

Landscape influences on climate-related lake shrinkage at high latitudes

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Abstract

Climate-related declines in lake area have been identified across circumpolar regions and have been characterized by substantial spatial heterogeneity. An improved understanding of the mechanisms underlying lake area trends is necessary to predict where change is most likely to occur and to identify implications for high latitude reservoirs of carbon. Here, using a population of ca. 2300 lakes with statistically significant increasing and decreasing lake area trends spanning longitudinal and latitudinal gradients of ca. 1000 km in Alaska, we present evidence for a mechanism of lake area decline that involves the loss of surface water to groundwater systems. We show that lakes with significant declines in lake area were more likely to be located: (1) in burned areas; (2) on coarser, well-drained soils; and (3) farther from rivers compared to lakes that were increasing. These results indicate that postfire processes such as permafrost degradation, which also results from a warming climate, may promote lake drainage, particularly in coarse-textured soils and farther from rivers where overland flooding is less likely and downslope flow paths and negative hydraulic gradients between surface water and groundwater systems are more common. Movement of surface water to groundwater systems may lead to a deepening of subsurface flow paths and longer hydraulic residence time which has been linked to increased soil respiration and CO₂ release to the atmosphere. By quantifying relationships between statewide coarse resolution maps of landscape characteristics and spatially heterogeneous responses of lakes to environmental change, we provide a means to identify at-risk lakes and landscapes and plan for a changing climate.

Keywords: Alaska, drainage, groundwater, National Wildlife Refuge, permafrost, talik, terrestrialization, thermokarst, waterfowl, wetlands

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Introduction

Declines in lake number and area have been identified across high latitude ecosystems (Smith *et al.*, 2005; Riordan *et al.*, 2006; Labrecque *et al.*, 2009; Carroll *et al.*, 2011; Chen *et al.*, 2012), and these changes have been coincident with a warming climate. Northern lakes and wetlands, particularly those in federally protected National Wildlife Refuge (NWR) lands, provide critical breeding habitat for international populations of migratory waterfowl and shorebirds and are sources of biodiversity that provide both local and far-reaching ecosystem services along migratory routes.

Net declining trends have also been characterized by spatial heterogeneity (Riordan *et al.*, 2006; Carroll *et al.*, 2011; Roach *et al.*, 2011; Chen *et al.*, 2012; Rover *et al.*, 2012) with increasing lakes interspersed among shrinking lakes, highlighting a potential for resiliency at fine

spatial scales. The ability to identify these pockets of resiliency is an important first step in managing and planning for a new future landscape. Such spatially explicit information may (1) clarify whether the features and number of stable or new habitats can continue to support individual species and overall species richness, (2) prioritize allocation of resources among refuges, and (3) inform the delineation of future management boundaries. To meet this need, we must identify explicit quantitative relationships between coarse resolution landscape characteristics and the probability that a lake will increase or decrease in size.

The identification of these relationships may elucidate the dominant mechanism of lake decline across a large spatial extent (longitudinal and latitudinal gradients spanning ca. 1000 km). A better understanding of the dominant pathway involved in water loss may clarify the net direction and magnitude of effects on high latitude stores of carbon which constitute a substantial portion of the global belowground carbon pool (Tarnocai *et al.*, 2009). Studies conducted across relatively small

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spatial extents (<200 km) have provided localized support for several mechanisms of declining lake area including (1) increased evapotranspiration (Smol & Douglas, 2007), (2) permafrost degradation leading to the loss of surface water to shallow or deep groundwater systems (Yoshikawa & Hinzman, 2003; Karlsson *et al.*, 2012; Jepsen *et al.*, 2013), and (3) thermo-erosion and lateral breaching of lake shorelines (Jones *et al.*, 2011; MacDonald *et al.*, 2012). In addition, floating mat encroachment and terrestrialization (i.e., peatland development) have been identified as important components of the mechanism of lake surface area loss across a large spatial extent (ca. 800 km) in boreal Alaska (Roach *et al.*, 2011) and may be a response to a more proximate climate-driven mechanism such as permafrost degradation (Payette *et al.*, 2004) or increased evaporation.

