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Landscape-scale characterization of Arctic tundra vegetation composition, structure, and function with a multi-sensor unoccupied aerial system

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Abstract

The Arctic is experiencing some of the most rapid climate change on Earth, with strong impacts on tundra ecosystems that are characterized by high land-surface and vegetation heterogeneity. Previous studies have explored this complexity using satellite remote sensing, however these typically coarse spatial resolution data have generally missed sub-pixel heterogeneity, leaving critical gaps in our understanding of tundra vegetation dynamics from the community to landscape scales. To address these gaps, we collected very high-resolution (1–5 cm) optical, structural, and thermal data at three low-Arctic tundra sites on the Seward Peninsula, Alaska, using a multi-sensor unoccupied aerial system (UAS). We examined the application of these data to studying tundra vegetation dynamics, by quantifying (a) canopy height and thermoregulation (leaf–air temperature) of representative plant functional types (PFTs), (b) fine-scale patterns of vegetation composition across landscapes, and (c) impacts of fine-scale vegetation composition on landscape-scale variation of canopy height and thermoregulation. Our results show that deciduous tall shrubs (those that can potentially grow >2 m) had a strong cooling effect, with canopy temperatures significantly lower than local air temperatures and other PFTs. Increased cover of tall shrubs also had the potential to reduce the cover of low-stature PFTs across the landscape, potentially associated with their closed canopy (i.e. increased light competition) and strong thermoregulation. To understand the connections between fine-scale vegetation composition and large-scale ecosystem processes, we produced a random forest model which showed that fine-scale PFT composition accounted for 86.8% and 74.2% of the landscape-scale variation in canopy height and thermoregulation, respectively. These findings highlight the importance of spatially detailed characterization of tundra PFTs to improve our ecological understanding and model representation of tundra vegetation, also transcend our study to show the need for continued collection of similar datasets to better understand the impacts of surface heterogeneity on the mapping and modeling of tundra ecosystem dynamics, as well as assist with conservation management and biodiversity monitoring strategies.

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1. Introduction

The most rapid, regional temperature increases in recent decades have occurred in the Arctic, with wide-spread impacts on tundra vegetation dynamics (Post et al 2009, Schuur et al 2015 Elmendorf et al 2012). Increased shrub and graminoid cover has been observed across the Arctic (Sturm et al 2001, Myers-Smith et al 2011, Elmendorf et al 2012, Tremblay et al 2012), leading to major shifts in the taxonomic and functional composition of tundra plant communities (Myers-Smith et al 2011, Pajunen et al 2011) and, subsequently, potential modification of ecosystem structure and function (Pearson et al 2013, Myers-Smith et al 2015, Vowles and Björk 2019). These changes include an observed pan-arctic ‘greening’ trend detected by coarse-scale satellite observations (Myneni et al 1997, Ju et al 2016). However, tundra landscapes display a large degree of spatial heterogeneity (Beck and Goetz 2011, Epstein et al 2012, Reichele et al 2018), which can introduce significant uncertainties in the quantification of vegetation dynamics across these landscapes with coarse-resolution observations (Myers-Smith et al 2020). To accurately assess the impacts of climate change on high-latitude ecosystems, a finer-scale understanding of tundra vegetation composition, structure, and function, as well as scaling processes that transmit fine-scale patterns to large-scale ecosystem impacts, is critically needed.

Tundra ecosystems are characterized by low-stature plants (e.g. moss, lichen, graminoids, and dwarf shrubs), and are vulnerable to climate change (Chapin et al 1992, Callaghan et al 1993). The establishment and expansion of low to tall shrubs into tundra ecosystems can cause substantial changes in community assembly, with a shuffling of strategies related to resource allocation, energy balance and water cycling, as well as with potentially large impacts on plant and animal biodiversity (Myers-Smith et al 2011, Zhang et al 2018, Vowles and Björk 2019).

Typically, the formation of a closed shrub canopy significantly alters understory light and nutrient availability, increasing competition for resources and restricting the growth of other plant forms (Klein et al 2004, Elmendorf et al 2012, Brathen and Lortie 2015). However, shrub litter accumulation improves soil resources (DeMarco et al 2011, 2014, Salmon et al 2019), and as such, an intermediate shrub cover may facilitate the seedling recruitment of certain species (Gonzalez and Ghermandi 2019). These multifaceted plant competition and facilitation relationships create a complex pattern of tundra vegetation composition, additionally modified by resource availability, topography, and climate change.

Tundra plant species also differ in their canopy structure and functional properties (Yang et al 2020), including leaf thermoregulation (i.e. the ability of a leaf to regulate its temperature under changing environments; Watling et al 2008, Michaletz et al 2016), which can have large-scale impacts on ecosystem structure and function given changes in dominant vegetation composition (Bourgeron et al 1999, Cushman et al 2010). For example, tall shrub species tend to have efficient leaf temperature regulation through canopy transpiration, leaf angle distribution, and within-canopy leaf shadowing, which collectively contribute to a cooler micro-environment in tall shrub communities during the growing season (Blok et al 2010, Myers-Smith et al 2011). On the other end of the structural spectrum, ground-hugging lichens are observed to have a high surface temperature and low water content (Chapin et al 1996, Yang et al 2020). Hence, an increase in lichen cover may lead to higher ecosystem vulnerability to disturbances, such as drought and wildfire during which dry lichens are more vulnerable to being consumed than other green vegetation (Joly et al 2009), and alter soil thermal regimes (Porada et al 2016).

