Plant Soil (2017) 421:31–42
DOI 10.1007/s11104-017-3411-x

REGULAR ARTICLE

Sensitivity of carbon stores in boreal forest moss mats - effects of vegetation, topography and climate

Robert J. Smith · Sarah Jovan · Andrew N. Gray · Bruce McCune

Received: 22 March 2017 / Accepted: 4 September 2017 / Published online: 26 September 2017

Abstract
Background and aims In northern regions, moss and lichen mats are the major carbon-cycling interface between soils and the atmosphere. We aimed to quantify sensitivity of ground layer nutrient stores to environmental predictors, to better understand interactions with vegetation, topography and climatic conditions.
Methods With non-destructive forest inventory techniques, we estimated distributions of biomass, carbon and nitrogen among moss/lichen ground layers in a 1.1 million-ha watershed within Alaska's boreal forest region. Using nonparametric multiplicative regression, we fit response surfaces and quantified sensitivity to environmental predictors.
Results Across 96 sites, half the ground layer biomass values were in the range 4750–18,900 kg ha^{-1} (25th to 75th percentiles). Carbon and nitrogen stores peaked in older stands and those with little forb cover (suggesting low disturbance) and low incident radiation. Among functional groups, the most abundant were nitrogen-fixing feather mosses, which formed extensive carpets. Nutrient stores were most sensitive to local vegetation and topography predictors, but less sensitive to regional climate.
Conclusions Moss and lichen mats in boreal forests are substantial carbon and nitrogen stores, with consequences for carbon sequestration and ecosystem productivity. Their environmental sensitivity suggests that ground layer nutrient stores could decrease if global changes promote vascular vegetation expansions and intensifying wildfire regimes.

Keywords Boreal forests · Carbon sequestration · Climate change sensitivity · Interior Alaska · Nitrogen cycling · Nonparametric multiplicative regression · Soil-atmosphere transition · Soil nutrients · Wildfire regimes

Responsible Editor: Jeffrey Walck.

R. J. Smith (✉) · B. McCune
Department of Botany and Plant Pathology, Oregon State University, 2082 Cordley Hall, Corvallis, OR 97331, USA
e-mail: smithr2@oregonstate.edu

S. Jovan · A. N. Gray
USDA Forest Service, Portland Forestry Sciences Laboratory, 620 SW Main, Suite 400, Portland, OR 97205, USA

Introduction

High-latitude forests are central to understanding global changes because of biophysical feedbacks between vegetation, soils, and the atmosphere (Bonan 2008). Carbon exchange in boreal forests is mediated in no small part by the "ground layer", which is the three-dimensional stratum of mosses and lichens that occupy terrestrial surfaces. Ground layers (which include both living and dead organic material) are categorically neither soils nor above-ground vegetation, but instead occupy a unique transitional interface where soils and the atmosphere meet (Fig. 1). Terrestrial mosses and lichens have long been recognized as pivotal actors in global climate feedbacks and local nutrient budgets (e.g., Rennie 1807; Geikie 1866; Stålfelt 1937; Gorham 1953; Tamm

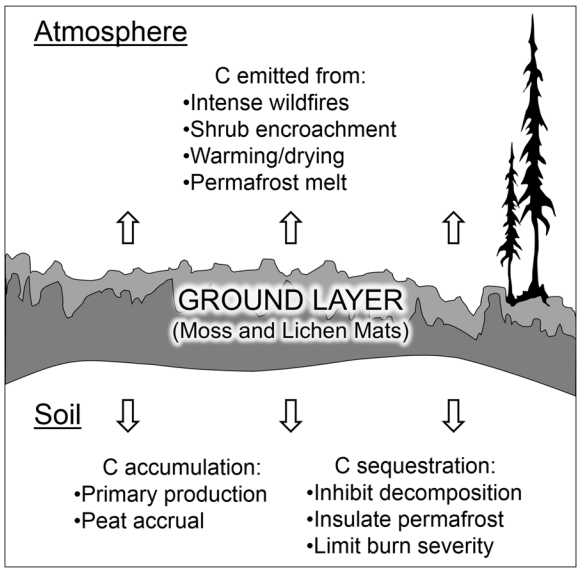

Fig. 1 Conceptual carbon balance in moss and lichen mats at the soil–atmosphere interface. Carbon storage is in both aboveground and transitional organic matter. In addition to regulating carbon cycling, ground layer organisms have many other functions (Table 1)

1953). Recent global changes (e.g., changes in air temperature trends, moisture patterns and disturbance regimes) have revived interest in quantifying how much carbon and nitrogen are stored in ground layers, and on the environmental conditions under which nutrients are accumulated and sequestered. If northern high-latitude climates continue to warm following recent trends (Chapin et al. 2014), thawing permafrost and peat decomposition beneath ground layers may accelerate CH_4 and CO_2 releases that could further amplify climatic warming (McGuire et al. 2009).

Moss mats account for one-fifth of all net carbon uptake and more than half of nitrogen fixation in boreal forest understories (Lindo et al. 2013; Hasselquist et al. 2016). The carbon storage capacity of ground layers is potentially huge since moss-dominated peatlands currently store about 33% of the world's terrestrial carbon (Yu 2012), most often in poorly drained tundra and boreal forests presumed to be of minor commercial value. Ecosystem engineers like peat-forming *Sphagnum* mosses simultaneously take up atmospheric carbon and inhibit decomposition by altering the pH and water content of soils (Clymo et al. 1998). Despite large carbon sequestration potential, it is unclear whether ground layers might switch from sinks to sources under projected global changes.

Carbon storage in subarctic ground layers may face a variety of challenges. In high-latitude habitats, an increase in surface temperatures and CO_2 concentrations promotes growth of tall shrubs that outcompete shorter-statured lichens and mosses (Cornelissen et al. 2001; Elmendorf et al. 2012; Lang et al. 2012). A particular concern are forage lichens on which caribou and other wildlife depend, and whose decline would have socio-economic impacts on hunting, tourism and subsistence practices (Joly et al. 2009). Another factor promoting ground layer carbon losses is the intensifying pattern of boreal forest wildfires. Recently, large wildfires resulted in greater carbon emissions than at any point in the last several thousand years (Turetsky et al. 2011; Kelly et al. 2013; Hu et al. 2015). They also occurred later in the growing season when ground layers have dried, which increased both burn depth and combustive carbon losses (Kasischke and Chapin 2008).

