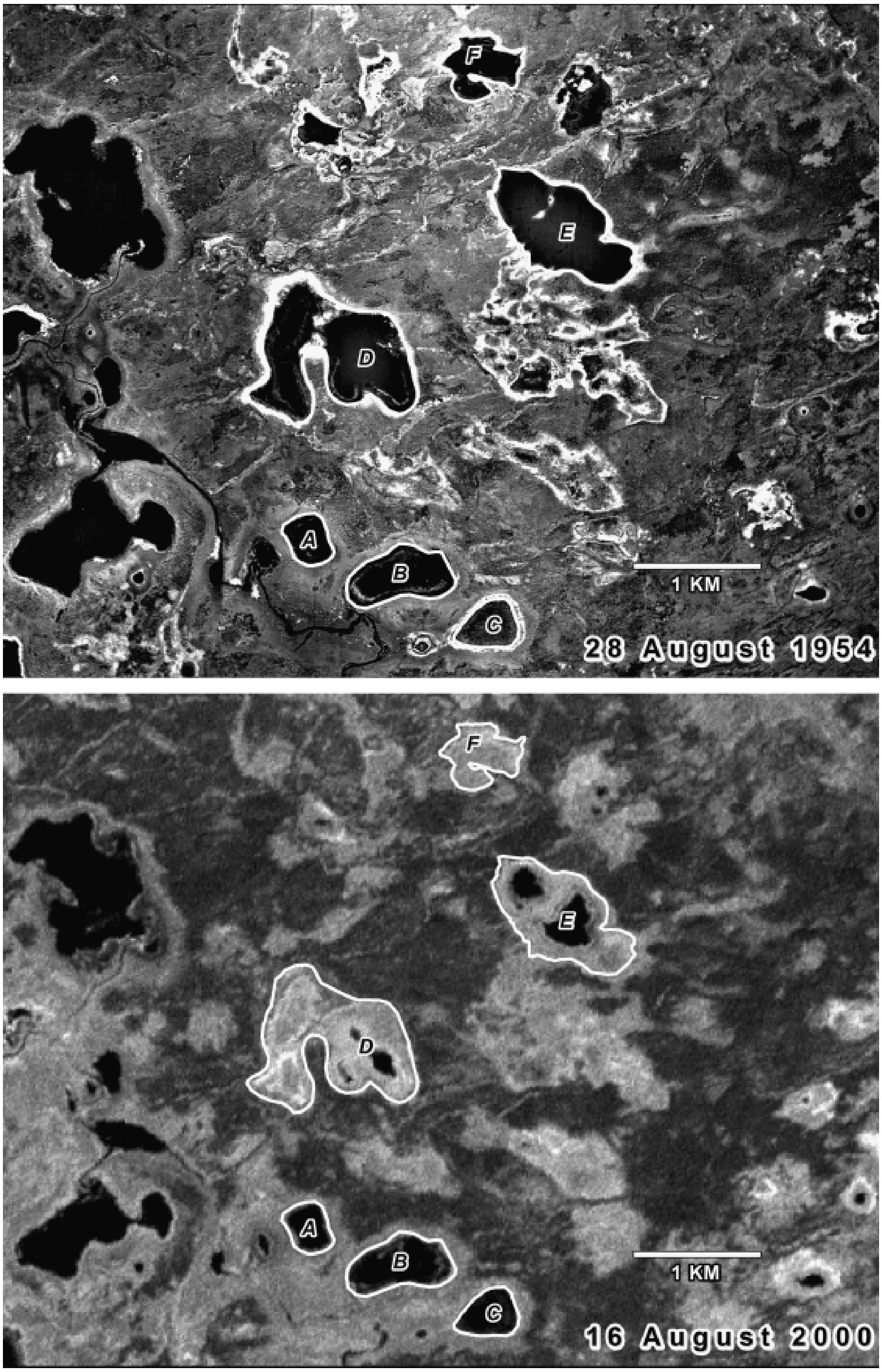

Fig. 1 Heterogeneous pattern of shrinking lakes in the Yukon Flats East study region. For example, lakes A, B, and C exhibit little change in surface area, while lakes D, E, and F shrank substantially since the 1950s (reproduced from Riordan *et al*., 2006).

date the mechanisms underlying broad-scale loss in lake area.

Potential sources of heterogeneity

The objective of this study was to identify the primary mechanisms underlying the fine-scale heterogeneity in closed-basin lake area changes in National Wildlife Refuges in Alaskan boreal forest. The heterogeneous distribution of lakes with stable, increasing, and decreasing area within boreal forest may be the result of heterogeneous (1) permafrost stability, (2) hydraulic gradients, and/or (3) lake and catchment topography.

Permafrost [soil, rock, or water that remains at or below 0 °C for 2 or more years (van Everdingen, 2005)] is particularly sensitive to the effects of climate warming (Vitt *et al*., 1994; Osterkamp *et al*., 2000; Jorgenson *et al*., 2001; Jorgenson & Osterkamp, 2005; Osterkamp, 2005). However, the magnitude and rate of its response to increased temperatures (i.e., relative stability) can vary at a fine scale as a result of heterogeneous snow cover, soil moisture, soil organic content, topography, and human or wildlife disturbance (Nelson *et al*., 1999; Anisimov *et al*., 2002). Lakes with more unstable permafrost may be more susceptible to lateral permafrost degradation (i.e., thermokarst formation) which can lead to an increase in lake area (Jorgenson & Osterkamp, 2005). They may also be more susceptible to vertical permafrost degradation underneath the lake (i.e., talik growth) which can proceed until the lake is no longer isolated from groundwater systems via a permafrost aquiclude (Swanson, 1996; Vörösmarty *et al*., 2001). Once a permafrost aquiclude is removed, lake area may either increase or decrease depending on the relative pressure gradient (i.e., hydraulic gradient) that is present between surface water and formerly subpermafrost groundwater systems (Britton, 1957; Kane & Slaughter, 1973; Billings & Peterson, 1980; Woo, 1986; Jorgenson *et al*., 2001; Yoshikawa & Hinzman, 2003). The complex network of aquifers and the heterogeneous distribution of permafrost in the boreal forest may result in opposing hydraulic gradients at neighboring lakes.

Alternatively, neighboring lakes may have different lake and catchment topography which may differentially affect their susceptibility to lake area change. Lakes with larger catchments may receive greater water inputs from precipitation or snowmelt runoff while lakes with a greater surface area relative to water volume may be more susceptible to climate-induced losses in lake area resulting from increased evaporation rates and/or increased rates of terrestrial infilling (Campbell *et al*., 1997; Jorgenson & Shur, 2007). One source of fine-scale heterogeneity in lake bathymetry in the boreal forest is the presence of heterogeneous permafrost ice content which effects the size of depressions and thermokarst lakes resulting from permafrost degradation (Hopkins, 1949; Burn & Smith, 1990; Burn, 1992; Hinzman *et al*., 1997; Jorgenson & Osterkamp, 2005; Jorgenson & Shur, 2007).

Study design

The fine-scale heterogeneity in lake area change enabled the spatial and temporal pairing of decreasing and nondecreasing lakes to control for broad-scale differences in temperature, precipitation, and substrate heterogeneity in order to isolate the primary mechanisms responsible for lake area change. Several heterogeneity-related mechanisms could explain the differential responses of a population of paired lakes.

The three mechanisms considered to explain lake area reduction were: (1) taliks beneath lakes expanded into subpermafrost groundwater systems causing lakes to drain in the presence of a negative hydraulic gradient (Britton, 1957; Billings & Peterson, 1980; Woo, 1986; Yoshikawa & Hinzman, 2003) (Fig. 2a); (2) surface water evaporation exceeded water inputs leading to receding shorelines, drier conditions, and increased nutrient concentrations and lake productivity (Schindler *et al*., 1990; Klein *et al*., 2005; Smol & Douglas, 2007) (Fig. 2b); or (3) floating mat vegetation encroached towards the center of the lake obscuring surface water in remotely sensed imagery and causing increased rates of transpiration and basin infilling with organic matter (i.e., terrrestrialization) (Gates, 1942; Dansereau & Segadas-Vianna, 1951; Drury, 1956; Tallis, 1983; Kratz & DeWitt, 1986; Hu & Davis, 1995; Campbell *et al*., 1997) (Fig. 2c).

The three mechanisms considered to explain lake area stability or increase were: (1) permafrost remained stable and acted as an aquiclude (Swanson, 1996; Vörösmarty *et al*., 2001) minimizing surface and subpermafrost groundwater interactions (Fig. 2d); (2) taliks underneath lakes expanded to subpermafrost groundwater systems and the presence of a positive hydraulic gradient led to artesian conditions recharging the lake (Kane & Slaughter, 1973; Jorgenson *et al*., 2001) (Fig. 2e); or (3) ice-rich permafrost degraded laterally (i.e., thermokarst) facilitating lake expansion (Jorgenson & Osterkamp, 2005) (Fig. 2f).

For eight variables (Table 1), *a priori* expectations for the direction of mean differences between paired decreasing and nondecreasing lakes for all nine possible combinations (i.e., scenarios) of the proposed decreasing vs. nondecreasing mechanisms were generated (Fig. 2). Observed results from statistical tests of the null hypotheses of no difference between paired decreasing and nondecreasing lakes were then compared with these predictions to identify which mechanisms were most likely to be primarily responsible for the fine-scale heterogeneity in lake area change.

Materials and methods

Study design

Differences in characteristics between paired closed-basin lakes, where one lake had lost area since the 1950s and the other lake had not, were evaluated. Closed-basin lakes were defined as those with no detectable connection to any river or stream system. Assessment was restricted to closed-basin lakes because the potential effects of climatic variables such as evaporation, evapotranspiration, and permafrost stability on water levels are often masked by stream flow into and out of open-basin lakes (Anderson *et al*., 2007). Mechanisms of long-term area change in open-basin lakes would likely

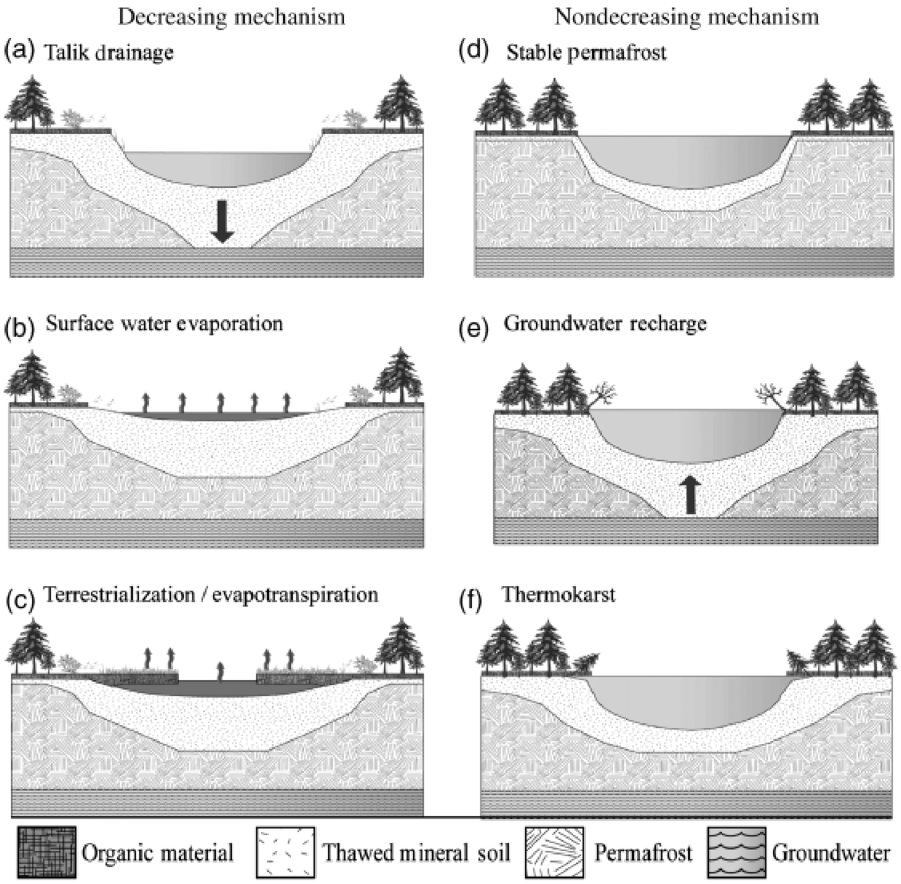

Fig. 2 Diagrammatic representation of the three decreasing [(a) talik drainage, (b) surface water evaporation, (c) terrestrialization/evapotranspiration] and three nondecreasing [(d) stable permafrost, (e) groundwater recharge, (f) thermokarst] mechanisms that were evaluated to explain the fine-scale heterogeneity in decreasing and nondecreasing lakes.

include changes in the pattern and magnitude of river and stream flow which were not addressed in this study.

