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### **Aboveground biomass corresponds strongly with drone-derived canopy height but weakly with greenness (NDVI) in a shrub tundra landscape**

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## Aboveground biomass corresponds strongly with drone-derived canopy height but weakly with greenness (NDVI) in a shrub tundra landscape

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4 1 **Aboveground biomass corresponds strongly with drone-derived canopy**  
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6 2 **height but weakly with greenness (NDVI) in a shrub tundra landscape**  
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43 19 **Keywords**

44 20 Vegetation Change; Aboveground Vascular Biomass; Vegetation greenness; Normalised  
45 21 Difference Vegetation Index (NDVI); Drones; Arctic Tundra Ecosystems; Structure-from-  
46 22 Motion Photogrammetry  
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1  
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3 **23 Abstract**  
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5 24 Arctic landscapes are changing rapidly in response to warming, but future predictions are  
6  
7 25 hindered by difficulties in scaling ecological relationships from plots to biomes. Unmanned  
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9 26 aerial systems (hereafter 'drones') are increasingly used to observe Arctic ecosystems over  
10  
11 27 broader extents than can be measured using ground-based approaches and facilitate the  
12  
13 28 interpretation of coarse-grained remotely-sensed datasets. However, more information is  
14  
15 29 needed about how drone-acquired remote sensing observations correspond with ecosystem  
16  
17 30 attributes such as aboveground biomass. Working across a willow shrub-dominated alluvial  
18  
19 31 fan at a focal study site in the Canadian Arctic, we conducted peak growing season drone  
20  
21 32 surveys with an RGB camera and a multispectral multi-camera array. We derived  
22  
23 33 photogrammetric reconstructions of canopy height and normalised difference vegetation index  
24  
25 34 (NDVI) maps along with *in situ* point-intercept measurements and aboveground vascular  
26  
27 35 biomass harvests from 36, 0.25 m<sup>2</sup> plots. We found high correspondence between canopy  
28  
29 36 height measured using *in situ* point-intercept methods compared to drone-photogrammetry  
30  
31 37 (concordance correlation coefficient = 0.808), although the photogrammetry heights were  
32  
33 38 positively biased by 0.14 m relative to point-intercept heights. Canopy height was strongly and  
34  
35 39 linearly related to aboveground biomass, with similar coefficients of determination for point  
36  
37 40 framing ( $R^2 = 0.92$ ) and drone-based methods ( $R^2 = 0.90$ ). NDVI was positively related to  
38  
39 41 aboveground biomass, phytomass and leaf biomass. However, NDVI only explained a small  
40  
41 42 proportion of the variance in biomass ( $R^2$  between 0.14 and 0.23 for logged total biomass)  
42  
43 43 and we found moss cover influenced the NDVI-phytomass relationship. Vascular plant  
44  
45 44 biomass is challenging to infer from drone-derived NDVI, particularly in ecosystems where  
46  
47 45 bryophytes cover a large proportion of the land surface. Our findings suggest caution with  
48  
49 46 broadly attributing change in fine-grained NDVI to biomass differences across biologically and  
50  
51 47 topographically complex tundra landscapes. By comparing structural, spectral and on-the-  
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53 48 ground ecological measurements, we can improve understanding of tundra vegetation change  
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55 49 as inferred from remote sensing.  
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## 1. Introduction

Arctic ecosystems are warming rapidly (IPCC, 2013) and plant communities are responding (Elmendorf et al., 2012b, 2015; Myers-Smith et al., 2011, 2019). Shrub growth is climate sensitive (Elmendorf et al., 2012a; Myers-Smith et al., 2020) and increases in shrub abundance and decreases in bare ground in plant communities have been reported at sites around the tundra biome (Elmendorf et al., 2012b; Myers-Smith et al., 2011). However, there is limited understanding of the controls on vegetation change in tundra plant communities (Myers-Smith et al., 2020; Post et al., 2019). We do not yet have standardised methods of quantifying changes in tundra plant canopy structures and growth across the landscape and there are few allometric relationships relating observable plant dimensions to aboveground biomass in Arctic ecosystems (Berner et al., 2015). One of the key challenges in tundra ecological monitoring is acquiring scale-appropriate observations due to the small growth forms of many plants in this large extent and often less accessible biome (Fisher et al., 2018).

Remote-sensing approaches have been widely employed to gather information about changing Arctic landscapes (Bartsch et al., 2020; Berner et al., 2015; Jia et al., 2009; Myers-Smith et al., 2020; Walker et al., 2003a). In tundra ecosystems, there is a critical scale gap between biome-wide coarse-grain observations from satellite-based remote sensing (with pixels typically measuring between 64 km<sup>2</sup> to 100 m<sup>2</sup>) and *in-situ* observations collected at fine spatial scales typically over a few meters (Bartsch et al., 2020; Myers-Smith et al., 2020; Riihimäki et al., 2019; Santin-Janin et al., 2009). Bridging this scale gap requires the integration of observations at intermediate scales. Unmanned aerial systems (hereafter 'drones') are one possible platform for deploying sensors to collect high-resolution data at landscape scales (Anderson, 2016), which have now become widely used for collecting environmental data (Assmann et al., 2018; Howell et al., 2020; Karl et al., 2020). However, empirical work is needed to relate remotely-sensed attributes to ecological variables and inform scientific interpretations (Räsänen et al., 2019).

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3 79 Fine-scale measurements of three-dimensional plant structure can inform biomass prediction  
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5 80 (Cunliffe et al., 2016; Fraser et al., 2016; Greaves et al., 2017, 2015; Poley and McDermid,  
6  
7 81 2020). Such methods have been demonstrated with ground-based and airborne light detection  
8  
9 82 and ranging (LiDAR) observations in Arctic tundra landscapes (Greaves et al., 2017, 2015),  
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11 83 but also with aerial photogrammetry surveys leveraging advances in computer vision  
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13 84 approaches (Alonzo et al., 2020; Fraser et al., 2019, 2016). However, few studies have tested  
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15 85 the correspondence between photogrammetrically determined canopy height and *in situ*  
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17 86 measurements Arctic plants. Such testing is necessary to inform the successful integration of  
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19 87 drone-derived products into existing ecological monitoring programmes in the tundra biome.  
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23  
24 89 Spectral reflectance measurements from optical remote sensing have long been used for  
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26 90 vegetation studies (Jia et al., 2003; Myers-Smith et al., 2020; Walker et al., 2003a). Spectral  
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28 91 reflectance data can be used to calculate vegetation indices such as the normalised difference  
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30 92 vegetation index (NDVI), which contrasts the reflectance in the red portion of the spectrum  
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32 93 that is maximally absorbed by chlorophyll with the near-infrared (NIR) portion that is highly  
33  
34 94 reflected by leaf and canopy structures (Buchhorn et al., 2016). Several studies have shown  
35  
36 95 that NDVI can be good predictor of photosynthetic tissue biomass (here after phytomass) in  
37  
38 96 Arctic ecosystems (Boelman et al., 2003; Hogrefe et al., 2017; Walker et al., 2003a), and NDVI  
39  
40 97 has often also been considered a predictor of total aboveground biomass (Berner et al., 2018;  
41  
42 98 Myers-Smith et al., 2020). However, different plant tissues have different reflectance  
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44 99 properties (Bratsch et al., 2017; Räsänen et al., 2019), and aboveground biomass is  
45  
46 100 dominated by non-photosynthetic tissues, such as woody stems, in many communities such  
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48 101 as shrublands (Epstein et al., 2012). Logistical challenges have limited the number of empirical  
49  
50 102 studies that have been able to test the relationship between NDVI and *total* aboveground  
51  
52 103 biomass (Berner et al., 2018; although see Boelman et al., 2003; Goswami et al., 2015).  
53  
54 104 Furthermore, there is commonly a scale mismatch between the extent sampled for spectral  
55  
56 105 reflectance (i.e., the ground sampling distance of a remotely-sensed pixel) and the extent over  
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58 106 which aboveground biomass is quantified (Berner et al., 2018; Karlsen et al., 2018). The  
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3 107 capacity of peak NDVI to explain variation in total biomass requires further evaluation given  
4  
5 108 the widespread consideration of NDVI as a predictor of total aboveground biomass, combined  
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7 109 with the increasing accessibility of spectral reflectance data at ever-finer spatial resolutions  
8  
9 110 (Berner et al., 2018; Fraser et al., 2017; Riihimäki et al., 2019).

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13  
14 112 In this study, we conducted spatially explicit-comparisons between ground-based and drone-  
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16 113 based measurements of canopy height, NDVI and biomass to address biomass monitoring in  
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18 114 tundra ecosystems. We worked across a *Salix richardsonii* to graminoid ecotone on a shrub-  
19  
20 115 dominated alluvial fan at a focal tundra research site on Qikiqtaruk – Herschel Island. We  
21  
22 116 examined whether drone data collection combined with image-based modelling approaches  
23  
24 117 yielded high-fidelity measurements of vegetation attributes. We tested the correspondence  
25  
26 118 among (i) canopy height models derived from aerial photogrammetry and *in-situ* point-  
27  
28 119 intercept methods, (ii) canopy height and aboveground biomass of vascular plants, and (iii)  
29  
30 120 NDVI values obtained at different spatial grains and total vascular plant biomass,  
31  
32 121 photosynthetic biomass and leaf biomass. Our analyses tested the extent to which drone-  
33  
34 122 based methods can be used to monitor vegetation canopies to infer tundra biomass and  
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36 123 productivity.