Despite their critical importance, our ability to accurately characterize tundra vegetation composition, structure, and thermoregulation has been largely challenged by the short growing season, remote environment, and the high level of spatial heterogeneity (Stow et al 2004, Beamish et al 2020, Myers-Smith et al 2020). In the past few decades, the most accurate characterization of tundra vegetation has been conducted mainly via ground-based plot surveys (Metcalfe et al 2018, Walker et al 2018), which has largely improved our understanding of tundra vegetation dynamics. However, in-situ surveys are time-consuming and limited in their spatial and temporal coverage, which has resulted in limited data on high-latitude plant functional types (PFTs; Schimel et al 2013, Diepstraten et al 2018). In particular, the structure, function, and composition patterns of low-stature PFTs (i.e. moss, lichen, and graminoids) are not as well-characterized compared to forb and shrub PFTs (Vowles and Björk 2019). On the other hand, satellite remote sensing provides much more continuous coverage over large spatial and temporal scales and has facilitated a better understanding of broad changes in high latitude ecosystems in recent years (Myneni et al 1997, Beck et al 2011, Ju and Masek 2016, Beamish et al 2020). However, the commonly-used satellite data (e.g. Moderate Resolution Imaging Spectroradiometer (500 m), Landsat (30 m), and Sentinel-2 (10 m)) have typically been insufficient for differentiating low-stature tundra species or PFTs or elucidating the fine-scale patterns that drive changes in vegetation composition, structure, and function (Myers-Smith et al 2020, Siewert and Olofsson 2020, Assmann et al 2020).

Multi-sensor, very-high-resolution (VHR; 1 ∼ 10 cm) remotely sensed data collected by unoccupied aerial systems (UASs) have transformed the way that ecologists view, describe, and quantify vegetation status and dynamics (Anderson and Gaston 2013,
Yao et al (2019). The analysis of UAS data has shown great efficiency for disentangling the fine-scale patterns of vegetation dynamics and linking these patterns to large-scale variation in ecosystem structure and function (Anderson and Gaston 2013, Fraser et al 2016, Juszak et al 2017, Riihimäki et al 2019, Yang et al 2020). This includes spatially detailed characterization of vegetation composition, structure, and function (Greaves et al 2015, Saarinen et al 2018, Alonzo et al 2020, Assmann et al 2020, Zhao et al 2021) to determine the drivers of large-scale variation in albedo, biomass, gross primary productivity, evapotranspiration, etc (Cunliffe et al 2020). In this paper, we examined the utility of VHR, multi-sensor UAS data for characterizing tundra vegetation composition, structure, and function, using a newly developed, multi-sensor UAS (called the ‘Osprey’; Yang et al 2020). We focused on three questions: (a) How do tundra PFTs differ in canopy height and thermoregulation? (b) What are the fine-scale patterns of vegetation composition across tundra landscapes? and (c) How does fine-scale vegetation composition drive the large-scale variation in canopy height and thermoregulation? For this, we acquired, processed, and validated VHR optical, structural, and thermal data at three low-Arctic tundra sites using the Osprey UAS. We mapped representative tundra species and PFTs from the UAS images through random forest (RF) classification. Based on the mapped PFTs, combined with in-situ and UAS data, we then analyzed the structure, thermoregulation, and composition of different tundra PFTs, in line with the above three questions.

2. Materials and methods

2.1. Study sites

Three tundra field sites in the Seward Peninsula (figure 1, Council, Kougarok, Teller), established by the Next-Generation Ecosystem Experiments Arctic (NGEE-Arctic, https://ngee-arctic.ornl.gov/) project, were used in this study. The Seward Peninsula is located on the western coast of the U.S. state of Alaska (figure 1), an area highly sensitive to climate change. The three field sites represent a highly dynamic transition from wet meadow tundra adjacent to the tundra-forest ecotone at Council, to a drier, interior hillslope of alder shrubland and alder savanna at Kougarok, and then to a wet, coastal tundra hillslope dominated by willow shrubland and wet meadow tundra at Teller. The vegetation composition, topography, and meteorology of these three field sites have been previously described in Lloyd et al (2003), Kim et al (2014), Leger et al (2019), Salmon et al (2019), and Yang et al (2020). The three sites include a variety of common PFTs for the western Arctic (table 1). In addition, vegetation composition showed a high degree of variation within and among the three field sites modified by diverse environmental conditions, enabling a thorough investigation of vegetation composition across a range of abiotic conditions.

2.2. Field campaign

2.2.1. UAS data collection and processing

In July 2018, we conducted a field campaign to collect VHR optical, structural, and thermal UAS images. The Osprey (Yang et al 2020) was flown over our three field sites, with pre-determined data collection missions designed to cover representative plant community types (PCTs, Breen et al 2020). During each flight, a portable weather station was deployed in the proximity of the flight area (sensors installed ~1.5 m above ground, <100 m to the center of each UAS flight) to gather ambient weather/environmental conditions, including air temperature, radiation, humidity, and wind speed. In this campaign, a total of 20 data collection flights were performed, and we chose one representative flight from each site (collected around solar noon) with the highest data quality and spatial coverage for this study (acquisition dates: Council, 22 July; Teller, 23 July; Kougarok, 26 July). The total area of the three flights was ~18 ha and spanned a wide range of tundra PCTs (figure S1 (available online at stacks.iop.org/ERL/16/085005/mmedia)).

Using the workflow developed in Yang et al (2020), we processed the Osprey collections to generate an optical red-green-blue (RGB) ortho-mosaic image, a thermal infrared (TIR; 7–14 μm) ortho-mosaic image, and a canopy height model (CHM) for each flight. To produce the CHM, we derived a digital surface model (DSM) and digital elevation model (DEM), and then calculated the CHM as the height difference between the DSM and DEM (see Yang et al 2020). The final pixel resolution of the RGB, CHM, and TIR surfaces were ~1, 2, and 5 cm, respectively.