Paired lakes were located 0.2–1.8 km apart and all data were collected for both pair members on the same day or on 2 consecutive days. This paired design enabled the direct detection of fine-scale mechanisms of lake area change that may have been masked or biased by study area or within-season differences. The paired design controlled for extraneous sources of broad-scale spatial (e.g., among study area variance in substrate characteristics) and temporal (e.g., within summer variability in precipitation and thawing) heterogeneity. For example, the design enabled the direct comparison of oxygen isotopic composition between paired lakes by controlling for broad-scale variability in precipitation and enabled the direct comparisons of thaw depth between paired lakes by controlling for within-season thaw progression.

Study areas

Lake pairs were located in four study areas that ranged in size from 630 to 2020 km^2 (Fig. 3) in Alaskan boreal forest. These areas were selected because previous work had estimated rates of change for closed-basin lakes in these areas since the 1950s (−4% to −31%) and provided an initial dataset for selection of potential lake pairs (Riordan *et al.*, 2006).

The boreal forest is characterized by a dynamic mosaic of spruce forests, shrub areas dominated by willows, bogs, and fens dominated by mosses, sedges, and lakes. Principal lake types in Alaska include thermokarst lakes, fluvial lakes such as oxbows, glacial lakes such as kettles and tarns, and moraine-dammed lakes (Arp & Jones, 2009). Lakes included in this study are likely of the former two types because the study areas were located in lowland areas that were unglaciated in the Pleistocene (Manley & Kaufman, 2002). The areas were underlain by either continuous or discontinuous permafrost (Brown *et al.*, 2001; Jorgenson *et al.*, 2008). The permafrost layer in these areas affects surface and subsurface hydrology by acting as an aquiclude which leads to an abundance of relatively shallow lakes and wetlands that would otherwise be unusual for the dry climate found in interior Alaska.

Lake area change analysis and lake pair selection

A population of paired decreasing and nondecreasing lakes that were float plane accessible and <1.8 km apart was identified using data presented by Riordan *et al.* (2006). Float plane accessibility and distance between lakes was assessed using

Table 1 Scenario expectations for eight variables used to discriminate between mechanistic scenarios

	Paired lake scenario		Expectation at decreasing compared with nondecreasing lake							
	Decreasing mechanism	Nondecreasing mechanism	$\delta^{18}O$*	Cond	S : V index	Bank slope (°)	Floating mat width (m)	Peat depth at shoreline (cm)	Thaw depth – shoreline (cm)	Thaw depth – forest boundary (cm)
A	Talik drainage	Groundwater Recharge	+	−	0	0	0	0	0	0
B	Talik drainage	Stable Permafrost			−	+	0	0	+	
C	Talik drainage	Thermokarst			−	+	0	0		
D	Surface water evaporation	Groundwater Recharge	+		+	−	0	0	−	
E	Surface water evaporation	Stable Permafrost	+	+	+	−	0	0	0	0
F	Surface water evaporation	Thermokarst	+	+	+	−	0	0		−
G	Terrestrialization/evapotranspiration	Groundwater Recharge	+		+	−	+	+	−	
H	Terrestrialization/evapotranspiration	Stable Permafrost	0	+	+	−	+	+	0	0
I	Terrestrialization/evapotranspiration	Thermokarst	0	+	+	−	+	+		−

*$[(R_{sample}/R_{standard})-1] \times 1000‰$, where R is the ratio of oxygen isotopes ($^{18}O/^{16}O$) in sample and standard ocean water, respectively.
A '+' indicates that the variable was expected to be greater at the decreasing lake, a '−' indicates that the variable was expected to be lower at the decreasing lake, and a '0' indicates that no difference was expected between paired lakes for the corresponding hypothesis. Blank boxes indicate that the expected direction of the difference was unclear. Cond, electrical conductivity ($\mu S\,cm^{-1}$); S : V index, surface to volume index.

aerial reconnaissance and Geographic Information System (GIS) analysis. Lake pairs were then ranked based on the difference in magnitude of change between decreasing and nondecreasing lakes and sampled in this order until either six paired lakes per study area were sampled or all remaining lake pairs had been discarded due to changing float plane accessibility during the season. In order to improve our ability to account for inter- and intraannual variability in trend detection, initial estimates of lake area change were verified with a regression analysis that included at least six image dates for each lake from the 1950s to 2002, with at least two images from early season (May–June) and two images from late season (July–August). Lake boundaries were manually digitized from historical black and white aerial photography from the 1950s, color infrared aerial photography from 1978 to 1984, and satellite imagery from the Landsat Enhanced Thematic Mapper Plus sensor (ETM +) and the Landsat Thematic Mapper sensor (TM) from 1991 to 2002. All images were georectified to the UTM map projection, NAD27, using a linear affine transformation model and nearest neighbor resampling. Each model was based on well-defined image-based control points using the statewide coverage of 1 : 63 360 topographic maps and had a root mean squared error (RMSE) of <1 pixel, corresponding to 2–9 m for the aerial photographs and 15–30 m for the Landsat TM/ETM + images. Each image was rectified using at least 25 control points and a density of at least 0.5 points per km^2. A linear regression (SAS Institute, Inc., 2003) was performed for each lake to identify whether there was a significant trend in lake area (m^2) from 1950 to 2002. Date of image acquisition expressed as days beginning on January 1, 1900 was used as the independent variable in order to simultaneously account for day, month, and year in the regression model. Lakes with a significant ($P<0.05$) negative effect of day on lake area were classified as decreasing lakes. Lakes with a significant ($P<0.05$) positive effect or a nonsignificant ($P>0.05$) effect of day on lake area were classified as nondecreasing lakes (Table 2). Lakes with positive or no effect of day on lake area were combined into one category because the primary interest was in identifying mechanisms for area reduction. Based on this analysis, 15 lake pairs that consisted of one decreasing lake and one nondecreasing lake were retained (Table 2). These 15 pairs included five pairs in the Yukon Flats West study area, three pairs in the Yukon Flats East study area, four pairs in the Kaiyuh Flats study area, and three pairs in the Tetlin study area (Fig. 3, Table 2).

Scenario expectations

The nine possible combinations of the three hypothetical mechanisms for decreasing lakes and the three hypothetical mechanisms for nondecreasing lakes were referred to as Scenarios A–I (Table 1). Assuming that the nondecreasing lakes could be used as control sites for decreasing lakes, a '+' indicates that the variable was expected to be greater, a '−' indicates that the variable was expected to be lower, and a '0' indicates that the variable was not expected to be different at decreasing lakes compared with paired nondecreasing lakes. Expected differences were classified as unknown when the

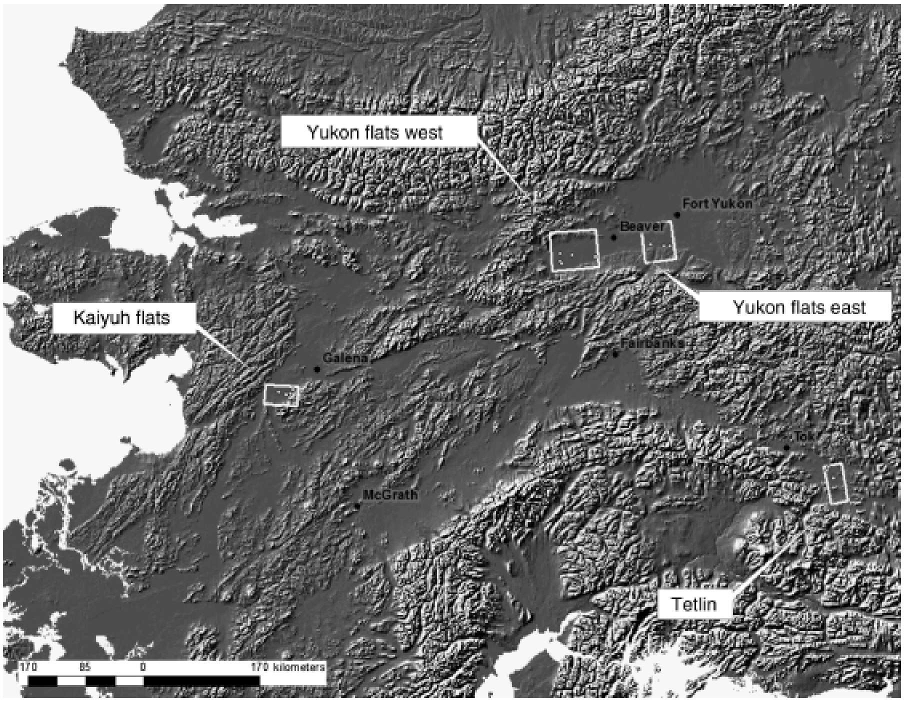

Fig. 3 Map of Alaska showing boundaries of study areas and the locations of the 15 lake pairs included in this study.

direction of the difference was unclear. Variables and the direction of the difference expected between decreasing and nondecreasing lakes for each scenario are as follows.

Variable 1: ^{18}O Enrichment. Oxygen isotope ratios can be used to clarify the relative role of evaporation compared with water inputs in a lake's hydrological budget (Anderson *et al*., 2007; Clegg & Hu, 2010; Turner *et al*., 2010). For a closed-basin lake, water inputs can be from groundwater, surface runoff derived from snowmelt or precipitation, or precipitation falling directly on a lake surface. Evaporation leads to enrichment of lake ^{18}O, because the lighter isotope (^{16}O) has weaker bonds causing it to fractionate during evaporation. In contrast, precipitation and especially groundwater and snowmelt tend to be depleted in ^{18}O (Craig, 1961; Payne, 1970; Gat, 1996; Turner *et al*., 2010). Therefore, the degree of isotopic enrichment of a lake may indicate the relative difference between evaporation and water inputs in a lake's water balance. If a reduction in lake area was due to surface water evaporation that exceeded water inputs, the lake would be expected to be relatively enriched in ^{18}O compared with a lake with stable or increasing water levels.