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## 40 41 125 **2. Methods**

### 42 43 126 **2.1. Site description**

44  
45 127 We conducted our study on Qikiqtaruk - Herschel Island in the Canadian Arctic. Tundra  
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47 128 vegetation communities here range from graminoid- to shrub-dominated and are underlain by  
48  
49 129 organic soils and ice-rich permafrost. This site has undergone marked ecological changes in  
50  
51 130 community composition, increases in canopy height and vegetation abundance, decreases in  
52  
53 131 bare ground, and an advance in leaf emergence and flowering over nearly two decades of  
54  
55 132 ecological monitoring (Myers-Smith et al., 2019).

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### 59 60 134 **2.2. Field sampling**

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2  
3 135 Our study area encompassed a graminoid-shrub ecotone at the edge of a wet willow shrub-  
4  
5 136 dominated alluvial fan (69.571°N, 138.893°W) (Figure 1). We established two adjacent sites,  
6  
7 137 a 0.5-hectare area to the north was allocated for monitoring canopy structure and biomass  
8  
9 138 change over time (coordinates in Table S4), and an adjacent sampling area to the south  
10  
11 139 contained the harvest plots for calibrating allometric relationships between height or NDVI and  
12  
13 140 biomass. Both the monitoring and harvesting areas were selected to be representative of the  
14  
15 141 full distribution of canopy heights that we observed in the field (see Figure S8 for comparison  
16  
17 142 of value distributions).  
18  
19

20 143

21  
22 144 To constrain the photogrammetric modelling and locate the point clouds in a coordinate  
23  
24 145 reference system, 26 ground control markers (265 mm x 265 mm) were deployed across the  
25  
26 146 entire area and geolocated to a relative 3D accuracy of  $\leq 0.015$  m with an RTK-GNSS survey  
27  
28 147 instrument (Leica GS10). Coordinates were relative to a local benchmark, geolocated in  
29  
30 148 absolute terms to  $\pm 0.003$  m in X and Y, and  $\pm 0.008$  m in Z (95% confidence interval), using  
31  
32 149 the AUSPOS web service. The markers were situated to be visible from the air, and the high  
33  
34 150 density of markers (ca. 26 markers per  $\text{ha}^{-1}$ ) facilitated image alignment for stable  
35  
36 151 reconstruction in the texturally complex scene (Poley and McDermid, 2020).  
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40  
41 153 In June 2016, we selected 36 plots of 50 cm x 50 cm for detailed observation within our  
42  
43 154 harvesting area (Figure 1d). The plots were arranged in twelve blocks of three replicates,  
44  
45 155 stratified across the range of canopy heights in order to estimate the allometric models more  
46  
47 156 efficiently as well as to determine the form of the relationship between mean canopy height  
48  
49 157 and biomass (Warton et al., 2006). Plots contained no standing water during the period of  
50  
51 158 observations. The dimensions of the harvest plots were selected to be large enough to contain  
52  
53 159 representative samples of plant material and to reduce the possible effects of co-registration  
54  
55 160 errors. The corners of each harvest plot were precisely geolocated using the GNSS. To  
56  
57 161 minimise the GNSS survey staff sinking into the often-soft ground, we used a ca. 25  $\text{cm}^2$  'foot'  
58  
59 162 on the bottom of the staff to dissipate pressure.  
60



163

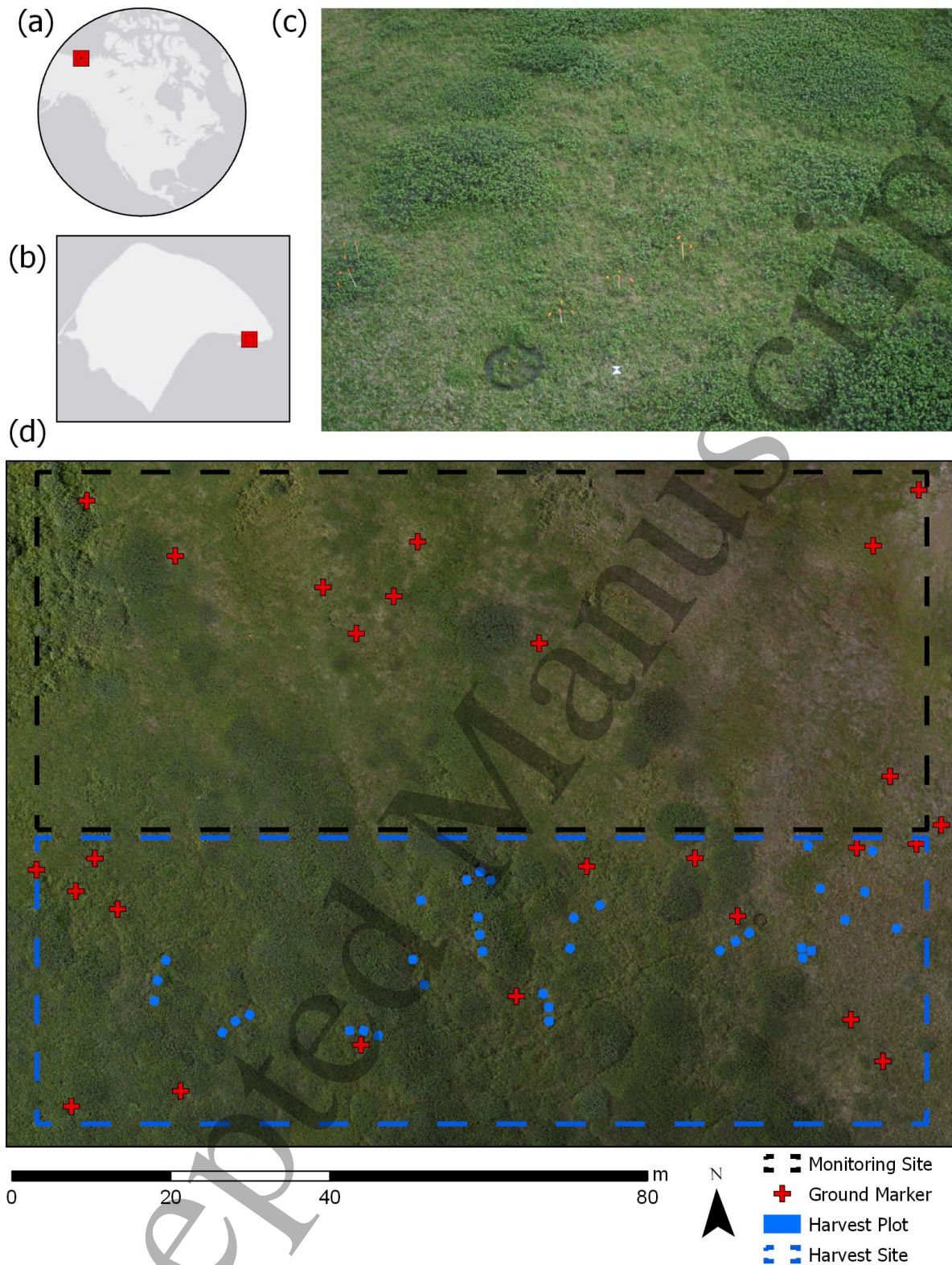
164 To enable canopy height to be modelled across the monitoring area, we undertook a walkover  
165 survey with the GNSS to measure the ground elevation at intervals along transects, which  
166 yielded 911 observations with an average spacing of 1 point per 10 m<sup>2</sup>. We excluded 36  
167 regularly spaced ground observations for validation purposes and interpolated a terrain model  
168 from the remaining observations using inverse distance weighting (power = 3, search radius  
169 = 7, cell size = 0.1 m).

170

171 On the 30<sup>th</sup> and 31<sup>st</sup> of July 2016 after the drone surveys were completed, each of the 36, 50  
172 x 50 cm plots were surveyed using point-intercept methods similar to ITEX protocols (Molau  
173 and Mølgaard, 1996; Myers-Smith et al., 2019). We placed a grid with 36 points at 10 cm  
174 intervals over each plot. At each point, we placed a metal pin vertically and recorded the  
175 maximum height of the canopy above the moss/litter layer representing the ground surface.  
176 Wind speeds were generally light during our ground surveys and our point-intercept  
177 observations did not appear to be influenced by the limited movement of the low stature  
178 canopies.