Plant thermoregulation reflects the ability of a plant to regulate its water and energy exchanges under ambient environmental conditions (Fauset et al 2018, Deva et al 2020). In this study, we defined it as the difference between leaf and local air temperature (ΔT). Typically, a high ΔT indicates a strong thermoregulation capacity while a low ΔT indicates a weak thermoregulation capacity. Here, air temperature (T_air) was provided by the weather station and the ΔT for each flight was calculated by subtracting the mean
Figure 1. Location of the Seward Peninsula and the three study sites of NGEE Arctic project, i.e. Teller, Kougarok, and Council. The black rectangles show the area of the UAS flights used in this study.

Table 1. Plant functional types (PFTs) used in this study and corresponding plant species.

| PFT               | PFT definition based on Walker et al (2000) and Swanson et al (2015) | Common name of species included in this study | USDA scientific name |
|-------------------|-----------------------------------------------------------------------|-----------------------------------------------|----------------------|
| Deciduous tall shrub (DTS) | Deciduous erect shrub with potential maximum height >200 cm | Siberian alder                               | Alnus viridis subsp. fruticosa |
|                   |                                                                       | Diamond-leaf willow                          | Salix pulchra        |
| Deciduous low shrub (DLS)   | Deciduous erect woody shrub 40–200 cm tall                           | Resin birch                                  | Betula glandulosa    |
|                   |                                                                       | Arctic dwarf birch                           | Betula nana          |
|                   |                                                                       | Bog blueberry                                | Vaccinium uliginosum |
|                   |                                                                       | Mountain bearberry                           | Arctous alpina       |
| Deciduous dwarf shrub (DDS)  | Deciduous woody shrub below 40 cm tall                                | Alaskan mountain-avens                      | Dryas octopetala subsp. alaskensis |
| Evergreen shrub (ES)       | Non-deciduous erect/prostrate dwarf woody shrub below 40 cm tall     | Black crowberry                             | Empetrum nigrum subsp. hermaphroditum |
| Graminoid (GR)            | Tussock/non-tussock narrow-leaf herbaceous vascular plant (grasses, sedges, rushes) | Common cotton-grass                         | Eriophorum angustifolium |
| Brophyte (BR)             | Cryptogamic (reproduces by spores) nonvascular plant that occurs in mesic to wet sites (all bryophytes including mosses and liverworts) | Tussock cotton-grass                        | Eriophorum vaginatum var. vaginatum |
| Lichen (LI)              | Cryptogamic (reproduces by spores) nonvascular plant-like organism that occurs in dry sites (comprised of fungi + algae or cyanobacteria) | Reindeer lichen                            | Cladina spp. (mainly C. arbuscula, C. rangiferina, C. stellaris, C. stygia) |
|                           |                                                                       | Dark fruticose lichen                        | Mainly Alectoria nigricans, A. ochroleuca, Bryocaulon divergens |
in-flight $T_{air}$ (Teller: 21.12 °C, Kougarok: 21.5 °C, Council: 21.35 °C; see table S1 and figure S2 for more details) from the UAS TIR data. It is noted that we performed the UAS flights under clear-sky and reasonably stable weather conditions. Air temperature showed little to no variation within and across flights (figure S2(a)). Solar radiation, another variable that may strongly affect surface temperature, was also reasonably stable during each flight and was close to the standard solar conditions within the study region (figure S2(b) and table S1).

2.2.2. Ground measurements
To validate our UAS-derived CHM and TIR mosaic, we collected in-situ canopy height and temperature measurements. For the CHM, we selected 24 targets of individual tall shrubs (i.e. alder and willow) or distinct patches of low and dwarf shrubs within the Kougarok flight. Using a graduated height pole, we measured the mean canopy height of each ground target, by averaging height measurements from multiple parts (>3 locations) of the target. The geographic coordinates for the center of each target were recorded with a Trimble Geo7x differential global positioning system (dGPS). We post-processed the dGPS data using the Pathfinder Office software (Trimble Inc.) and provided target locations with spatial registration errors less than 10 cm.

Evaluating the absolute temperature of UAS-collected TIR is challenging given issues related to spatial mismatch, offset in the time of collection between UAS imagery and ground truth, and highly variable local environmental conditions (e.g. wind and clouds). In addition, its impractical to collect ground-truth data in close proximity to our UAS flights. Thus, we focused on validating the calculated $\Delta T$, which was relatively consistent over a period of time given that it generally tracks environmental conditions. For this, we selected a group of validation targets at each site which included representative plant species. On each flight day, we measured the ‘skin’ temperature and surrounding air temperature (~1 m above ground) for each target using an Apogee MI-210 radiometer and a Kestrel 5500 weather meter, respectively. To avoid substantial changes in ambient conditions, we conducted the measurements within ±1 h of the UAS flights. This resulted in a total of 294 pairs of ground-based surface and air temperature measurements across all three sites. The $\Delta T$ between the ground-based skin and air temperatures were then used for validation of the UAS-derived $\Delta T$.

2.3. Data analysis
2.3.1. Validating UAS-derived CHM and $\Delta T$ data
The UAS-based mean canopy height for each of the in-situ targets was derived from the CHM image and compared with the in-situ measurements. To this end, we manually identified the 24 in-situ targets in the Kougarok imagery using their dGPSs and in-situ photos, and created a region of interest (ROI) for each in the Environment for Visualizing Images software (version 5.5; Harris Geospatial Solutions, Inc.). The mean canopy height of each target was then calculated by averaging the CHM of all pixels in the ROI. We used linear regression to compare the in-situ and UAS-derived heights. The coefficient of determination ($R^2$), root mean squared error (RMSE), and % bias, were calculated to quantify their agreement.

