



## LETTER

## Lichen cover mapping for caribou ranges in interior Alaska and Yukon

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Matthew J Macander<sup>1</sup> , Eric C Palm<sup>2,10</sup> , Gerald V Frost<sup>1</sup> , Jim D Herriges<sup>3</sup>, Peter R Nelson<sup>4</sup>, Carl Roland<sup>5</sup>, Kelsey L M Russell<sup>6</sup>, Mike J Suitor<sup>7</sup>, Torsten W Bentzen<sup>8</sup>, Kyle Joly<sup>5</sup>, Scott J Goetz<sup>9</sup> and Mark Hebblewhite<sup>2</sup>

<sup>1</sup> ABR, Inc.—Environmental Research & Services, Fairbanks, AK 99708, United States of America

<sup>2</sup> W A Franke College of Forestry and Conservation, University of Montana, Missoula, MT 59812, United States of America

<sup>3</sup> Bureau of Land Management, Fairbanks, AK 99709, United States of America

<sup>4</sup> University of Maine-Fort Kent, Fort Kent, Maine 04743, United States of America

<sup>5</sup> National Park Service, Fairbanks, AK 99709, United States of America

<sup>6</sup> Department of Environment, Yukon Government, Whitehorse, YT Y1A 4Y9, Canada

<sup>7</sup> Department of Environment, Yukon Government, Dawson City, YT Y0B 1G0, Canada

<sup>8</sup> Alaska Department of Fish and Game, Fairbanks, AK 99701, United States of America

<sup>9</sup> School of Informatics, Computing, and Cyber Systems, Northern Arizona University, Flagstaff, AZ 86011-5693, United States of America

<sup>10</sup> Author to whom any correspondence should be addressed.

E-mail: [eric.palm@umontana.edu](mailto:eric.palm@umontana.edu)

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Supplementary material for this article is available [online](#)

**Abstract**

Previous research indicates that the effects of climate warming, including shrub expansion and increased fire frequency may lead to declining lichen abundance in arctic tundra and northern alpine areas. Lichens are important forage for caribou (*Rangifer tarandus*), whose populations are declining throughout most of North America. To clarify how lichen cover might affect caribou resource selection, ecologists require better data on the spatial distribution and abundance of lichen. Here, we use a combination of field data and satellite imagery to model lichen cover for a 583 200 km<sup>2</sup> area that fully encompasses nine caribou ranges in interior Alaska and Yukon. We aggregated data from *in situ* vegetation plots, aerial survey polygons and unmanned aerial vehicle (UAV) imagery to align with 30 m resolution Landsat pixels. We used these data to train a random forest model with a suite of environmental and spectral predictors to estimate lichen cover. We validated our lichen cover model using reserved training data and existing external datasets, and found that reserved data from aerial survey polygons ( $R^2 = 0.77$ ) and UAV imagery ( $R^2 = 0.71$ ) provided the best fit. We used our lichen cover map to evaluate the influence of estimated lichen cover on caribou resource selection in the Fortymile Herd from 2012 to 2018 during summer and winter. In both seasons, caribou avoided lichen-poor areas (0%–5% lichen cover) and showed stronger selection as lichen cover increased to ~30%, above which selection leveled off. Our results suggest that terrestrial lichen cover is an important factor influencing caribou resource selection in northern boreal forests across seasons. Our lichen cover map goes beyond existing maps of lichen abundance and distribution because it incorporates extensive field data for model training and validation and estimates lichen cover over a much larger spatial extent. We expect our landscape-scale map will be useful for understanding trends in lichen abundance and distribution, as well as for caribou research, management and conservation.

**1. Introduction**

Lichens are major contributors to overall biodiversity and biomass in many Arctic and subarctic ecosystems around the world. These long-lived and slow-growing organisms play important roles in ecosystem function

by being among the first species to colonize newly exposed surfaces (Cutler 2010). Lichens also fix nitrogen (Cornelissen *et al* 2001) and provide crucial forage, especially during winter, for arctic and subarctic herbivores such as caribou and reindeer (*Rangifer tarandus*; Heggberget *et al* 2002, Joly *et al* 2007). However, multiple



**Figure 1.** Photos showing mats of *Cladonia stellaris* (left) and *Cladonia rangiferina* (dominant species on right) in the Fortymile caribou herd range in interior Alaska. Photos by MJM and ECP.

factors directly related to climate change may lead to decreased lichen abundance in high-latitude areas.

Experimental and observational studies in arctic tundra and northern alpine areas show that climate warming has facilitated widespread expansion of shrubs (Myers-Smith *et al* 2011), which outcompete terricolous (occurring on the ground) lichen through shading and litter accumulation (Joly *et al* 2009, Elmendorf *et al* 2012a, Fraser *et al* 2014). Increases in shrub density, height, and spatial coverage decrease surface albedo, increase evapotranspiration, and increase accumulation of snow and litter, which may promote more shrub growth and reduce lichen abundance (Sturm *et al* 2001, Joly *et al* 2009, Blok *et al* 2011, Loranty *et al* 2011). However, evidence linking warming temperatures and declining lichen abundance in circumpolar areas is not consistent throughout plot-scale studies (Elmendorf *et al* 2012b).

In boreal regions, forest fire has long been a major driver of lichen abundance and distribution. Over hundreds of years fire can prevent late-successional replacement of lichen by feathermosses and forest litter, yet lichen requires decades to fully recover after a fire (Klein 1982, Payette *et al* 2000, Coxson and Marsh 2001, Jandt *et al* 2008). The increasing frequency, spatial extent, and severity of fires observed in western North America's boreal forests and Arctic tundra during recent decades (Hu *et al* 2010, Kasischke *et al* 2010) may lead to lichen declines (Collins *et al* 2011). Therefore, climate change in both arctic and subarctic regions may significantly reduce lichen cover through shrub expansion and altered fire regimes.

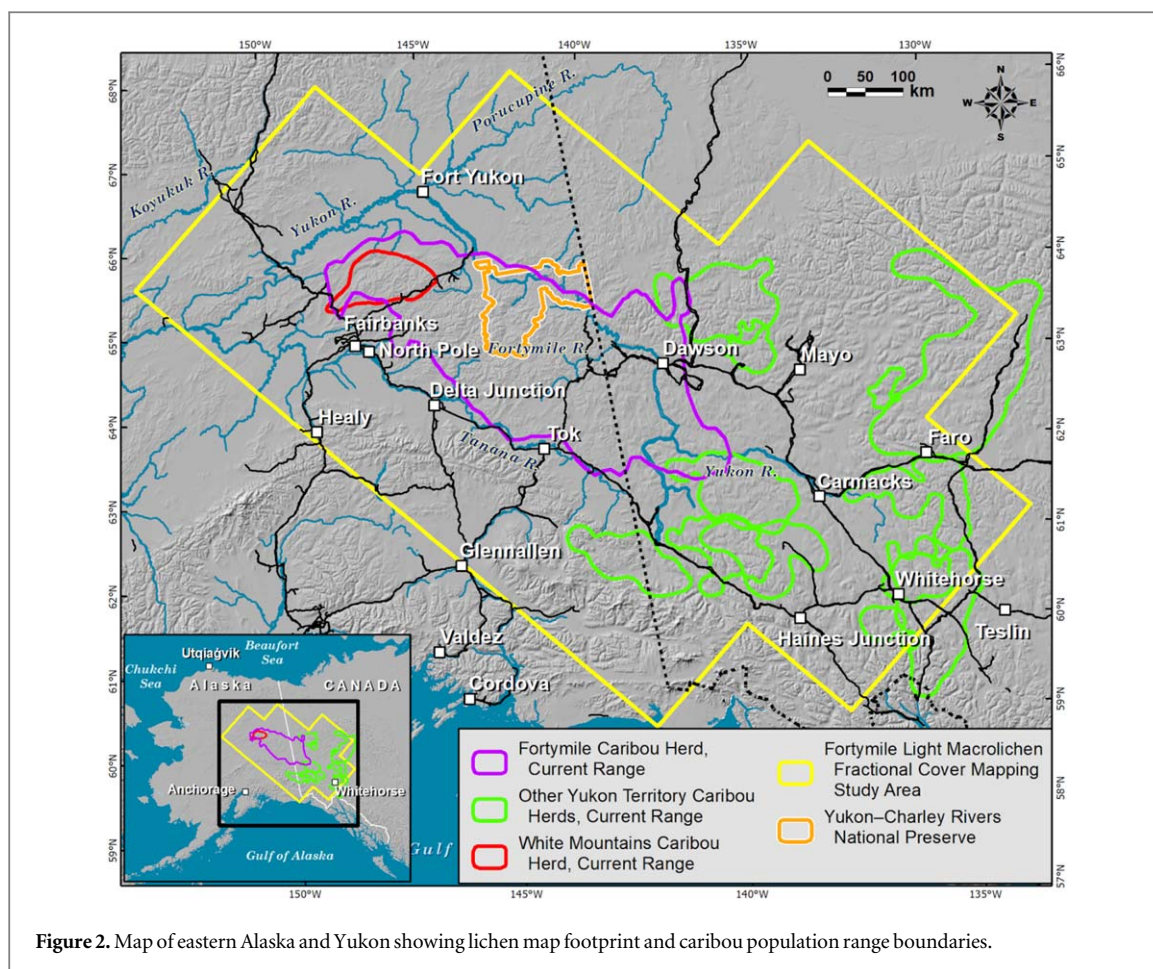
Terricolous lichens provide an easily digestible source of carbohydrates for caribou in winter, when the availability of high-protein forage is limited (Person *et al* 1980, Parker *et al* 2009). Changing fire regimes, through their effects on lichen and shrub expansion (Fraser *et al* 2014), may influence the movements, distribution, and nutritional ecology of caribou, which depend on habitats with forage lichen during winter (Joly *et al* 2003, Collins *et al* 2011).