In contrast with surface water evaporation, isotopes do not fractionate when roots take up water (Gonfiantini *et al*., 1965; Dawson & Ehleringer, 1991; Gat, 1996; Gibson & Edwards, 2002). Instead, evaporative enrichment during transpiration occurs within the leaf water (Gonfiantini *et al*., 1965; Cooper *et al*., 1991; Gat, 1996) and is reflected in the isotopic composition of plant cellulose (Epstein *et al*., 1977; DeNiro & Epstein, 1979). Thus, a reduction in lake water balance due to transpiration would not affect lake water oxygen isotopic composition.

Subpermafrost groundwater is relatively depleted in the heavier isotopes due to isolation from evaporative effects (Gat, 1996). Thus groundwater recharge to a lake through an open talik in the presence of a positive hydraulic gradient (i.e., artesian conditions) would result in a large influx of water that was relatively depleted in ^{18}O compared with a lake not receiving a comparable influx of subpermafrost groundwater. Thus, greater relative enrichment of oxygen isotopes at decreasing lakes compared with paired nondecreasing lakes (+) was expected if either surface water evaporation was the primary decreasing mechanism (i.e., isotopic enrichment at the decreasing lake) or if groundwater recharge was the nondecreasing mechanism (i.e., depletion of heavier isotopes at the nondecreasing lake) (Table 1: Scenarios A, D, E, F, and G). No net difference in oxygen isotope enrichment was expected if terrestrialization/evapotranspiration was the decreasing mechanism and if stable permafrost or thermokarst was the nondecreasing mechanism (Table 1: Scenarios H and I) because neither of these mechanisms are likely to have a substantial effect on lake oxygen isotopic composition. The expectation for talik drainage as a decreasing mechanism in combination with stable permafrost or thermokarst as a nondecreasing mechanism was classified as unknown (Table 1: Scenarios B and C) because talik drainage could have either no effect or a slight depleting effect on ^{18}O depending on whether drainage was actively occurring or if an equilibrium had been reached involving steady state exchange with subpermafrost groundwater. For Scenario A, it was assumed that even if talik drainage had reached equilibrium, groundwater recharge to nondecreasing lakes through an open talik would still lead to relatively more depleted ^{18}O at nondecreasing lakes compared with paired decreasing lakes.

Table 2 Results from linear regression models of lake area (m^2) against date of image acquisition expressed as day beginning on January 1, 1900 for each sampled decreasing (D) and nondecreasing (N) lake

Refuge/Lake	Slope (m^2/day)	R^2	Coefficient of variation
Yukon Flats West			
Lake 1D	−19.45	0.864*	0.541
Lake 1N	–	0.341	0.043
Lake 2D	−4.04	0.697*	0.278
Lake 2N	–	0.328	0.026
Lake 3D	−11.16	0.865*	0.338
Lake 3N	–	0.0001	0.032
Lake 4D	−2.09	0.788*	0.272
Lake 4N	–	0.324	0.123
Lake 5D	−7.27	0.874*	0.542
Lake 5N	–	0.006	0.138
Yukon Flats East			
Lake 6D	−0.71	0.910*	0.950
Lake 6N	–	0.533	0.040
Lake 7D	−0.25	0.977*	0.622
Lake 7N	0.37	0.816*	0.058
Lake 8D	−1.13	0.740*	0.824
Lake 8N	–	0.058	0.592
Kaiyuh			
Lake 9D	−0.37	0.885*	0.586
Lake 9N	–	0.042	0.067
Lake 10D	−0.37	0.888*	0.455
Lake 10N	–	0.368	0.166
Lake 11D	−0.17	0.908*	0.244
Lake 11N	–	0.537	0.176
Lake 12D	−0.10	0.993*	0.314
Lake 12N	–	0.286	0.069
Tetlin			
Lake 13D	−0.08	0.909*	0.187
Lake 13N	0.14	0.925*	0.160
Lake 14D	−0.14	0.782*	0.388
Lake 14N	–	0.278	0.197
Lake 15D	−0.33	0.771*	0.386
Lake 15N	–	0.175	0.048

*Significant at $\alpha = 0.05$.
Data for regression models was derived from imagery from at least six time periods from the 1950s to 2002. Imagery included black and white aerial photography from the 1950s, color infrared aerial photography from 1977 to 1981, and Landsat TM and ETM + images from 1991 to 2002. Lakes with significant ($P < 0.05$) negative effects of day on lake area were classified as decreasing. Lakes with significant ($P < 0.05$) positive or nonsignificant ($P > 0.05$) effects of day on lake area were classified as nondecreasing. Coefficients of variation are shown to demonstrate the degree of interannual variability in lake area for decreasing and nondecreasing lakes.

Variable 2: Electrical conductivity. Similar to oxygen isotopic composition, electrical conductivity can be used to identify the relative inputs and outputs affecting lake water balance. Lakes receiving formerly subpermafrost groundwater tend to have a higher electrical conductivity than precipitation fed lakes because subpermafrost groundwater is typically enriched in cations due to a longer residence time in contact with earth materials (Rouse *et al*., 1997; Yoshikawa & Hinzman, 2003). In contrast with oxygen isotopes which give different signals for evaporation and transpiration, electrical conductivity may be increased by both evaporation and transpiration, thus reflecting the net evapotranspiration rate of a lake. Evaporation of water from the surface of a lake directly increases electrical conductivity by concentrating dissolved ions in the lake water (Smol & Douglas, 2007). Aquatic macrophytes can indirectly increase electrical conductivity over the course of several years by removing water from a lake through transpiration and leaching nutrients into the water column upon death and decomposition of plant tissues in fall and winter (Boyd & Hess, 1970; Gaudet, 1977; Carpenter, 1980; Johnston, 1991; Kroger *et al*., 2007). For example, *Typha latifolia* and *Phragmites australis*, common species found at study lakes, lost 90–93% of their potassium, sodium, nitrogen, and phosphorus to the water column after 20 days of submerged tissue senescence (Boyd & Hess, 1970; Nichols & Keeney, 1972; Gaudet, 1977).

Because surface water evaporation, terrestrialization/evapotranspiration, and groundwater recharge all lead to greater electrical conductivity, scenarios that combined the former two decreasing mechanisms with the latter nondecreasing mechanism were classified as unknown since it was not possible to assess the relative effects of these mechanisms on electrical conductivity (Table 1: Scenarios D and G). For scenarios that compared surface water evaporation and terrestrialization/evapotranspiration as decreasing mechanisms with stable permafrost and thermokarst as nondecreasing mechanisms (Table 1: Scenarios E, F, H, and I), a greater electrical conductivity was expected at decreasing lakes compared with paired nondecreasing lakes (+). Scenarios that compared talik drainage as a decreasing mechanism with stable permafrost and thermokarst as nondecreasing mechanisms (Table 1: Scenarios B and C) were classified as unknown because talik drainage may have either no effect or cause a slight increase in conductivity depending on whether the lake has reached equilibrium with subpermafrost groundwater. However, for Scenario A (Table 1), it was expected that even if talik drainage had reached equilibrium with subpermafrost groundwater at the decreasing lake, groundwater recharge due to artesian conditions at the nondecreasing lake would have had a positive overall effect on electrical conductivity resulting in a relatively lower conductivity at decreasing lakes compared with paired nondecreasing lakes (−).

Variable 3: Surface : volume index. Surface to volume index was used to estimate current lake bathymetry. Shallow lakes with a greater surface to volume index may have greater direct evaporation rates and/or greater rates of floating mat encroachment, basin infilling, and therefore greater evapotranspiration rates. Thus, a greater surface to volume index (+) was expected at decreasing lakes compared with paired nondecreasing lakes if surface water evaporation or terrestrialization/evapotranspiration was the primary decreasing mechanism (Table 1: Scenarios D–I). In contrast, open taliks are more likely to form at deeper lakes with smaller surface to volume indices due to the increased thermal conductivity of the lake water as the volume of water increases (Brewer, 1958; Mackay, 1992; Burn, 2002; Yoshikawa & Hinzman, 2003). Thus, a smaller surface to volume index (−) was expected at decreasing lakes compared with paired nondecreasing lakes if talik drainage was the primary decreasing mechanism and groundwater recharge via an open talik was not the primary nondecreasing mechanism (Table 1: Scenarios B and C). For Scenario A (Table 1), no difference was expected in surface to volume ratio (0) because both the talik drainage and groundwater recharge hypotheses involve the formation of open taliks underneath lakes that are sufficiently deep.

Variable 4: Bank slope. The slope of the banks between shoreline (terrestrial edge of the floating mat if present) and the forest boundary was used to estimate former lake bathymetry. Using the same logic as stated above for surface : volume index, shallower bank slopes (−) were expected at decreasing lakes compared with paired nondecreasing lakes if surface water evaporation or terrestrialization/evapotranspiration was the primary decreasing mechanism (Table 1: Scenarios D–I). Similarly, steeper bank slopes (+) were expected at decreasing lakes compared with paired nondecreasing lakes if talik drainage was the primary decreasing mechanism and stable permafrost or thermokarst was the nondecreasing mechanism (Table 1: Scenarios B and C) and no difference (0) was expected if talik drainage was the decreasing mechanism and groundwater recharge via an open talik was the nondecreasing mechanism (Table 1: Scenario A).

Variable 5: Floating mat width. The width of floating mat vegetation on a lake surface may be indicative of the rate of floating mat encroachment and terrestrialization (Dansereau & Segadas-Vianna, 1951; Drury, 1956; Kratz & DeWitt, 1986). Thus, decreasing lakes were expected to have wider floating mats compared with paired nondecreasing lakes (+) if terrestrialization/evapotranspiration (i.e., floating mat encroachment) was the primary decreasing mechanism (Table 1: Scenarios G–I). No difference (0) in floating mat width was expected for Scenarios A–F (Table 1) because floating mat encroachment is only relevant to the terrestrialization/evapotranspiration mechanism.

Variable 6: Peat depth. The depth of peat at the shoreline of decreasing lakes may be indicative of the rate of organic matter accumulation resulting from the establishment and encroachment of floating mats and the subsequent basin infilling associated with terrestrialization (Dansereau & Segadas-Vianna, 1951; Drury, 1956; Kratz & DeWitt, 1986). Thus, decreasing lakes were expected to have greater shoreline peat depth compared with paired nondecreasing lakes (+) if terrestrialization/evapotranspiration (i.e., floating mat encroachment) was the primary decreasing mechanism (Table 1: Scenarios G–I). No difference (0) in peat depth was expected for Scenarios A–F (Table 1) because, in contrast with the peat-forming process of terrestrialization, evaporation, and talik drainage are not expected to have as large of an effect on the accumulation of organic matter at the shoreline.