The validation of UAS-derived $\Delta T$ was performed using a PFT-based method given the challenges of direct comparison between ground and UAS data (e.g. shadows and matching exact measurements locations). In addition, a portion of the in-situ targets were located outside the UAS flight boundaries, due to limited areas and terrain covered by the flights and the challenges of collecting temperature ground-truth data quickly and within the specific flightlines of each data collection mission. Thus, to evaluate our $\Delta T$ calculations, we first grouped the in-situ measured species into PFTs based on table 1, and calculated the mean and variance of the in-situ collected $\Delta T$ for each PFT. Second, we calculated the mean and variance of the UAS-derived $\Delta T$ for each PFT by aligning the $\Delta T$ and PFT maps (see section 2.3.2). The mean and variance of each PFT were then compared between the two datasets. We also conducted an unpaired t-test for each PFT to examine if there was a significant difference between the in-situ and UAS-derived $\Delta T$s.

2.3.2. Mapping representative plant species and PFTs from UAS data
The representative plant species were mapped using an object-based classification, similar to Yang et al. (2020), where we segmented the layer-stack of RGB, CHM, and $\Delta T$ (scale = 20, shape = 0.2) in eCognition (version 8.9; Trimble Inc.) and derived 13 distinct ‘object’ features, including object mean and variance in blue, green, red, CHM, and $\Delta T$, respectively; object area; object border length; and object-averaged green chromatic coordinate (GCC) index (Leduc and Knudby 2018). These ‘object’ features were then used as input to a RF classifier (we used 100 trees in this study) run in Python (version 3.7). Training samples for the RF classifier (~1000 objects for each flight) were visually selected from the layer stack of RGB, CHM, and $\Delta T$ with in-situ survey information and our expert knowledge about the study sites. Here we used a flight-specific strategy to select training samples and perform classification, where one RF classifier was trained for each flight using the samples (~1000 objects) selected from the flight. This strategy avoids the effects of inter-flight differences in illumination on the classification. To assess mapping accuracy, we calculated confusion matrix and overall accuracy (Story and Congalton 1986, Ismail and Jusoff 2008) for each flight, with an additional set of validation samples (~1000 objects). In this process,
13 species classes (table 1) and four non-vegetation classes (dead plant material, shadow, rocks/soil, and water) were identified from the UAS images.

In this study, our analysis focused on PFTs as they (a) form the basis for vegetation descriptions in Earth system models (ESMs; Wullschleger et al. 2014, Fisher et al. 2017), (b) condense broad complexity of individual species by capturing the variation in canopy structure and function (Chapin et al. 1996, Woodward et al. 1996, Walker et al. 2000), and (c) have higher mapping accuracy than individual species, which reduces the analysis uncertainty caused by misclassification (Yang et al. 2020). We merged the species classes into seven PFTs according to table 1 (Walker 2000, Swanson et al. 2015) and calculated the confusion matrix and overall accuracy for the mapped PFTs. Here, the four non-vegetation classes were also merged into a non-vegetation (NV) component class.

2.3.3. Characterizing canopy height and thermoregulation of different PFTs

The canopy height and ∆T of representative PFTs were analyzed by aligning the mapped PFTs with the CHM and ∆T images. Using data from all three flights, we calculated the mean, standard deviation, and density distribution of CHM and ∆T for each PFT. Tukey tests were conducted to examine the significance of difference in CHM and ∆T among PFTs.

To further explore the patterns and drivers of canopy property variation across PFTs, we performed a principal component analysis (PCA, n = 3) on the combination of GCC, CHM, and ∆T, using 'prcomp' in R (R Core Team 2020). Here, the GCC was used as an indicator of vegetation greenness (Leduc and Knudby 2018). The GCC, CHM, ∆T, and belonging PFT of all eCognition-derived objects for the three UAS flights were derived and used for the PCA. The percent variance explained by each principal component (PC) was calculated, and the loadings of GCC, CHM, ∆T for each PC were also derived to indicate their contribution to the PCs.

2.3.4. Quantifying fine-scale vegetation composition patterns across landscapes

The fine-scale PFT composition patterns were explored using a quadrat-based method, where we divided the UAS images into equal-sized quadrats (5 × 5 m; figure 2) and considered each quadrat as a 'plot community', as similar to Rocchini et al. (2017) and Rossi et al. (2020). The quadrat size was determined by maximizing per-quadrat structural and functional 'α' diversity across sites (see figure S3). In each quadrat, we calculated the fractional cover (FCover) for each of the seven mapped PFTs (figure 2(a)) and produced a spatially continuous PFT FCover map for each UAS flight. The average CHM and ∆T were also calculated for each quadrat.

Here, we focused on how spatial changes in the FCover of a PFT impacted other PFTs within the quadrats. For this, the Pearson correlation coefficient (PCC) was calculated on the quadrant FCover between any two of the seven PFTs, to describe the strength and direction (positive or negative) of their associations. We considered two PFTs to have a positive or negative relationship if a statistically significant PCC was acquired. PCC in this analysis describes the relationship between two PFTs and their FCovers. It does not suggest that that PFTs are the sole or primary factor impacting the FCover between PFTs, as other factors (i.e. topography, soil moisture, and nutrient availability) not investigated in this study may influence the FCover of the studied PFTs (Callaghan et al. 1993).