The abundance of lakes in dry Arctic and subarctic climates is largely due to the presence of permafrost which acts as an aquiclude, limiting exchange between surface water and groundwater systems. In Alaska, permafrost has thawed in response to climate warming (Osterkamp & Romanovsky, 1999; Osterkamp, 2007) and in response to forest fire due to removal of surface moss and organic horizons (Swanson, 1996; Burn, 1998). Once permafrost thaws, substrate permeability then becomes largely controlled by soil texture. In particular, coarse-textured sandy soils may promote drainage (Burn, 2002), while fine-grained silty soils can act as an aquiclude similar to permafrost and promote surface water ponding. On permeable soils, deep permafrost thaw underneath lakes (i.e., taliks) can lead to drainage (Yoshikawa & Hinzman, 2003) or lake expansion (Kane & Slaughter, 1973; Jorgenson *et al.*, 2001) depending on the direction of hydraulic pressure gradients between surface water and subsurface groundwater systems (i.e., negative vs. positive). Shallow permafrost thaw on lake catchments with coarse-textured soils can also lead to a reduction in lake area due to increased water infiltration into a deepening active layer. This can lead to the loss of surface water to shallow groundwater systems and can also reduce the amount of runoff available to recharge lakes which is an important component of lake water balances in high latitude regions (Barber & Finney, 2000).

The degradation of ice-rich permafrost (i.e., thermokarst), commonly found in fine-grained silty soils (Jorgenson & Osterkamp, 2005), can also lead to increases in lake area (Burn & Smith, 1990; Roach *et al.*, 2011). However, net declines in lake area have been observed predominantly in discontinuous permafrost regions that have relatively unstable permafrost, while increases or negligible changes have been found in continuous permafrost regions (Smith *et al.*, 2005; Riordan *et al.*, 2006). Such findings have led to a hypothesis that

regional lake responses to permafrost degradation may occur along a continuum (Smith *et al.*, 2005) with initial thawing in relatively stable permafrost zones leading to a transitory increase in lake area due to thermokarst followed by declining lake area as permafrost continues to degrade.

Given the heterogeneous nature of change, the ability to manage and plan for a new future landscape depends on the ability to use readily available indices to identify lakes and regions that have a high probability of risk or resilience in a changing climate. Thus, the primary objective of this study was to quantify relationships between coarse resolution landscape characteristics and spatially heterogeneous responses of lakes to environmental change. Here, we (1) estimate the direction and magnitude of lake area trends at multiple spatial extents, (2) use these individual lake trend estimates to develop a probabilistic model to predict the likelihood that a lake will decrease or increase based on landscape characteristics, and (3) use this model to infer the dominant mechanism of lake decline and its associated implications.

Materials and methods

Study areas

Ten study areas (927–4537 sq km) were located within eight Alaskan NWRs in boreal and polar ecoregions: Tetlin, Yukon Flats, Kanuti, Selawik, Koyukuk, Innoko, Togiak, and Becharof (Fig. 1). The Yukon Flats NWR contained three study areas (West, Central, and East) due to the presence of a wide longitudinal gradient (ca. 200 km) within this refuge and preliminary suggestions of differential lake trends along this gradient. Study area boundaries were delineated to (1) maximize overlap with NWR lands of particular value to wildlife populations and other ongoing studies identified through consultations with U.S. Fish and Wildlife Service land managers, and (2) maximize overlap of cloud-free satellite imagery.

Image processing

Six overlapping Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) scenes were obtained for each study area from the United States Geological Survey (USGS) Earth Resources Observation and Science Center. We used only six images per study area due to the time constraints involved in image processing and interpretation for 10 study areas. Most of the time series began in 1985–1986 (Table S1). Exceptions to this were the Togiak and Tetlin time series and the southern time series for the Innoko study area which began in 1989, 1995, and 1991, respectively, because useable imagery was not available prior to these dates due to (1) presence of clouds that can obscure lakes and create shadows that are spectrally similar to surface water and (2) limited availability of Landsat scenes during the Earth Observation Satellite Com-

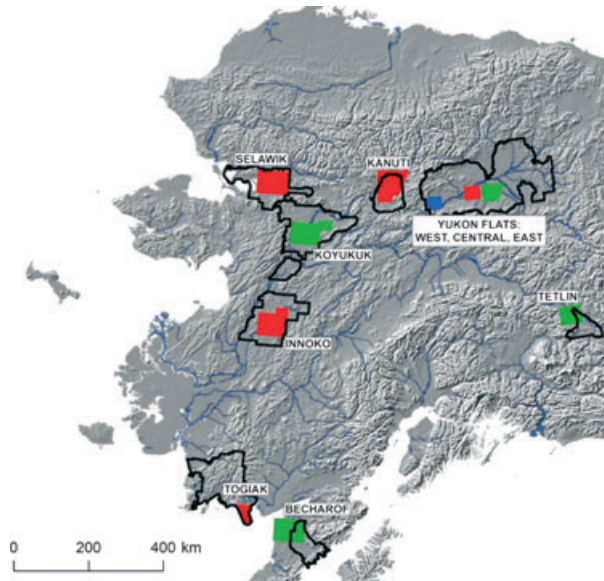


Fig. 1 The direction of study area trends in lake area since ca. 1985. Study areas with significant ($\alpha = 0.05$) decreasing trends are colored red. Study areas with significant ($\alpha = 0.05$) increasing trends are colored blue. Study areas with nonsignificant trends are colored green. Alaskan National Wildlife Refuge boundaries are shown in black.