Most caribou populations in arctic, subarctic and boreal regions of western North America are declining (Vors and Boyce 2009, Hebblewhite 2017). Managers are concerned that the effects of climate change on lichen abundance and distribution may alter caribou population dynamics for many northern caribou populations that are subject to less human disturbance than those farther south (Joly *et al* 2010, Gustine *et al* 2014, Mallory and Boyce 2017). Recent observations from the Fortymile Herd in interior Alaska and western Yukon may indicate nutritional limitation, including low calf weights, low parturition (birth) rates of three-year-old females and population range expansion (Boertje *et al* 2017). These data suggest caribou may be struggling to meet energy requirements (Boertje *et al* 2017).

Lichens eaten by caribou in Alaska and Yukon are primarily terricolous, light-colored macrolichens (i.e. fruticose and foliose growth forms) from the *Cetraria* and *Cladonia* genera (figure 1; nomenclature following Esslinger *et al* 2019 except for *Cetraria* following McCune and Geiser 2009, henceforth, 'light macrolichens;' Rees *et al* 2004, Joly and Cameron 2018). Spatially-explicit maps depicting lichen distribution and abundance are necessary to quantify changes to caribou forage availability and assess relationships between lichen forage and caribou population dynamics (Parker *et al* 2009).

However, creating lichen cover distribution maps is difficult due to the challenge of consistently linking remotely-sensed spectral reflectance to lichen cover, volume, and biomass (Nelson *et al* 2013, Falldorf *et al* 2014, Rickbeil *et al* 2017). Terricolous lichen occurs in mats that often encompass a few square meters or less and can be difficult to detect and map over large spatial extents using satellite imagery. Existing published lichen maps based on satellite imagery generally have focused on relatively small spatial extents (Nelson *et al* 2013, Falldorf *et al* 2014) or have not incorporated *in situ* sampling data for training and validation (Rickbeil *et al* 2017).

The goal of our study was to estimate current cover of light macrolichens across a large spatial extent



covering the range of the Fortymile Herd and adjacent caribou ranges in Alaska and Yukon (figure 2). Managers and researchers are interested in using the resulting lichen cover map as a predictive layer in caribou resource selection analyses to gain a better understanding of the spatial and nutritional ecology of caribou in the region. We demonstrate an application of our lichen map, using step selection functions (SSFs; Fortin *et al* 2005, Thurfjell *et al* 2014), to test our hypothesis that lichen cover affects seasonal resource selection of female Fortymile Herd caribou. We predict that caribou will select areas with higher lichen cover, and that strength of selection for high lichen cover will be strongest in winter, when deciduous vegetation has senesced.

## 2. Methods

### 2.1. Study area

We modeled current (circa 2015) fractional cover of light macrolichens across 583 200 km<sup>2</sup> of east-central Alaska, central and southern Yukon, and far north-western British Columbia. We selected this area to fully encompass the ranges of the Fortymile (100 000 km<sup>2</sup>), White Mountains (6500 km<sup>2</sup>), Aishihik (10 000 km<sup>2</sup>), Clear Creek (3000 km<sup>2</sup>), Chisana (8000 km<sup>2</sup>), Hart River (13 000 km<sup>2</sup>), Klaza (11 000 km<sup>2</sup>), Kluane (8000 km<sup>2</sup>), Pelly (9000 km<sup>2</sup>)

and Laberge (5000 km<sup>2</sup>) caribou ranges (figure 2). The study area consists of rolling hills, subalpine and alpine areas, and large forested river valleys stretching from Alaska's White Mountains in the northwest to near Whitehorse, Yukon in the southeast. The historical fire rotation in interior Alaska's boreal forest is 100–200 years (Lynch *et al* 2004, Kasischke *et al* 2010). Approximately 73% of the study area and 61% of the Fortymile Herd range remains unburned since the 1940s (figure A1), according to fire occurrence data from the Alaska Large Fire Database (ALFD; Kasischke *et al* 2002) and the Canadian National Fire Database (CNFD; Stocks *et al* 2002).

### 2.2. Primary training and validation data

#### 2.2.1. Existing vegetation data

We used existing *in situ* plot data from 528 plots across 29 sites in Yukon-Charley Rivers National Preserve (YUCH) collected from 2006 to 2015 as part of the US National Park Service's Central Alaska Network vegetation monitoring program (Roland *et al* 2004, Roland *et al* 2019; table 1; figure A2; see appendix A1 for sampling details). We used data from 486 of these plots (27 sites) to train models and reserved data from 42 plots (2 sites) for validation. We used existing visual aerial estimates ( $n = 838$  polygons) of lichen cover collected by Environment Yukon during helicopter-based vegetation surveys of three areas in Yukon:

**Table 1.** Summary of training and validation datasets used for modeling fractional lichen cover in the Fortymile caribou (*Rangifer tarandus granti*) range in Alaska and Yukon, 2006–2017.

| Dataset                             | <i>n</i> | Location      | Years      | Cover type   | Size   | Notes  | Modeling status                  |
|-------------------------------------|----------|---------------|------------|--|--|--|----------------------------------|
| UAV survey                          | 22       | Alaska, Yukon | 2017       | Image-based, sum to 100%   | 0.25 m <sup>2</sup> quadrats, 2–30 ha<br>image | Lichen to species or color group               | Training, reserved<br>validation |
| BLM CIR imagery                     | 15       | Alaska        | 2015–2016  | Photo-interpretation. Lichen cover only                                    | 1000–2000 ha                                   | Highly variable image quality                  | Validation                       |
| Yukon aerial survey polygons        | 738      | Yukon         | 2010–2016  | Aerial visual, sum to 100%   | 0.4–40 ha                                      | Light macrolichens to genus                    | Training, reserved<br>validation |
| Yukon–Charley vegetation plots      | 528      | Alaska        | 2006–2013  | Point-intercept any-hit cover (Coulloudon <i>et al</i> 1999), sum to >100% | 0.02 ha  | Point-intercept to lifeform; quadrats to genus | Training, reserved<br>validation |
| Forest Inventory and Analysis sites | 44       | Alaska        | 2012–2013  |  |  |  | Validation                       |
| BLM White Mountains plots           | 386      | Alaska        | 2007, 2012 | Point-intercept, sum to 100%   |  | Lichen to forage or non-forage                 | Validation                       |

Dawson City (summer 2010), Klaza caribou range (summer 2013) and Hart River/Clear Creek caribou ranges (summer 2016). These polygons ranged from 5 to 439 Landsat pixels in area. We randomly sampled five 30 m resolution pixels from each of 684 polygons for training the lichen cover model and reserved pixels from the remaining 154 polygons for validation. The model training and validation splits were determined randomly by assigning each site (YUCH plot or Environment Yukon aerial survey polygon) a uniformly distributed random number between 0 and 1. Sites with a value  $<0.8$  were used for training and all others were used for validation.