Understanding how global changes will interact with carbon cycling at the soil–atmosphere interface (Fig. 1) requires estimating status and trends in carbon pools. Quantifying forest floor and soil carbon now takes a central role in national forest inventories of the United States, Canada, Sweden, and other nations with boreal forests (Woodall et al. 2012; Bona et al. 2013; Swedish NFI 2013). For example, the US Forest Service's Forest Inventory and Analysis (FIA) program now focuses on interior Alaska, which is the last large region of the United States without a systematic forest inventory (Mueller and Irvine 2015). Boreal forests of interior Alaska have a great variety and abundance of ground layer mosses and lichens, although ground layers have never before been measured systematically over such large landscapes. Overlooking ground layers in forest inventory protocols would grossly underestimate carbon stores (Bona et al. 2013).

We aimed to estimate ground layer biomass, carbon, nitrogen, and ecosystem functions from a systematic forest inventory at 96 sites in the Tanana River valley of interior Alaska. Data were from a pilot for the FIA Interior Alaska Inventory, which aims to sample more than four thousand plots throughout the entirety of interior Alaska over the next decade (Mueller and Irvine 2015). Primary objectives were to identify the best environmental predictors of each ground layer attribute, to quantify their environmental sensitivity, and to estimate potentially nonlinear response surfaces. We initially expected greater sensitivity to climate predictors, relative to topography or vegetation, because of climatic control of

photosynthesis and respiration that determine carbon balance. We discuss our findings in the context of regional changes and carbon balances, and also explore opportunities to unify inventory data with emerging methods for predictive carbon estimation.

Materials and methods

Study area and sampling design

Our study was part of a first-year pilot project for the FIA Interior Alaska Inventory (Mueller and Irvine 2015), a multi-year effort that combines field plot and airborne sampling to document status and trends of forest soils, trees, vegetation, fuels, downed woody materials, and other forest attributes. The study area was the Tanana River valley of interior Alaska, north of the Alaska Range and south of the Yukon-Tanana uplands, in an area bounded by 61.5–66.5 °N and 141–153 °W (Fig. 2). Most of the area was coniferous boreal forest dominated by black spruce and white spruce (*Picea mariana* and *P. glauca*), in addition to extensive areas of deciduous hardwoods forest including aspen, paper birch and balsam poplar (*Populus tremuloides, Betula neoalaskana, Populus balsamifera*). Habitats included a heterogeneous mixture

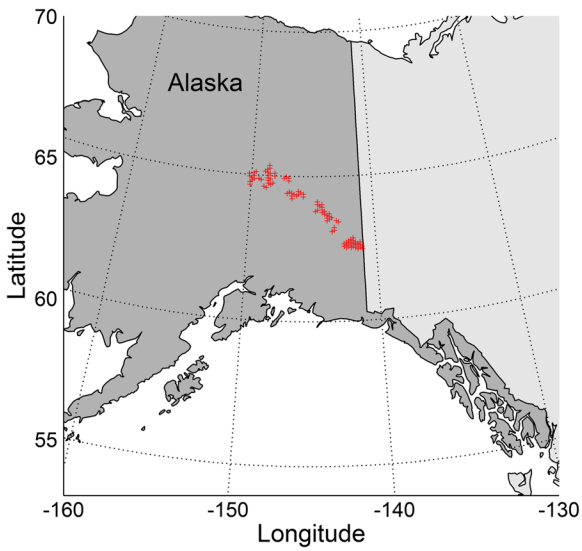

Fig. 2 Map of the study area in interior Alaska. Cross symbols indicate locations of 96 plots in the Tanana River valley of interior Alaska, within which ground layers were measured in June–August of 2014. The study area was the Tanana River valley of interior Alaska, north of the Alaska Range and south of the Yukon-Tanana uplands. Plot locations are fuzzed for privacy

of lowland and upland sites. For the pilot study conducted June–August of 2014, FIA crews measured 96 plots at sites systematically located on 1.1 million ha of forested public lands (Tanana Valley State Forest and Tetlin National Wildlife Refuge). Plots, each of 0.38 ha area, were evenly spaced on a regular hexagonal grid to facilitate airborne surveys (not reported here), with one plot per 9712-ha polygon overlaying the study area (Pattison et al. 2017). Among other measurements described below, crews used the Ground Layer Indicator (Smith et al. 2015) to measure ground layer attributes.

Ground layer attributes

First, we estimated ground layer attributes at each of the 96 sites using the FIA Ground Layer Indicator (Smith et al. 2015), which is a nondestructive method that uses prior calibrations to convert field-measured depth and cover of moss and lichen functional groups into a plot-level estimate of biomass, carbon, and nitrogen for each functional group (Table 1). Field measurements were restricted to mosses and lichens growing over terrestrial substrates, which included other mosses, small rocks, soils or downed woody materials that lacked bark. Workers did not collect or harvest plant material and were not required to know species' identities. Each plot had 32 rectangular microquads of 20 × 50 cm (1000 cm^{-2} area). In each microquad, and for each functional group in the predefined set (Table 1), workers visually estimated cover classes (with breakpoints at 0%, 0.1%, 1%, 2%, 5%, 10%, 25%, 50%, 75%, 95%, 99%, 100%), and measured depth to the nearest cm using a slender steel rod (7 mm diameter, 23 cm length, marked at 1-cm intervals, with a narrowly pointed tip); this gives a field-based measure of volume. The field method includes green photosynthetic material and undecomposed fibric material (live or dead), but excludes partially or fully decomposed peat that may form in deeper layers. Depth measurements are intentionally truncated at 40 cm deep, and therefore are expected to give conservative estimates. With the Ground Layer Indicator, a potentially large number of plots can be evaluated rapidly since the field measurements take less than 2 h per plot (Smith et al. 2015). A further benefit is the capacity to quantify the relative importance of ecosystem functions based on a defined set of functional groups (Table 1). Examples of ground layer ecosystem functions include wildlife forage, biological N-fixation, paludification and water table modification, soil cooling, soil and detritus binding, animal habitat, interception and

Table 1 Functional groups and their estimated abundances at 96 plots on forested lands in the Tanana River region of interior Alaska