pany (EOSAT) privatization period of 1984–1999. All time series ended in 2007–2009.

Each time series of six TM/ETM+ scenes included three early season (pre-July 10) and three late season (post-July 10) scenes (Table S1) with the exception of the Kanuti time series, which included four late season scenes and only two early season scenes due to early season cloud interference. The inclusion of imagery from a range of dates (Table S1) within the summer season improved our ability to account for intra-annual variability when estimating long-term annual trends in lake area.

The short wave infrared (SWIR) Band 5 was used to classify water from TM/ETM+ scenes because this band is the most useful in discriminating water from nonwater pixels (Frazier & Page, 2000; Roach *et al.*, 2012). Digital Numbers (DNs) were converted to Top-Of-Atmosphere (TOA) reflectance (Chander *et al.*, 2009) to reduce scene-to-scene variability. Reflectance was then scaled from 0.0–0.63 floating point to 0–255 integer (1-byte) values.

All imagery was co-registered to the UTM map projection, NAD27, using a linear affine transformation model and nearest neighbor re-sampling. The statewide coverage of 1 : 63 360 topographic maps obtained from the USGS Alaska Geospatial Data Clearinghouse (<http://agdc.usgs.gov/data/>) was used as a source for control points. A single co-registration model was used for each extent/time series to minimize image positional error as a source of bias in the time series analysis. Each satellite image co-registration model was based on at least 30 control points and a root mean squared error of less than 23 m. Co-registered Landsat TM/ETM+ images had a pixel size of 30 m.

Image interpretation

Water was classified from Landsat images using a density slicing approach (Roach *et al.*, 2012). A unique SWIR Band 5 threshold value for discriminating water from nonwater pixels was identified for each image by minimizing the difference between training lake area classified from Landsat images and the area of the lakes manually delineated from high resolution aerial photographs. Training lakes were selected that were stable in size between the Landsat image and high-resolution aerial photographs, represented a range of lake sizes and covered a wide spatial extent.

A visual inspection of polygons and imagery was conducted to identify rivers and wetlands (wet, ground surfaces) that were misclassified as lake water pixels. The misclassification of wetlands as open water can be particularly problematic when using an automated approach to classify water and nonwater from Landsat imagery (Roach *et al.*, 2012). To identify these misclassifications, after instituting a minimum lake size threshold, we visually inspected the spectral characteristics of lakes that suddenly appeared or enlarged in some seasons or years and, if misclassified, removed them from the analysis. Clouds and cloud shadows misclassified as water were masked and considered as missing data. If atmospheric interference was present in Band 1 or thermal Band 6, the image was discarded and replaced with another one.

Trend analysis

To summarize lake polygons that may have coalesced or broke apart into discrete entities that could be tracked through time, we defined lake area as either the polygon or group of polygons within the combined maximum extent of that water body throughout the time series. Lakes that were smaller than 5850 m² (midpoint between six and seven 30 m pixels) in all images were removed from the analysis to reduce omission and commission errors (Roach *et al.*, 2012). If larger than 5850 m² in at least one image the lake was retained and values smaller than 5850 m² were assigned a constant value of half the detection limit (i.e., 2925 m²) (Helsel, 2005). All islands smaller than 5850 m² were classified as water.

Previous estimates of lake area change have often been based solely on the difference between imagery from only two dates (c.f., Yoshikawa & Hinzman, 2003; Smith *et al.*, 2005; Riordan *et al.*, 2006; Labrecque *et al.*, 2009) and, thus, have not accounted for within- and among-year variability. In contrast, we used a regression analysis with Landsat images from 6 years and a wide range of dates within summer (Table S1) to detect trends that explicitly accounted for both interannual and intra-annual variability. This increased both the statistical power to detect linear trends and the accuracy of trend estimates which provided a means to project future change in lake area that will be essential for assessing potential implications of lake change for the global carbon budget and fish and wildlife habitats.