### 2.2.2. Additional vegetation data and coincident UAV imagery

We collected additional terrestrial lichen-cover data and high-resolution RGB imagery in summer 2017 from UAVs at 22 forested and alpine sites across interior Alaska and western Yukon within three caribou ranges: Fortymile ( $n = 13$ ), Hart River ( $n = 8$ ), and Clear Creek ( $n = 1$ ; table 1; figure A2). We chose sites that were easy to access ( $\leq 6$  km from a road) and had relatively high lichen cover. At each site, we visually estimated the percent cover (top-hit cover, sensu Karl *et al* 2017) of terrestrial lichen and vegetation in ten  $0.25 \text{ m}^2$  square ground quadrats spaced 10 m apart along a 100 m transect. We marked quadrat corners on the ground with 1 m long PVC pipe or wood lath to ensure the quadrats were clearly visible in the UAV imagery and to eliminate the need for precise ground control points. We grouped lichen species into color groups (white, gray, yellow, green, brown, black, orange) and estimated percent cover for each group within quadrats. Cover estimates for terrestrial lichen and vegetation species totaled 100% for each quadrat, allowing for direct comparisons with cover estimates derived from classified two-dimensional nadir RGB imagery.

We flew a DJI Phantom 4 Pro unmanned aerial vehicle (UAV) with a 20-megapixel camera sensor over a 2–6 ha rectangular grid at 30 m above ground level (AGL) that fully encompassed the 100 m transect and captured nadir RGB imagery at  $\sim 0.8$  cm pixel resolution at each site (figure A3). Whenever possible, we flew UAVs under overcast skies to minimize shadows in the resulting imagery. We used a fixed white balance for each flight to minimize spectral variation across sites. All flights had 80%–85% image overlap along the flight path (endlap) and 70% overlap between flight lines (sidelap). At seven of the Fortymile sites, we collected additional nadir RGB imagery from a DJI Phantom 3A with a 12 megapixel camera sensor at 46–70 m AGL over 5–29 ha, yielding 2.0–3.2 cm pixel resolutions.

We uploaded raw UAV imagery to Pix4Dmapper Cloud (Pix 4D S.A. 2017), where we used structure-from-motion processing to produce several products for each site, including a two-dimensional RGB

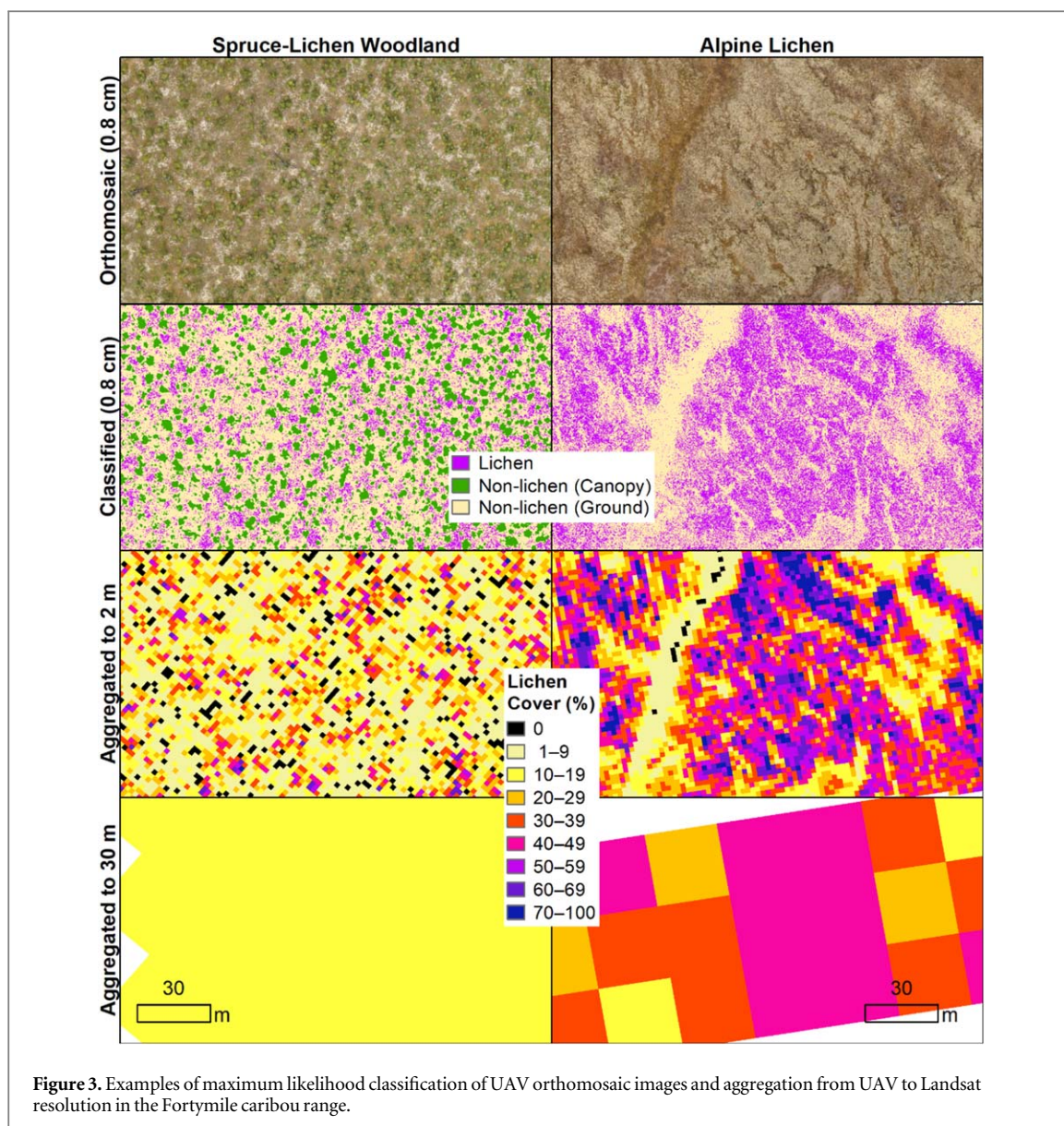
orthomosaic image, a digital surface model (DSM) and a digital terrain model (DTM). Using guidance from quadrat photos (see below), we visually classified each of the 29 RGB orthomosaics to ‘light macrolichens’ (white, gray, and yellow color groups), ‘Other’, and ‘No Data’. The ‘Other’ class included canopy, dark lichens, other vegetation, and non-vegetated surfaces, while ‘No Data’ included shadows and areas off the edge of the mosaic. In sites with shrubs and/or trees, we mapped the canopy using a canopy height model (CHM) generated by subtracting DTM values from DSM values. Then, we extracted the ground layer for spectral classification by masking out all pixels that were  $>20$  cm in height in the CHM layer—a threshold that corresponds to the cutoff between dwarf and low shrub in the Alaska Vegetation Classification (Vioreck *et al* 1992).

We conducted a supervised spectral classification of the ground layer using a maximum-likelihood algorithm in Multispec software (Biehl and Landgrebe 2002). We created training polygons throughout each UAV orthomosaic in ArcMap (ESRI 2017) using photo-interpretation. We used ground photographs of the sampling quadrats from a Nikon D3300 camera as references to calibrate the photo-interpretation. We classified each UAV mosaic independently due to variations in light and color balance among mosaics. As a measure of classification accuracy, we compared lichen cover estimates derived from classified UAV imagery with ocular cover estimates for each  $0.25 \text{ m}^2$  sampling quadrat and found good agreement between the two (10.3% mean absolute error; figure A4). Visually-estimated lichen cover within quadrats averaged 6.3% higher than classification-derived lichen cover.

We overlaid our classified UAV imagery with 30 m resolution Landsat pixels and used the ‘raster’ package in Program R (Hijmans 2019) to aggregate UAV pixels by calculating the proportion of each UAV pixel class within Landsat pixels (figure 3). We masked out ‘No Data’ UAV pixels that composed  $>25\%$  of a Landsat pixel and then recalculated light macrolichen percent cover within all remaining UAV pixels. Finally, we merged the 30 m lichen cover summaries into a single raster image to use as training data. Imagery data from 19 of the 22 total UAV sites provided fractional lichen cover training data for 1437 Landsat pixels. We reserved three UAV sites (90 Landsat pixels) for validation using the same random number assignment procedure as for the vegetation datasets (section 2.2.1).