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180

181 Figure 1. Overview of the study site encompassing a graminoid-shrub ecotone. The panels  
 182 indicate: location of Qikiqtaruk – Herschel Island in the Western Canadian Arctic (a), location  
 183 of the study site on an alluvial fan to the east of the Island at  $69.571^{\circ}\text{N}$ ,  $138.893^{\circ}\text{W}$  (b), an  
 184 aerial oblique photograph of the graminoid to shrub ecotone, looking southwest (c), and true

1  
2  
3 185 colour orthomosaic at 4 mm spatial resolution (d). The orange flags (in c) indicate some of the  
4  
5 186 36 harvest plots (blue squares in d) and the wide squares (in c) indicate some of the 26 ground  
6  
7 187 control markers (red crosses in d).  
8

9 188

### 11 189 2.3. Biomass harvest

13 190 Our sampling at the end of July coincided with the period of peak biomass across the growing  
14  
15 191 season at this location. Within each of the 36 sub-plots, all standing vascular plants were  
16  
17 192 harvested down to the top of the moss/litter layer (after Walker et al., 2003a) on the 31<sup>st</sup> of  
18  
19 193 July and 1<sup>st</sup> of August 2016. Harvested biomass was separated into three partitions: (i) woody  
20  
21 194 stems, (ii) shrub leaves (including catkins that accounted for less than 10% of the 'leaf'  
22  
23 195 biomass), and (iii) herbaceous material (consisting of mainly graminoids and equisetum, but  
24  
25 196 also some forbs). *Salix richardsonii* produces catkins before leaves in June and the seeds are  
26  
27 197 mostly dispersed by mid-July. At the time of drone data collection and biomass harvesting,  
28  
29 198 most catkins had dispersed their seeds and were senesced. Biomass was dried at ca. 35°C  
30  
31 199 for  $\geq 70$  hours, until it reached a constant weight ( $<0.2\%$  change) over a 24-hour period.  
32  
33

34 200

35 201

### 37 202 2.4. Aerial surveys

#### 39 203 2.4.1. Aerial survey for canopy height modelling

41 204 To obtain aerial images for modelling of canopy heights, we used a 24 megapixel camera  
42  
43 205 (Sony  $\alpha$ 6000), equipped with a prime lens (Sony SEL 20 mm F2.8), carried on a Tarot 680  
44  
45 206 hexacopter controlled with a PixHawk running open source ArduPilot (<http://ardupilot.org>)  
46  
47 207 software (Table 1). Two sets of survey flights were undertaken, the first obtaining nadir  
48  
49 208 imagery and the second obtaining oblique (ca. 20° from nadir). Images were obtained with a  
50  
51 209 spatial grain of ca. 4-6 mm at the canopy top (Cunliffe and Anderson, 2019). The camera was  
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53 210 triggered by the flight controller based on distance travelled, with both sets of flights together  
54  
55 211 capturing  $\geq 22$  photos for every part of the study area (equivalent to forward overlap of 75%  
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57 212 and sidelap of 65% for each flight). We collected 673 RGB photographs over the survey area.  
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3 213 Mission flight speeds ensured that motion blur during shutter exposure was less than one third  
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5 214 of the ground sampling distance. Image data were originally recorded in lossless RAW-file  
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7 215 format (Sony ARW), and were converted to uncompressed TIFF using Sony's Image Data  
8  
9 216 Converter (v4).

10  
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#### 13 14 218 2.4.1. Aerial survey for spectral reflectance

15  
16 219 To obtain images for modelling spectral reflectance, we used Parrot Sequoia (Paris, France)  
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18 220 multi-camera arrays (firmware 1.0.0), to record the Red (640-680 nm) and Near-infrared (770-  
19  
20 221 820 nm) bands with an instantaneous-field-of-view of 61.9° (across flight line) and 48.5° (along  
21  
22 222 flight line) (Parrot, 2017). Recent studies indicate a generally good, but sometimes mixed  
23  
24 223 correspondence between surface reflectance measured with Sequoia or similar multi-camera  
25  
26 224 arrays and satellite observations (e.g. from Sentinel-2) (Díaz-Delgado et al., 2019; Fawcett et  
27  
28 225 al., 2020; Fernández-Guisuraga et al., 2018; Franzini et al., 2019; Khaliq et al., 2019; Matese  
29  
30 226 et al., 2015). We reduced issues associated with the precision of the Sequoia observations  
31  
32 227 (Fawcett and Anderson, 2019) as much as possible by adhering to best practices (Assmann  
33  
34 228 et al., 2018). To learn more about the consistency of the drone-derived NDVI products under  
35  
36 229 real-world operational conditions, we conducted four multispectral surveys under different  
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38 230 spatial grain and illumination conditions, using different survey altitude, sun elevation and  
39  
40 231 cloud conditions (Assmann et al., 2018; Fawcett et al., 2020; Stow et al., 2019).

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45 233 The Sequoia sensors were mounted on multi-rotor (as above) and flying-wing (Zeta Phantom  
46  
47 234 FX-61) platforms with PixHawk flight controllers. We undertook four multispectral surveys over  
48  
49 235 two days, at altitudes of 19 m, 50 m, 120 m and 121 m above ground level, to sample a range  
50  
51 236 of spatial resolutions and illumination conditions with respect to cloud cover and sun  
52  
53 237 illumination angle (Table 1). The three multirotor flights carried the same Sequoia sensor,  
54  
55 238 while the flying-wing carried a second Sequoia sensor. A MicaSense spectral reflection  
56  
57 239 calibration panel reflecting ca. 50% of light was imaged before and after each survey, and the  
58  
59 240 image considered to be the most representative of illumination conditions during the survey

241 was used for empirical line calibration of spectral reflectance during processing (Assmann et  
 242 al., 2018). The reflectance values of the panel were measured under laboratory conditions  
 243 before and after the field campaign, and we used the mean of these two measurements to  
 244 minimise errors arising from degradation in panel reflectance (Assmann et al., 2018). The  
 245 Sequoia was triggered using a two-second intervalometer to achieve an overlap of at least  
 246 five images across the study area.

247

248 Table 1. Description of drone surveys. (A) and (B) refer to the two Parrot Sequoia sensors,  
 249 and local time refers to the middle of the survey period.

Sensor	Altitude agl [m]	GSD [m]	Date	Local time (UTC- 8)	Solar elevation (degrees)	Platform	Mean wind speed [m s <sup>-1</sup> ]	Cloud conditions
Sony α6000	19	0.005	25 <sup>th</sup> July 2016	13:20	39.9	Multirotor	3.4	Thin cirrus (sun not obscured)
Parrot Sequoia (A)	19	0.018	26 <sup>th</sup> July 2016	17:34	27.3	Multirotor	3.1	Thin cirrus (sun not obscured)
Parrot Sequoia (A)	50	0.047	30 <sup>th</sup> July 2016	13:10	38.7	Multirotor	4.2	Scattered cumulus (sun not obscured)
Parrot Sequoia (B)	120	0.119	30 <sup>th</sup> July 2016	13:21	38.7	Flying wing	4.9	Cumulus (sun obscured)
Parrot Sequoia (A)	121	0.121	26 <sup>th</sup> July 2016	19:50	15.6	Multirotor	3.1	Scattered cumulus (sun not obscured)

250

## 251 2.5. Image based modelling

### 252 2.5.1. Processing for canopy height models

253 The aerial images were processed using structure-from-motion photogrammetry on a high  
 254 performance workstation with a workflow based on Cunliffe *et al.* (2016). Geotagged image  
 255 data and marker coordinates were imported into Agisoft PhotoScan (v1.2.4) and converted  
 256 into a common coordinate reference system (WGS84 UTM 7N; EPSG:32607). Image quality  
 257 was assessed using PhotoScan's image quality tool, which assesses the sharpness of the  
 258 sharpest part of each photograph; all images had a sharpness of  $\geq 0.77$ . Photos were matched  
 259 and cameras aligned using the highest quality setting, key point limit of 100,000, unlimited tie  
 260 points, generic and reference pair preselection were enabled, and adaptive camera model  
 261 fitting was disabled. Camera location accuracy was set to 25 m, marker location accuracy was

1  
2  
3 262 set to 0.01 m, marker projection accuracy was set to two pixels, and tie point accuracy was  
4  
5 263 set to one.  
6

7 264  
8

9 265 The sparse cloud was filtered and tie points with reprojection error above 0.55 were excluded  
10  
11 266 from further analysis. We reviewed the estimated camera positions to verify their plausibility  
12  
13 267 and removed any obviously erroneous tie points from the sparse cloud. Geolocated markers  
14  
15 268 were manually placed on all projected images for each of the 26 ground control points (Cunliffe  
16  
17 269 et al., 2016; Kachamba et al., 2016). Three markers used for independent accuracy  
18  
19 270 assessment were deselected at this stage. The bundle adjustment was then optimised using  
20  
21 271 the filtered cloud of tie points and the following lens parameters: focal length ( $f$ ), principal point  
22  
23 272 ( $c_x$ ,  $c_y$ ), radial distortion ( $k_1$ ,  $k_2$ ,  $k_3$ ), tangential distortion ( $p_1$ ,  $p_2$ ), aspect ratio and skew  
24  
25 273 coefficients ( $b_1$ ,  $b_2$ ). Out of 673 images, 95% (636) were aligned and used for the multi-view  
26  
27 274 stereopsis (dense cloud generation) using the ultrahigh quality setting, mild depth filtering and  
28  
29 275 point colour calculation enabled. The dense point cloud was exported in the .laze format, with  
30  
31 276 point coordinate and RGB attributes.  
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34 277  
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36 278 The dense point cloud was analysed in PDAL (v1.9.1 PDAL Contributors, 2020). The corner  
37  
38 279 coordinates were used to subset points for each harvest plot. Within each plot, the normalised  
39  
40 280 height above ground (hereafter height) of each point was calculated relative to the horizontally  
41  
42 281 closest corner coordinate. Any points with a calculated negative height above the inferred  
43  
44 282 ground surface were set to zero. In a few instances where corner marker posts were visible in  
45  
46 283 the point cloud, these points were removed manually from the point cloud. We determined the  
47  
48 284 maximum height for each cell across a 0.01 m grid using the rasterstats package (v0.13.1).  
49  
50 285 For cells containing no points, maximum heights were interpolated with inverse distance  
51  
52 286 weighting considering an array of 11 x 11 cells using a power term of two, and cells with no  
53  
54 287 neighbouring points in that area remained empty. We used the 1-cm spatial grain when  
55  
56 288 creating the canopy height model (CHM) to preserve the fine-scale detail in the point cloud  
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1  
2  
3 289 (Alonzo et al., 2020; Cunliffe et al., 2016; Wallace et al., 2017). Plot-level mean height was  
4  
5 290 then extracted from this grid of the local maximum elevations.  
6