2.3.5 Determining the effects of fine-scale vegetation composition on large-scale variation in canopy height and thermoregulation

The spatial turnover of vegetation composition drives the large-scale variation in ecosystem structure and function (i.e. β functional diversity: variation across communities), along with varying vegetation properties adapted to local environments. In this study, we examined the importance of PFT composition for describing landscape-scale variation in CHM and ∆T, by modeling their changes across quadrats. The variation of two quadrat variables associated with CHM and ∆T was modeled, including the (a) mean and (b) α diversity (i.e. variation within communities; figure 2(b)) of quadrant CHM and ∆T. The mean CHM and ∆T for each quadrat were calculated as described in section 2.3.4. To describe α diversity, we used the Rao’s Quadratic (Q) index (equation (1), Rao 1982)

\[ Q = \frac{1}{n} \sum_{i=1}^{n} \sum_{j=1}^{n} d_{ij} \times p_i \times p_j, \]

where n is the total number of species present in a quadrat; d_{ij} is the dissimilarity between species i and j in the measured variable (i.e. CHM or ∆T), and p_i and p_j are the abundances of species i and j. Generally, a larger Q indicates a higher α diversity. We applied a modification reported by Rochchini et al. (2017) to calculate Q from our UAS images, which was defined as the average dissimilarity between any two pixels in a quadrat (figure 2(b)). To avoid the effects of salt-and-pepper noises (an impulse type of noise that commonly existing in high-resolution images, especially when pixel size is smaller than the studied objects; Azzeh et al. 2018), we used the object-level CHM and ∆T as input for calculating Q indices. In addition, we normalized the CHM and ∆T to 0–1, in order to standardize the range of Q.

To inspect the importance of each PFT for explaining the landscape-scale variation in CHM and ∆T, we conducted RF modeling (equation (2)) on combined data from the three sites:
Figure 2. Illustration of quadrat-based method for calculating fractional cover (FCover) and $\alpha$ diversity from UAS classification and canopy property map (i.e. $\Delta T$ and CHM). (a) Calculation of FCover from UAS classification map, where $N_i$ is the number of UAS image pixels belonging to a PFT and $N_q$ is the total number of UAS image pixels in the quadrat (i.e. 500 × 500). (b) Calculation of $\alpha$ diversity from vegetation property map, where $n$ is the total number of UAS pixels in the quadrat and $d_{ij}$ is the dissimilarity in CHM or $\Delta T$ between pixel $i$ and $j$.

\[
R_q = \sum_{i=1}^{n} \left[ f(FCover_i) + f(P_i) \right] + \varepsilon,
\]

where $R_q$ is the mean or $\alpha$ diversity of quadrat $q$ based on either CHM or $\Delta T$; $FCover_i$ and $P_i$ are the fractional cover of the $i$th PFT and its averaged CHM or $\Delta T$ within quadrat $q$, respectively; $n$ is the number of mapped PFTs plus a NV component; $\varepsilon$ is the residual error in $R_q$ that cannot be explained by $FCover$ and $P$ (i.e. functional redundancy). Using the scikit-learn module in Python, we performed the RF modeling and derived the variable importance for projection (VIP) for each predictor variable. In this process, a total of four RF models were developed: mean of CHM, $\alpha$ diversity of CHM, mean of $\Delta T$, and $\alpha$ diversity of $\Delta T$.

To inspect the contribution of PFT composition, we then used a stepwise modeling technique where we removed $FCover$ and $P$ from equation (2), alternatively. Through this, we calculated the percentage of variance in $R_q$ explained by FCover and $P$, respectively.

3. Results

3.1. UAS data, validation, and PFT mapping results
We derived canopy TIR and CHM from our UAS collected images (figures 3 and S4). The linear regression validation of the CHM produced a regression slope of 0.85, with an $R^2$ of 0.96, RMSE of 0.14 m, and % bias of 0.17 (figure 4(a)), indicating good quality of the UAS-derived canopy height. The $\Delta T$ derived from UAS TIR also agreed well with our in-situ measurements for most PFTs ($p > 0.1$), except for bryophytes

where the in-situ $\Delta T$ was significantly higher than that from UAS TIR ($p < 0.1$) (figure 4(b)). Importantly, both the in-situ and UAS-derived $\Delta T$ captured significant variation among PFTs, which confirmed the viability of UAS thermal imaging.

The representative plant species and PFTs were mapped using a fusion of RGB, CHM, and $\Delta T$ images (figure 5). We identified 13 individual species from the high-resolution UAS images. These mapped species had an overall accuracy of 86.4%, 88.8%, and 90.5% for Kougarok, Teller, and Council, respectively (table 2). We aggregated these species maps into PFT descriptions, which we labeled deciduous tall shrub (DTS), deciduous low shrub (DLS), deciduous dwarf shrub (DDS), evergreen shrub (ES), graminoid (GR), bryophyte (BR), and lichen (LI) classes (figure 5(b) and table 1). Unsurprisingly, the PFT maps had much higher accuracy (Kougarok: 93.2%, Teller: 94.5%, Council: 93.9%, table 2) than the original species maps, but overall, both species and PFT maps were of high quality and resolution.

3.2. Canopy height and $\Delta T$ of PFTs
The canopy height of DTS was significantly taller and more variable than other PFTs, with a mean CHM of 0.99 ± 0.61 m (figure 6(a)). In our flight regions, DTS reached as high as ~2.5 m. DLS also showed a slightly larger mean canopy height (0.26 ± 0.14 m) than other low-stature PFTs (i.e. LI, BR, ES, DDS). We found no significant difference in height among remaining PFTs ($p$-value > 0.1). In contrast, $\Delta T$ exhibited distinct means and high variation across PFTs (figure 6(b)). The distribution of $\Delta T$ for the DTS (~3.03 ± 2.41 °C) was significantly lower than...
Figure 3. Image products at Teller site derived from the Osprey UAS platform, including optical RGB, thermal infrared (TIR) temperature, and canopy height model (CHM). The spatial resolution is 1, 5, and 2 cm, respectively. See figure S4 for the equivalent images from Kougarok and Council.