Functional group	Functions	Biomass (kg ha^{-1})		C (kg ha^{-1})		N (kg ha^{-1})		Cover (%)	
		Mean	*SE*	Mean	*SE*	Mean	*SE*	Mean	*SE*
Biotic soil crust	Soil trapping, soil water influx, disturbance indicator	3.0	2.3	1.4	1.0	< 0.1	< 0.1	< 0.1	< 0.1
Eutrophic lichens	Indicate nutrient over-enrichment	0.4	0.3	0.2	0.2	< 0.1	< 0.1	< 0.1	< 0.1
Forage lichens	Wildlife forage (caribou, etc.)	446.4	146.7	198.1	65.1	2.7	0.9	2.7	0.8
Foliose lichens	Invertebrate habitat, bare site colonization	8.7	6.5	3.8	2.9	0.1	0.1	0.1	0.1
Fruticose lichens	Invertebrate habitat, bare site colonization	70.4	32.5	31.2	14.4	0.5	0.2	0.7	0.3
N-fixing foliose lichens	N-fixation, C:N modification	158.4	66.8	70.3	29.6	4.1	1.7	1.9	0.8
N-fixing fruticose lichens	N-fixation, increases albedo	34.1	9.9	15.1	4.4	0.9	0.3	0.3	0.1
Feather mosses	Rainfall interception, soil cooling	734	266.9	325.8	118.5	8.9	3.2	3.2	1.2
N-fixing feather mosses	Broad-area N-fixation, soil cooling	7799.2	1384.2	3461.5	614.4	88.9	15.8	25.3	4.1
Sphagnum peat-mosses	Carbon storage (peat), water regulation, soil cooling	2244.8	646.8	996.3	287.1	21.1	6.1	5.0	1.5
Turf mosses	Soil accrual, bare site colonization	1030.2	343.3	457.2	152.4	10.3	3.4	6.7	1.8
Flat liverworts	Soil/detritus binding, water infiltration	23.6	10.6	10.5	4.7	0.4	0.2	0.2	0.1
Leafy liverworts	Soil/detritus binding, water infiltration	18.9	11.5	8.4	5.1	0.3	0.2	0.1	0.1

Each of the mutually exclusive groups integrates growth forms, potential indicator status and ecosystem effects. Functions follow Smith et al. (2015) based on literature references therein

retention of precipitation, and many other functional effects on ecosystems. Nondestructive biomass estimates were based on a bulk density calibration curve, generated by previous destructive sampling in the same locality, which described bulk density as a negative exponential function of mat depth (Smith et al. 2015). Biomass for each microquad was then calculated as the arithmetic product of the estimated bulk density and the field-measured volume. Estimated mean biomass for a given plot was simply the mean of all 32 microquads, scaled to kg ha^{-1}. Carbon and nitrogen content for each functional group were then calculated as proportions of biomass based on previous destructive sampling with lab analysis, described more fully by Smith et al. (2015). For all ground layer attributes, we then calculated summary statistics and generated histograms of biomass among different functional groups. We used R software version 3.3.1 (R Core Team 2016) for most analyses besides the nonlinear regression of environmental predictors (below).

Uncertainty analyses

Because biomass estimates were based on a preexisting bulk density calibration curve, and because errors may propagate throughout the estimation procedure, we estimated the effects of measurement and model uncertainty using a three-tiered hierarchical bootstrap resampling analysis. Bootstrap resampling (drawing independent observations with replacement to construct a sampling distribution) is a nonparametric approach that allows determining error rates of a prediction without making assumptions about model forms or statistical distributions (Manly 2007). It is commonly used to account for uncertainty in estimates of forest biomass (Rice et al. 2004; Saatchi et al. 2007; Montesano et al. 2014). Specifically, we resampled with replacement from the original calibration dataset of destructive

samples, each replicate having the same size as the calibration dataset (n = 150 observations), then used each bootstrap replicate to recalculate new bulk density calibration curves, new microquad biomass estimates and new plot-level biomass estimates. We repeated this procedure for each of 999 bootstrap replicates, and calculated root mean square error (RMSE) as a measure of the quality of each estimate. The outcome was to quantify how uncertainty propagates to predictive error (RMSE) through each of three distinct levels: 1) the bulk density calibration model, 2) predicted biomass of microquads within plots, and 3) predicted biomass of entire plots. The original formulation of the Ground Layer Indicator (Smith et al. 2015) also used bootstrap methods to identify minimum sampling requirements with respect to number of microquads per plot.

Environmental predictors

We used nonlinear regression methods to evaluate responses of four ground layer attributes: plot mean biomass, mean total carbon content, mean total nitrogen content and the total number of functional groups (functional group richness, FGR). Candidate predictors (Table 2) included vegetation, climate, and topographic variables. Vegetation variables were from field measurements taken concurrently with ground layer measurements according to FIA protocols (FIA 2014a; b). For example, litter depth was the average of eight point measurements per plot; seedling count was the average counts of trees <2.54 cm diameter in four microplots of 13.5 m^2 area each; and stand age was the average of at least three tree cores per plot (FIA 2014a; b). Vegetation cover was ocular estimation of vertically-projected canopy cover for each layer (trees, shrubs, forbs and grasses), which we later transformed by taking the arcsine-square-root to emphasize differences in values towards the ends of the 0–100% measurement scale. Climate variables were annual mean 30-year normals (1981–2010) extracted from the ClimateNA database (Wang et al. 2012). Some topographic variables were

Table 2 Candidate predictors tested to model responses of biomass, carbon, nitrogen and functional group richness

Symbol	Predictor	Type	Description	Units	Ref.
litt	Litter depth	Vegetation	Depth of litter overlying mosses and lichens	cm	a
seed	Seedling count	Vegetation	Number of tree seedlings occurring in subplots	count	a
age	Stand age	Vegetation	Field-estimated age of the plot trees, from 3 cores	years	a
tree	Tree cover	Vegetation	Arcsine-square-root transformed cover of trees	proportion	a
shrub	Shrub cover	Vegetation	Arcsine-square-root transformed cover of shrubs	proportion	a
forb	Forb cover	Vegetation	Arcsine-square-root transformed cover of forbs	proportion	a
grass	Grass cover	Vegetation	Arcsine-square-root transformed cover of grasses	proportion	a
slope	Slope	Topographic	Angle of slope	degrees	a
asp	Folded aspect	Topographic	Slope direction, increasing along a NE–SW axis	degrees	b
pdir	Potential direct incident radiation	Topographic	Potential annual direct incident solar radiation a slope receives, based on slope, aspect, and latitude	MJ cm^{-2} y^{-1}	b
htld	Heat load	Topographic	Potential heat index of a slope, accounts for both radiation and southwestness of aspect	unitless	b
mat	Mean annual temperature	Climate	Mean annual air temperature	°C	c
td	Continentality	Climate	Temp difference between warmest/coldest months	°C	c
map	Mean annual precipitation	Climate	Mean annual precipitation	mm	c
ahm	Annual heat moisture index	Climate	Ratio of temperature to precipitation	unitless	c
ffp	Frost-free period	Climate	Length of the frost-free period	d	c
pas	Percent precip as snow	Climate	Percent of annual precip in snow form	%	c
cmd	Climatic moisture deficit	Climate	Hargreaves climatic moisture deficit	mm	c

[a] FIA (2014a)

[b] McCune and Keon (2002)

[c] Wang et al. (2012)

measured on site (aspect, slope), while others (potential direct incident radiation, heat load) were subsequently calculated as a function of slope and aspect following Eq. 2 in McCune and Keon (2002).Potential direct incident radiation (PDIR) expresses the expected amount of radiation which a given slope receives annually, in units of MJ cm^{-2} y^{-1}. Forest types were defined by dominant live tree species (FIA 2014a).