We estimated two types of trends since ca. 1985: (1) trends of individual lakes ($n = 22\,960$) and (2) mean trend for study areas ($n = 10$). For all regression models, lake area (m²) was the

dependent variable and required natural log-transformation to normalize right skewed lake area distributions. Year and day-of-summer were explanatory variables to estimate annual and intra-annual trends, respectively. Year and day-of-summer were coded relative to the earliest date of image acquisition for each time series and were divided by 100 to enable model convergence. Year and day-of-summer slopes represented the geometric percent change in lake area per year and per day-of-summer, respectively (Flanders *et al.*, 1992).

Individual lake trends were estimated by pooling lakes into a single regression model for each study area. Models included indicator variables for each lake and all interactions between the indicator variables and main effects to obtain lake-specific annual and intra-annual slopes.

Study area trends were estimated using a mixed effects regression model for each study area. Mixed effects models allowed for overall fixed effects in year and day-of-summer and random variations from those effects for each individual lake (SAS Institute Inc., 2002–2010; Proc Mixed). Day-of-summer was included as an independent variable in both the individual lake and study area model only if significant at $\alpha = 0.05$ in the study area model. Temporal autocorrelation was estimated using an exponential autocovariance model. The parameters of the mixed effect study area trend model were estimated by setting the covariance parameters for intercept, year, and day-of-summer to be equal to the variances of the respective intercept, year, and day-of-summer effects from individual lake regression models. This was done because the restricted maximum likelihood estimates of these parameters were unrealistically small, underestimating the variance among individual lake intercepts and slopes.

Study area trend models also included a binary categorical variable to indicate whether lakes were included in a small (ca. 3%) subsample that had temporal records extending back to ca. 1948 by manually delineating historical aerial photography. Interactions between this binary variable and year and day-of-summer were included to estimate separate population trends for groups with long and short temporal records. Post-1948 trends are not described here due to their small sample. Their inclusion in statistical analyses made no material difference in post-1985 trend estimates.

Logistic regression analysis

We used a multivariate logistic regression model to predict the probability that a lake will decrease or increase in size based on landscape characteristics using those lakes with significantly ($\alpha = 0.05$) decreasing ($n = 1930$) and increasing ($n = 652$) annual trends from the 10 study areas (SAS Institute Inc., 2002–2010; Proc Glimmix). We used only those lakes with statistically significant ($\alpha = 0.05$) trends to increase the likelihood that our binary response variable (decreasing vs. increasing) was estimated with little error. The landscape variables we considered were: (1) distance from nearest river (USGS 1 : 2 000 000 Digital Line Graphs dataset, <http://agdc.usgs.gov/data/>), (2) elevation (USGS 300 m Digital Elevation Model, <http://agdc.usgs.gov/data/>), (3) soil texture as an ordinal variable ranging from fine

to coarse (Jorgenson *et al.*, 2008), (4) permafrost extent as an ordinal variable ranging from continuous to unfrozen (Jorgenson *et al.*, 2008), (5) permafrost ice content as an ordinal variable ranging from high ice to unfrozen (Jorgenson *et al.*, 2008), and (6) the presence/absence of a wildfire during 1942–2007 (Wildland Fire Dataset for Alaska, <http://agdc.usgs.gov/data/>).

We randomly selected 80% of the lakes with significant trends to build the model. The remaining 20% were used as a hold-out sample to evaluate predictive power using conditional fitted values and a probability threshold value for the classification of decreasing and increasing lakes that was equal to the value where the predicted prevalence was equal to the observed prevalence (i.e., greater than or less than 0.65) (Freeman & Moisen, 2008). Maximum likelihood based on Laplace approximation was used to estimate the parameters of a generalized linear mixed effects model with a logit link. Because lakes within study areas were not statistically independent, study area was included as a random intercept. Spatial autocorrelation was estimated using a radial smoothing function with 50 knots that uniformly covered the convex hull of the data locations which were computed by a modified Federov search algorithm (Cook & Nachtsheim, 1980) (SAS Institute Inc., 2002–2010; Proc Optex).

All variables except for wildfire were standardized by subtracting the mean and dividing by two times the standard deviation (Gelman, 2008). All possible variable combinations were considered except those that included collinear variables (Pearson's r or Cramer's $V > 0.5$ for continuous and ordinal/binary variables, respectively). The final model was the model with the lowest Akaike's Information Criteria (AIC). Competing models ($\Delta AIC < 2$) were not averaged because additional variables had parameter estimates with wide confidence intervals overlapping zero and the inclusion of these additional variables did not change the parameters estimated by the lowest AIC model.