Figure 4. Validation of UAS products. (a) Scatter plot of UAS derived canopy height against ground measurements; (b) PFT-based comparison between UAS derived $\Delta T$ and those derived from ground Apogee and Kestrel measurements. DTS: deciduous tall shrub, DLS: deciduous low shrub, DDS: deciduous dwarf shrub, ES: evergreen shrub, GR: graminoid, LI: lichen, BR: bryophyte. * in (b) indicates that UAS derived $\Delta T$ is significantly different from ground-based $\Delta T$.

other PFTs and was mostly below zero. We found that areas dominated by lichen cover had the warmest surface temperatures (LI: $2.81 \pm 1.75 \, ^\circ C$) across the UAS flight regions (figure 6(b)). ES also showed higher surface temperature, with a mean $\Delta T$ of $2.56 \pm 1.19 \, ^\circ C$. The distribution of $\Delta T$ for other PFTs was located between DTS and LI, with considerable variation within each PFT.

The PCA analysis showed that GCC and $\Delta T$ best describe the canopy variation among PFTs, except for DTS, by having nearly opposite directions (paralleled with the PFT eclipses) on the PC1 vs. PC2 space (figure S5). Instead, variation within DTS was mainly related to CHM. Nevertheless, large overlaps were observed among PFTs, indicating a high level of similarity in optical,
Figure 5. Mapped species (a) and PFTs (b) for the studied UAS flights. The legend boundary color in (a) indicates the PFT belongingness of the mapped species. DTS: deciduous tall shrub, DLS: deciduous low shrub, DDS: deciduous dwarf shrub, ES: evergreen shrub, GR: graminoid, LI: lichen, BR: bryophyte, NV: non-vegetation components (i.e. the combination of dead plant material, schist rock/soil, shadow, and water).

Table 2. UAS image classification accuracy (percentage of training samples that are correctly classified) and kappa coefficient.

| Species | Overall accuracy (%) | Kappa coefficient | Overall accuracy (%) | Kappa coefficient |
|---------|----------------------|-------------------|----------------------|-------------------|
| Teller  | 88.8                 | 0.87              | 93.2                 | 0.91              |
| Kougarok| 85.2                 | 0.83              | 94.5                 | 0.92              |
| Council | 90.1                 | 0.89              | 93.9                 | 0.92              |
Figure 6. Density distribution of CHM and $\Delta T$ of studied PFTs derived from the three UAS flights. (a) CHM; (b) $\Delta T$. DTS: tall shrub, DLS: low shrub, DDS: dwarf shrub, ES: evergreen shrub, GR: graminoid, LI: lichen, BR: bryophyte, NV: non-vegetation. * indicates if the mean of the distribution is significantly greater than 0 for CHM or significantly different from 0 for $\Delta T$. One hundred samples were randomly selected from each distribution for the $t$-test to avoid the effect of large sample size on $p$-value.

Figure 7. (a) FCover of studied PFTs plotted against quadrat-mean canopy temperature. The PFT FCover was binned by $\Delta T$ with an interval of 0.5 $^\circ$C and the standard deviation in each bin was plotted as grey ribbon. The three cutouts indicated three different plant communities, from left to right: alder tall shrubland, mixed shrub-sedge tussock tundra, and dryas lichen dwarf shrub tundra. (b) Pearson correlation coefficients (PCC) derived from quadrat-based FCover and canopy mean GCC, CHM and $\Delta T$. blue box: PCC among the FCover of different PFTs; red box: PCC among GCC, CHM, and $\Delta T$; green box: PCC between FCover and canopy GCC, $\Delta T$, and CHM. × indicates PCCs that are tested not significant. Bonferroni correction was applied to adjust the significance level for multiple hypothesis testing. DTS: deciduous tall shrub, DLS: deciduous low shrub, DDS: deciduous dwarf shrub, ES: evergreen shrub, GR: graminoid, LI: lichen, BR: bryophyte.

3.3. Fine-scale patterns of tundra vegetation composition
The FCover of mapped PFTs showed strong correlations with canopy $\Delta T$ at the quadrat scale (figure 7(a)). In general, the FCover of DTS (green line in figure 7(a)) increased with decreasing quadrat $\Delta T$. Low-stature PFTs were mostly found where DTS had low FCover (bottom right in figure 7(a)), with ‘hot’ canopies (i.e. high $\Delta T$). However, low-stature PFTs are less common when DTS became dominant and the community $\Delta T$ dropped to below zero (bottom left in figure 7(a)). In addition, both DLS and GR displayed a bell-shaped relationship with changing community $\Delta T$, with a higher potential to co-occur with DTS when the latter had a mid-range FCover (middle part in figure 7(a)).