7 291

#### 9 292 2.5.2. Processing for spectral reflectance

11 293 The multispectral images were processed using Pix4Dmapper Pro (v4.0.25). We implemented  
12  
13 294 radiometric corrections using downwelling sun irradiance and pre- or post-flight images of  
14  
15 295 reflectance panels following Assmann *et al.* (2018). Ground control markers were manually  
16  
17 296 placed in  $\geq 15$  images, and then automatic placement was employed and manually verified.  
18  
19 297 Normalised difference vegetation index (NDVI) maps were generated using the 'AG  
20  
21 298 Multispectral Template' at the native resolution of the GSD (Table 1). The R Package  
22  
23 299 'exactextractr' (Baston, 2019, v0.1.1) was used to extract the mean NDVI of each plot, using  
24  
25 300 areal weighting to avoid the edge effects associated with inclusion or exclusion of boundary  
26  
27 301 pixels. Solar elevations were calculated using the 'suncalc' package (v0.5.0) (Thieurmel and  
28  
29 302 Elmarhraoui, 2019). To examine pairwise pixel covariance, we resampled NDVI,  
30  
31 303 photogrammetrically-derived canopy height and NDVI-derived canopy height to a common  
32  
33 304 0.25 m spatial resolution with bilinear interpolation.  
34  
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36 305

#### 39 306 2.6. Landscape biomass estimation

41 307 To demonstrate how this approach might support upscaling studies, we estimated  
42  
43 308 aboveground vascular biomass density for the monitoring area based on modelled canopy  
44  
45 309 height and NDVI using the allometric functions calibrated from the adjacent harvest plots  
46  
47 310 (Figures 3 and S5, Tables S1 and S2). This analysis was undertaken using the 'raster'  
48  
49 311 package v. 3.1-5 (Hijmans and et al., 2020) and visualised using the package 'rasterVis' v.  
50  
51 312 0.47 (Lamigueiro and Hijmans, 2019). We calculated upper and lower estimates for biomass  
52  
53 313 in the monitoring plot, using the standard error of the allometric equations, in order to account  
54  
55 314 for this source of uncertainty in the landscape estimates.  
56  
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58 315

#### 59 316 2.7. Statistical analysis

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2  
3 317 Statistical analysis was conducted in R (v3.6.1) (R Core Team, 2019). To compare agreement  
4  
5 318 between point framing and structure-from-motion metrics of canopy height, we calculated  
6  
7 319 concordance correlation coefficients using the 'DescTools' package (after Lin, 1989) and we  
8  
9 320 described this relationship with a power function fitted with ordinary least squares regression  
10  
11 321 because using a positive exponent means the model passes through the origin. We used least  
12  
13 322 squares optimisation to fit linear models between canopy height and aboveground biomass,  
14  
15 323 with intercepts constrained through the origin as plants with zero height above ground have  
16  
17 324 no biomass above ground. The intercept terms in the unconstrained point-intercept and  
18  
19 325 photogrammetry canopy height-biomass models were not statistically significant ( $p = 0.78$  and  
20  
21 326  $p = 0.25$ , respectively) and constraining model intercepts made only small differences to model  
22  
23 327 slopes (Table S1). We reported errors as standard deviations unless otherwise stated.  
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25

26 328

27  
28 329 We used least squares optimisation to fit exponential models between NDVI and three  
29  
30 330 vascular plant biomass pools: (i) total aboveground biomass, (ii) phytomass (calculated as the  
31  
32 331 sum of shrub leaves and herbaceous material), and (iii) the biomass of shrub leaves.  
33  
34 332 Comparisons between remotely-sensed NDVI and biomass usually have a substantial  
35  
36 333 mismatch in observation extents due to the larger grain of satellite products relative to smaller  
37  
38 334 extents of directly measured harvest plots (Bartsch et al., 2020; Berner et al., 2018). In our  
39  
40 335 study, we undertook spatially explicit drone-based sampling of corresponding areas, so thus  
41  
42 336 our biomass and NDVI measurements do not have this scale mismatch. Because non-  
43  
44 337 harvested moss can contribute to the differential reflectance of red and near-infrared energy,  
45  
46 338 we hypothesized that the proportion of moss cover might influence the relationships between  
47  
48 339 NDVI and biomass. We extracted the proportion of moss cover from our point-intercept  
49  
50 340 observations and tested the influence of moss cover on NDVI-biomass relationships by adding  
51  
52 341 an interaction term in our model of the relationship between NDVI and phytomass. The code  
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54 342 for statistical analyses and data visualisation is available from  
55  
56 343 <https://github.com/AndrewCunliffe/OrcaManuscript>.  
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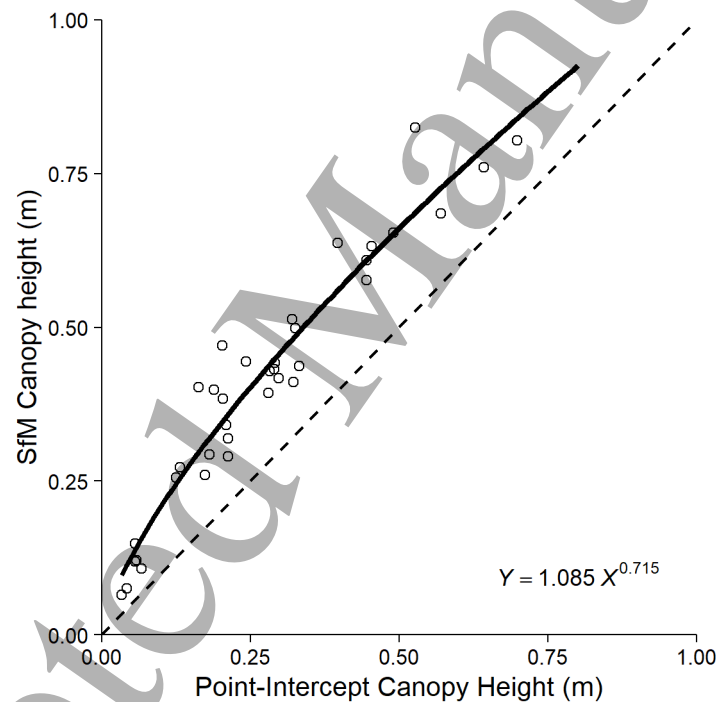


### 344 3. Results

#### 345 3.1. Drone photogrammetry captured variation in plant canopy height

346 We found strong agreement between canopy heights as observed with point-intercept method  
 347 and structure-from-motion photogrammetry (Figures 2 and S1). The photogrammetrically-  
 348 derived canopy heights had a consistent positive bias relative to point-intercept heights, with  
 349 a median difference of  $0.14 \pm 0.05$  m ( $\pm$  SD). Differences in mean canopy height between  
 350 methods were smaller for the shortest and tallest plots, and greatest for the plots of  
 351 intermediate heights (Figure S1). The concordance correlation coefficient was 0.79 (with 95%  
 352 confidence intervals of 0.68 to 0.86).

353



354

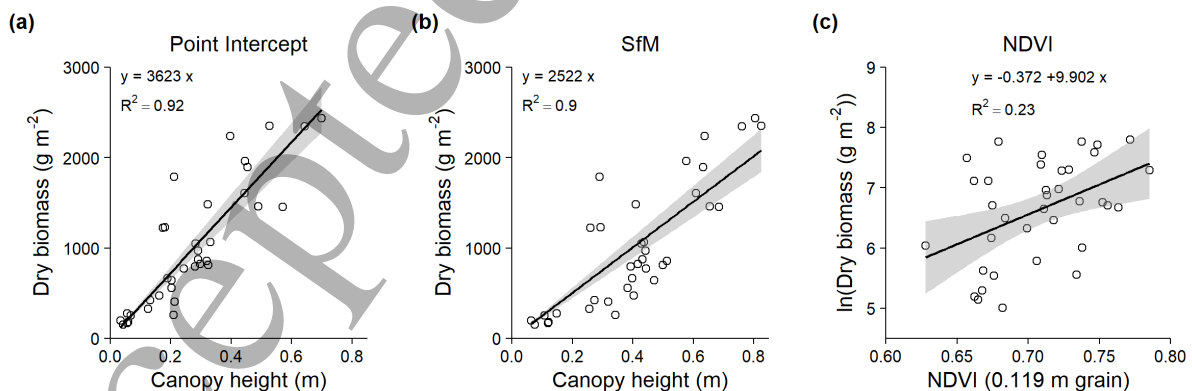
355 Figure 2. Canopy heights observed with point-intercept methods were positively correlated  
 356 with canopy heights observed with structure-from-motion photogrammetry (SfM) at the plot  
 357 level. Open circles represent observed values. The dotted line shows the 1:1 relationship for  
 358 reference and the solid line is a power model. Mean canopy heights measured with SfM were  
 359 consistently positively biased, on average by 0.14 m, relative to mean canopy heights  
 360 measured with point-intercept .