### 2.3. Remote sensing datasets, framework and model development

We used three types of training data to model fractional cover of light macrolichens, including terrestrial lichen cover estimates from the *in situ* plots, aerial survey polygons, and UAV imagery. Prior to using these data for training, we applied the lichen



cover estimate for each YUCH *in situ* plot to the Landsat pixel overlapping the plot center. We used Google Earth Engine to apply the overall lichen cover estimate from each aerial survey polygon to five randomly selected Landsat pixels within that polygon. The pooled data from all three datasets was used to train a random forest model that applied a suite of environmental and spectral predictors to estimate lichen cover throughout the study area. In addition to validating our model with reserved training data from *in situ* plots, aerial survey polygons, and UAV imagery, we also used additional existing lichen cover data for validation (details below in 2.3.3 and 2.3.4), including data from *in situ* plots, aerial imagery, and an existing lichen cover map that overlapped a portion of our study area.

### 2.3.1. Spectral predictors

We used Google Earth Engine (Gorelick *et al* 2017) to generate surface reflectance percentile composites

from all available Tier 1 Landsat 7 ETM+ and Landsat 8 OLI images acquired in May–September during 2014–2017. We filtered images to remove clouds, snow, shadows, and water. Then, for each band (blue, green, red, near-infrared, SWIR1, and SWIR2), we extracted the 10th, 25th, 50th, 75th, and 90th percentiles as predictors (figure A5). Similarly, we calculated six spectral indices (table A1) for every image and extracted the same percentiles for each index layer. While some previous studies (Nordberg and Allard 2002, Falldorf *et al* 2014, Rickbeil *et al* 2017) have used the Normalized Difference Lichen Index (NDLI), we note that this index is a simple reformulation of the Normalized Difference Snow Index (NDSI; Hall *et al* 1995). Because there is no difference in the information content of the two formulations, we used the longer-established NDSI as a spectral predictor. The percentile composites effectively represent the range of spectral conditions that occur during the snow-free season, even though that season can vary by elevation

and topographic position. We visually inspected the composites and rejected the minimum (0%) and maximum (100%) composites due to excessive noise from unmasked clouds, shadows, haze and snow.

### 2.3.2. Environmental predictors

We used elevation data from the Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) Breakline Emphasis 7.5 arc-second product (Danielson and Gesch 2011). We estimated percent tree cover for 2016 using Hansen *et al*'s (2013) global forest cover and forest cover loss datasets by using 2000 tree cover estimates and assigning areas with forest loss from 2000–2016 to 0% tree cover. We used the maximum water extent from 1984 to 2015 from the JRC Global Surface Water Mapping Layers v1.0 (Pekel *et al* 2016) to exclude areas that we assumed had no lichen cover, but we did not include water extent as a model predictor. These global layers were resampled and reprojected to the coordinate system of our final lichen cover map using nearest neighbor resampling. The global forest cover and surface water layers were nominally 30 m resolution, while the GMTED2010 was nominally 225 m resolution and was primarily used to distinguish broad-scale terrain differences (e.g. mountainous areas versus low valleys). Although we did not use fire occurrence data as predictors in our lichen cover model, we summarized estimated lichen cover values by fire year using polygon data from the ALFD and the CNFD.

### 2.3.3. Model development and evaluation

We developed random forest models (Breiman 2001) in Google Earth Engine using selected data from existing field datasets and 2017 UAV imagery. Approximately 20% of each training dataset was reserved for validation. In our random forest models, we used a random forest classifier with 10 trees, the regression mode, and a random seed of 1. We compared the performance of models with raw surface reflectance predictors versus those with topographically-corrected surface reflectance predictors (Soenen *et al* 2005) using reserved validation data. We selected the best model based on root mean square error (RMSE) and mean absolute error (MAE) using the reserved validation data.

Validating an extensive map derived from remote sensing can be challenging but it is a very important step. We used multiple approaches to characterize the performance and uncertainty of our map: (1) pooling all reserved training data, (2) validating against each reserved training dataset separately, (3) validating against selected independent plot datasets not used in model training, (4) cross-validation of training data predicted in 'out-of-bag' mode, (5) a stratified sample of photo-interpreted points using color infra-red (CIR) imagery from the Bureau of Land Management (BLM), and (6) a comparison to an existing Klaza caribou range lichen cover map created using Landsat 5 imagery and Environment Yukon aerial imagery as

training data (Caslys Consulting Ltd 2014; see appendix A2 for details on Klaza lichen map).

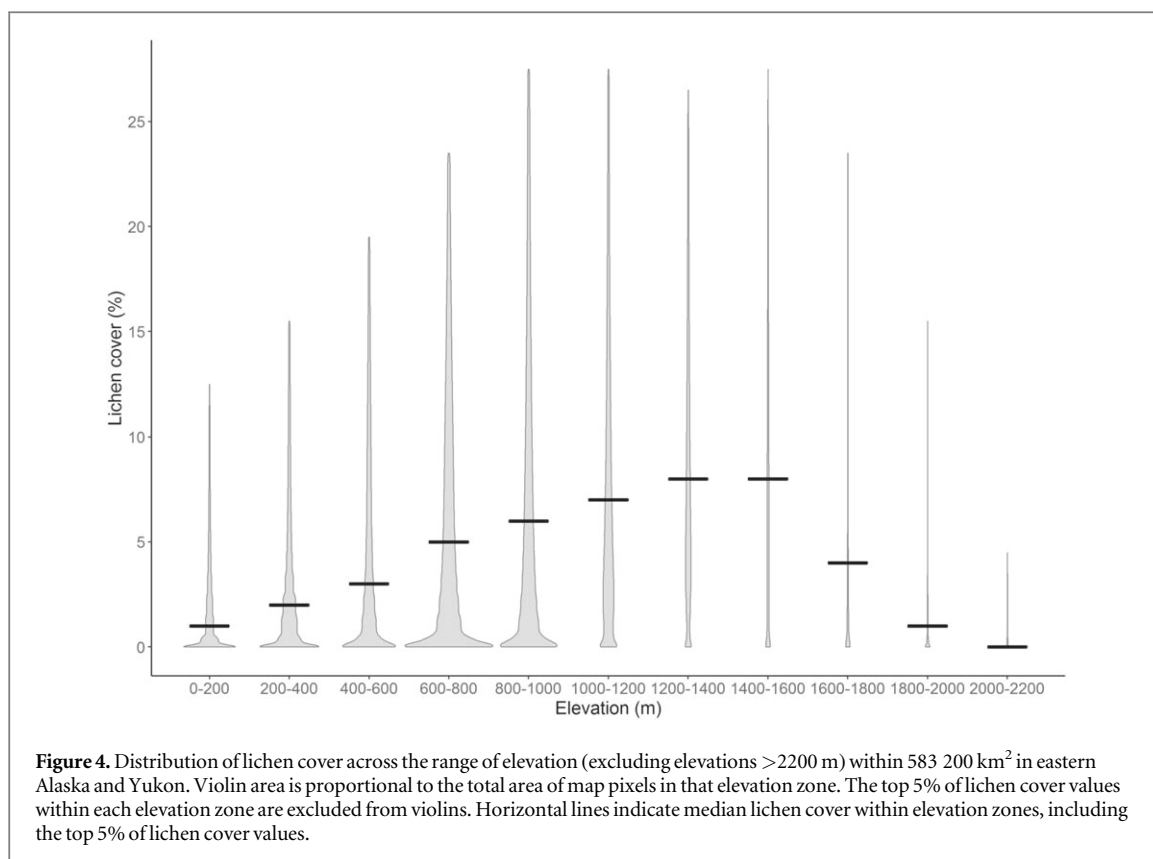
### 2.3.4. Additional remote sensing validation data

We validated the final model using existing BLM point-intercept vegetation data from 386 plots in burned and unburned areas of the White Mountains, Alaska, collected in 2007 and 2012 (table 1). We also used US Forest Service (USFS) Forest Inventory and Analysis (FIA) lichen cover data from 45 sites in interior Alaska in 2012–2013. In addition, we used BLM aerial imagery from 2015 to 2016 collected from a Nikon DSLR camera modified to capture CIR to validate our model (see appendix A3 for details on BLM CIR imagery). The BLM CIR imagery encompassed 11 of the 22 UAV sample sites from 2018 but covered much larger areas (967–2062 ha).