To select predictors and fit models, we used nonparametric multiplicative regression (NPMR: McCune 2006) in HyperNiche version 2.25 (McCune and Mefford 2011). NPMR is a kernel regression method that estimates mean responses as a smoothed function of all possible interactions of an optimized subset of predictors. For this, we used a local mean model with a Gaussian kernel and HyperNiche's default parsimony criteria settings (overfitting control setting = "medium", minimum average neighborhood size = 7.5, improvement criterion = 5, and minimum data-to-predictor ratio = 10), with model fit assessed by leave-one-out cross-validated R^2 (xR^2). Preliminary analyses (not reported) using $\log_{10}$-transformations of biomass, carbon, and nitrogen did not improve predictive capacity, and were not required to meet NPMR model assumptions, therefore we used untransformed data throughout. We performed randomization tests (100 randomizations per regression model) to test the null hypothesis that the fit of each selected model was no better than obtained at random. We calculated sensitivity as a measure of the relative importance of each environmental predictor. Specifically, sensitivity was calculated as the mean absolute difference in each response that resulted from perturbing each predictor ±5% of its range, expressed as a proportion of the range of the response variable. Therefore, sensitivity values = 0 would indicate that perturbing a predictor has no effect on the response, while values = 1 would indicate that perturbing a predictor yields an equal-magnitude change in the response variable.

Results

Ground layer attributes and uncertainty

At 96 plots located in the Tanana River valley of interior Alaska, ground layer biomass averaged 12,397 kg ha^{-1} (± 1345 sample standard error), including 5515 ± 583 kg ha^{-1} of carbon and 137 ± 15 kg ha^{-1} of nitrogen. The middle 50% of biomass values were in the range 4750–18,900 kg ha^{-1} (range from 25th to 75th percentiles)(Fig. 3). The frequency and relative abundances of functional groups varied across the Tanana landscape (Fig. 4). For example, nitrogen-fixing mosses (with cyanobacterial associates) were most frequent across the study area, and were often the most locally abundant functional group in a given plot. *Sphagnum* peatmosses occurred in fewer plots, but often achieved highest within-plot biomass. Forage lichens were moderate in frequency but also had considerable biomass where encountered (Fig. 4). On average there were 6.6 ± 1.9 functional groups per plot. Black spruce forest types in the Tanana River area had the greatest mean biomass (19,234 ± 2062 kg ha^{-1}) relative to other forest types. As a per-plot average, estimated mean biomass and mean nutrient content in black spruce forest types were roughly double that of white spruce forest types, and nearly four times that of most hardwood forest types (Table 3). Bootstrapped 95% confidence intervals for prediction error (RMSE) were assessed at the levels of the bulk density calibration model, the microquad estimates, and the plot estimates (Fig. 5). For the bulk density calibration model, the 95% bootstrap confidence interval for prediction error was 0.017–0.027 g cm^{-3}; for the microquad estimates it was 1.41–29.94 g per 1000 cm^{-2} microquad; and for the plot estimates it was 167.6–3917.8 kg ha^{-1} (Fig. 5).

Environmental predictors

The best predictors of biomass, carbon stores, and nitrogen stores were related to vegetation (stand age, forb cover and litter depth) and insolation (PDIR) (Table 4). Response surfaces and sensitivity to each of these environmental predictors were essentially identical for the three nutrient variables (biomass, carbon and nitrogen), as expected since the nutrient response variables were roughly proportional to each other. Estimated ground layer carbon and nitrogen were greatest in older stands, and were lowest in plots with high forb cover and high PDIR (Fig. 6). Variation in functional group richness was best explained by vegetation (seedling count and tree cover), and it was weakly sensitive to

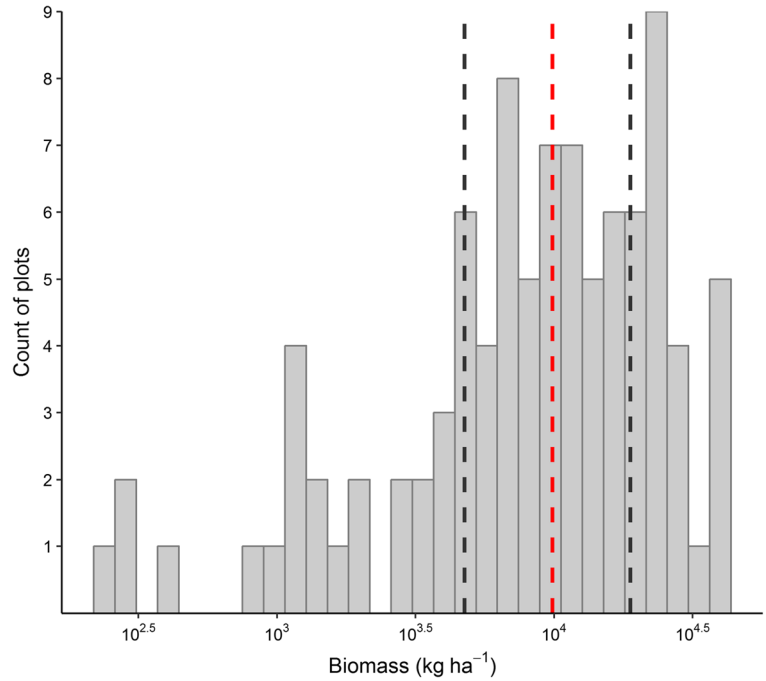

Fig. 3 Histogram of plot-level biomass (kg ha^{-1}) for 96 plots in the Tanana River valley of interior Alaska. Dashed lines indicate the median (red) and 25th and 75th percentiles (black) of the distribution of values. The middle 50% of biomass values were in the range 4750–18,900 kg ha^{-1} (range from 25th to 75th percentiles). Note that values on the horizontal axis are on a $\log_{10}$ scale

a climate proxy (percent precipitation as snow) (Table 4). Model fit, based on leave-one-out cross-validated R^2, ranged from xR^2 = 0.27–0.34 for the four models. All four regression