Variable 7: Thaw depth at shoreline. Thaw depth (depth to frozen ground, cm) is influenced by many factors including surface temperature, thermal properties of the surface cover and substrate, soil moisture, and the duration and thickness of snow cover (Brown *et al*., 2000). These factors also influence the stability of permafrost and, therefore, a relatively shallow thaw depth is often used as an easily obtainable indicator of relative permafrost stability (Brown *et al*., 2000). Thus, thaw depth at the shoreline of a lake may be indicative of relative permafrost stability underneath the lake (i.e., vertical permafrost degradation and talik enlargement). In contrast, greater thaw depth at the forest boundary may be indicative of lateral permafrost degradation that is often associated with thermokarst formation and lake growth. Because the effects of vertical and lateral permafrost degradation may be difficult to isolate from one another, expectations for thaw depth at shoreline were classified as unknown when there was a difference expected for thaw depth at the forest boundary (Table 1: Scenarios C, F, and I). For Scenario B (Table 1), it was expected that the presence of an open talik at decreasing lakes compared with stable permafrost at the paired nondecreasing lakes would be associated with a greater thaw depth at the shoreline (+) at decreasing lakes compared with paired nondecreasing lakes. Similarly, a shallower relative thaw depth at the shoreline of decreasing lakes compared with paired nondecreasing lakes (−) was expected when groundwater recharge (i.e., open talik with a positive hydraulic gradient) was the primary nondecreasing mechanism and talik drainage (i.e., open talik with a negative hydraulic gradient) was not the primary decreasing mechanism (Table 1: Scenarios D and G). No difference in thaw depth at shoreline (0) was expected if open taliks were present at both decreasing and nondecreasing lakes (Table 1: Scenario A) or if neither decreasing nor nondecreasing mechanisms involved permafrost degradation (Table 1: Scenarios E and H).

Variable 8: Thaw depth at forest boundary. Greater thaw depth at the forest boundary may be indicative of lateral permafrost degradation that is often associated with thermokarst formation and lake growth. The expectation for thaw depth at the forest boundary was classified as unknown whenever there was a difference expected for thaw depth at shoreline because the effects of vertical and lateral permafrost degradation may be difficult to isolate (Table 1: Scenarios B, C, D, and G). With the exception of Scenario C, in which the expectation was classified as unknown due an opposing signal for thaw depth at shoreline, a shallower relative thaw depth (more stable permafrost) at the forest boundary of decreasing lakes (−) was expected when thermokarst (i.e., unstable permafrost) was the nondecreasing mechanism (Table 1: Scenarios F and I). No difference in thaw depth at the forest boundary (0) was expected if both decreasing and nondecreasing mechanisms were associated with similar levels of permafrost stability (Table 1: Scenario A) or did not involve permafrost degradation (Table 1: Scenarios E and H).

Supplemental Variable 9: Tree age. A ninth variable, tree age, was also estimated on the banks of paired lakes. While these data were not critical to the discrimination among competing scenarios, they were used to elucidate the nature of vegetation changes associated with lake area reduction. Younger trees on the banks of decreasing lakes compared with paired nondecreasing lakes may indicate that former lake beds were becoming drier (terrestrial species were invading the former lake bed) (Vasander *et al*., 1993; Jukaine & Laiho, 1995; Klein *et al*., 2005) rather than remaining wet as would be expected if terrestrialization and the resulting peatlands expanded into surrounding forests (i.e., paludification) (Klinger, 1996). To investigate this further, a linear regression of relative tree age against transect position was performed for decreasing lakes to identify whether the age of trees at decreasing lakes was directly related to distance from shoreline (i.e., past receding water levels).

Transect sampling

Sampling was conducted from June 29 to August 28 in 2006 and 2007. All measurements were made along two randomly oriented transects that were perpendicular to one another, passed through the center of each lake and ended at the adjacent forest boundary. Terrestrial measurements were made at the shoreline, at the forest boundary, and at the midpoint between shoreline and the forest boundary. Shoreline was defined as the point where open water or floating mat vegetation transitioned to dry ground (i.e., water table below the ground surface). The forest boundary was defined as the point along the transect where tree cover became dominant (i.e., ratio of tree to shrub and herbaceous vegetation areal cover was greater than one). At nondecreasing lake transects, the forest boundary was often located at or near the shoreline. In these cases ($n = 4$), the locations were classified as forest boundary with shoreline data being absent in order to avoid erroneous results that could arise from comparing ecosystem types with different moisture content. For example, if these locations had been classified as shoreline they would have been expected to have shallower thaw depths compared with shoreline locations of decreasing lakes as a result of the lower soil moisture content of a more forested ecosystem type.

Water samples were collected at nominal depths of 30 cm at the center of each lake because thorough mixing was assumed for this sample of shallow lakes. Water samples were analyzed for oxygen isotopic composition by the Alaska Stable Isotope Facility at the University of Alaska Fairbanks. Stable isotope data was obtained using continuous-flow isotope ratio mass spectrometry (CFIRMS). Instrumentation was a Thermo DeltaV Isotope ratio mass spectrometer interfaced with a Thermo thermal conversation elemental analyzer (TC/EA). Stable isotope ratios were reported in δ notation as parts per thousand (‰) deviation from the international standards of Vienna standard mean ocean water (V-SMOW). Electrical conductivity ($\mu S\,cm^{-1}$) was measured on-site at the center of each lake with an Oakton™ electrical conductivity meter. Water depth measurements (m) were made at nominal intervals of 5 m along each transect from the edge of floating mat vegetation through the center of the lake. All lakes were shallow enough to allow direct measurement of water depth with a marked string attached to a weight. As an index of surface area, the distance (m) was estimated along each transect from shoreline to shoreline including floating mat vegetation on the surface of the lake. It is important to note that this field-based estimation may not be equivalent to estimates of surface area derived from remotely sensed imagery which may exclude floating mat vegetation. As an index of lake volume, the trapezoidal method (Cox, 2007) was used to estimate the cross-sectional area (m^2) of water underneath each transect, extrapolating to estimate water depth underneath the floating mat. A bathymetric profile was then obtained for each transect by dividing the surface area index by the volume index.

The steepness of lake banks was estimated by measuring the slope (degrees) of the ground surface along each transect at the shoreline, the forest boundary, and at the midpoint between the shoreline and the forest boundary. Slope was measured with a clinometer placed on a 1 m straight steel probe parallel to the ground surface.

The width (m) of the floating mat vegetation was estimated along each transect starting at the shoreline and ending at open water. Floating mat vegetation was defined as any expanse of herbaceous or shrub vegetation rooted in a thick mat of organic material floating on the water surface and did not include emergent vegetation species rooted at the lake bottom.

Thaw depth (depth to frozen ground, cm) was measured at the shoreline and at the forest boundary with a 3 m steel probe pushed into the ground until frozen ground was reached. When frozen ground was not reached, a minimum thaw depth value of 300 cm was assigned. Peat depth (cm) was measured at the shoreline by digging until mineral soil was reached or to a depth of 40 cm. When mineral soil was not present at 40 cm, a minimum peat depth of 40 cm was assigned. When frozen organic soil was reached before mineral soil, a peat depth equivalent to depth to the frozen layer was assigned.

Dendrochronology was used to estimate the age of trees and shrubs along each transect. Ages were estimated for the tree or shrub species located closest to six evenly spaced intervals along each transect from shoreline to the forest boundary. Transect position was denoted with an ordinal integer scale ranging from 1 for the shoreline position to 6 for the forest boundary position. Stems were collected from small trees and shrubs and a Suunto™ increment borer was used to obtain cores at the root collar of larger trees. Stems and cores were sanded and rings were counted using a magnifying lens.

For some variables, sample sizes were less than the original 15 lake pairs due either to equipment failure ($\delta^{18}O$ and tree age) or to the absence of shoreline data (peat depth at shoreline and thaw depth at shoreline). To avoid pseudoreplication, surface to volume indices, bank slopes, width of floating mats, thaw depths, peat depths, and relative tree ages from the transects at each lake were averaged to obtain a single composite value for each sampled lake.

Statistical analysis of differences in lake characteristics

The Shapiro–Wilk test with an α-level of 0.05 was used to test the null hypothesis that the paired differences for each variable came from a normally distributed population. Five variables (electrical conductivity, bank slope, floating mat width, thaw depth at shoreline, and thaw depth at forest boundary) required natural log transformation of the raw data in order to normalize the distributions of paired differences.

Linear regression was used to estimate the relationship between average relative tree age and transect position at decreasing lakes (SAS Institute Inc., 2003). Tree ages were converted to relative age by dividing by the oldest tree age along each transect to enable combination of data from all lakes into a single analysis. The untransformed relative ages were left skewed and ranged from 0.05 to 1. These data were normalized with an arcsine (radians) square root transformation which is the standard transformation for skewed proportion data that range from 0 to 1(Ahrens *et al*., 1990).

Two-tailed paired *t*-tests (SAS Institute Inc., 2003) were conducted to test the null hypotheses that the mean differences in lake characteristics between paired decreasing and nondecreasing lakes were 0. When a null hypothesis was rejected, the result (+ or −) was assigned based on the direction of the mean difference between paired decreasing and nondecreasing lakes.

A single paired *t*-test with an α level of 0.05 was used to compare tree age (Supplemental Variable 9) between decreasing and nondecreasing lakes. Multiple paired *t*-tests for the remaining eight variables (Table 1) were used to discriminate among competing mechanistic scenarios because a multivariate logistic regression approach resulted in complete separation.

For the eight discriminatory variables (Table 1), Holm's Sequentially Selective Bonferroni Method (Holm, 1979) was used to reduce the Type I error rate when making multiple comparisons (i.e., the probability of rejecting any one of the eight independent variable null hypotheses when true). Experiment-wise α level was set at 0.1 *a priori* to reduce the Type II error rate when making multiple comparisons (i.e., probability of accepting any one of the eight null hypotheses when false) (Manderscheid, 1965). Thus, to declare experiment-wise significance at $\alpha = 0.1$, individual variable *P*-values had to be much lower than 0.05.

Conditional probabilities were calculated for each of the nine possible scenarios of contrasting paired-lake mechanisms (Table 1: Scenarios A–I). Conditional probabilities update the probability of a certain event (e.g. a scenario) based on new information (e.g. observed results). The formula used to calculate conditional probabilities was: $P_C = P_{scen}/P_{res}$, where P_C is the conditional probability, P_{scen} the random probability of scenario, and P_{res} the random probability of the number of results that match variable expectations for the specified scenario (Casella & Berger, 2002). Unknown expectations were excluded from the calculations of conditional probabilities. Under the assumption that the outcomes for the eight variables in Table 1 are independent events, P_{scen} is the random probability that any combination of x of the three possible results (+, −, 0) would occur ($1/3^x$, where x = the number of known expectations). P_{res} is the random probability of observing y number of results that match the expectations ($1/3^y$). Higher probabilities indicate a higher likelihood for the scenarios. Although the assumption of independence is most likely false, leading to inflated probabilities, the calculation of these conditional probabilities did enable the rank ordering and comparison of competing scenarios. The scenario that had the best match between predicted and observed results (i.e., the greatest probability given the results) was then identified.