361

362 3.2. Canopy height explained variation in total biomass across plots

363 We found canopy height explained most of the variation in the aboveground biomass of  
 364 vascular plants across the *Salix richardsonii*-dominated graminoid-shrub ecotone. The  
 365 biomass models had slopes of  $3623 \pm 177 \text{ g m}^{-1}$  and  $2522 \pm 143 \text{ g m}^{-1}$ , explaining 0.92 and  
 366 0.90 of the variance for point-intercept and SfM-derived canopy heights respectively (Figure  
 367 3). Total aboveground biomass within the sampled plots ranged from  $149 \text{ g m}^{-2}$  to  $2,431 \text{ g m}^{-2}$   
 368 with a mean of  $1012 \pm 699 \text{ g m}^{-2}$ . Shrubs (woody material and leaves) accounted for the  
 369 majority of biomass in 32 of the 36 plots. The biomass of shrub leaves was positively related  
 370 to total biomass (slope =  $19 \text{ g m}^{-2}$ ) and explained 70% of the variation in total biomass (Figure  
 371 5a). However, phytomass, calculated as the sum of shrub leaves and herbaceous material  
 372 typically accounted for less than 10% of total biomass (Figure S3), and did not correspond  
 373 with total biomass (Figure 5b). Herbaceous material (largely equisetum and some forbs)  
 374 typically accounted for half of the phytomass in each harvest plot, ranging from 3% to 87% of  
 375 the phytomass. The mass of leaf material was a reasonable predictor of total biomass ( $y =$   
 376  $-63.7 + 19.04 x$ ;  $R^2 = 0.70$ ; Figure 5a); however, phytomass was a poor predictor of total  
 377 biomass ( $y = -1185 + 0.8471x$ ;  $R^2 = 0.01$ ; Figure 5b).

378



379

380 Figure 3. Aboveground biomass was strongly predicted by canopy height, but less strongly by  
 381 NDVI. For each harvest plot, the mean canopy height was measured with point-intercept (a)  
 382 and structure-from-motion photogrammetry (b), and mean NDVI was extracted from the 0.119

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2  
3 383 m grain raster (c). Linear models with constrained intercepts were fitted using least mean  
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5 384 squares optimisation, with constrained intercepts for the canopy height models. The linear  
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7 385 model fit is a simplification of the likely saturating relationships that we would expect to find  
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9 386 across the full variation of NDVI and biomass values.

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12 387

### 13 14 15 388 3.3. NDVI weakly explained variation in biomass

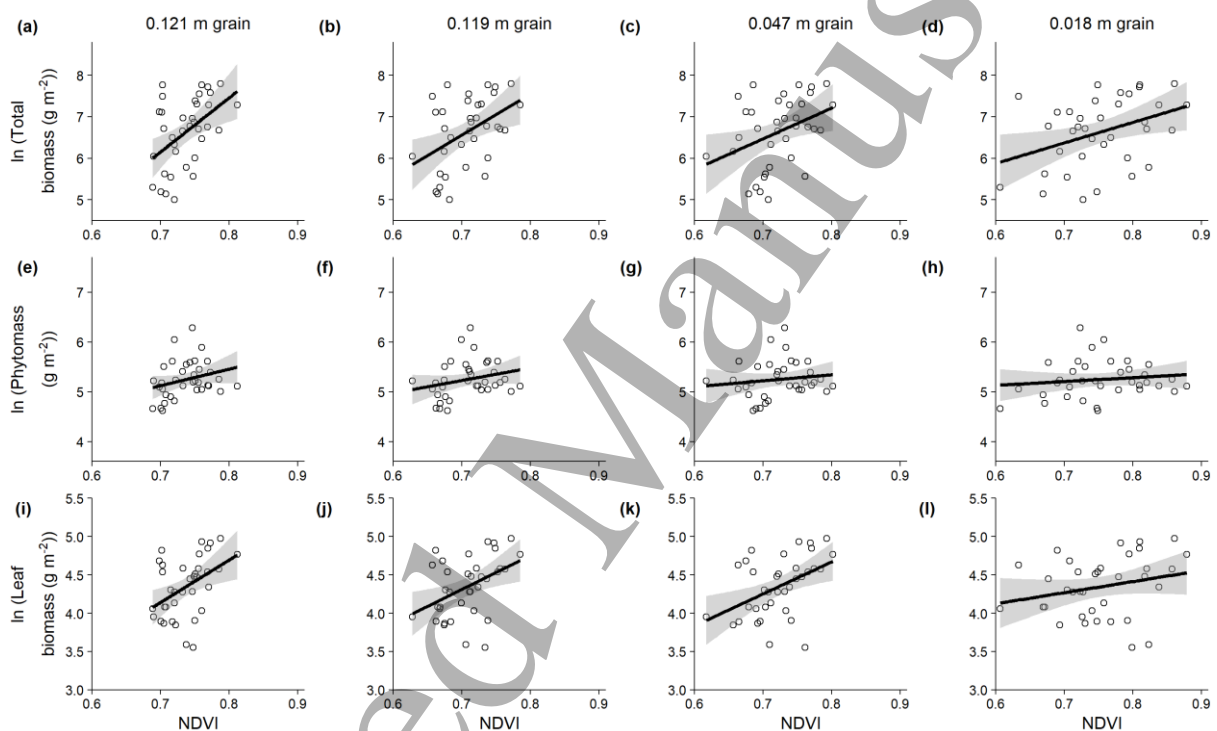
16  
17 389 We found that NDVI positively corresponded with total aboveground biomass, phytomass and  
18  
19 390 shrub leaf biomass (Figures 3c, 4 and S3, Tables 2 and S2). However, NDVI explained less  
20  
21 391 than a quarter of the variance in total aboveground biomass (14% to 23%), phytomass (2% to  
22  
23 392 7%) and leaf biomass (6% to 21%) across all four spatial grains investigated (Figure 4, Table  
24  
25 393 2). The predictive relationships weakened slightly as the spatial grain of the NDVI rasters  
26  
27 394 became finer from 0.121 m to 0.018 m, with larger residual standard errors and smaller  
28  
29 395 coefficients of determination (Table 2). With a coarser spatial grain, the overall mean and  
30  
31 396 variability amongst plot NDVI values was lower, although the relationship at the coarsest  
32  
33 397 spatial grain (0.121 m) deviated slightly from this pattern (Figure S4a). We speculate that this  
34  
35 398 may relate to more pronounced bi-directional reflectance experienced during this particular  
36  
37 399 drone survey that was conducted with a lower sun elevation of just 15.6 degrees (Table 1).  
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39  
40 400 We tested whether the proportion of moss cover influenced the relationship between NDVI  
41  
42 401 and total biomass, phytomass and the three biomass pools (Table S3, Figure S6), and though  
43  
44 402 the interaction effects were similar with stronger NDVI-biomass relationships among plots with  
45  
46 403 lower moss cover, the interaction was only significant ( $p < 0.05$ ) for the phytomass relationship  
47  
48 404 for the 0.121 m raster (Figure 5c).

49  
50  
51 405

52  
53  
54 406 To understand the performance of NDVI as a predictor of biomass, it is informative to examine  
55  
56 407 the pairwise pixel covariance between NDVI and canopy height, as canopy height is a strong  
57  
58 408 predictor of biomass (Figure 6). We found a generally positive relationship between NDVI and  
59  
60 409 canopy height, although the relationship was weaker at canopy heights below 0.2 m and once

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2  
3 410 NDVI saturated at ca. 0.75. This relationship was consistent across all four spatial grains of  
4  
5 411 NDVI sampled, and suggests NDVI-biomass transfer functions will be more uncertain where  
6  
7 412 canopies are low (< 0.2 m) or NDVI is high (> 0.75). We used an NDVI-height transfer function  
8  
9 413 developed by Bartsch *et al.* (2020) to predict canopy height from NDVI and compare these  
10  
11 414 predictions to photogrammetrically-derived canopy height (Figure S10), and found that while  
12  
13 415 there was a generally positive relationship, the slope differed by a factor of ca. five. Models  
14  
15 416 fitted to predict canopy height as a function of NDVI are reported in Table S5.

417

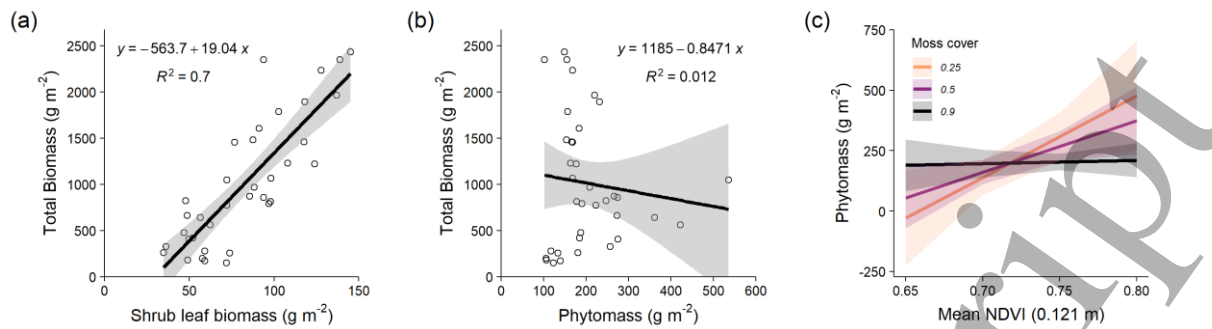


418

419 Figure 4. Mean NDVI was positively, but weakly related to total biomass, phytomass and leaf  
420 biomass at the plot level. Open circles represent observations, and black lines are linear  
421 models fitted to the log transformed biomass data described in Table 2. Exponential models  
422 fitted to non-transformed biomass data are presented in Figure S5 and Table S2.