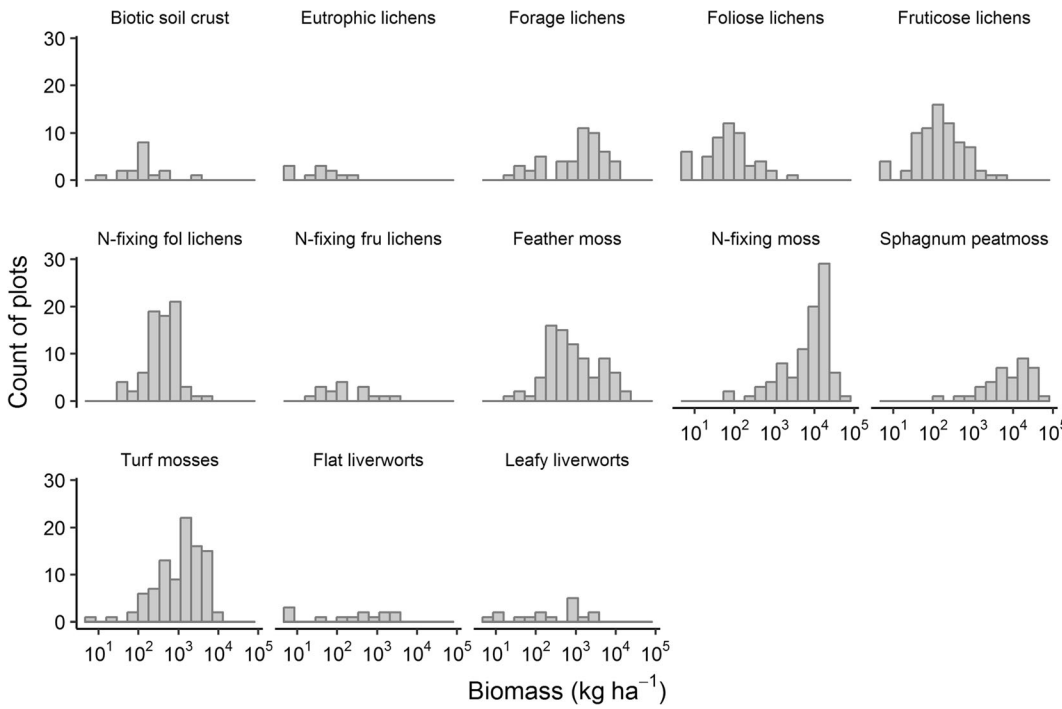

Fig. 4 Histograms of biomass ($\log_{10}$ scale) for 13 functional groups at 96 plots in the Tanana River valley of interior Alaska. N-fixing feather mosses were the most abundant and most frequent functional groupp. *Sphagnum* peatmosses occurred at fewer sites but tended to have high biomass when present. Relative distributions and abundances of functional groups can indicate their ecosystem effects across landscapes

Table 3 Estimated ground layer biomass, C and N by forest type for forested lands in the Tanana River region of interior Alaska

Forest type	Biomass (kg ha^{-1})		C (kg ha^{-1})		N (kg ha^{-1})	
	Mean	*SE*	Mean	*SE*	Mean	*SE*
White spruce	9370	2130	4147	942	106	24
Black spruce	19,234	2062	8541	919	210	21
Aspen	5290	1905	2354	852	58	21
Paper birch	5268	852	2331	381	58	10
Balsam poplar	247	90	112	45	3	1
Nonstocked	2735	2735	1211	1211	28	28
Overall	12,397	1345	5515	583	137	15

Biomass is expressed on an oven-dry basis

models had better fit than expected at random (randomization p-values all <0.05).

Discussion

Biomass, carbon and nitrogen stores in boreal ground layers

Mat-forming mosses and lichens in boreal forests are key actors in the accumulation and storage of carbon at the primary interface where soils and the atmosphere meet. We found that ground layers were a substantial biomass and carbon pool in boreal forests of interior Alaska. Our finding of 4750–18,900 kg ha^{-1} biomass is within the range of variability observed in other ground layer studies in the Tanana River area (Barney and van Cleve 1973; Mack et al. 2008), though slightly higher than other reports that excluded fibric organic matter (Mead 1995; Ruess et al. 2003). This gives a baseline estimate of the current carbon pool in the ground layer, and suggests that plot remeasurements could indicate carbon pool trends over time in interior Alaska.

Nitrogen-fixing feather mosses are an often overlooked part of nutrient cycles, yet they comprised the most abundant and frequent functional group in the Tanana River study area (Table 1 and Fig. 4). Because of their extensive coverage in boreal regions and ability to fix atmospheric nitrogen, cyanobacteria-harboring feather mosses have large landscape nutrient effects. Their sheer abundance makes up for comparatively modest nitrogen fixation rates (when compared per unit mass with nitrogen-fixing lichens; Gavazov et al. 2010). Carbon fixation in moss mats represents about 20% of all understory net primary production (Hasselquist et al. 2016), and nearly 50% of understory nitrogen fixation in boreal forests (Lindo et al. 2013) and high-latitude tundra (Stewart et al. 2011). This understory nutrient cycling route regulates N availability to vascular plants, as well as C and N mineralization rates in soils that affect ecosystem fluxes of both C and N (Lindo et al. 2013). Therefore, we suggest that forest inventories and dynamic vegetation models may consider including biomass of mosses, especially nitrogen-fixing feather mosses, to correctly portray nutrient budgets in boreal forests.

Environmental sensitivity and consequences

We found that biomass, carbon stores and nitrogen stores were sensitive to a topographically-derived measure of incident radiation (PDIR). This suggests that mass accumulation in ground layers is tied to physical

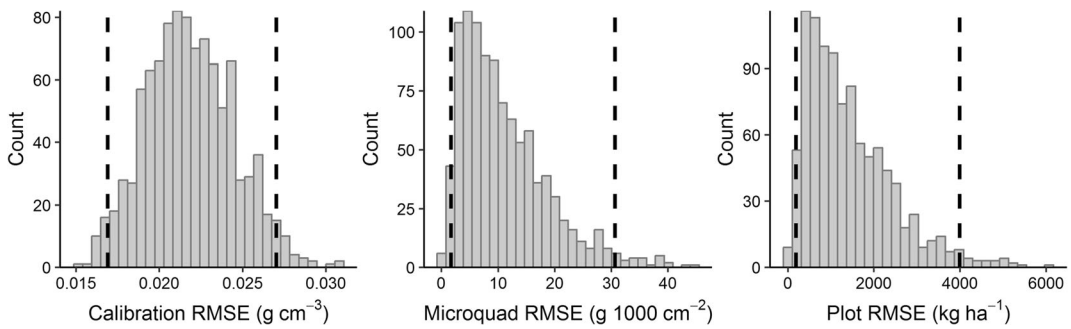

Fig. 5 Uncertainty analysis outcomes. Three-tiered hierarchical bootstrap resampling (999 replicates) gave measures of predictive error, measured as root mean square error (RMSE). Smaller RMSE values indicate lower predictive error. Outcomes are expressed for three distinct levels: 1) the bulk density calibration model, 2) predicted biomass of microquads within plots, and 3) predicted biomass of entire plots (from left to right). Dashed lines indicate the 25th and 75th percentiles of each distribution (lower and upper bounds of the interquartile range).