Results

Rates of change

There was an average net decline in lake area of 0.80% per year (SEM = 0.34%) across all 10 study areas (Table 1), and 0.72% per year (SEM = 0.02%) across all individual lakes. Five of 10 study areas had significant declining trends (Fig. 1; Table 1) and, of all lakes with significant trends, 75% were declining (Table S2). Net annual rates of change for study areas ranged from -2.96 to +0.34% per year (Table 1). There was also substantial heterogeneity in individual lake trends (Fig. 2, Figures S1–S9) even within study areas that had net decreasing and increasing trends. In many study areas, individual lake trends ranged from disappearance to a doubling of lake size since ca. 1985.

Inter- and intra-annual variability in lake area also were substantial. Individual lake coefficients of temporal variation in area were as large as 228% with a mean

Table 1 Net intra-annual and annual trends in lake area estimated for 10 study areas in Alaska by linear mixed effects models. Intra-annual and annual trends indicate the geometric percent change in lake area per day-of-summer and per year, respectively

Study area	Intercept \pm SEM	Intra-annual trend \pm SEM	Cumulative 90-day summer% change	Annual trend \pm SEM	Projected cumulative 50-year% change
Tetlin	9.67* \pm 0.08	-0.403* \pm 0.02	-30.4	0.07 \pm 0.13	3.6
Yukon Flats East	10.05* \pm 0.11	-0.562* \pm 0.05	-39.7	0.19 \pm 0.21	10.0
Yukon Flats Central	10.85* \pm 0.09	-0.178* \pm 0.03	-14.8	-2.96* \pm 0.18	-77.2
Yukon Flats West	9.7* \pm 0.09	0.142* \pm 0.04	13.6	0.34* \pm 0.13	18.5
Kanuti	10.11* \pm 0.03	-0.072* \pm 0.02	-6.3	-1.50* \pm 0.07	-52.8
Selawik	10.12* \pm 0.02	-0.054* \pm 0.01	-4.7	-0.81* \pm 0.04	-33.3
Koyukuk	9.68* \pm 0.03	-0.153* \pm 0.01	-12.9	-0.08 \pm 0.05	-3.9
Innoko	10.1* \pm 0.05	-0.217* \pm 0.02	-17.7	-1.54* \pm 0.10	-53.7
Togiak	10.54* \pm 0.07	-0.217* \pm 0.02	-17.7	-1.63* \pm 0.13	-55.7
Becharof	9.76* \pm 0.03	0.078* \pm 0.01	7.3	-0.05 \pm 0.04	-2.5
Average		-0.158	-11.7	-0.80	-24.7

*Significantly different from zero at $\alpha = 0.05$. SEM = Standard Error of the Mean.

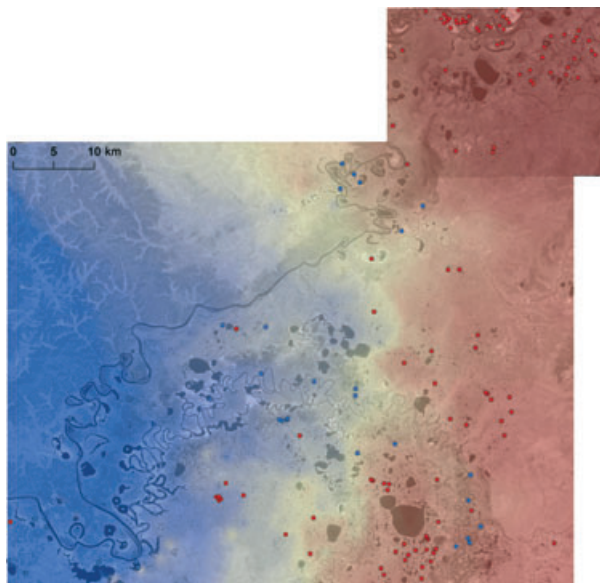


Fig. 2 Predicted probability surface of decreasing vs. increasing lake area in the Innoko study area based on logistic regression model. Colored surface generated by applying inverse distance weighted interpolation to predicted probabilities of decreasing for all lakes in the study area. Darker red shades indicate high probability of decreasing (maximum probability = 0.99). Darker blue shades indicate low probability of decreasing (minimum probability = 0.11). Intermediate shades (e.g., yellow) indicate intermediate probabilities. Colored dots are centroids of lakes with significant ($P < 0.05$) decreasing (red; $n = 110$) and increasing (blue; $n = 39$) trends used to build the logistic regression model. Other study areas are depicted in Supporting Figures S1–S9.

of 30% (SEM = 0.2%) (Table S2) and intra-annual rates of change, when compounded over a 90 day summer, yielded -100 to +56% changes in lake area.