## 2.4. Application of lichen cover model to caribou resource selection

We used step selection functions (SSF; Fortin *et al* 2005, Thurfjell *et al* 2014) to evaluate the influence of estimated lichen cover on adult female caribou resource selection in the Fortymile caribou range from 2012–2018 during summer and winter (see appendix A4 for more details on SSFs and caribou GPS location data). In an SSF, the step length is the distance between consecutive GPS locations, and the relative turning angle is the difference in bearing between consecutive steps (Fortin *et al* 2005). Using conditional logistic regression, we contrasted lichen cover at used steps with lichen cover at random 'available' steps that we presumed were available to the animal along its movement path (figure A6). In addition to lichen cover, we annotated both used and available locations with values for percent tree cover, elevation, slope, and snow cover frequency (Macander and Swingley 2017).

We defined summer as the period between the mean dates of peak calving and rut across all collared females and years (May 25–October 5) that we determined from daily movement speeds. Winter represented the remaining portion of the year. We derived movement distributions for each individual during both seasons at three step scales (2.5, 10 and 25 h), which roughly correspond to Johnson's (1980) third through fourth orders of habitat selection, by fitting gamma distributions to observed step lengths and von Mises distributions to observed turning angles. We used these distributions to generate five random displacements from used locations at time  $t$ , and local availability at time  $t + 1$ , for every step made by an individual for each of the three step scales. We clustered locations by animal in our conditional logistic regression models to account for the lack of independence between steps made by the same individual (Prima *et al* 2017).



### 3. Results

Mean modeled lichen cover values increased from 1.4% at 0–200 m elevation up to 8.1% at intermediate elevations in alpine areas (1400–1600 m; e.g. Blackstone Uplands, Ogilvie Mountains, Yukon-Tanana Uplands) then dropped towards zero at high elevations (e.g. Wrangell Mountains and Alaska Range; figures 4 and 5). Mean lichen cover was highest (8.1%) in areas with no record of fire in the ALFD and CNFD. Mean lichen cover within mapped burn perimeters ranged from 3.0% in areas burned in 2000–2009 to 5.9% in areas burned prior to 1950.

#### 3.1. Model validation

We examined model performance separately for each of the reserved validation datasets (table A2). The  $R^2$  was highest for Yukon aerial survey polygons and lowest for the YUCH vegetation monitoring plots. The best-fit line for the UAV plots was nearly 1:1, indicating consistent model performance results across the range of lichen cover values (figure 6). Results from cross-validation with the training data were very similar to the reserved data for the UAV sites, better than the reserved sites for Yukon aerial survey polygons, and worse than the reserved sites for the YUCH plots.

The BLM White Mountains vegetation plots from 2007 and 2012 had similar  $R^2$  and best-fit lines, and a larger RMSE than the reserved YUCH vegetation plots (figure 6). Both datasets are based on similar point-

intercept vegetation sampling methods and include plot data from the mid-2000s. There was good agreement between our map and recent FIA plots. Agreement between our map and the existing Klaza lichen map was poor when compared pixel-wise at 30 m resolution, but much better when both products were aggregated to 300 m. Photo-interpretation of 200 usable samples from BLM orthoimagery had an RMSE of 14.3% and showed that the model had fairly good performance at high observed lichen cover values.

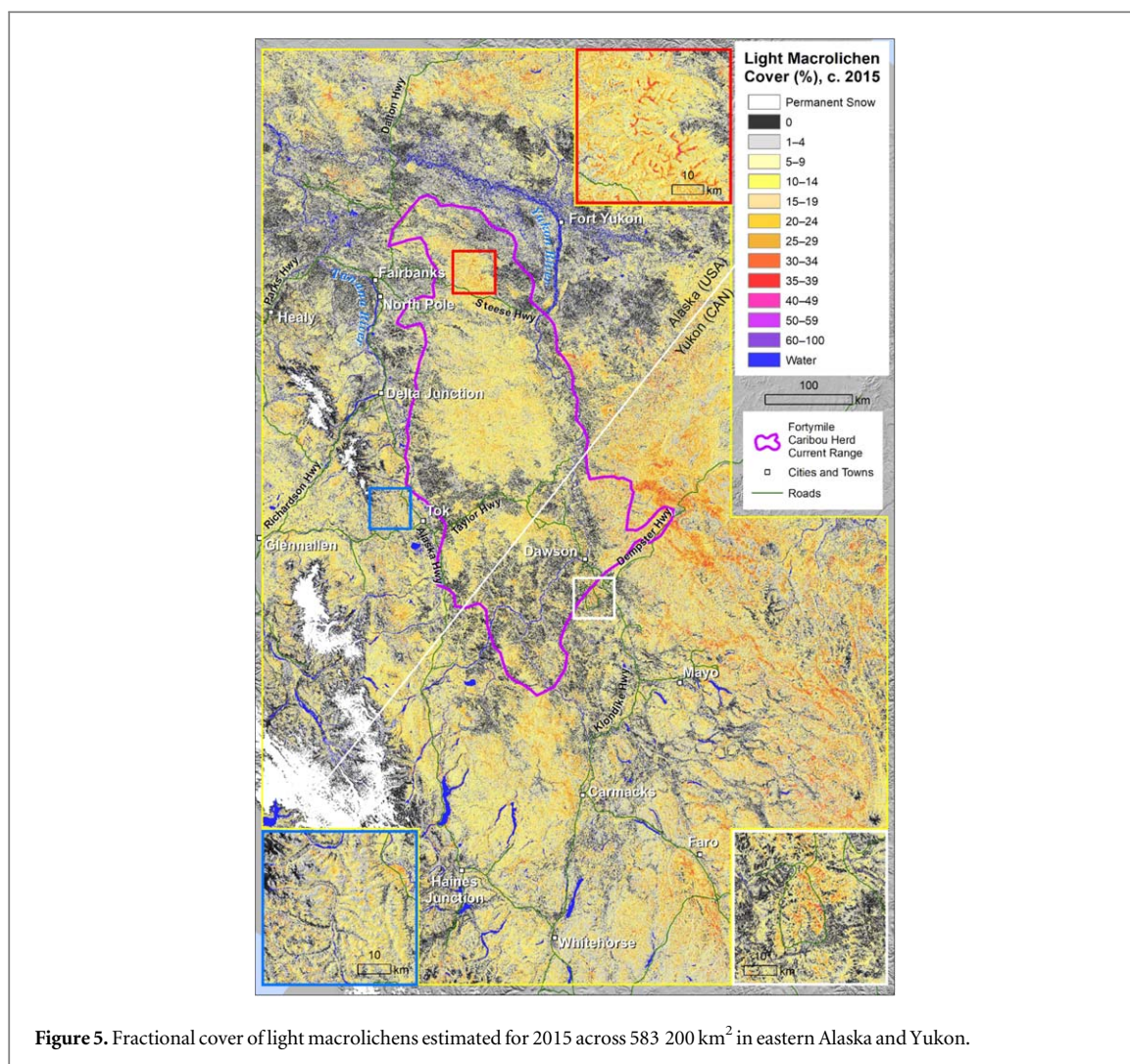
#### 3.2. Caribou-lichen resource selection analysis

Caribou generally avoided areas with lowest lichen cover (0%–5%) during both summer and winter seasons and selected areas with higher lichen cover (figures 7 and A7). There was little difference in selection strength for lichen cover between seasons and the response to lichen cover was consistent across spatiotemporal scales (figure A8). The best models for both winter and summer included a two-knot spline for lichen cover and quadratic terms for elevation, slope and snow cover frequency (table A3).

### 4. Discussion

We used data products derived from satellite imagery, *in situ* vegetation sampling plots and UAV imagery to estimate fractional cover of light macrolichens across 583 200 km<sup>2</sup> of boreal forest and alpine tundra in interior Alaska, western Yukon and northern British





**Figure 5.** Fractional cover of light macrolichens estimated for 2015 across 583 200 km<sup>2</sup> in eastern Alaska and Yukon.

Columbia. We found a strong, positive relationship between lichen cover and caribou resource selection. Based on these results, we expect our landscape-scale map will be useful for understanding trends in lichen abundance and distribution, as well as for caribou research, management and conservation.