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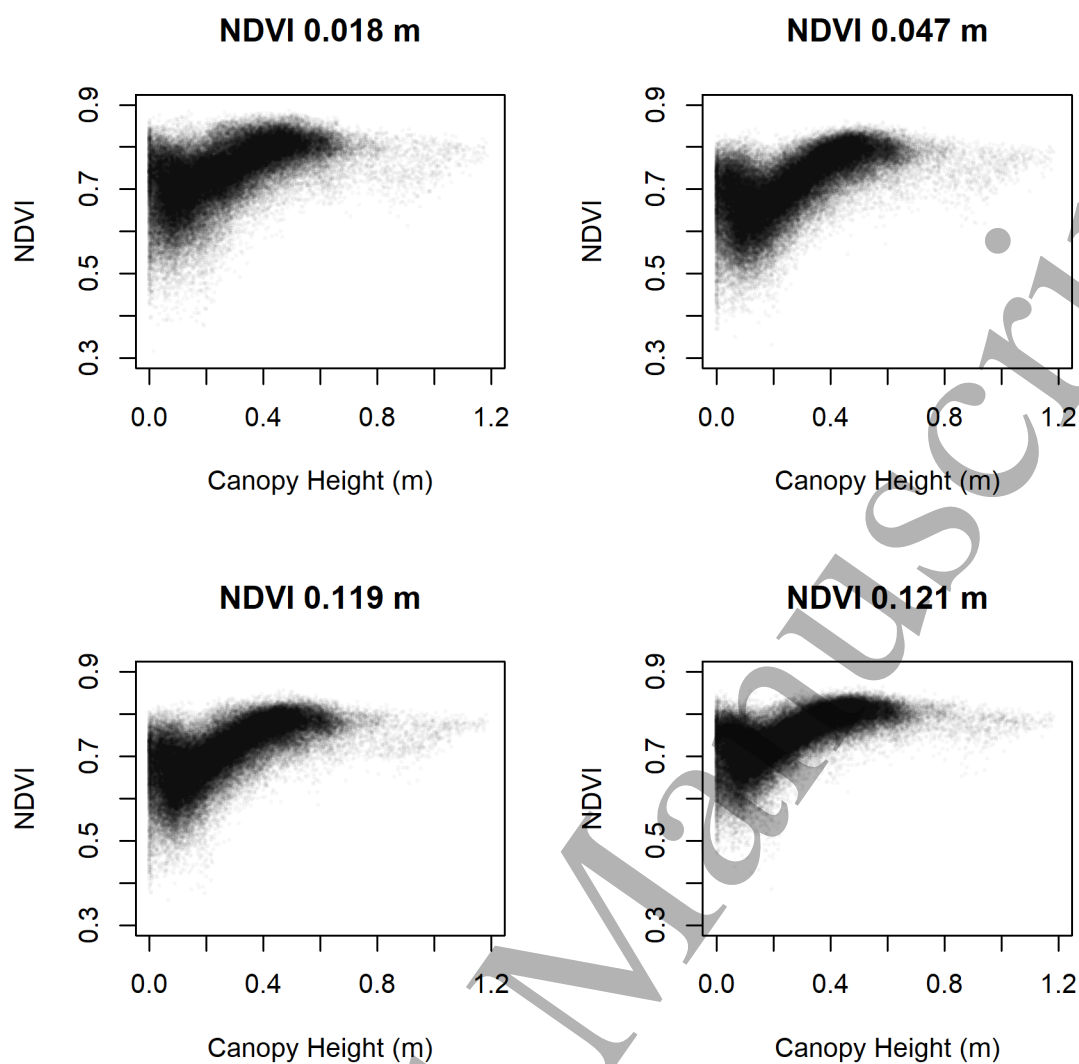
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424

425 Figure 5. Shrubs are the dominant species in this landscape, and total aboveground biomass  
 426 was predicted strongly by shrub leaf biomass, but not by overall phytomass. The mass of  
 427 shrub leaves explained 70% of the variation in total biomass (a), but phytomass, calculated  
 428 as the sum of shrub leaves and herbaceous material, explained none of the variation in total  
 429 biomass (b). The proportion of moss cover only had a significant influence on the relationship  
 430 between NDVI and phytomass for the 0.121 m grain raster (c). The relationship between NDVI  
 431 and phytomass was strong when moss cover was low, but weakened as moss cover increased  
 432 (See Figure S6 for non-significant interactions for other biomass pools and NDVI products).

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433

434 Figure 6. Pairwise pixel covariance between NDVI and canopy height inferred from the  
435 photogrammetry for the monitoring area, both resampled to a common 0.25 m spatial  
436 resolution. There is a general positive relationship between NDVI and canopy height, although  
437 this breaks down at canopy heights below 0.2 m and once NDVI saturates at ca. 0.75. Models  
438 fitted to predict canopy height as a function of NDVI are reported in Table S5.

439

440 Table 2. Parameters of linear models fitted to mean plot normalised difference vegetation  
 441 index (NDVI) and log-transformed total aboveground biomass, phytomass (leaf +  
 442 herbaceous), and leaf biomass. In all cases the model form was  $\ln(Y) = a + b X$  and  $n = 36$ .

Dependent variable	grain of NDVI in m	a	b	R <sup>2</sup>	RMSE
Total biomass	0.121	-2.976 ± 2.987	13.04 ± 4.049	0.23	0.7162
Total biomass	0.119	-0.372 ± 2.39	9.902 ± 3.373	0.20	0.7308
Total biomass	0.047	1.282 ± 2.244	7.412 ± 3.103	0.14	0.7571
Total biomass	0.018	2.909 ± 1.539	4.947 ± 2.037	0.15	0.7553
Phytomass	0.121	2.808 ± 1.479	3.307 ± 2.005	0.07	0.3547
Phytomass	0.119	3.464 ± 1.166	2.518 ± 1.646	0.06	0.3565
Phytomass	0.047	4.374 ± 1.082	1.207 ± 1.496	0.02	0.3651
Phytomass	0.018	4.664 ± 0.744	0.772 ± 0.985	0.02	0.3653
Leaf biomass	0.121	0.263 ± 1.428	5.54 ± 1.937	0.19	0.3426
Leaf biomass	0.119	1.213 ± 1.126	4.429 ± 1.589	0.19	0.3443
Leaf biomass	0.047	1.326 ± 1.005	4.183 ± 1.389	0.21	0.339
Leaf biomass	0.018	3.255 ± 0.754	1.45 ± 0.998	0.06	0.3703

443 The standard error of the parameter is shown by ±.

444

#### 445 3.4. Upscaling to landscape biomass estimations

446 We estimated aboveground vascular biomass density across the graminoid-shrub ecotone for  
 447 the 0.5 ha<sup>-1</sup> monitoring area (Figure 1d). Estimated biomass at this landscape-level differed  
 448 substantially between the five predictors, canopy height and NDVI at each of the four spatial  
 449 grains (Figure 6; Table 3). We calculated the difference in estimated biomass relative to the  
 450 CHM-derived biomass map, as we considered this to be the most accurate product (based on  
 451 the model performance and our knowledge of this site). Although we consider the CHM-  
 452 derived biomass estimate to be the most accurate, errors in the allometric model and in the  
 453 canopy heights from the interpolated terrain model and plant surface model will all contribute  
 454 uncertainty. For example, evaluation of the terrain model accuracy against 36 validation points  
 455 indicated a mean residual elevation of 0.029 m ± SD 0.035 m. Although small, the systematic