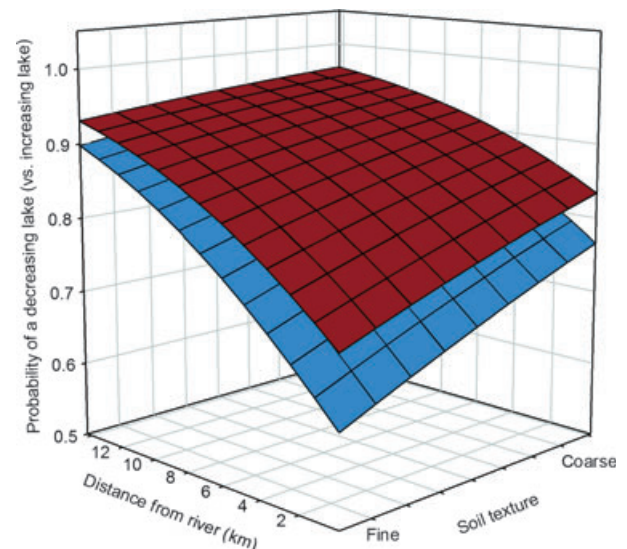


Fig. 3 Predicted probabilities of decreasing vs. increasing lake area from a logistic regression model of the effects of distance from river, soil texture, and the occurrence of a wildfire from 1942 to 2007. Red surface shows probabilities with fire occurrence. Blue surface shows probabilities in the absence of fire. For ease of demonstration, the mean intercept among all 10 study areas (i.e., fixed intercept effect) is shown.

Relationship between trends and landscape characteristics

The logistic regression model to predict the probability of a lake decreasing or increasing in size that had the lowest AIC included three predictor variables: soil texture, distance from nearest river, and the occurrence of wildfire (Fig. 3). All three effects were significantly different from zero at $\alpha = 0.05$. Elevation, permafrost extent, and permafrost ice content were not significant predictors of the direction of lake area trends and were

not included in the final model. Decreasing lake area was 2 and 1.4 times more likely on well-drained rocky and sandy soils, respectively, than on fine-grained silty soils and was 1.5 times more likely if a lake was within a wildfire boundary (Table 2). Decreasing lake area was also more likely farther from rivers (Fig. 3, Table 2) where lakes are less likely to be recharged by flooding and more likely to have downslope flow paths and negative hydraulic pressure gradients between surface water and subsurface groundwater systems. The model had moderate (Landis & Koch, 1977) predictive power based on the 20% hold-out sample (Table 3) ($\kappa \pm 95\%$ confidence interval = 0.43 ± 0.085 ; prevalence-adjusted bias-adjusted kappa statistic = 0.53, maximum attainable kappa = 0.84) (Sim & Wright, 2005).

Discussion

Rates of change

Annual rates of change for study areas may compound to yield substantial cumulative reductions in lake area (Fig. 4; Table 1). For example, lake area for the five declining study areas could be reduced by 30–80% within 50 years if annual rates of change continue (Fig. 4; Table 1). The one study area with a net increasing trend would not counteract reductions in other areas (Fig. 4; Table 1). Overall effects will likely alter the fundamental nature of surface water hydrology in Alaskan NWRs and, half of the refuge study areas are unlikely to maintain their value as waterfowl production areas in the face of 30–80% reductions in lake area.

Spatially heterogeneous decreasing and increasing lake trends could be due to natural lake life cycles (Billings & Peterson, 1980), even in a stable climate.

Table 3 Classification matrix of the number of correctly and incorrectly classified decreasing and increasing lakes using the logistic regression model applied to a 20% holdout sample with known trends

Predicted trend	Known trend		Total
	Decreasing	Increasing	
Decreasing	308	44	352
Increasing	77	87	164
Total	385	131	516