Results

The area of decreasing and nondecreasing lakes from the earliest imagery ranged from 0.38–44.64 ha ($\bar{x} = 9.35$ ha, SE = 3.77 ha, $n = 15$) to 0.46–15.66 ha ($\bar{x} = 3.40$ ha, SE = 1.19 ha, $n = 15$), respectively, and from the most current imagery ranged from 0.12–19.24 ha ($\bar{x} = 3.72$ ha, SE = 1.50 ha, $n = 15$) to 0.24–16.83 ha ($\bar{x} = 3.62$ ha, SE = 1.26 ha, $n = 15$), respectively. Two of the 15 nondecreasing lakes increased significantly ($P < 0.05$) in size since the 1950s, increasing by 13% and 46% of their total lake area from the earliest to the latest imagery date. The remaining 13 nondecreasing lakes had nonsignificant ($P > 0.05$) trends in lake area. Twelve of these 13 nondecreasing lakes had coefficients of variation that were < 0.20 (Table 2) suggesting that nonsignificant trends in lake area were the result of relative stability as opposed to large bi-directional changes in lake area. On average, the surface area of sampled decreasing lakes declined 61% (SE = 3.89%, $n = 15$) from the earliest to the latest imagery date, which corresponded to an average loss of 5.63 ha (SE = 2.42 ha, $n = 15$) of surface area per lake. The maximum depth of decreasing and nondecreasing lakes ranged from 0.42–1.64 m ($\bar{x} = 0.98$ m, SE = 0.09 m, $n = 15$) to 0.70–3.20 m ($\bar{x} = 1.97$ m, SE = 0.19 m, $n = 15$), respectively.

Trees were significantly ($P = 0.0003$, Fig. 4a) younger on the banks of decreasing lakes compared with nondecreasing lakes. In addition, the relative age of trees significantly ($P < 0.0001$; $R^2 = 0.55$, Fig. 5) increased with distance from shoreline at decreasing lakes indicating that the banks of decreasing lakes were succeeding toward drier forest vegetation types.

Decreasing lakes had significantly greater electrical conductivity ($P = 0.0331$, Fig. 4b), greater surface : volume indices ($P = 0.0001$, Fig. 4c), shallower bank slopes ($P < 0.0001$, Fig. 4d), wider floating mats ($P < 0.0001$, Fig. 4e), greater shoreline peat depths ($P = 0.0026$, Fig. 4f), and shallower thaw depths at the forest boundary ($P = 0.0151$, Fig. 4g). Each of these individual *P*-values was significant using the Holm's Sequentially Selective Bonferroni Method with an experiment-wise α level of 0.1. The conditional probability of obtaining these results (Fig. 4, Table 3) was highest (Table 4) for the scenario that postulated terrestrialization/evapotranspiration (Fig. 2c) as the primary driver of lake area reduction combined with thermokarst formation (Fig. 2f) as the primary mechanism for nondecreasing lake area (Table 1: Scenario I).

The observation of significantly greater surface to volume indices (Fig. 4c) and significantly shallower bank slopes (Fig. 4d) at decreasing lakes was inconsistent with talik drainage as a decreasing mechanism (Table 1: Scenarios B and C) because open taliks are more likely to form in deeper lakes. In addition, there

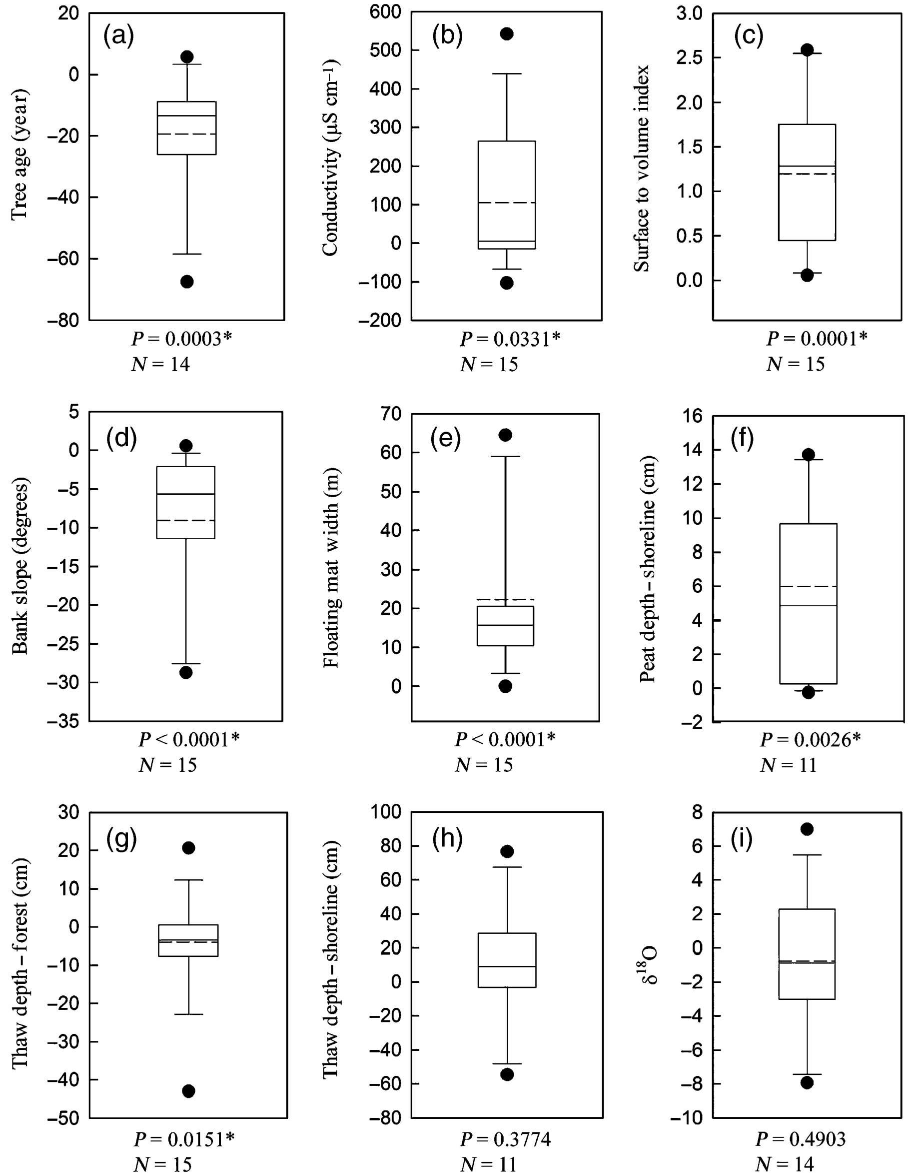

Fig. 4 Box plots of the difference in nine (a–i) lake characteristics between paired decreasing and nondecreasing lakes (decreasing minus nondecreasing). Untransformed data is plotted for ease of interpretation. The upper and lower box boundaries are the 75th and 25th percentiles, respectively. The error bars represent the 90th and 10th percentiles. Dots represent outliers that fall outside of the 90th and 10th percentiles. Within the box, the solid line represents the median value and the dotted line represents the mean value. The *P*-values shown are for the two-tailed paired *t*-tests of the null hypothesis that the difference between paired decreasing and nondecreasing lakes was 0. Five variables (electrical conductivity, bank slope, floating mat width, thaw depth at shoreline, and thaw depth at forest boundary) required natural log transformation of the raw data before conducting paired *t*-tests in order to normalize the distributions of paired differences. *Experiment-wise significance at the $\alpha = 0.10$ level using a Holm's sequential Bonferroni correction.

was no difference ($P = 0.3774$, Fig. 4h) in thaw depth at the shoreline between paired lakes and this observation did not lend support to the presence of greater talik enlargement at decreasing lakes compared with paired nondecreasing lakes (Table 1: Scenario B).

All scenarios with surface water evaporation as the primary decreasing mechanism (Table 1: Scenarios D–F) had expectations of greater ^{18}O enrichment at decreasing lakes compared with paired nondecreasing lakes and no such difference ($P = 0.4903$, Fig. 4i) in ^{18}O enrichment was observed. The lack of a difference in ^{18}O enrichment was primarily due to high variability in the direction of the difference between paired lakes indicating substantial heterogeneity in the relative role

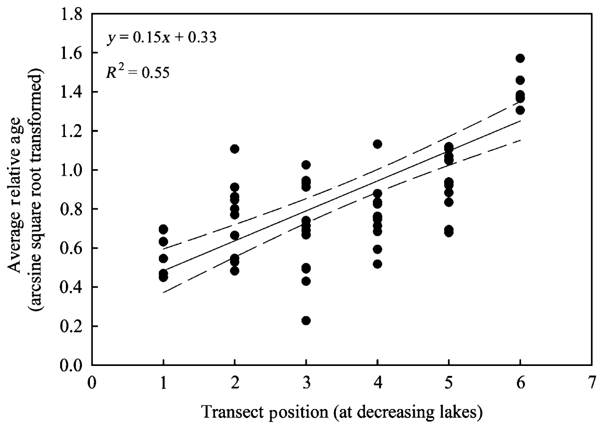

Fig. 5 Linear regression of arcsine square root transformed average relative tree age against transect position (1 = shoreline, 6 = forest boundary) for decreasing lakes showing 95% confidence intervals.

of evaporation and water inputs on water balances for this sample of lakes. Thus, the results did not support the presence of consistently greater surface water evaporation rates that exceeded water inputs at decreasing lakes (Table 1: Scenarios D–F). This result was, however, consistent with greater rates of transpiration at decreasing lakes that would result from wider floating mats of vegetation (Table 1: Scenarios H and I) and have no effect on relative isotopic enrichment (Gonfiantini *et al.*, 1965; Dawson & Ehleringer, 1991; Gat, 1996; Gibson & Edwards, 2002). In further support of terrestrialization/evapotranspiration as the mechanism for lake area reduction (Table 1: Scenarios H and I), greater electrical conductivity (Fig. 4b), floating mat width (Fig. 4e), and shoreline peat depth (Fig. 4f) were observed at decreasing lakes compared with paired nondecreasing lakes.

Thaw depth at the forest boundary was critical for discriminating between Scenarios H and I (Table 1) and

Table 3 Observed results from two-tailed paired *t*-tests for eight independent variables used to discriminate between mechanistic scenarios of lake area change

$\delta^{18}O$*	Electrical conductivity	Surface to volume index	Bank slope	Floating mat width	Peat depth at shoreline	Thaw depth at shoreline	Thaw depth at forest boundary
0	+	+	−	+	+	0	−

*$[(R_{sample}/R_{standard})-1] \times 1000‰$, where R is the ratio of oxygen isotopes ($^{18}O/^{16}O$) in sample and standard ocean water, respectively.

Paired *t*-tests were conducted to test the null hypothesis that the difference between paired decreasing and nondecreasing lakes was 0. When the null hypothesis was rejected, the result (+ or −) was assigned based on the direction of the mean difference between paired decreasing and nondecreasing lakes. A '+' indicates that the variable was significantly greater at the decreasing lake, a '−' indicates that the variable was significantly lower at the decreasing lake, and a '0' indicates that there was no significant difference between paired lakes. Experiment-wise significance was evaluated at $\alpha = 0.10$ using a Holm's sequential Bonferroni correction.

Table 4 Conditional probability of each combination (i.e., scenario) of decreasing and non-decreasing mechanisms given observed results

	Paired lake scenario				
	Decreasing mechanism	Nondecreasing mechanism	P_{scen}*	P_{res}	Conditional probability
A	Talik drainage	Groundwater recharge	$1/3^8$	$1/3$	0.00046
B	Talik drainage	Stable permafrost	$1/3^5$	0	0
C	Talik drainage	Thermokarst	$1/3^4$	0	0
D	Surface water evaporation	Groundwater recharge	$1/3^6$	$1/3^2$	0.01235
E	Surface water evaporation	Stable permafrost	$1/3^8$	$1/3^4$	0.01235
F	Surface water evaporation	Thermokarst	$1/3^7$	$1/3^4$	0.03704
G	Terrestrialization/evapotranspiration	Groundwater recharge	$1/3^6$	$1/3^4$	0.11111
H	Terrestrialization/evapotranspiration	Stable permafrost	$1/3^8$	$1/3^7$	0.33333
I	Terrestrialization/evapotranspiration	Thermokarst	$1/3^7$	$1/3^7$	1

*Conditional probability given results (P_C) = P_{scen}/P_{res} (Casella & Berger, 2002).