Table 4 Top predictors of ground layer biomass, total carbon, total nitrogen and functional group richness (FGR) as selected by nonparametric multiplicative regression, NPMR

Response	xR^2	N*	p	Predictor 1			Predictor 2			Predictor 3			Predictor 4		
				X	*Sens*	*Tol*	*X*	*Sens*	*Tol*	*X*	*Sens*	*Tol*	*X*	*Sens*	*Tol*
Biomass (kg ha^{-1})	0.31	4.9	0.03	age	0.35	21.5	pdir	0.23	0.09	forb	0.21	0.09	litt	0.09	2.72
Carbon (kg ha^{-1})	0.31	4.9	0.01	age	0.35	21.5	pdir	0.23	0.09	forb	0.21	0.09	litt	0.09	2.72
Nitrogen (kg ha^{-1})	0.27	5.4	0.01	age	0.31	21.5	pdir	0.20	0.09	forb	0.15	0.10	litt	0.08	2.63
FGR (count)	0.35	8.7	0.01	seed	0.55	10.3	tree	0.51	0.06	pas	0.08	97.7	–	–	–

See also the NPMR response surfaces (Fig. 3)

xR^2 *:* Cross-validated R^2 is the proportion of variation explained by each model, based on NPMR's leave-one-out cross-validation

N:* Neighborhood size is the average number of sample units used to estimate the response at a given point

p: Randomization *p*-value, the proportion of 100 randomized runs with fit ≥ observed fit

X: Predictor name (see Table 2 for symbols)

Sens: Sensitivity is a unitless measure of the relative importance of each predictor. Values = 0 indicate that perturbing a predictor has no effect on the response. Values = 1 indicate that perturbing a predictor yields an equal-magnitude change in the response variable

Tol: Tolerance is a measure of how broadly a point estimate depends on nearby plots in predictor unit space, representing one standard deviation of the Gaussian kernel

situations (e.g., north-facing slopes) where topography limits direct insolation that may otherwise prevent establishment of mosses and lichens. Yet, at the other extreme, heavy shading from dense herbaceous layers (especially tall shrubs) could lead to competitive exclusion of mosses and lichens (Cornelissen et al. 2001), a concept supported by our finding of decreased biomass at high forb abundances. Aside from its direct effects, PDIR may also be an indirect indicator of waterlogging and permafrost conditions that vary according to landscape position and topography. For example, growth and accumulation in ground layers depends in part on soil and groundwater attributes that were not directly measured during this inventory (e.g., watertable height, dissolved oxygen, phenolic content). Drought and falling water levels (from warming air temperatures and permafrost thawing) can reverse the anoxic, waterlogged conditions that inhibit decomposition from peat beneath ground layers, eventually leading to net carbon emissions (Gorham 1991; Fenner and Freeman 2011; Turetsky et al. 2011). Future efforts to estimate landscape carbon could benefit from using topographic landscape position as a proxy for important hydrologic and insolation attributes.

We documented more biomass and carbon in ground layers of old stands relative to young stands. This is consistent with evidence that moss and lichen mats are carbon sinks in older boreal forests, while they may be carbon sources following recent disturbances such as wildfires (Harden et al. 1997). This emphasizes the dual challenges that wildfires pose to carbon storage, not only for acute combustion losses, but also for legacy effects that may hinder carbon uptake even decades on. Biomass and elemental content also declined at high levels of forb cover, suggesting that post-fire conditions which promote forb growth in our study area could have corresponding negative effects on ground layers. In interior Alaska, forbs like fireweeds (*Chamerion* spp.) indicate strongly disturbed sites (Dyrness and Norum 1983), and could thus indicate poor areas for ground layer accumulation. We suspect that the negative association may not imply any direct impacts of vascular vegetation, but rather that vascular forbs and nonvascular ground layers may have contrasting recovery rates following disturbances.

Our finding of modest climate sensitivity was initially surprising given that climatic temperature and moisture should be strong controls on rates of photosynthetic carbon gain and respiratory carbon losses in ground layers and organic soils (Biasi et al. 2008). However, our study area was relatively homogeneous with regards to most climate values. Greater climatic sensitivity may