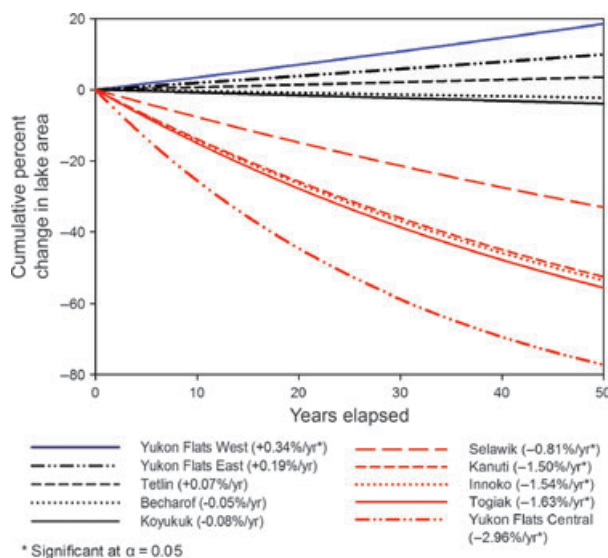


Fig. 4 Projected cumulative percent change in lake area for each of 10 study areas in Alaskan National Wildlife Refuges during the next 50 years assuming post-1985 annual rates of change continue. Red lines indicate study areas with decreasing trends. The blue line indicates the study area with an increasing trend. Black lines indicate study areas with nonsignificant trends. Asterisks indicate significance at $\alpha = 0.05$.

Table 2 Logistic regression coefficients and odds ratios quantifying the effects of landscape variables on the probability that a lake will have a decreasing or increasing lake area trend for 10 study areas in Alaska. Odds ratios represent the change in odds of a lake decreasing vs. increasing for the specified unit change in the predictor variable

Parameter	Coefficient	SE	P-value	Unit change	Odds ratios		
					Ratio	95% confidence limits	
Distance from river	0.469*	0.160	0.0035	1 km	1.126	1.040	1.219
Soil texture	0.438*	0.174	0.0122	Sandy vs. Silty	1.424	1.080	1.877
				Rocky vs. Sandy	1.424	1.080	1.877
				Rocky vs. Silty	2.028	1.167	3.525
Fire history (1942–2007)	0.427*	0.186	0.0216	Fire vs. No fire	1.533	1.065	2.206

*Significantly different from zero at $\alpha = 0.05$.

However, net declines in lake area within and among study areas indicated that a dynamic equilibrium was not always present at large spatial extents. A unidirectional external force such as climate change may be tipping the balance of decreasing and increasing lakes (Fig. 2, Figures S3, S5, S6, S8, Table S2).

Our observations of dramatic interannual and intra-annual variability in lake area emphasize the need to account for among and within-year variability when estimating long-term trends. The variable magnitude and direction of intra-annual trends among lakes and among study areas likely reflect differential influences of evapotranspiration, snow melt, precipitation, and glacial runoff on individual lake water balances.

Relationship between trends and landscape characteristics

There was no indication of a latitudinal (Arctic to subarctic) or longitudinal (continental to maritime) pattern in net study area trends (Fig. 1) suggesting that lake change may be driven by a complex interaction between climate forcing and fine-scale variability in lake hydrological processes influenced by permafrost degradation, substrate permeability and/or landscape position. The logistic regression analysis identified relationships between lake trends and landscape characteristics that were consistent with this expectation (Fig. 3). Our results indicated that wildfire and climate warming may promote decreasing lake area, likely by thawing permafrost (Swanson, 1996; Burn, 1998; Osterkamp & Romanovsky, 1999; Osterkamp, 2007), thus, increasing substrate permeability and drainage to either deep or shallow groundwater systems, particularly on coarse, well-drained soils, and farther from rivers. Lakes that are farther from rivers are more likely to have downslope flow paths and negative hydraulic gradients between surface water and groundwater systems and are less likely to be flooded by overland flow. Our study is the first to provide quantitative evidence for such a mechanism across a large spatial extent (longitudinal and latitudinal gradients spanning ca. 1000 km).

The degree of permafrost degradation is affected both by inherent permafrost stability, which is influenced by air temperature and local variation in substrate insulation, solar radiation, and topography (Jorgenson *et al.*, 2010), and external events such as wildfire (Burn, 1998). While our findings lend support to an influence of wildfire on decreasing lake area, likely through its effects on permafrost, the coarse resolution of permafrost extent maps may have limited our ability to detect the effects of inherent permafrost stability on individual lake trends. There was, however, a suggestion of a relationship between permafrost extent and net study area trends. The one study area

located entirely in continuous permafrost (Yukon Flats West) was the only study area to have a net increasing trend while study areas with net decreasing or negligible trends had more unstable permafrost. This finding is consistent with the hypothesis that initial thawing in relatively stable permafrost zones may lead to a transitory increase in lake area due to thermokarst (Burn & Smith, 1990; Roach *et al.*, 2011) while continued degradation in discontinuous permafrost regions, particularly those with coarse-grained soils and farther from rivers, may lead to declining lake area (Yoshikawa & Hinzman, 2003; Smith *et al.*, 2005).