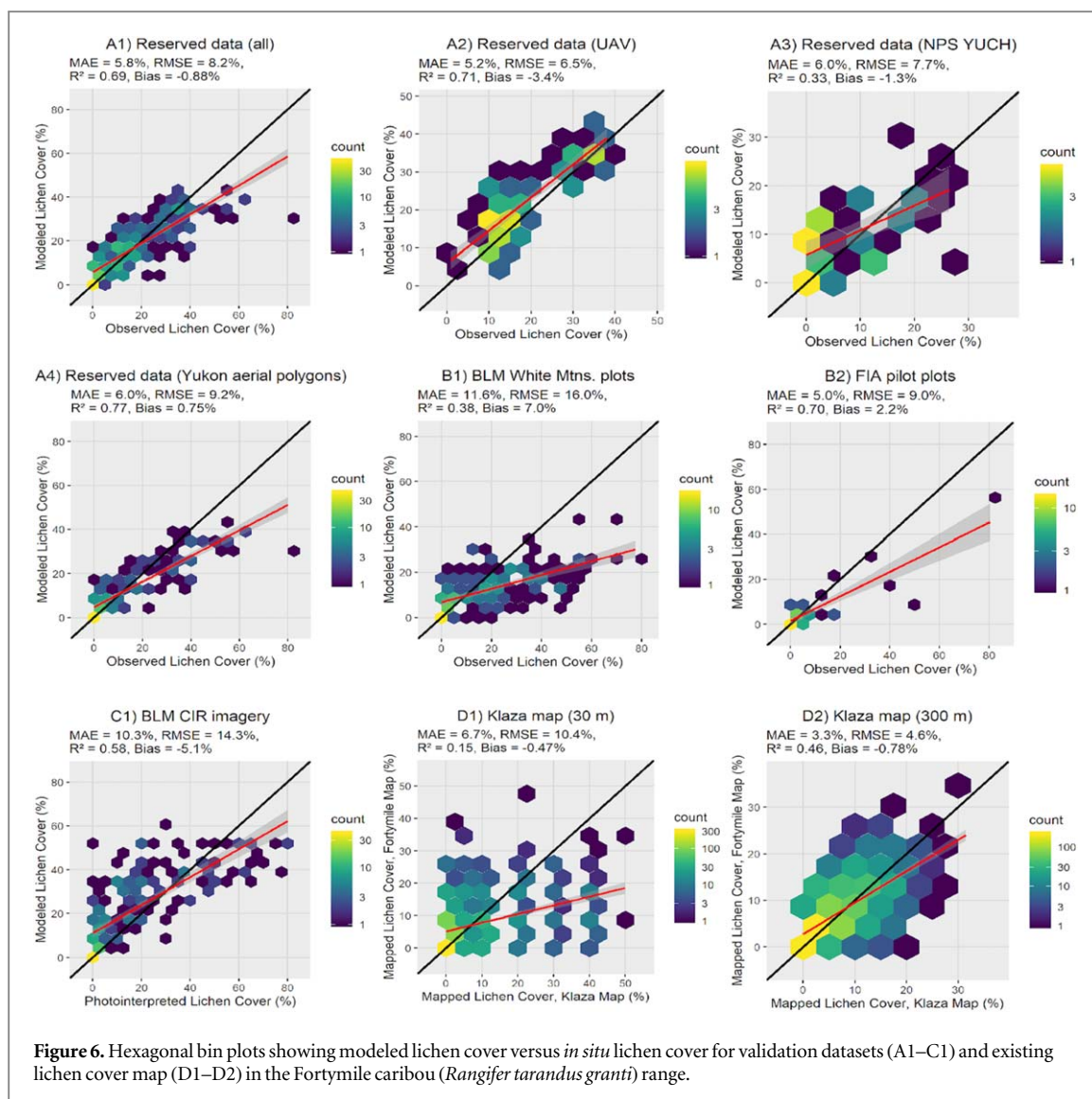
#### 4.1. Comparison to existing lichen maps

There are very few existing studies that have modeled lichen cover or volume at landscape scales. Falldorf *et al* (2014) estimated lichen volume for lichen-dominated alpine heath communities within an 8000 km<sup>2</sup> study area in Norway using two indices derived from Landsat imagery and training data from hundreds of ground-based measurements. Rickbeil *et al* (2017) used Falldorf *et al*'s (2014) equations to estimate lichen volume for all Landsat pixels classified as tundra by a MODIS-derived land cover layer within 700 000 km<sup>2</sup> in the Northwest Territories and Nunavut. Unlike Falldorf *et al* (2014), Rickbeil *et al* (2017) did not incorporate *in situ* training or validation data into their model, and the authors state that their estimates of lichen volume should not be interpreted as absolute values. Nelson *et al* (2013) estimated

percent cover of usnic (yellow) lichens and light macrolichens (yellow + white or gray color groups) across 12 000 km<sup>2</sup> of Denali National Park using a combination of vegetation plots, midsummer Landsat imagery, and topographic metrics.

Both Falldorf *et al* (2014) and Nelson *et al* (2013) reported better model performance using topographically-normalized reflectance predictors rather than raw predictors. During model development, we evaluated the use of topographically-normalized predictors based on the Modified Sun-Canopy-Sensor topographic correction function (Soenen *et al* 2005). We pursued models with raw surface reflectance predictors because they outperformed those with topographically-normalized predictors, though we expect our model with normalized predictors might have performed better with a more accurate digital elevation model across the entire study area. Further, our suite of predictors included six spectral indices, which collectively dampen the effects of topographic illumination.

Visual observations of lichen on the landscape indicate that it may be much more easily seen at certain times, for example after a period of warm weather



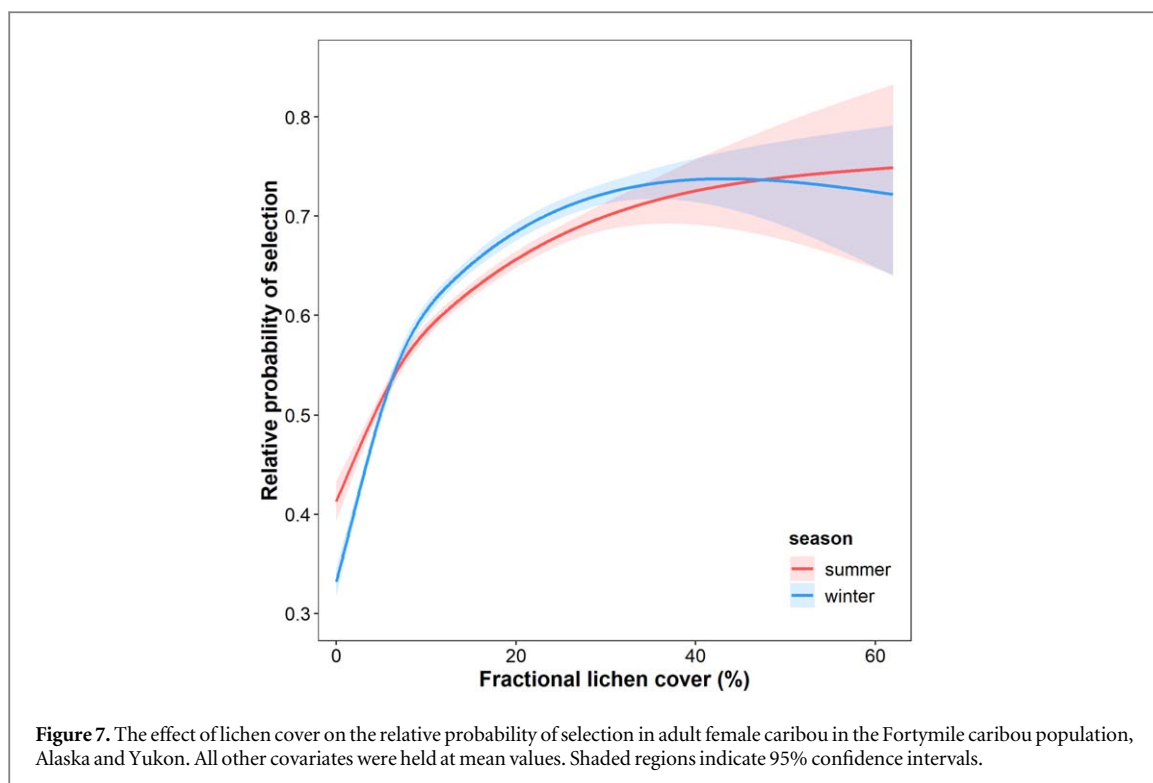
following abundant rain. Our percentile composite approach captured unusual spectral conditions that may be diagnostic, while avoiding the extreme outliers (minimum, maximum) that tend to be dominated by remnant cloud and shadow.