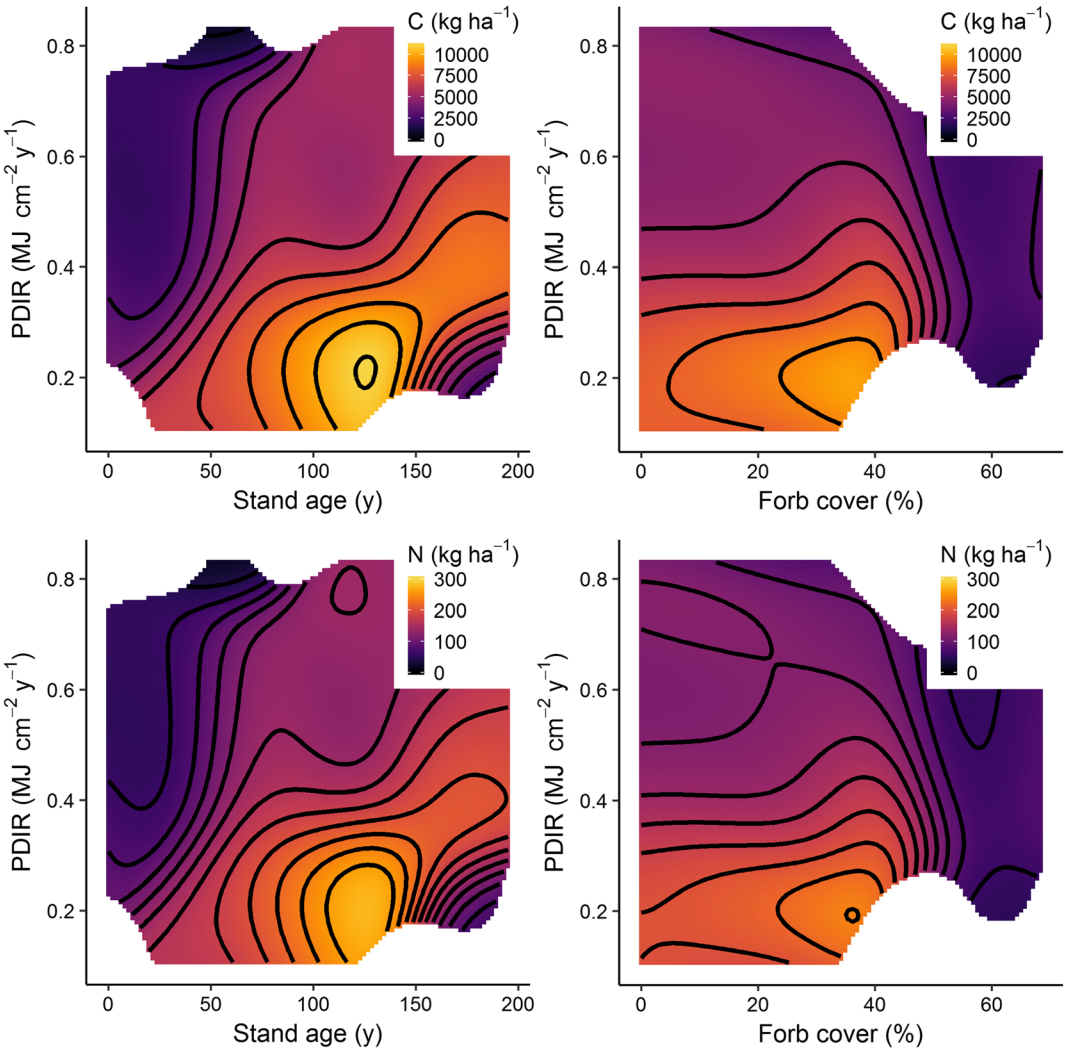

Fig. 6 Three-dimensional response surfaces showing mean carbon stores (top row) and mean nitrogen stores (bottom row) in response to potential direct incident radiation (PDIR) and vegetation attributes (stand age, forb cover). Both carbon and nitrogen, which were roughly proportional to each other, reached maximal values at high-to-intermediate stand ages, at low-to-intermediate forb cover, and at low insolation (PDIR). The NPMR model fitting process selects among many competing models to find the subset of variables that are most parsimonious in explaining variation in the response while maximizing fit; it identified PDIR, stand age, and forb cover as important predictors in explaining variation in the nutrient responses

be expected from steeper climatic gradients, for example, across the Alaska Range which induces a rainshadow in cold, dry, continental interior Alaska and separates northern areas from warmer maritime temperate forests closer to the Pacific coast.

Our findings provide a baseline from which to measure the direct and indirect effects of ongoing feedbacks between global changes, vascular vegetation, wildfire disturbances and moss/lichen ground layers. For example, atmospheric emissions from burned ground layers, as well as subsequent regrowth of fire-promoting vascular vegetation, could potentially amplify climate warming (Kasischke and Stocks 2000; Chapin et al. 2010; Turetsky et al. 2015). Insight into how ground layers contribute to these changes would benefit greatly from systematically collected data, which the FIA program is now implementing in the Tanana River region as part of a national forest inventory expansion. Anticipating regional changes in forests will require continued monitoring of vascular and nonvascular vegetation, as well as predictive approaches to estimating carbon pools.

Estimating carbon distributions

Mapping forest floor carbon (including litter, humus and fine woody debris) has been a valuable product of FIA inventories (Woodall et al. 2012; Wilson et al. 2013). Carbon estimation in ground layers could be linked with remote sensing approaches, which have recently been used for mapping forage lichen cover for caribou habitat (Nelson et al. 2013), fire effects on moss mats (Lewis et al. 2011), peatland drought status (Harris and Bryant 2009), ecosystem productivity of moss mats (Kushida et al. 2004), and forest floor organic carbon stores (Pastick et al. 2014). Lidar, hyperspectral and thermal imaging data could be calibrated with our ground layer biomass estimates to infer regional patterns through predictive modeling and imputation. Our determination of the key predictors of ground layer attributes (potential direct incident radiation, stand age and forb cover) should aid in refining remote sensing models by accounting for topography and vegetation covariates. Accurately estimating carbon pools may also require new FIA field techniques for sampling deep organic peat increments beyond 30 cm deep (Chimner et al. 2014). The union of field measurements, remote sensing and predictive modeling will provide opportunities for ground layer carbon estimation in a part of the United States that is at the forefront of ongoing global changes.

Acknowledgements This research was supported by Joint Venture Agreement 12-JVA-11261979 between the USDA Forest Service and Oregon State University. We thank Doug Daoust and Allison Nelson for project support, Bethany Schulz, Robert Pattison and Ken Winterberger for advising on the field method, and the Anchorage Forestry Sciences Laboratory for substantial contributions to field work. We are grateful to Jeffrey Walck and three anonymous reviewers for feedback that improved the manuscript.

References

Barney RJ, van Cleve K (1973) Black spruce fuel weights and biomass in two interior Alaska stands. Can J For Res 3:304–311

Biasi C, Meyer H, Rusalimova O et al (2008) Initial effects of experimental warming on carbon exchange rates, plant growth and microbial dynamics of a lichen-rich dwarf shrub tundra in Siberia. Plant Soil 307:191–205

Bona KA, Fyles JW, Shaw C, Kurz WA (2013) Are mosses required to accurately predict upland black spruce forest soil carbon in national-scale forest C accounting models? Ecosystems 16:1071–1086

Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320: 1444–1449

Chapin FS, McGuire AD, Ruess RW et al (2010) Resilience of Alaska's boreal forest to climatic change. Can J For Res 40: 1360–1370

Chapin FS, Trainor SF, Cochran P, et al (2014) Ch. 22: Alaska. In: Melillo JM, Richmond TC, Yohe GW (eds) Climate Change Impacts in the United States: The Third National Climate Assessment. U.S. Global Change Research Program, pp 514–536

Chimner RA, Ott CA, Perry CH, Kolka RK (2014) Developing and evaluating rapid field methods to estimate peat carbon. Wetlands 34:1241–1246

Clymo RS, Turunen J, Tolonen K (1998) Carbon accumulation in peatland. Oikos 81:368–388

Cornelissen JHC, Callaghan TV, Alatalo JM et al (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? J Ecol 89:984–994

Dyrness CT, Norum RA (1983) The effects of experimental fires on black spruce forest floors in interior Alaska. Can J For Res 13:879–893

Elmendorf SC, Henry GHR, Hollister RD et al (2012) Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nature Clim Change 2:453–457

Fenner N, Freeman C (2011) Drought-induced carbon loss in peatlands. Nat Geosci 4:895–900

FIA [Forest Inventory and Analysis Program] (2014a) Field Instructions for the Annual Inventory of Coastal Alaska 2014. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Anchorage, Alaska

FIA [Forest Inventory and Analysis Program] (2014b) Supplement to the Alaska Field Manual for installation of FIA Plots in the Tanana Valley Pilot in Interior Alaska. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Anchorage, Alaska

Gavazov KS, Soudzilovskaia NA, van Logtestijn RSP et al (2010) Isotopic analysis of cyanobacterial nitrogen fixation associated with subarctic lichen and bryophyte species. Plant Soil 333:507–517

Geikie J (1866) XXVIII. On the buried forests and peat mosses of Scotland, and the changes of climate which they indicate. T Roy Soc Edin-Earth 24:363–384

Gorham E (1953) Some early ideas concerning the nature, origin and development of peat lands. J Ecol 41:257–274

Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol Appl 1:182–195

Harden JW, O'Neill KP, Trumbore SE et al (1997) Moss and soil contributions to the annual net carbon flux of a maturing boreal forest. J Geophys Res 102:28805–28816

Harris A, Bryant RG (2009) A multi-scale remote sensing approach for monitoring northern peatland hydrology: Present possibilities and future challenges. J Environ Man 90:2178–2188

Hasselquist NJ, Metcalfe DB, Marshall JD et al (2016) Seasonality and nitrogen supply modify carbon partitioning in understory vegetation of a boreal coniferous forest. Ecology 97:671–683

Hu FS, Higuera PE, Duffy P et al (2015) Arctic tundra fires: Natural variability and responses to climate change. Front Ecol Environ 13:369–377

Joly K, Jandt RR, Klein DR (2009) Decrease of lichens in Arctic ecosystems: the role of wildfire, caribou, reindeer, competition and climate in north-western Alaska. Polar Res 28:433–442

Kasischke ES, Chapin FS (2008) Increasing vulnerability of Alaska's boreal forest as a result of climate warming and the changing fire regime. In: MacCracken M, Moore F, Topping JC Jr (eds) Sudden and Disruptive Climate Change: Exploring the Real Risks and How We Can Avoid Them. Earthscan, Sterling, pp 175–192

Kasischke ES, Stocks BJ (2000) Fire, Climate Change, and Carbon Cycling in the Boreal Forest. Springer Science & Business Media

Kelly R, Chipman ML, Higuera PE et al (2013) Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. PNAS 110:13055–13060

Kushida K, Kim Y, Tanaka N, Fukuda M (2004) Remote sensing of net ecosystem productivity based on component spectrum and soil respiration observation in a boreal forest, interior Alaska. J Geophy Res-Atmos 109:1–11

Lang SI, Cornelissen JHC, Shaver GR et al (2012) Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. Glob Change Biol 18:1096–1107

Lewis SA, Hudak AT, Ottmar RD et al (2011) Using hyperspectral imagery to estimate forest floor consumption from wildfire in boreal forests of Alaska, USA. Int J Wildland Fire 20:255–271

Lindo Z, Nilsson M-C, Gundale MJ (2013) Bryophyte-cyanobacteria associations as regulators of the northern latitude carbon balance in response to global change. Glob Change Biol 19:2022–2035

Mack MC, Treseder KK, Manies KL et al (2008) Recovery of aboveground plant biomass and productivity after fire in mesic and dry black spruce forests of interior Alaska. Ecosystems 11:209–225

Manly BFJ (2007) Randomization, Bootstrap and Monte Carlo Methods in Biology, 3rd edn. CRC Press, Boca Raton

McCune B (2006) Non-parametric habitat models with automatic interactions. J Veg Sci 17:819–830

McCune B, Keon D (2002) Equations for potential annual direct incident radiation and heat load. J Veg Sci 13:603–606

McCune B, Mefford M. 2011. Nonparametric Multiplicative Habitat Modeling. Version 2.25. MjM Software, Gleneden Beach, OR

McGuire AD, Anderson LG, Christensen TR et al (2009) Sensitivity of the carbon cycle in the Arctic to climate change. Ecol Monogr 79:523–555

Mead BR (1995) Plant Biomass in the Tanana River Basin, Alaska. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland

Montesano PM, Nelson RF, Dubayah RO et al (2014) The uncertainty of biomass estimates from LiDAR and SAR across a boreal forest structure gradient. Remote Sens Environ 154:398–407

Mueller B, Irvine D (2015) Collaborating for success: implementation of the interior Alaska inventory. In: Pushing Boundaries: New Directions in Inventory Techniques & Applications; Forest Inventory and Analysis (FIA) Symposium 2015. GTR-PNW-931. USDA Forest Service, Pacific Northwest Research Station, Portland, OR, p 197

Nelson PR, Roland C, Macander MJ, McCune B (2013) Detecting continuous lichen abundance for mapping winter caribou forage at landscape spatial scales. Remote Sens Environ 137:43–54

Pastick NJ, Rigge M, Wylie BK, et al (2014) Distribution and landscape controls of organic layer thickness and carbon within the Alaskan Yukon River Basin. Geoderma 230–231:79–94

Pattison RR, Andersen H-E, Gray AN et al (2017) Forests of the Tanana Valley State Forest and Tetlin National Wildlife Refuge Alaska - results of the 2014 pilot inventory. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rennie R (1807) Essays on the Natural History and Origin of Peat Moss. George Ramsay & Co., Edinburgh

Rice AH, Pyle EH, Saleska SR et al (2004) Carbon balance and vegetation dynamics in an old-growth Amazonian forest. Ecol Appl 14:55–71

Ruess RW, Hendrick RL, Burton AJ et al (2003) Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. Ecol Monogr 73:643–662

Saatchi SS, Houghton RA, Dos Santos Alvalá RC et al (2007) Distribution of aboveground live biomass in the Amazon basin. Glob Change Biol 13:816–837

Smith RJ, Benavides JC, Jovan S et al (2015) A rapid method for landscape assessment of carbon storage and ecosystem function in moss and lichen ground layers. Bryologist 118:32–45

Stålfelt MG (1937) Der Gasaustausch der Moose. Planta 27:30–60

Stewart KJ, Lamb EG, Coxson DS, Siciliano SD (2011) Bryophyte-cyanobacterial associations as a key factor in N_2-fixation across the Canadian Arctic. Plant Soil 344:335–346

Swedish National Forest Inventory (2013) Fältinstruktion 2013: RIS - Riksinventeringen av skog. SLU Institutionen för Skoglig Resurshushållning, Umeå, Sweden

Tamm CO (1953) Growth, yield and nutrition in carpets of a forest moss (*Hylocomium splendens*). Meddelanden Från Statens Skogsforskningsinstitut, Stockholm

Turetsky MR, Benscoter B, Page S et al (2015) Global vulnerability of peatlands to fire and carbon loss. Nat Geosci 8:11–14

Turetsky MR, Donahue WF, Benscoter BW (2011) Experimental drying intensifies burning and carbon losses in a northern peatland. Nat Commun 2:1–5

Wang T, Hamann A, Spittlehouse DL, Murdock TQ (2012) ClimateWNA—high-resolution spatial climate data for western North America. J Appl Meteorol Clim 51:16–29

Wilson BT, Woodall CW, Griffith DM (2013) Imputing forest carbon stock estimates from inventory plots to a nationally continuous coverage. Carbon Balance and Management 8:1–15

Woodall CW, Perry CH, Westfall JA (2012) An empirical assessment of forest floor carbon stock components across the United States. Forest Ecol Manag 269:1–9

Yu Z (2012) Northern peatland carbon stocks and dynamics: a review. Biogeosci Discuss 9:5073–5107