P_{scen}, random probability of scenario excluding unknown expectations; P_{res}, random probability of the number of results that match the variable expectations for the specified scenario.

isolating thermokarst as the primary nondecreasing mechanism. The presence of greater thaw depths at the forest boundary of nondecreasing lakes (Fig. 4g) was consistent with the expectation for Scenario I of more unstable permafrost at the forest boundary of nondecreasing lakes and did not support the expectation for Scenario H of more stable permafrost at the forest boundary of nondecreasing lakes. The lack of a difference in $\delta^{18}O$ signatures did not lend support to groundwater recharge as the primary nondecreasing mechanism (Table 1: Scenarios A, D, and G) because groundwater recharge would have led to relatively depleted ^{18}O at nondecreasing lakes compared with paired decreasing lakes (Payne, 1970; Gat, 1996; Turner *et al.*, 2010). Likewise, the electrical conductivity results did not lend support to subpermafrost groundwater recharge at nondecreasing lakes (Table 1: Scenario A). In addition, the lack of a difference in thaw depth at shoreline did not lend support to greater talik enlargement and, therefore, subpermafrost groundwater recharge at nondecreasing lakes (Table 1: Scenarios D and G). Thus, the results provided the strongest support for Scenario I, that terrestrialization/evapotranspiration was the primary mechanism for lake area reduction combined with thermokarst as the primary mechanism for nondecreasing area for this sample of lakes.

Discussion

This work is the first to use a widely distributed sample of lakes in the boreal forest to simultaneously evaluate a suite of hypotheses that might explain why one member of a pair of adjacent closed-basin lakes was decreasing in area while the other was not. The fine-scale mechanisms identified here are critical to understanding the implications of observed broad-scale reductions in lake number and area both in these study areas and in other study areas in discontinuous permafrost (Smith *et al.*, 2005; Riordan *et al.*, 2006) during the past ~50 years.

Nondecreasing lakes were deeper (mean difference in maximum depth = 1 m) with steeper banks and lower surface to volume indices than decreasing lakes (Fig. 4). Deeper lakes formed from thermokarst in relatively ice-rich permafrost may be more persistent features on the landscape while shallow lakes may be more susceptible to floating mat development, encroachment, and basin infilling (Jorgenson & Shur, 2007). Because the size and depth of thermokarst lakes is largely controlled by relative permafrost ice content (the higher the ice content, the greater the degree of subsidence) (Hopkins, 1949; Burn, 1992; Jorgenson & Shur, 2007), regions of relatively ice-poor permafrost may be dominated by shallow lakes that are more susceptible to losses in lake area resulting from terrestrialization (Payette *et al.*, 2004). The large degree of subsidence that occurs when deep lakes are formed may more effectively separate the former terrestrial system from the surface of the new thermokarst lake. In contrast, shallow subsidence in comparatively ice-poor permafrost may leave an overhanging organic mat in close contact with the new aquatic system that serves as a substrate for colonization by floating aquatic vegetation (Racine *et al.*, 1998). In addition, shallow lakes tend to have warmer water temperatures than deep lakes which may facilitate terrestrialization. Broad-scale maps of permafrost ice content have been developed based on the correlation of ice content with the thickness of surficial deposits and proximity to bedrock and could be useful in future studies to identify regional susceptibility to lake area reduction (Heginbottom & Radburn, 1992; Brown *et al.*, 2001).

The lack of a difference in $\delta^{18}O$ between paired lakes did not lend support to evaporation exceeding water inputs at decreasing lakes. While decreasing lakes may have had greater evaporation rates compared with nondecreasing lakes due to a greater surface to volume ratio, these increased evaporation rates may have been offset by greater runoff from relatively larger catchments at decreasing lakes thus leading to no net effect on lake water balance, and consequently $\delta^{18}O$, as a result of evaporation. Consistent with this concept, average transect length from shoreline to forest boundary (i.e., catchment area) was greater at decreasing lakes compared with nondecreasing lakes at 13 of the 15 lake pairs. Proportionately greater surface runoff at decreasing lakes may also deliver more dissolved ions to these aquatic systems further enhancing productivity and floating mat encroachment at these sites. The nonsignificant difference in $\delta^{18}O$ observed for our *population* of paired lakes was characterized by a large degree of variability in the direction and magnitude of $\delta^{18}O$ differences among individual lake pairs. Thus, it remains a possibility that evaporation may have exceeded water inputs at some decreasing lakes although not for the sampled population as a whole. There was no indication of regional differences in the direction and magnitude of $\delta^{18}O$ differences between paired lakes. Although $\delta^{18}O$ is a useful inferential tool for understanding the relative role of evaporation compared with water inputs in a lake's hydrological budget, it is limited in its ability to identify the absolute magnitudes and sources of water inputs and outputs (e.g., snowmelt, lateral flow, and subsurface flow). More thorough investigations of the various components of the water budgets at lakes in future studies may provide an additional context for the interpretation of oxygen isotope results.

The observations of decreasing lake area were most likely the result of the encroachment of floating mat vegetation on the surface of the lake while decreases in both lake area and volume may result from increased transpiration rates that result from increased aquatic vegetation. Observations of δ^{18}O and electrical conductivity were consistent with increased transpiration rates that have no effect on lake δ^{18}O (Gonfiantini *et al*., 1965; Dawson & Ehleringer, 1991; Gat, 1996; Gibson & Edwards, 2002) but may cause an increase in lake ion concentrations. Similarly, Simpson *et al*. (1987) concluded that a water deficit accompanied by increased ion concentrations and no change in δ^{18} O was primarily due to transpiration. Evapotranspiration from floating sedge fens and sphagnum bogs can be an important component of a lake water balance and can exceed evaporation from a pan or open water surface (Sturges, 1968; Clymo, 1973; Rutherford & Byers, 1973; Nichols & Brown, 1980; Koerselman & Beltman, 1988). Thus, an initial loss in surface area due to encroaching floating mat vegetation provides a mechanism for, and thus potentially precedes, losses in water volume resulting from transpiration. In contrast with evaporation and talik drainage which would lead to receding shorelines and a loss in water volume proportional to remotely detected losses in surface area, terrestrialization initially obscures surface water potentially leading to overestimates of remotely inferred water volume loss.

Terrestrialization was originally described as an autogenic successional process by which an open water aquatic system transitions to a terrestrial system via a specific sequence of wetland communities (Clements, 1916; Tallis, 1983). Later work has emphasized the dynamic nature of this process and has demonstrated that terrestrialization can involve a wide variety of successional trajectories which can be greatly influenced by external allogenic processes related to climate (Walker, 1970; Tallis, 1983). For example, an ombrotrophic raised bog phase is most likely to occur in wet climates where rainfall is sufficient to support *Sphagnum* growth and the accumulation of peat in isolation from minerotrophic waters. In contrast, terrestrialization in drier climates tends to proceed towards a mesophytic forested community (Tallis, 1983). The observation of younger trees and shrubs at infilling lakes may be indicative of a trajectory towards a forested ecosystem as would be expected in regions of interior Alaska with low precipitation.

Terrestrialization usually involves a minerotrophic floating fen phase at some point during its trajectory. This phase is characterized by aquatic systems with high productivity (Tallis, 1983; Hu & Davis, 1995) and rapid rates of mat encroachment onto open water. Previous studies have documented rates of floating mat encroachment of 42 m over 24 years (Gates, 1942) and complete overgrowth of a 92 m × 18 m open water area by a floating mat over 3 years (Jewell & Brown, 1929). Our observations of encroaching floating mats over shallow lakes with relatively high electrical conductivities in the Yukon Flats and Tetlin study areas over the past ~50 years may be indicative of this minerotrophic fen phase of peatland development. In contrast, even though decreasing lakes in the Kaiyuh Flats had higher electrical conductivities compared with nondecreasing lakes, the average electrical conductivity of all sampled lakes in the Kaiyuh Flats ($\bar{x} = 42\,\mu S\,cm^{-1}$, $SE = 3.3\,\mu S\,cm^{-1}$) was lower than the average electrical conductivity of lakes in the other study areas ($\bar{x} = 269\,\mu S\,cm^{-1}$, $SE = 37.6\,\mu S\,cm^{-1}$) suggesting that this region may be relatively more ombrotrophic.

While terrestrialization likely involves some autogenic internal processes (Kratz & DeWitt, 1986; Korhola, 1992; Hu & Davis, 1995), several studies have identified climate warming as an important external force in initiating and accelerating terrestrialization during warm, dry periods of the Holocene (Nicholson & Vitt, 1994; Hu & Davis, 1995; Korhola, 1995; Campbell *et al*., 1997). Observations of floating mat encroachment at multiple independent sites located in four areas that had weak (R^2 from 0.068 to 0.17) but significant positive linear trends in mean annual temperature ($P < 0.05$) and annual total PET ($P < 0.1$) since the 1950s (Riordan *et al*., 2006) suggests that a drier, warmer climate may have initiated or accelerated terrestrialization at these sites. Contemporary climate warming may facilitate floating mat development by lengthening the growing season (Smith *et al*., 2004; Euskirchen *et al*., 2006), thereby increasing water temperatures, carbon uptake, vegetation growth (Keeling *et al*., 1996; Myneni *et al*., 1997), and evapotranspiration rates (Oechel *et al*., 2000) which can increase aquatic system productivity.

In contrast with evaporation and talik drainage, which would involve receding shorelines and an immediate shift to drier conditions, terrestrialization involves the gradual infilling of a lake basin with organic matter which would convert a lake to a temporary carbon sink providing an initial negative feedback to climate warming (Whiting & Chanton, 2001; Payette *et al*., 2004). The observation of greater peat depths at the shorelines of decreasing lakes is indicative of this increased carbon storage. An additional negative feedback may result if the development of broad-leaved macrophytes on the surface of the lake leads to increased albedo. Alternatively, the development of sedge vegetation may serve as a positive feedback by facilitating methane release (King *et al*., 1998).

While terrestrialization may lead to a transient increase in carbon storage at the water's edge, a transition to drier conditions on lake banks may lead to higher decomposition rates, increased fire frequency (Pitkanen *et al*., 1999) and greater CO_2 efflux (Gorman, 1991; Gignac & Vitt, 1994; Chapin *et al*., 2000; Keyser *et al*., 2000; McGuire *et al*., 2000). The observation of new tree recruitment on decreasing lake banks suggests that as terrestrialization proceeds, transpiration rates may eventually exceed the water retaining capacity of the newly formed peat leading to drier conditions that can support new tree growth and higher decomposition rates. The net effect of drier conditions on carbon storage will depend on the balance between enhanced CO_2 efflux, increased carbon storage in new tree biomass, and decreased methane efflux associated with a declining water table (Roulet *et al*., 1992; Laine *et al*., 1996; Minkkinen *et al*., 2002; Hargreaves *et al*., 2003). An improved understanding of the net effect of terrestrialization on carbon storage, albedo, and global radiative forcing should be the focus of future research.