The PCC analysis showed that DTS had negative ($-0.2\sim-0.6$) correlations with most PFTs, except for DDS and ES (figure 7(b)). This suggests that increasing FCover of DTS in plot communities reduced that of other PFTs. The FCover of DDS and ES had a significant positive correlation (PCC: 0.6), signifying that both PFTs increase on the other’s FCover. Lastly, LI had a strong negative correlation with canopy GCC (PCC: $-0.7$), but a positive correlation with canopy $\Delta T$ (PCC: 0.5).
3.4. Effects of fine-scale vegetation composition on large-scale variation in canopy height and $\Delta T$

The VIP of each PFT derived from our four RF models was used to explore their importance for describing the landscape-scale variation in CHM and $\Delta T$ (figure 8). As expected, DTS had the highest VIP for explaining both the mean and $\alpha$ diversity in CHM, followed by DLS (figures 8(a) and (b)). However, DLS showed the highest VIP for modeling the spatial variation in mean $\Delta T$, likely as a result of its broad distribution across the landscape (figures 8(c) and 5). Similarly, GR showed the highest VIP for describing the spatial variation in the $\alpha$ diversity of $\Delta T$ (figure 8(d)). But overall, the spatial variation in $\Delta T$ had more diverse contributions from different PFTs than CHM.

The stepwise RF modeling showed that PFT composition (i.e. FCover) accounted for 74.2% and 86.8% of the landscape-scale variation in mean $\Delta T$ and CHM, respectively, which was slightly less than the PFT properties (i.e. P) (85.5%, and 93.4% respectively) (table 3). However, PFT composition explained more of the variance in $\alpha$ diversity than PFT properties (67.8% and 78.7% for FCover; 65.18% and 77.67% for P) for both $\Delta T$ and CHM. The combination of PFT composition and property (i.e. FCover + P) thus accounted for 89.6% and 98.2% of the spatial variation in mean $\Delta T$ and CHM (table 3), respectively, while a larger portion of the variance in $\alpha$ diversity (21.2%, 13.8% for $\Delta T$ and CHM, respectively) could not be explained by PFT.

4. Discussion and conclusion

High-latitude tundra landscapes are rapidly warming, with wide-spread implications for vegetation (Chapin et al 1996, Pearson et al 2013). In order to adequately assess impacts on these ecosystems, a fine-scale understanding of tundra vegetation composition, structure, and function is critically needed, as well as the impacts of scale on characterizing these
patterns over broad regions. Presently, however, our ability to understand tundra vegetation dynamics and processes is challenged by the high level of spatial heterogeneity within tundra landscapes (Beamish et al. 2020, Myer-Smith et al. 2020), as well as a lack of observations at fine spatial scales (Schimel et al. 2015). To address these challenges, we collected VHR, multisensor UAS data across three low-Arctic tundra sites located in western Alaska using our Osprey platform (Yang et al. 2020). We illustrate that these data are effective for detailed analyses of vegetation structure and function across tundra PFTs, providing datasets of similar fidelity as direct, in-situ measurements. The high-resolution mapping of PFTs provides a new avenue to characterize fine-scale vegetation composition patterns and link these patterns with landscape-scale variation in ecosystem properties. In addition, using such data, we were able to illustrate how the distribution of DTSs can significantly affect the structure, function, composition, and diversity of tundra landscapes.

4.1. How do tundra PFTs differ in canopy height and thermoregulation?

We first sought to understand how tundra PFTs differ in canopy height and thermal functioning. We observed that DTSs were unique on the landscape in their structure, function, and distribution, with important implications for other PFTs. This defines a critical need to characterize tall shrubs in the tundra biome (Alonzo et al. 2018 and 2020). However, no significant height differences were detected among low-stature PFTs, which indicates that canopy height may not be a critical parameter to differentiate these PFTs; from our analysis, it is also not clear how height for these PFTs plays a role in competition for resources, such as light or whether other resources (e.g., water, nutrients) are more important for controlling plant species distribution. The ‘skin’ temperature of DTSs was also found to be significantly lower than other PFTs and typically below local air temperature (ΔT < 0), suggesting higher rates of canopy cooling via evapotranspiration (Clark 2019, figure 6(b)). This ‘cooling effect’ suggests a stronger thermoregulation capacity of tall shrubs than other PFTs (Myer-Smith et al. 2011, Bring et al. 2016). Consequently, an increase in tall shrub cover, as predicted with climate change, could lead to localized cooling of tundra landscapes during the growing season, and potentially exerts negative feedbacks to permafrost thaw (Blok et al. 2010, Frost et al. 2018). However, some tall shrub species, such as alder, tend to have lower visible albedos that amplifies warming (Myers-Smith et al. 2011, Grunberg et al. 2020). High tall shrub covers can also increase winter snowpack which creates positive feedbacks to permafrost thaw (Bonfils et al. 2012, Grünberg et al. 2020). These complex interactions between vegetation structure, function, and optical properties can strongly regulate climate feedbacks (Zhang et al. 2018), which however could be further complicated by plant-herbivore interactions, where large herbivores, like muskoxen, moose, and reindeer, have been shown to decrease shrub abundance in the Arctic (Olofsson et al. 2009, Ravolainen et al. 2011, Christie et al. 2015, Yu et al. 2017).

Lichen was found to have a lower thermoregulation capacity (i.e. higher ΔT) than other PFTs (figures 4(b) and 6(b)), likely because of their non-vascular structure and low water content (Chapin et al. 1993). Evergreen shrub also had hot canopies (i.e. low thermoregulation capacity). Our field survey shows that they commonly exist at high elevations (e.g. hillslope summits) encompassed by schist rocks and lichens, which were observed to have high surface temperatures (Yang et al. 2020). This hot background thus likely contributes to the high temperature of evergreen shrubs. However, taller PFTs generally have a stronger thermoregulation capacity than lower PFTs, with a PCC of −0.5 between CHM and ΔT (figure 8). More critically, a high thermal variation was found within all PFTs (figure 6(b)), highlighting the necessity of characterizing intra-PFT thermal variation for understanding tundra vegetation dynamics.