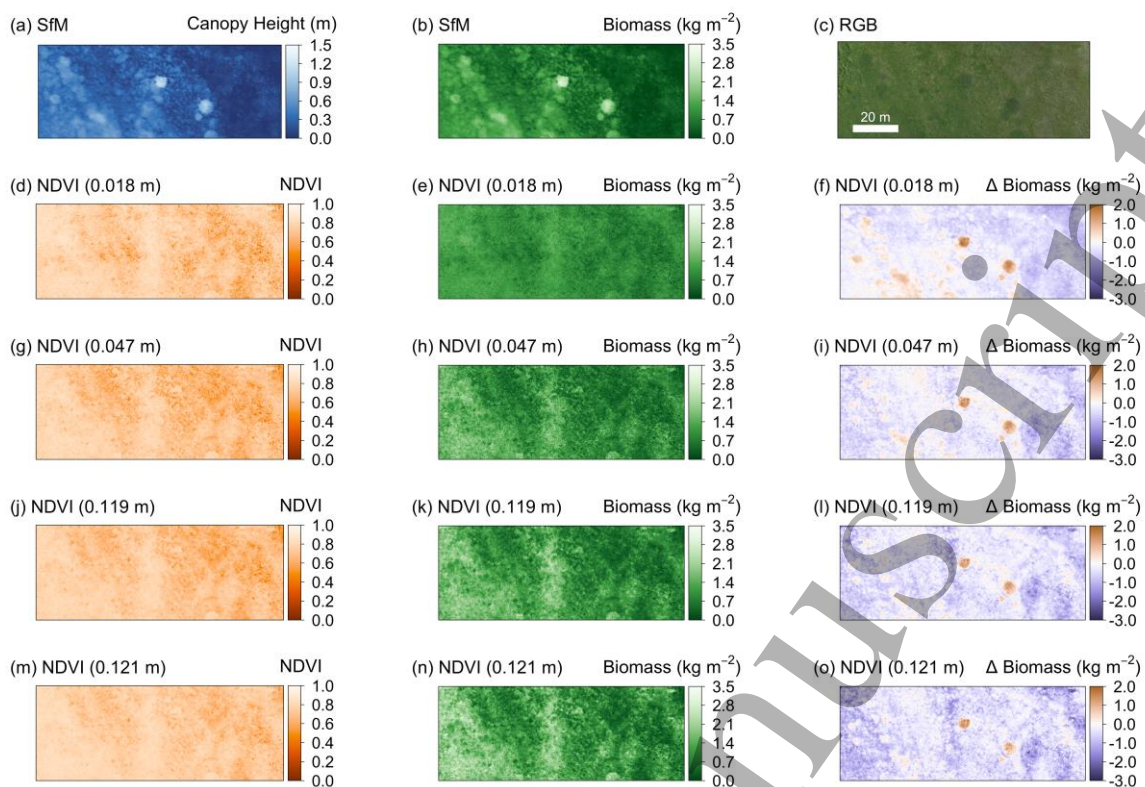
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3 456 bias of 0.029 m in the interpolated terrain model (Figure S7) amounts to 10% of the 0.278 m  
4  
5 457 mean canopy height estimated for the monitoring area, and so would equals a 10%  
6  
7 458 underestimate of biomass inferred from the CHM. The allometric models were fitted using  
8  
9 459 similar distributions of canopy height and NDVI values to those found across the adjacent  
10  
11 460 monitoring site. The distribution for the harvested samples of the two coarser NDVI rasters  
12  
13 461 (0.121 and 0.119 m) had slightly truncated tails, which may have contributed to greater  
14  
15 462 uncertainty in the model fit (Figure S8).  
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20 464 We found substantial differences in the estimated average biomass inferred from the five  
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22 465 datasets (Table 3). NDVI-based biomass estimates are generally greater than the height-  
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24 466 based estimates (Figure 7f,i,l,o; Figure S9), apart from areas with taller shrubs near the centre  
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26 467 of the monitoring area. Estimated biomass was positively correlated with the spatial grain of  
27  
28 468 the NDVI maps, mainly due to differences in the allometric models between different grain  
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30 469 sizes (Table S2, Figure S5). However, the biomass estimates from NDVI were highly uncertain  
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32 470 as demonstrated by the range of possible values (Table 3).  
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473 Figure 7. Landscape-level biomass maps estimated from the canopy height model and NDVI  
 474 for four spatial grains, using the allometric equations obtained above. Canopy height model  
 475 (a), biomass-inferred from canopy height (b), RGB orthomosaic (c), NDVI reflectance (d), (g),  
 476 (j), (m), biomass-inferred from NDVI \*e),(h), (k), (n), and biomass difference maps relative to  
 477 the biomass map inferred from canopy height (f), (i), (l), (o).

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479 Table 3. Biomass density in the monitoring area estimated using the allometric equations  
 480 obtained above. Lower and upper bounds are calculated using the standard errors for the  
 481 equation coefficients (Table S2).

Predictor	Biomass (g m <sup>-2</sup> )		
	Best estimate	Lower bound	Upper bound
CHM	672	634	710
NDVI 0.018 m	972	-128	26,704
NDVI 0.047 m	989	-301	205,831
NDVI 0.119 m	1087	-357	324,568
NDVI 0.121 m	1195	-501	752,362

482

#### 483 **4. Discussion**

484 We found that canopy heights across a graminoid-shrub ecotone could be measured over fine  
 485 (cm) spatial scales using structure-from-motion photogrammetry. Heights derived from drone  
 486 photogrammetry corresponded strongly with those obtained using conventional point-intercept  
 487 methods (Figure 2) (Molau and Mølgaard, 1996; Myers-Smith et al., 2019). Canopy heights  
 488 were positively correlated with vascular plant biomass (Figure 3), indicating that  
 489 photogrammetry-derived data can be used to accurately estimate aboveground tundra  
 490 biomass. However, vegetation greenness as measured by NDVI only weakly corresponded  
 491 with vascular plant biomass and was influenced by the amount of moss cover on the ground  
 492 (Figure 5c, Figure S6). The relationship between fine-grain peak NDVI and biomass can be  
 493 influenced by moss or other types of evergreen vegetation cover. Nonlinear make the NDVI-  
 494 biomass relationships particularly sensitive to the range and quality of the sample used to fit  
 495 the curve. Our findings suggest that the relationship between fine-grain peak NDVI and  
 496 biomass can be influenced by moss or other types of evergreen vegetation cover. Our study  
 497 highlights that drone-derived canopy height can inform monitoring of vegetation change over  
 498 larger and more representative extents, and thus improve projections of plant responses to  
 499 warming in tundra ecosystems.

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3 500  
45 501 *Photogrammetry-derived canopy heights were taller than in situ measured canopy heights*

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7 502 We found a positive bias in canopy heights measured with point-intercept relative to  
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9 503 photogrammetry, which we attribute to differences in the way the two approaches quantify  
10  
11 504 canopy architecture. The photogrammetry-derived heights in our study may have also been  
12  
13 505 slightly exaggerated by slight depression at the plot corners by the survey staff on the ground  
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15 506 surface at the top of the moss layer (ca. 2 - 3 cm) The plot-level terrain models will have  
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17 507 smaller vertical errors than the model applied across the monitoring area (Figure S7), because  
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19 508 elevations were interpolated over smaller horizontal distances (< 0.71 m). It is also possible  
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21 509 that the fewer point-intercept observations within each harvest plot (n = 36) may under sample  
22  
23 510 canopy structure relative to the photogrammetry (n ≤ 2500). Several studies have now  
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25 511 reported strong correspondence between canopy heights reconstructed with photogrammetry  
26  
27 512 and *in situ* measurements (Alonzo et al., 2020; Karl et al., 2020; Poley and McDermid, 2020).  
28  
29 513 For example, Clement and Fraser (2017) reported similarly good correspondence between *in-*  
30  
31 514 *situ* versus photogrammetrically-derived *maximum* canopy heights for 20 shrubs measured at  
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33 515 an Arctic tundra site near Iqaluktuuttiaq (Cambridge Bay). However, such comparisons are  
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35 516 hindered by the sensitivity of maximum height measurements to outliers in these often noisy  
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37 517 point clouds (Cunliffe et al., 2016). The comprehensive review by Poley and McDermid (2020)  
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39 518 discusses such inter-comparisons of different canopy height measurements in further detail,  
40  
41 519 but they were unable draw general conclusions because all sets of observations are sensitive  
42  
43 520 to the ways in which they are collected, processed and analysed (Cunliffe et al., 2016; Fraser  
44  
45 521 et al., 2019; Wallace et al., 2017). Our findings suggest that, when applied in a consistent m  
46  
47 522 canopy height manner, drone photogrammetry is an appropriate tool for monitoring shrub  
48  
49 523 canopy heights in such ecosystems.

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53 52454 525 *Canopy heights predicted aboveground biomass*

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56 526 Canopy height strongly predicted aboveground biomass for the *Salix richardsonii*-dominated  
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58 527 community that we studied, which corroborates similar reports for photogrammetry across a  
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3 528 range of biomes and plant communities (Alonzo et al., 2020; Bendig et al., 2015; Grüner et  
4  
5 529 al., 2019; Howell et al., 2020; Karl et al., 2020; Selsam et al., 2017; Wijesingha et al., 2019).  
6  
7 530 Estimating aboveground biomass from canopy height models depends on having an  
8  
9 531 underlying terrain model of sufficient quality to describe topographic variability (Cunliffe et al.,  
10  
11 532 2016; Fraser et al., 2019; Poley and McDermid, 2020). In this study, we derived our terrain  
12  
13 533 model using RTK-GNSS observations, which can be a viable option for characterising  
14  
15 534 topography over extents of up to a few hectares. In ecosystems where canopies are spatially  
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17 535 or temporally discontinuous, terrain models could also be derived directly from  
18  
19 536 photogrammetric point clouds (Cunliffe et al., 2016; Fraser et al., 2019). Terrain models  
20  
21 537 derived using other survey techniques could also be co-registered in a hybrid approach  
22  
23 538 (Dandois and Ellis, 2013). However, propagation of uncertainties including co-registration  
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25 539 error is vital for understanding the limits of detection of genuine change in canopy height  
26  
27 540 (James et al., 2017).  
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#### 33 542 *Refining predictions of biomass from canopy height*