While the results lend strong support to terrestrialization as the primary mechanism in lake area reduction, it remains a possibility that evaporation or talik drainage mechanisms may be occurring in conjunction with or may have facilitated terrestrialization before field sampling. Although the results did not support the involvement of talik drainage in lake area reduction, logistical constraints prevented the use of ground penetrating radar and piezometers to directly detect the presence of taliks and the direction of the hydraulic gradient. In addition, more reliable and fine-scaled descriptions of surficial geology, parent material, and lake origin (e.g., silty floodplain vs. eolian sand sheets) may be able to further elucidate susceptibility to permafrost thaw and the roles of surface and subsurface flow at lake sites.

Among the various lake area reduction hypotheses considered, terrestrialization may have the most positive implications for ecosystem services. The involvement of terrestrialization suggests that (1) losses of water volume may occur at a slower rate than that inferred from remotely sensed losses in lake area, (2) the losses in water volume that do occur may lead to initial increases in carbon storage in former lake basins, and (3) the loss of open water area to floating mat vegetation may lead to an initial increase in high-quality waterfowl nesting habitat (Krapu *et al*., 1979; Bouffard *et al*., 1988; Arnold *et al*., 1993; Solberg & Higgins, 1993) compared with evaporation or talik drainage. The net effect of heterogeneous lake area change in the boreal forest will depend on specific regional balances of lake area growth and reduction.

Acknowledgements

We thank Robert Warren and Kevin Wyatt for help with field work and Bruce Finney for assistance with isotope analyses. US Fish and Wildlife Service (FWS) staff at Yukon Flats, Tetlin, and Koyukuk/Nowitna National Wildlife Refuges helped with logistics and float plane access to field sites. Funding was provided by FWS, US Geological Survey Climate Effects Network, the University of Alaska Fairbanks (UAF) Special President's Fund, and a UAF Graduate School Thesis Completion Fellowship. We thank Eric J. Taylor, Jennifer Harden, A. Dave McGuire, and Joshua Rose for their assistance and reviews of earlier drafts. Any use of trade names is for descriptive purposes only and does not imply endorsement by the US Government.

References

Ahrens WH, Cox DJ, Budhwar G (1990) Use of the arcsine and square root transformations for subjectively determined percentage data. *Weed Science*, **38**, 452–458.

Anderson LA, Abbott MB, Finney BP, Burns SJ (2007) Late Holocene moisture balance variability in the southwest Yukon Territory, Canada. *Quaternary Science Reviews*, **26**, 130–141.

Anisimov OA, Shiklomanov NI, Nelson FE (2002) Variability of seasonal thaw depth in permafrost regions: a stochastic modeling approach. *Ecological Modelling*, **153**, 217–227.

Arnold TW, Sorenson MD, Rotella JJ (1993) Relative success of overwater and upland mallard nests in southwestern Manitoba. *Journal of Wildlife Management*, **57**, 578–581.

Arp CD, Jones BM (2009) *Geography of Alaska lake districts: identification, description, and analysis of lake-rich regions of a diverse and dynamic state*. U.S. Geological Survey Scientific Investigations Report 2008-5215, 40 pp.

Billings WD, Peterson KM (1980) Vegetational change and ice-wedge polygons through the thaw-lake cycle in arctic Alaska. *Arctic and Alpine Research*, **12**, 413–432.

Bouffard SH, Sharp DE, Evans CC (1988) Overwater nesting by ducks: a review and management implications. In: *Eighth Great Plains Wildlife Damage Control Workshop Proceeding*. *USDA Forest Service General Technical Report*, RM-154, US Forest Service, Ft Collins, CO (eds Uresk DW, Schenbeck GL, Sefkin R), pp. 153–158.

Boyd CE, Hess LW (1970) Factors influencing shoot production and mineral nutrient levels in *Typha latifolia*. *Ecology*, **51**, 296–300.

Brewer MC (1958) Some results of geothermal investigations of permafrost in Northern Alaska. *Transactions, American Geophysical Union*, **39**, 19–26.

Britton ME (1957) Vegetation of the arctic tundra. In: *Arctic Biology* (ed. Hansen HP), pp. 26–72. Oregon State University Press, Corvallis.

Brown J, Ferrians O Jr, Heginbottom JA, Melnikov ES (2001) *Circum-Arctic Map of Permafrost and Ground-Ice Conditions*. National Snow and Ice Data Center/World Center for Glaciology, Digital Media, Boulder, CO.

Brown J, Hinkel KM, Nelson FE (2000) The Circumpolar Active Layer Monitoring (CALM) Program: research designs and initial results. *Polar Geography*, **24**, 165–258.

Burn CR (1992) Canadian landform examples – 24. Thermokarst lakes. *The Canadian Geographer*, **36**, 81–85.

Burn CR (2002) Tundra lakes and permafrost, Richards Island, western Arctic coast, Canada. *Canadian Journal of Earth Sciences*, **39**, 1281–1298.

Burn CR, Smith MW (1990) Development of thermokarst lakes during the Holocene at sites near Mayo, Yukon Territory. *Permafrost and Periglacial Processes*, **1**, 161–176.

Campbell DR, Duthie HC, Warner BG (1997) Post-glacial development of a kettle-hole peatland in southern Ontario. *Ecoscience*, **4**, 404–418.

Carpenter SR (1980) Enrichment of Lake Wingra, Wisconsin, by submerged macrophyte decay. *Ecology*, **61**, 1145–1155.

Casella G, Berger RL (2002) *Statistical Inference*. Duxbury, Pacific Grove, CA.

Chapin III FS, McGuire AD, Randerson J *et al*. (2000) Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biology*, **6**, 211–223.

Clegg BF, Hu FS (2010) An oxygen-isotope record of Holocene climate change in the south-central Brooks Range, Alaska. *Quaternary Science Reviews*, **29**, 928–939.

Clements FE (1916) *Plant Succession*. Carnegie Institution of Washington, Washington, DC.

Clymo RS (1973) The growth of sphagnum: some effects of environment. *Journal of Ecology*, **61**, 849–869.

Cooper LW, DeNiro MJ, Keeley JE (1991) The relationship between stable oxygen and hydrogen isotope ratios of water in astomatal plants. In: *Stable Isotope Geochemistry: A Tribute to Sam Epstein* (eds Taylor HP, O'Neill JR, Kaplan IR), pp. 247–255. Geochemical Society, San Antonio.

Cox MG (2007) The area under a curve specified by measured values. *Metrologia*, **44**, 365–378.

Craig H (1961) Standards for reporting concentrations of deuterium and oxygen-18 in natural waters. *Science*, **133**, 1833–1834.

Dansereau P, Segadas-Vianna F (1951) Ecological study of the peat bogs of eastern North America. *Canadian Journal of Botany*, **30**, 490–520.

Dawson TE, Ehleringer JR (1991) Streamside trees that do not use stream water. *Nature*, **350**, 335–337.

DeNiro MJ, Epstein S (1979) Relationship between the oxygen isotope ratios of terrestrial plant cellulose, carbon dioxide, and water. *Science*, **204**, 51–53.

Drury WH (1956) *Bog Flats and Physiographic Processes in the Upper Kuskokwim River Region, Alaska* (eds Rollins RC, Foster RC), The Gray Herbarium of Harvard University, Cambridge, 131pp.

Epstein S, Thompson P, Yapp CJ (1977) Oxygen and hydrogen isotopic ratios in plant cellulose. *Science*, **198**, 1209–1215.

Euskirchen ES, McGuire AD, Kicklighter DW *et al*. (2006) Recent shifts in the dynamics governing growing season length and productivity in terrestrial high-latitude ecosystems. *Global Change Biology*, **12**, 731–750.

Gat JR (1996) Oxygen and hydrogen isotopes in the hydrologic cycle. *Annual Review of Earth and Planetary Sciences*, **24**, 225–262.

Gates FC (1942) The bogs of northern lower Michigan. *Ecological Monographs*, **12**, 213–254.

Gaudet JJ (1977) Uptake, accumulation and loss of nutrients by papyrus in tropical swamps. *Ecology*, **58**, 415–422.

Gibson JJ, Edwards TWD (2002) Regional water balance trends and evaporation-transpiration partitioning from a stable isotope survey of lakes in northern Canada. *Global Biogeochemical Cycles*, **16**, 1–18.

Gignac LD, Vitt DH (1994) Responses of northern peatlands to climate change: effects on bryophytes. *The Journal of the Hattori Botanical Laboratory*, **75**, 119–132.

Gonfiantini R, Gratziu S, Tangiorgi E (1965) Oxygen isotopic composition of water in leaves. In: *Isotopes and Radiation in Soil-Plant Nutrition Studies* (pp. 405–410. International Atomic Energy Association, Vienna.

Gorman E (1991) Northern peatlands: role in the carbon cycle and probable responses to climate warming. *Ecological Applications*, **1**, 182–195.

Hargreaves KJ, Milne R, Cannell MGR (2003) Carbon balance of afforested peatland in Scotland. *Forestry*, **76**, 299–317.

Hassol SJ (2004) *ACIA, Impacts of a Warming Arctic: Arctic Climate Impact Assessment*. Cambridge University Press, Cambridge.

Heginbottom JA, Radburn LK (1992) Permafrost and ground ice conditions of northwestern Canada; Geological Survey of Canada, Map 1691A, scale 1:1,000,000. Digitized by S. Smith, Geological Survey of Canada. Boulder, CO: National Snow and Ice Data Center/World Data Center for Glaciology. Digital Media.

Hinzman LD, Bettez ND, Bolton WR *et al*. (2005) Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change*, **72**, 251–298.

Hinzman LD, Goering DJ, Kinney TC, Li S (1997) Numeric simulation of thermokarst formation during disturbance. In: *Disturbance and Recovery in Arctic Lands: An Ecological Perspective* (ed. Crawford RM), pp. 191–211. Kluwer Academic Publishers, Dordrecht.

Holm S (1979) A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, **6**, 65–70.

Hopkins DM (1949) Thaw lakes and thaw sinks in the Imuruk Lake area, Seward Peninsula, Alaska. *The Journal of Geology*, **57**, 119–131.

Hu FS, Davis RB (1995) Postglacial development of a Maine bog and paleoenvironmental implications. *Canadian Journal of Botany*, **73**, 638–649.

Jewell ME, Brown HW (1929) Studies on northern Michigan bog lakes. *Ecology*, **10**, 427–475.

Johnston CA (1991) Sediment and nutrient retention by freshwater wetlands: effects on surface water quality. *Critical Reviews in Environmental Control*, **21**, 491–565.

Jorgenson MT, Osterkamp TE (2005) Response of boreal ecosystems to varying modes of permafrost degradation. *Canadian Journal of Forest Research*, **35**, 2100–2111.

Jorgenson MT, Racine CH, Walter JC, Osterkamp TE (2001) Permafrost degradation and ecological changes associated with a warming climate in central Alaska. *Climate Change*, **48**, 551–579.

Jorgenson MT, Shur Y (2007) Evolution of lakes and basins in northern Alaska and discussion of the thaw lake cycle. *Journal of Geophysical Research*, **112** F02S17, doi: 10.1029/2006JF000531.