Falldorf *et al* (2014) developed their lichen volume estimator for a homogeneous, lichen-rich landscape. Our study area included a variety of land cover types, including forested areas and alpine tundra, that precluded the use of a single lichen volume estimator such as that in Falldorf *et al* (2014). Further, while lichen volume or lichen biomass are likely more directly relevant to caribou than lichen cover, these data were not available for the YUCH plots and aerial survey polygons that we used to train and validate our model. Instead, we modeled lichen cover, which is positively correlated with volume and biomass in most locations (Dunford *et al* 2006, Moen *et al* 2007, Collins *et al* 2011), and thus reflects the patterns of forage abundance for caribou. We note, however, that if core portions of the Fortymile caribou range were heavily

grazed, the relationship between lichen cover and biomass may be weak in those areas. Nonetheless, our model combined with additional biomass data (Hebblewhite, unpubl. data) could subsequently be used to explore the effects of caribou grazing intensity. Our results showing highest lichen cover on non-glaciated alpine slopes at intermediate elevations is consistent with results from past studies in Alaska that did not generate map products (Holt *et al* 2008) or else did so for a limited spatial extent (Nelson *et al* 2013).

#### 4.2. Sources of uncertainty

While the lichen cover model performed well overall, there was a bias towards overestimating lichen cover at low lichen cover values and underestimating lichen cover at high lichen cover values (figure 6). The overestimates at low lichen cover were mostly related to erroneously mapping areas with zero or negligible lichen cover as having low lichen cover, i.e. 10% or less. These areas were generally correctly mapped as no to low lichen cover. No and low lichen cover areas



occurring with other vegetation were challenging to distinguish because the lichen cover was largely obscured by canopy and shadow in many of these areas. High lichen cover areas tended to be patchy at Landsat scale (e.g. figure 3 bottom panel). High-resolution image-based lichen cover summaries such as the UAV aggregation (figures 6 and A2) and the stratified photo interpretation (figures 6 and C1) were most suitable for characterizing the spatial heterogeneity of lichen cover and these validation datasets also showed smaller biases for higher lichen cover areas. This suggests that including more UAV blocks in future mapping efforts may improve model performance for lichen-rich areas.

We did not systematically assess the robustness of our modeled lichen cover estimates to the use of different percentile composites as spectral predictors. However, we do not expect the specific percentiles selected to be important if noise from unmasked clouds, shadows, haze, and snow is minimized. We caution that excessive noise in the 10% and 90% percentile composites could be problematic for studies with fewer Landsat observations and/or less effective masking.

#### 4.3. Application of lichen maps to caribou resource selection

Results from our resource selection analysis supported our hypothesis that lichen cover influences caribou resource selection and demonstrates the utility of lichen cover mapping for caribou management efforts. Even when accounting for the effects of topography, tree cover and snow cover frequency, caribou selected

areas with higher lichen cover. During both winter and summer, caribou selection for lichen cover increased steadily until ~30% lichen cover (figure 7). Estimated lichen cover values >30% were very rare (<1% by area) across the Fortymile caribou range. Our results suggest that lichen may be important forage for Fortymile caribou not only during winter but also after vegetation senescence in late summer and early fall, consistent with a recent diet analysis of caribou in the Western Arctic Herd (Joly and Cameron 2018).

Our resource selection results corroborate those from past studies that were based primarily on field site observations, which found caribou select areas with high lichen cover. Woodland caribou in Canada's Jasper and Banff National Parks selected locations with high terrestrial lichen cover (Shepherd *et al* 2007); migratory caribou from the Western Arctic Herd selected areas with higher percent cover and volume of lichen during winter compared to random locations (Joly *et al* 2010); the Nelchina Herd, whose range is to the Fortymile Herd range, selected areas with high lichen cover and biomass (Collins *et al* 2011), and caribou in Denali National Park increased their use of areas with high lichen abundance through winter (Nelson *et al* 2018).

#### 4.4. Implications for future research

We believe our use of high-resolution UAV imagery helps bridge the gap between fine-scale *in situ* sampling and satellite imagery, demonstrating a relatively inexpensive and efficient way to collect data on vegetation cover with relevance to wildlife management. Imagery from UAVs provided data to calibrate

and validate our regional lichen cover models over large spatial extents and provided a baseline for tracking lichen cover over time at field sites. A larger footprint from UAV flights would provide even more model training data, although additional research on the trade-off between larger image footprint versus decreased spatial resolution would be valuable for future mapping efforts.

Our mapping of lichen cover distribution across several caribou ranges in central Alaska and Yukon provides a useful baseline for future efforts estimating lichen cover change over time. Change analyses would be potentially valuable for exploring longer-term population dynamics of caribou relative to their resource selection and nominal range distributions, as well as for assessing the effectiveness of caribou management actions and the potential impacts of climate change.

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## Data availability statement

The data that support the findings of this study are available upon request from the authors.

## ORCID iDs

Matthew J Macander  <https://orcid.org/0000-0003-2808-208X>

Eric C Palm  <https://orcid.org/0000-0002-5330-4804>

Gerald V Frost  <https://orcid.org/0000-0002-5134-0334>

Scott J Goetz  <https://orcid.org/0000-0002-6326-4308>

Mark Hebblewhite  <https://orcid.org/0000-0001-5382-1361>

## References

- Biehl L and Landgrebe D 2002 MultiSpec—a tool for multispectral–hyperspectral image data analysis *Comput. Geosci.* **28** 1153–9
- Blok D, Schaepman-Strub G, Bartholomeus H, Heijmans M M P D, Maximov T C and Berendse F 2011 The response of Arctic vegetation to the summer climate: relation between shrub cover, NDVI, surface albedo and temperature *Environ. Res. Lett.* **6** 035502
- Boertje R D, Gardner C L, Ellis M M, Bentzen T W and Gross J A 2017 Demography of an increasing caribou herd with restricted wolf control *J. Wildlife Manage.* **81** 429–48
- Breiman L 2001 Random forests *Mach. Learn.* **45** 5–32
- Caslys Consulting Ltd 2014 Mapping lichen forage in the Klaza caribou herd range using a revised land cover. Summary report prepared for Environment Yukon, Whitehorse, Yukon. Saanichton, British Columbia. 36 pp
- Collins W B, Dale B W, Adams L G, McElwain D E and Joly K 2011 Fire, grazing history, lichen abundance, and winter distribution of caribou in Alaska's taiga *J. Wildl. Manage.* **75** 369–77
- Cornelissen J H C *et al* 2001 Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Ecology* **89** 984–94
- Coulloudon B *et al* 1999 Sampling vegetation attributes *Interagency Technical Reference* 1734–4 US Department of Interior, Bureau of Land Management
- Coxson D S and Marsh J 2001 Lichen chronosequences (postfire and postharvest) in lodgepole pine (*Pinus contorta*) forests of northern interior British Columbia *Can. J. Botany* **146A** 1449–64
- Cutler N 2010 Long-term primary succession: a comparison of non-spatial and spatially explicit inferential techniques *Plant Ecol.* **208** 123–36
- Danielson J J and Gesch D B 2011 Global multi-resolution terrain elevation data 2010 (GMTED2010) *Report No.* 2011-1073 US Geological Survey (<https://doi.org/10.3133/ofr20111073>)
- Dunford J S, McLoughlin P D, Dalerum F and Boutin S 2006 Lichen abundance in the peatlands of northern Alberta: implications for boreal caribou *Ecoscience* **13** 469–74
- Elmendorf S C *et al* 2012a Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time *Ecol. Lett.* **15** 164–75
- Elmendorf S C *et al* 2012b Plot-scale evidence of tundra vegetation change and links to recent summer warming *Nat. Clim. Change* **2** 453–7
- Esslinger T *et al* 2019 A cumulative checklist for the lichen-forming, lichenicolous and allied fungi of the continental United States