While this model provided a mechanistic explanation for patterns of lake change within study areas, the coarse nature of available data limited its ability to explain finer scale heterogeneity (Fig. 2, Figures S1–S9). The current scale of model predictions is commensurate with management strategies such as land exchange. However, availability of finer resolution maps of permafrost, substrate, lake bathymetry, lake inflow to evaporation ratios, and other hydrological processes may further improve the predictive power of models and their utility for finer scale objectives.

The loss of surface water to either shallow or deep groundwater systems may have substantial effects on basin-wide carbon cycling between terrestrial and aquatic systems (Striegl *et al.*, 2005). An increase in winter groundwater flow has been documented throughout the Yukon River Basin of Alaska since ca. 1940s and is thought to be a direct result of permafrost thawing and increased infiltration of surface water to shallow groundwater systems (Walvoord & Striegl, 2007; Brabets & Walvoord, 2009; Jepsen *et al.*, 2013). Increased groundwater in the Yukon River Basin and the resulting deeper flow paths and longer hydraulic residence time have been linked to increased respiration of dissolved organic carbon (DOC) in terrestrial systems and decreased DOC export to rivers and oceans (Striegl *et al.*, 2005). Thus, the loss of lake surface water to groundwater systems may facilitate the release of high latitude reservoirs of carbon to the atmosphere which could provide a substantial positive feedback to climate warming (Harden *et al.*, 2012).

Lake drainage and wildfire may also facilitate the growth of floating mat vegetation on lake surfaces as lakes become shallower, water temperatures increase, and nutrients are released. Encroachment of floating mat vegetation has been identified as a primary process involved in decreasing lake area in Alaska (Roach *et al.*, 2011) and is a well-documented phase of terrestrialization, an infilling process that converts lakes to peatland systems (Hu & Davis, 1995; Campbell *et al.*, 1997). This accumulation of organic matter in lake basins may at least partially offset a terrestrial increase in CO₂ release

due to deeper flow paths (Payette *et al.*, 2004; Roach *et al.*, 2011; Jones *et al.*, 2012). However, peatland development can also increase methane efflux, which is a more powerful greenhouse gas than carbon dioxide. These potential effects of terrestrialization should be considered when evaluating the net effect of declining lake area on carbon budgets and radiative forcing.

This study identifies soil drainage properties, proximity to rivers, and wildfire as factors that may influence the spatially heterogeneous responses of lakes to climate change and thawing permafrost. We contend that climate warming and resulting permafrost degradation will have the greatest probability of causing lake decline in burned areas with well-drained soils and farther from rivers where overland flooding is more unlikely and downslope flow paths and negative hydraulic gradients between surface water and groundwater systems are more common. The quantification of the effects of broadly mapped landscape characteristics on the probability that a lake will decrease or increase in size is an important step toward predicting the future of the Arctic landscape. This information will assist local land managers and national strategic planners in identifying lakes with high and low risk of decline to prepare for and adapt to a changing climate.

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Supporting Information

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

Figure S1. Predicted probabilities of decreasing vs. increasing lake area in the Tetlin study area based on logistic regression model.

Figure S2. Predicted probabilities of decreasing vs. increasing lake area in the Yukon Flats East study area based on logistic regression model.

Figure S3. Predicted probabilities of decreasing vs. increasing lake area in the Yukon Flats Central study area based on logistic regression model.

Figure S4. Predicted probabilities of decreasing vs. increasing lake area in the Yukon Flats West study area based on logistic regression model.

Figure S5. Predicted probabilities of decreasing vs. increasing lake area in the Kanuti study area based on logistic regression model.

Figure S6. Predicted probabilities of decreasing vs. increasing lake area in the Selawik study area based on logistic regression model.

Figure S7. Predicted probabilities of decreasing vs. increasing lake area in the Koyukuk study area based on logistic regression model.

Figure S8. Predicted probabilities of decreasing vs. increasing lake area in the Togiak study area based on logistic regression model.

Figure S9. Predicted probabilities of decreasing vs. increasing lake area in the Becharof study area based on logistic regression model.

Table S1. Dates of each series of Landsat TM/ETM+ imagery used to estimate annual trends in lake area.

Table S2. Summary statistics by study area of individual lake coefficients of variation in area, intra-annual lake area trends and annual lake area trends since ca. 1985.