Jorgenson MT, Yoshikawa K, Kanveskiy M *et al*. (2008) Permafrost characteristics of Alaska. In: *Proceedings of the Ninth International Conference on Permafrost, 29 June–3 July 2008, Fairbanks, Alaska* (eds Kane DL, Hinkel KM), pp. 121–122. Institute of Northern Engineering, University of Alaska Fairbanks, Fairbanks.

Jukaine HV, Laiho R (1995) Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. *Journal of Applied Ecology*, **32**, 785–802.

Kane DL, Slaughter CW (1973) Recharge of a central Alaska lake by subpermafrost groundwater. In: *Permafrost. Proceedings of the 2nd International Conference, Yakutsk* (eds Pewe TL, MacKay JR), pp. 458–462. North American Contribution, National Academy of Sciences, Washington, DC.

Kaufman DS, Schneider DP, McKay NP *et al*. (2009) Recent warming reverses long-term arctic cooling. *Science*, **325**, 1236–1239.

Keeling CD, Chin JFS, Whorf TP (1996) Increased activity of northern vegetation inferred from atmospheric CO_2 measurements. *Nature*, **382**, 146–149.

Keyser AR, Kimball JS, Nemani RR, Running SW (2000) Simulating the effects of climate change on the carbon balance of North American high-latitude forests. *Global Change Biology*, **6**, 185–195.

King JY, Reeburgh WS, Regli SK (1998) Methane emission and transport by arctic sedges in Alaska: results of a vegetation removal experiment. *Journal of Geophysical Research*, **103**, D00052, doi: 10.1029/98JD00052.

Klein E, Berg EE, Dial R (2005) Wetland drying and succession across the Kenai Peninsula Lowlands, south-central Alaska. *Canadian Journal of Forest Research*, **35**, 1931–1941.

Klinger LF (1996) The myth of the classic hydrosphere model of bog succession. *Arctic and Alpine Research*, **28**, 1–9.

Koerselman W, Beltman B (1988) Evapotranspiration from fens in relation to Penman's potential free water evaporation (E_0) and pan evaporation. *Aquatic Botany*, **31**, 307–320.

Korhola A (1992) Mire induction, ecosystem dynamics and lateral extension on raised bogs in the southern coastal area of Finland. *Fennia*, **170**, 25–94.

Korhola A (1995) Lake terrestrialization as a mode of mire formation: a regional review. *Publications of the National Board of Waters and the Environment*, **207**, 11–21.

Krapu GL, Talent LG, Dwyer TJ (1979) Marsh nesting by mallards. *Wildlife Society Bulletin*, **7**, 104–110.

Kratz TK, DeWitt CB (1986) Internal factors controlling peatland-lake ecosystem development. *Ecology*, **67**, 100–107.

Kroger R, Holland MM, Moore MT, Cooper CM (2007) Plant senescence: a mechanism for nutrient release in temperate agricultural wetlands. *Environmental Pollution*, **146**, 114–119.

Laine J, Silvola J, Tolonen K *et al*. (1996) Effect of water-level drawdown on global climatic warming: northern peatlands. *Ambio*, **25**, 179–184.

Mackay JR (1992) Lake stability in an ice-rich permafrost environment: examples from the Western Arctic coast. In: *Aquatic Ecosystems in Semi-arid Regions: Implications for Resource Management*. *N.H.R.I. Symposium Series 7* (eds Robarts RD, Bothwell ML), pp. 1–26. Environment Canada, Saskatoon.

Manderscheid LV (1965) Significance Levels. 0.05, 0.01, or ? *Journal of Farm Economics*, **47**, 1381–1385.

Manley W, Kaufman D (2002) *Alaska PaleoGlacier*. Institute of Arctic and Alpine Research (INSTAAR), University of Colorado, Atlas: Boulder, CO.

McGuire AD, Sitch S, Clein JS *et al*. (2000) Carbon balance of the terrestrial biosphere in the twentieth century: analyses of CO_2, climate, and land use effects with four process-based ecosystem models. *Global Biogeochemical Cycles*, **15**, 183–206.

Minkkinen J, Korhonen R, Savolainen I, Laine J (2002) Carbon balance and radiative forcing of Finnish peatlands 1900–2100 – the impact of forestry drainage. *Global Change Biology*, **8**, 785–799.

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981–1991. *Nature*, **386**, 698–702.

Nelson FE, Shiklomanov NI, Mueller GR (1999) Variability of active-layer thickness at multiple spatial scales, north-central Alaska, USA. *Arctic, Antarctic, and Alpine Research*, **31**, 158–165.

Nichols DS, Brown JM (1980) Evaporation from a sphagnum moss surface. *Journal of Hydrology*, **48**, 289–302.

Nichols DS, Keeney DR (1972) Nitrogen and phosphorus release from decaying water milfoil. *Hydrobiologia*, **42**, 509–525.

Nicholson BJ, Vitt DH (1994) Wetland development at Elk Island National Park, Alberta, Canada. *Journal of Paleolimnology*, **12**, 19–34.

Oechel WC, Vourlitis GL, Hastings SJ, Zulueta RC, Hinzman L, Kane D (2000) Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. *Nature*, **406**, 978–981.

Osterkamp TE (2005) The recent warming of permafrost in Alaska. *Global and Planetary Change*, **49**, 187–202.

Osterkamp TE, Vierek L, Shur Y, Jorgenson MT, Racine T, Doyle A, Boone RD (2000) Observations of thermokarst and its impact on boreal forests in Alaska, USA. *Arctic and Alpine Research*, **32**, 303–315.

Payette S, Delwaide A, Caccianiga M, Beauchemin M (2004) Accelerated thawing of subarctic peatland permafrost over the last 50 years. *Geophysical Research Letters*, **31**, L18208, doi: 10.1029/2004GL020358.

Payne BR (1970) Water balance of lake Chala and its relation to groundwater from tritium and stable isotope data. *Journal of Hydrology*, **11**, 47–58.

Pitkanen A, Turunen J, Tolonen K (1999) The role of fire in the carbon dynamics of a mire, eastern Finland. *Holocene*, **9**, 453–462.

Racine CH, Jorgenson MT, Walters JC (1998) *Permafrost*. *Proceedings of the 7th International Conference, Yellowknife*. Collection Nordicana No 55, pp. 927–933.

Riordan B, Verbyla D, McGuire AD (2006) Shrinking ponds in subarctic Alaska based on 1950–2002 remotely sensed images. *Journal of Geophysical Research*, **111**, G04002, doi: 10.1029/2005JG000150.
Roulet N, Moore T, Bubier J, Lafleur P (1992) Northern fens: methane flux and climatic change. *Tellus*, **44B**, 100–105.
Rouse WR, Douglas MS, Hecky RE *et al*. (1997) Effects of climate change on the freshwaters of arctic and subarctic North America. In: *Freshwater Ecosystems and Climate Change in North America* (ed. Cushing CE), pp. 55–84. John Wiley & Sons, Chichester.
Rutherford RJ, Byers GL (1973) Controlling wetland water by suppressing evaporation. *Canadian Agricultural Engineering*, **15**, 9–11.
SAS Institute Inc. (2003) *SAS 9.1.3 for Windows*. SAS Institute Inc., Cary, NC.
Schindler DW, Beaty KG, Fee EJ *et al*. (1990) Effects of climatic warming on lakes of the central boreal forest. *Science*, **250**, 967–970.
Serreze MC, Walsh JE, Chapin III FS *et al*. (2000) Observational evidence of recent change in the northern high-latitude environment. *Climatic Change*, **46**, 159–207.
Simpson HJ, Hamza MS, White JWC, Nada A, Awad MA (1987) Evaporative enrichment of deuterium and ^{18}O in arid zone irrigation. In: *Isotope Techniques in Water Resources Development Proceedings of a Symposium*, 30 March–30 April 1987, Vienna, Austria, pp. 241–256. IAEA Division of Publications, Vienna.
Smith LC, Sheng Y, MacDonald GM, Hinzman LD (2005) Disappearing arctic lakes. *Science*, **308**, 1429.
Smith NV, Saatchi SS, Randerson JT (2004) Trends in high northern latitude soil freeze and thaw cycle from 1988 to 2002. *Journal of Geophysical Research*, **109** D12101, doi: 10.1029/2003JD004472.
Smol JP, Douglas MS (2007) Crossing the final ecological threshold in high arctic ponds. *Proceedings of the National Academy of Sciences*, **104**, 12395–12397.
Solberg KL, Higgins KF (1993) Overwater nesting by ducks in northeastern South Dakota. *The Prairie Naturalist*, **25**, 19–22.
Sturges DA (1968) Evaporation at a Wyoming mountain bog. *Journal of Soil Water Conservation*, **23**, 23–25.
Swanson DK (1996) Susceptibility of permafrost soils to deep thaw after forest fires in interior Alaska, USA, and some ecological implications. *Arctic and Alpine Research*, **28**, 217–227.
Tallis JH (1983) Changes in wetland communities. In: *Ecosystems of the World* (ed. Gore AJP), pp. 311–347. Elsevier, Amsterdam.
Turner KW, Wolfe BB, Edwards TWD (2010) Characterizing the role of hydrological processes on lake water balances in the Old Crow Flats, Yukon Territory, Canada, using water isotope tracers. *Journal of Hydrology*, **386**, 103–117.
van Everdingen R (1998 revised May 2005) *Multi-Language Glossary of Permafrost and Related Ground-Ice Terms*. National Snow and Ice Data Center/World Data Center for Glaciology, Boulder, CO.
Vasander H, Kuusipalo J, Lindham T (1993) Vegetation changes after drainage and fertilization in pine mires. *Suo*, **44**, 1–9.
Vitt DH, Halsey LA, Zoltai SC (1994) The bog landforms of continental western Canada in relation to climate and permafrost patterns. *Arctic and Alpine Research*, **26**, 1–13.
Vörösmarty CJ, Hinzman LD, Peterson BJ *et al*. (2001) *The Hydrologic Cycle and its Role in Arctic and Global Environmental Change: A Rationale and Strategy for Synthesis Study*. Arctic Research Consortium of the US. 84pp.
Walker D (1970) Direction and rate in some British post-glacial hydroseres. In: *Studies in the Vegetational History of the British Isles* (eds Walker D, West RG), pp. 117–139. University Press of Cambridge, Cambridge.
Whiting GJ, Chanton JP (2001) Greenhouse carbon balance of wetlands: methane emission versus carbon sequestration. *Tellus*, **53B**, 521–528.
Wiens JA (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.
Woo MK (1986) Permafrost hydrology in North America. *Atmosphere-Ocean*, **24**, 201–234.
Yoshikawa K, Hinzman LD (2003) Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost near Council, Alaska. *Permafrost and Periglacial Processes*, **14**, 151–160.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Data from 15 paired decreasing and non-decreasing lakes in the Alaska boreal forest, 2006–2007, used for general comparisons and to evaluate nine possible combinations of three decreasing and three non-decreasing hypotheses (i.e., scenarios) using paired *t*-tests of the difference between lake types with Holm's sequential Bonferroni correction.
Appendix S2. Topographical characteristics, climate data, and percent change in lake surface area for the four study areas. Elevation, slope, and aspect derived from Alaska 300 m Digital Elevation Model. Climate data and percent change in lake surface area were adapted from Riordan *et al*., 2006. For information on weather station locations and methods used to generate climate and lake area change data see Riordan *et al*., 2006.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.