- and Canada, Version 23 *Opuscula Philolichenum* **18** 102–378 (<http://sweetgum.nybg.org/philolichenum/>)
- ESRI 2017 *ArcGIS Desktop: Release 10.5.1* (Redlands, CA: Environmental Systems Research Institute)
- Falldorf T, Strand O, Panzacchi M and Tømmervik H 2014 Estimating lichen volume and reindeer winter pasture quality from Landsat imagery *Remote Sens. Environ.* **140** 573–9
- Fortin D, Beyer H L, Boyce M S, Smith D W, Duchesne T and Mao J S 2005 Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park *Ecology* **86** 1320–30
- Fraser R H, Lantz T C, Olthof I, Kokelj S V and Sims R A 2014 Warming-induced shrub expansion and lichen decline in the Western Canadian Arctic *Ecosystems* **17** 1151–68
- Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D and Moore R 2017 Google Earth Engine: planetary-scale geospatial analysis for everyone *Remote Sens. Environ.* **202** 18–27
- Gustine D D, Brinkman T J, Lindgren M A, Schmidt J I, Rupp T S and Adams L G 2014 Climate-driven effects of fire on winter habitat for Caribou in the Alaskan-Yukon Arctic *PLoS One* **9** e100588
- Hall D K, Riggs G A and Salomonson V V 1995 Development of methods for mapping global snow cover using moderate resolution imaging spectroradiometer data *Remote Sens. Environ.* **54** 127–40
- Hansen M C *et al* 2013 High-resolution global maps of 21st-century forest cover change *Science* **342** 850–3
- Hebblewhite M 2017 Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry *Biol. Conservation* **206** 102–11
- Heggberget T M, Gaare E and Ball J P 2002 Reindeer (*Rangifer tarandus*) and climate change: importance of winter forage *Rangifer* **22** 13
- Hijmans R J 2019 Raster: Geographic Data Analysis and Modeling. R package version 2.8-19 (<https://CRAN.R-project.org/package=raster>)
- Holt E A, McCune B and Neitlich P 2008 Grazing and fire impacts on macrolichen communities of the Seward Peninsula, Alaska, USA *Bryologist* **111** 68–83
- Hu F S, Higuera P E, Walsh J E, Chapman W L, Duffy P A, Brubaker L B and Chipman M L 2010 Tundra burning in Alaska: linkages to climatic change and sea ice retreat *J. Geophys. Res.: Biogeosci.* **115** 1–8
- Jandt R, Joly K, Meyers R C and Racine C 2008 Slow recovery of lichen on burned caribou winter range in Alaska Tundra: potential influences of climate warming and other disturbance factors *Arctic, Antarct., Alpine Res.* **40** 89–95
- Johnson D H 1980 The comparison of usage and availability measurements for evaluating resource preference *Ecology* **61** 65–71
- Joly K, Dale B W, Collins W B and Adams L G 2003 Winter habitat use by female caribou in relation to wildland fires in interior Alaska *Can. J. Zool.* **81** 1192–201
- Joly K, Cole M J and Jandt R R 2007 Diets of overwintering Caribou, *Rangifer tarandus*, track decadal changes in Arctic Tundra vegetation *Can. Field-Naturalist* **121** 379–83
- Joly K, Jandt R R and Klein D R 2009 Decrease of lichens in arctic ecosystems: role of wildfire, caribou and reindeer, competition, and climate change *Polar Res.* **28** 433–42
- Joly K, Chapin F S and Klein D R 2010 Winter Habitat Selection by Caribou in Relation to Lichen Abundance, Wildfires, Grazing, and Landscape Characteristics in Northwest Alaska *Ecoscience* **17** 321–33
- Joly K and Cameron M D 2018 Early fall and late winter diets of migratory caribou in northwest Alaska *Rangifer* **38** 27–38
- Karl J W, McCord S E and Hadley B C 2017 A comparison of cover calculation techniques for relating point-intercept vegetation sampling to remote sensing imagery *Ecol. Indic.* **73** 156–65
- Kasischke E S *et al* 2010 Alaska's changing fire regime—implications for the vulnerability of its boreal forests *Can. J. For. Res.* **40** 1313–24
- Kasischke E S, Williams D and Barry D 2002 Analysis of the patterns of large fires in the boreal forest region of Alaska *Int. J. Wildland Fire* **11** 131–44
- Klein D R 1982 Fire, Lichens, and Caribou *J. Range Manage.* **35** 390–5
- Loranty M M, Goetz S J and Beck P S A 2011 Tundra vegetation effects on pan-Arctic albedo *Environ. Res. Lett.* **6** 024014
- Lynch J A, Hollis J L and Hu F S 2004 Climatic and landscape controls of the boreal forest fire regime: holocene records from Alaska *J. Ecol.* **92** 477–89
- Macander M J and Swingley C S 2017 Landsat snow persistence and snow regime mapping for Alaska, and lichen cover mapping for Yukon–Charley Rivers National Preserve. Final report for USGS Alaska Science Center, Anchorage, AK by ABR, Inc. Fairbanks, AK. 88 pp
- Mallory C D and Boyce M S 2017 Observed and predicted effects of climate change on Arctic caribou and reindeer *Environ. Rev.* **25** 1–13
- McCune B and Geiser L 2009 *Macrolichens of the Pacific Northwest* (Corvallis, OR: Oregon State University Press)
- Moen J, Danell O and Holt R 2007 Non-destructive estimation of lichen biomass *Rangifer* **27** 41–6
- Myers-smith I H *et al* 2011 Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities *Environ. Res. Lett.* **6** 045509
- Nelson P R, Joly K, Roland C A and McCune B 2018 Evaluating relocation extent versus covariate resolution in habitat selection models across spatiotemporal scales *Ecol. Inf.* **48** 245–56
- Nelson P R, Roland C, Macander M J and McCune B 2013 Detecting continuous lichen abundance for mapping winter caribou forage at landscape spatial scales *Remote Sens. Environ.* **137** 43–54
- Nordberg M-L and Allard A 2002 A remote sensing methodology for monitoring lichen cover *Can. J. Remote Sens.* **28** 262–74
- Parker K L, Barboza P S and Gillingham M P 2009 Nutrition integrates environmental responses of ungulates *Funct. Ecol.* **23** 57–69
- Payette S, Bhury N, Delwaide A and Simard M 2000 Origin of the lichen woodland at its southern range limit in eastern Canada: the catastrophic impact of insect defoliators and fire on the spruce-moss forest *Can. J. For. Res.* **30** 288–305
- Pekel J-F, Cottam A, Gorelick N and Belward A S 2016 High-resolution mapping of global surface water and its long-term changes *Nature* **540** 418–22
- Person S J, Pegau R E, White R G and Luick J R 1980 *In vitro* and Nylon-Bag Digestibilities of Reindeer and Caribou Forages *J. Wildlife Manage.* **44** 613–22
- Pix4D S.A. 2017 Pix4D version 3.4. Lausanne, Switzerland
- Prima M C, Duchesne T and Fortin D 2017 Robust inference from conditional logistic regression applied to movement and habitat selection analysis *PLoS One* **12** 1–13
- Rees W G, Tutubalina O V and Golubeva E I 2004 Reflectance spectra of subarctic lichens between 400 and 2400 nm *Remote Sens. Environ.* **90** 281–92
- Roland C A, Oakley K, Debevec E M and Loomis T 2004 Monitoring vegetation structure and composition at multiple scales in the Central Alaska Network *NPS Technical Report CAKN-001* National Park Service, Central Alaska Network Inventory and Monitoring Program (<https://irma.nps.gov/DataStore/Reference/Profile/2190295>)
- Roland C A, Schmidt J H, Winder S G, Stehn S E and Nicklen E F 2019 Regional variation in interior Alaskan boreal forests is driven by fire disturbance, topography, and climate *Ecol. Monogr.* **0** e01369
- Rickbeil G J M, Hermosilla T, Coops N C, White J C and Wolfer M A 2017 Estimating changes in lichen mat volume through time and related effects on barren ground caribou (*Rangifer tarandus groenlandicus*) movement *PLoS One* **12** 1–16
- Shepherd L, Schmiegelow F and Macdonald E 2007 Managing fire for woodland caribou in Jasper and Banff National Parks *Rangifer* **17** 129–40

- Soenen S A, Peddle D R and Coburn. C A 2005 SCS+C: a modified Sun-canopy-sensor topographic correction in forested terrain *IEEE Trans. Geosci. Remote Sens.* **43** 2148–59
- Stocks B J *et al* 2002 Large forest fires in Canada 1959–1997 *J. Geophys. Res.: Atmos.* **107** FFR 5–12
- Sturm M, McFadden J P, Liston G E, Stuart Chapin F, Racine C H and Holmgren. J 2001 Snow-shrub interactions in Arctic Tundra: a hypothesis with climatic implications *J. Clim.* **14** 336–44
- Thurfjell H, Ciuti S and Boyce M S 2014 Applications of step-selection functions in ecology and conservation *Movement Ecol.* **2** 1–12
- Viereck L A, Dyrness C T, Batten A R and Wenzlick. K J 1992 The Alaska Vegetation Classification *General Technical Report PNW-GTR-286* Pacific Northwest Research Station
- Vors L S and Boyce M S 2009 Global declines of caribou and reindeer *Glob. Change Biol.* **15** 2626–33