4.2. What are the fine-scale patterns of vegetation composition across tundra landscapes?

The DTS PFT was found to play a critical role in vegetation composition at the plot community scale, commonly reducing the abundance of other PFTs, as indicated by our PCC analysis (figures 7 and 8). This role is associated with their strong thermoregulation capacity, which creates cooler micro-environments (as discussed above) and simultaneously changes energy balance and nutrient availability (Myers-Smith et al. 2011). Particularly, low-stature PFTs had lower FCover in regions dominated by DTSs, although a higher co-occurrence potential was observed among PFTs when the latter has a mid-range FCover. This is consistent with previous findings that an intermediate cover of DTSs in tundra landscapes may have a ‘nursing’ effect (Padilla and Pugnaire 2006), by altering soil resource and micro-environments that facilitates the establishment of other plants (Gonzalez and Ghermandi 2019). However, this nursing effect may by nullified by the large reduction in energy and nutrient availability when DTSs become dominant (i.e. high FCover).

We also showed that deciduous low shrubs and graminoids both exhibit a bell-shaped relationship with changing community ΔT (i.e. negative at high ΔTs and positive at low ΔTs; figure 7). The negative relation at high ΔTs (right bottom in figure 7) suggests that a transition from low-statured communities (e.g. PCT4; figure S1) to graminoid or deciduous low shrub-dominated communities (e.g. PCT1 and 6; figure S1) can increase the thermoregulation capacity...
of the ecosystem. However, the positive correlation at low $\Delta T$s is likely caused by the dominance of DTS PFT, rather than manifesting a warming effect of the two PFTs.

It is worth mentioning that this study focused on exploring the landscape patterns of vegetation composition that are governed by both biotic (e.g. topography, soil water and nutrient availability, permafrost thaw depth) and abiotic factors (e.g. competition and facilitation). From the results, we still cannot tell which factor may have contributed to the relationships among PFTs. Further studies are needed to analyze the effects of biotic and abiotic factors on the above observed patterns, to determine cause-and-effect relationships (Myers-Smith et al 2011).

4.3. How does fine-scale vegetation composition drive the large-scale variation in canopy height and thermoregulation?

The landscape-scale variation in CHM was found to be well accounted for by PFT (98.2%), likely as a result of the dominant effects of DTS PFT (figure 8 and table 3), while a lower percentage (89.6%) was found for $\Delta T$. However, PFT composition (FCover) alone (74.2% and 86.8%) explains less of the landscape variation in the $\Delta T$ and CHM than the varying PFT property (85.5% and 93.4%), which highlights the necessity of quantifying functional variation within-PFT to improve our understanding and model representation of tundra vegetation dynamics. Moreover, a large portion of the variation in $\alpha$ diversity was not explained by PFT (unexplained variance: 21.2%, 13.8% for $\Delta T$ and CHM, respectively), indicating that species-level information may be needed for studying tundra plant functional diversity across landscapes.

Collectively, these findings show that the use of static (or fixed) traits (e.g. structure and thermal functioning in this study) in current ESMs to represent tundra PFTs may be inadequate. The representation of PFT trait variation across space and environmental gradients is necessary to improve predictions of tundra ecosystem dynamics (Wullschleger et al 2014). Additionally, a more detailed classification of PFTs, including shrub height, may also be useful to represent tundra ecosystem diversity in ESMs (Sulman et al 2021), of which the currently represented tundra PFTs are fewer than those studied in this paper (common model represented PFTs: evergreen and deciduous shrubs, graminoids, forbs, moss, and lichen; Wullschleger et al 2014).

4.4. Conclusions

In this paper, we demonstrated the utility of VHR, multi-sensor UAS data for studying fine-scale patterns of tundra vegetation. The findings provided valuable insights on tundra vegetation composition, structure, and function. First, a high degree of variation in thermal functioning was found among PFTs, with DTSs having a strong ‘cooling effect’ under peak growing season conditions. Second, DTSs played a critical role in structuring local vegetation composition, commonly reducing the abundance of other PFTs. Third, PFTs could be effective to describe landscape variation in canopy height and thermal functioning. Nevertheless, characterizing intra-PFT variation, as well as a more detailed PFT classification, may be needed to improve our ecological understanding and model representation of tundra vegetation dynamics. It should be noted that the spatial coverage of UAS flights is yet limited and the observed patterns may not be the case for other community types, such as alpine, riverine, and boreal forest communities. The fusion of UAS, airborne, and satellite data will be explored in the future to inspect these patterns over larger spatial scales. In addition, though provided with a very-high resolution, UAS remote sensing cannot identify understory plants hidden by tall shrub canopies. This may lead to a slightly underestimated FCover of low-stature PFTs in regions dominated by tall shrubs. However, such an underestimation may have little effect on the overall patterns revealed in this study, given the observed dominant FCover of tall shrubs and minor FCover of low-stature PFTs in those regions. But future studies may improve this by combining UAS LiDAR data. Lastly, this study used a single DTS PFT to represent the entire pool of tall shrub species observed at our three study sites (e.g. Alnus viridis subsp. Fruticose, Salix pulchra, and Betula glandulosa). In fact, these tall shrub species and many others that are not included in this study (e.g. Salix richardsonii and Salix alaxensis) may vary in their canopy structure and other biophysical properties, which leads to variation in their thermal functioning. In future analyses, we will include more detailed tall shrub classification to investigate the difference among tall shrub species. In conclusion, the outputs of this study highlight the importance of fine-scale information for understanding tundra vegetation dynamics, which transcends our study to show the need for continued collection of such datasets.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://doi.org/10.5440/1778212.

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