34 543 Relationships between plant dimensions and biomass are sensitive to the ways in which these  
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36 544 measurements are obtained (Cunliffe et al., 2020). Cross-site data syntheses therefore require  
37  
38 545 the use of standardised protocols for data collection and processing (such as HiLDEN  
39  
40 546 <https://arcticdrones.org/>, Assmann et al., 2018; Cunliffe and Anderson, 2019). As noted by  
41  
42 547 Pätzig *et al.* (2020), there is a need for further coordinated work to calibrate the relationship  
43  
44 548 between photogrammetric-inferred canopy height and aboveground biomass for different  
45  
46 549 taxonomic groups. There is also a need to quantify the sensitivity of these relationships to key  
47  
48 550 parameters (e.g., the spatial resolution of the input data, the implementation of multi-view  
49  
50 551 stereopsis and the spatial grain of analysis, sensu Wallace et al., 2017; Zarco-Tejada et al.,  
51  
52 552 2014), as well as to differences in environmental conditions (e.g., illumination and wind-  
53  
54 553 induced movement of plant canopies, Dandois et al., 2015; Frey et al., 2018).  
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57

58 554

59 555 *Vegetation greenness only weakly corresponded with biomass*

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3 556 We found that NDVI only weakly predicted the aboveground biomass of vascular plants,  
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5 557 explaining at most 23% of the variation in total biomass, and even less of the variance in  
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7 558 phytomass or leaf biomass (Figures 4 and S3, Tables 2 and S4). Inferring aboveground  
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9 559 biomass from NDVI is predicated on the assumptions that (i) NDVI is a good predictor of  
10  
11 560 phytomass, and (ii) that phytomass is a good predictor of total biomass. We found that while  
12  
13 561 NDVI had some capacity to explain variance in phytomass (Figure 4, Table 2), phytomass was  
14  
15 562 a very weak predictor of total biomass (Figure 5b). Across spatial grains, predictive  
16  
17 563 relationships weakened slightly as the spatial grain of the NDVI rasters became finer from  
18  
19 564 0.121 m to 0.018 m (Table 2). We attribute two main causes for the weak correspondence  
20  
21 565 between NDVI and biomass. Firstly, although leaf biomass was a strong predictor of total  
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23 566 aboveground biomass, leaf biomass accounted for typically only half of the phytomass in each  
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25 567 plot, and phytomass (including herbaceous material and shrub leaves) only weakly  
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27 568 corresponded with total biomass (Figure 5). Vegetation indices that integrate all  
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29 569 photosynthetically active material are often poor predictors of total biomass (Bratsch et al.,  
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31 570 2017; Räsänen et al., 2019). Secondly, we found indications that moss cover influenced the  
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33 571 relationship between NDVI and phytomass. The direction of the relationship was consistent;  
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35 572 however, the interaction effect was only statistically significant in one of the 12 combinations  
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37 573 of NDVI raster and biomass pool tested (Table S3). We found that the relationship between  
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39 574 NDVI and vascular phytomass was mediated by the amount of moss cover beneath the  
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41 575 sampled vegetation and weakened as moss cover increased (Figures 5C and S6). Vegetation  
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43 576 species composition therefore affects the biomass NDVI-relationship.  
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51 578 The relationship between NDVI and biomass in this setting is approximated by the relationship  
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53 579 between NDVI and canopy height across the monitoring site. NDVI was generally positively  
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55 580 related to canopy height across all four NDVI rasters (Figure 6); however, the relationship was  
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57 581 very weak at canopy heights below 0.2 m and NDVI values above ca. 0.75. NDVI-biomass  
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59 582 transfer functions will thus be more uncertain where canopies are low (< 0.2 m) possibly due  
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3 583 to increased signal from bryophytes or NDVI saturates at around 0.75. Canopy heights inferred  
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5 584 from NDVI using the NDVI-height transfer function developed by Bartsch *et al.* (2020) were  
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7 585 linearly related to canopy heights inferred from photogrammetry, although were positively  
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9 586 biased by a factor of ca. five and subject to the same issues around the shorter (< 0.2 m)  
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11 587 canopies and once NDVI saturated. This bias suggests that NDVI-biomass transfer functions  
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13 588 will need to be calibrated more specifically for different situations.  
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19 590 The weak correspondence between NDVI and phytomass that we observed contrasts with  
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21 591 reports of stronger positive relationships between NDVI and aboveground biomass derived  
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23 592 from datasets compiled across different spatial scales (Boelman *et al.*, 2003; Goswami *et al.*,  
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25 593 2015; Walker *et al.*, 2003b). NDVI has a saturating relationship with biomass and NDVI-  
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27 594 biomass relationships can be confounded by a variety of ecological variables, land-surface  
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29 595 properties and view angle effects (Buchhorn *et al.*, 2016; Karlsen *et al.*, 2018; Myers-Smith *et*  
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31 596 *al.*, 2020; Walker *et al.*, 2003a). Our findings are consistent with the well-known saturation  
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33 597 effect (e.g., Berner *et al.*, 2018), and we may have found better correspondence between  
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35 598 NDVI and biomass if we had sampled over a wider range of NDVI values beyond those that  
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37 599 were most prevalent at our study site. The unmeasured biomass associated with moss was  
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39 600 likely small compared with the biomass associated with the vascular plants at this site (Reid  
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41 601 *et al.*, 2012), but if we had included moss in our biomass harvests, this might have modified  
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43 602 relationships between NDVI and biomass. Our results highlight the need for caution when  
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45 603 deriving total biomass maps from vegetation indices in high latitude ecosystems with variable  
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47 604 land cover. The biome-wide tundra greening patterns and trends observed with large-grain  
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49 605 satellite datasets are unlikely to directly represent plant functional attributes such as canopy  
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51 606 height or biomass *in situ* (Myers-Smith *et al.*, 2020). Thus, to improve our understanding of  
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53 607 vegetation greening in tundra ecosystems across vegetation types and geographic gradients,  
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55 608 we need data collection across scales from focal sites to the tundra biome (Fisher *et al.*, 2018;  
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57 609 Miller *et al.*, 2019; Myers-Smith *et al.*, 2020).  
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611 *Landscape-estimates of biomass*

612 The spatially continuous estimates of canopy height and inferred vascular plant biomass  
613 across our monitoring site (Figure 6, Table 3) are well suited for upscaling studies. These  
614 kinds of highly accurate and precise products help to overcome limitations with incomplete  
615 characterisations of plant communities due to labour intensive and resource limited *in situ*  
616 monitoring programs (Alonzo et al., 2020; Bartsch et al., 2020; Myers-Smith et al., 2019). Of  
617 particular concern are the difficulties comparing observations from very different spatial  
618 extents, between remotely-sensed observations and small, potentially non-representative *in*  
619 *situ* plots. Biomass estimated from NDVI was highly uncertain (Table 3), even when only  
620 accounting for uncertainty in the coefficients of our exponential models without accounting for  
621 uncertainties in the NDVI values themselves. Drone-derived products are useful for calibrating  
622 and validating biomass retrievals of these properties from coarse-scale observations, and for  
623 testing key of assumptions underpinning novel retrievals approaches (Bartsch et al., 2020).  
624 Photogrammetric approaches to monitoring plant canopies can also be deployed over even  
625 larger extents using similar data from airborne surveys (Alonzo et al., 2020).

626

627 **5. Conclusion**

628 This study expands the empirical understanding of how fine-grained remotely-sensed  
629 observations relate to vegetation attributes. By comparing structural, spectral reflectance and  
630 on-the-ground ecological metrics, we can improve our understanding of the scaling  
631 relationships from fine- to coarse-scale observations of tundra vegetation change. Drone-  
632 collected data are already helping us to fill in the missing landscape-scale gap in tundra  
633 ecological monitoring, and future work must use coordinated protocols to underpin biome-  
634 scale data synthesis (e.g. HiLDEN <https://arcticdrones.org/> and Cunliffe and Anderson, 2019).  
635 We found strong agreement in canopy heights measured using *in-situ* point-intercept methods  
636 compared to drone-photogrammetry. Canopy height was strongly and linearly related to the

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3 637 aboveground biomass of vascular plants, explaining ca. 90% of the observed variability in the  
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5 638 biomass. Vegetation 'greenness' measured as NDVI across four independent multispectral  
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7 639 surveys explained only a small proportion of the variability in the biomass of vascular plants  
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9 640 and was influenced by moss cover, suggesting caution should be used when attributing  
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11 641 differences in NDVI to differences in either vascular plant biomass or phytomass. Our  
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13 642 comparison of structural, spectral and *in-situ* ecological measurements contributes to  
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15 643 improved understanding of tundra vegetation as inferred from remote sensing and thus  
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17 644 informs monitoring projections tundra vegetation change with warming.  
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3 646 **Statement of contribution**  
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5 647 A.M.C and I.H.M.-S. conceived the research idea. A.M.C., J.A. and I.H.M.-S. developed the  
6  
7 648 experimental design. I.H.M.-S. acquired the funding. A.M.C., J.A., J.T.K. and I.H.M.-S.  
8  
9 649 undertook the investigation. A.M.C. and G.D. completed the analysis, and A.M.C., J.A. and  
10  
11 650 G.D. completed the data visualisation. A.M.C. led the writing of the manuscript. All authors  
12  
13 651 contributed to the final version of the manuscript.  
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18 653 **Data accessibility**  
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20 654 The data that support the findings of this study are openly available at the following DOI:  
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22 655 <https://doi.org/10.5285/61C5097B-6717-4692-A8A4-D32CCA0E61A9>.  
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26 657 **Conflicts of interest**  
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28 658 The authors declare no conflicts of interest.  
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