

Can reindeer husbandry management slow down the shrubification of the Arctic?

Megha Verma^{1,2}

Henrike Schulte to Bühne²

Mailys Lopes²

Dorothee Ehrich³

Svetlana Sokovnina⁴

Stijn P. Hofhuis⁵

Nathalie Pettorelli^{2*}

**Corresponding author. Email: Nathalie.Pettorelli@ioz.ac.uk, telephone: (+44) 020 7449 6334*

1: Department of Life Sciences, Imperial College London, Buckhurst Road, SL5 7PY Ascot, UK.

2: Institute of Zoology, Zoological Society of London, Regent's Park, NW1 4RY London, UK.

3: Department of Arctic and Marine Biology, UiT – The Arctic University of Tromsø, 9037 Tromsø, Norway.

4: Arctic research station, Institute of Plant and Animal Ecology Ural Branch Russian academy of Sciences, 629400, Zelenaya Gorka 21, Labytnangi, Yamal-Nenets Autonomous District, Russia.

5: Resource Ecology Group, Wageningen University, Droevendaalsesteeg 3a, 6708PB Wageningen, the Netherlands

Declarations of interest: None

Abstract

Rapid climate change is threatening the stability and functioning of Arctic ecosystems. As the Arctic warms, shrubs have been widely observed to expand, which has potentially serious consequences for global climate regulation and for the ecological processes characterising these ecosystems. However, it is currently unclear why this shrubification has been spatially uneven across the Arctic, with herbivory being suggested as a key regulating factor. By taking advantage of freely available satellite imagery spanning three decades, we mapped changes in shrub cover in the Yamal Peninsula and related these to changes in summer temperature and reindeer population size. We found no evidence that shrubs had expanded in the study site, despite increasing summer temperatures. At the same time, herbivore pressure increased significantly, with the local reindeer population size growing by about 75%. Altogether, our results thus point towards increases in large herbivore pressures having compensated for the warming of the Peninsula, halting the shrubification of the area. This suggests that strategic semi-domesticated reindeer husbandry, which is a common practice across the Eurasian Arctic, could represent an efficient environmental management strategy for maintaining open tundra landscapes in the face of rapid climate changes.

Keywords: satellite remote sensing, Arctic, tundra, shrubification, climate change, grazing, semi-domesticated reindeer

1 **1. Introduction**

2 Climate change is expected to accelerate in the 21st century, creating unprecedented environmental
3 challenges for human communities around the world while altering species ranges (Chen et al. 2011;
4 Pinsky et al. 2013), rearranging species communities (Bertrand et al. 2011; Nooten et al. 2014;
5 Dieleman et al. 2015; Liu et al. 2018) and changing ecosystem processes and functioning (Schuur et al.
6 2008; Durán et al. 2013; Roxy et al. 2016). This is especially true in the Arctic, where temperatures
7 have increased at about twice the global average rate during recent decades (Bekryaev et al. 2010).
8 These rapid and drastic changes in climatic conditions have led to many places in the Arctic showing
9 increases in the distribution and vigour of woody vegetation. This so-called “shrubification” (Myers-
10 Smith et al. 2011) occurs as woody vegetation expands to new areas, fills gaps between existing
11 patches, and/or grows taller. Shrubification is thought to be directly and indirectly controlled by
12 climate change. Specifically, longer and warmer growing seasons (Blok et al. 2011), interactions
13 between the timing of snow melt and nutrient cycling, and positive feedback loops of shrub cover on
14 microclimate (Sturm et al. 2005; Wookey et al. 2009; Rixen et al. 2010) are all expected to promote
15 increases in the distribution and vigour of woody vegetation. The shrubification of the Arctic can alter
16 a large range of ecosystem processes and functions in tundras, including climate control and nutrient
17 cycling (Myers-Smith et al. 2011). For instance, it can lead to decreased surface albedo (Strum et al.
18 2005) and faster snow melt in spring (Marsh, 2010), thereby potentially promoting the acceleration
19 of global climate change. Shrub expansion can moreover be associated with an increase in passerine
20 bird diversity (Ims & Henden 2012), but also with a loss in plant species diversity, especially lichen,
21 which may have direct consequences for consumers such as reindeer/caribous (*Rangifer tarandus*;
22 Joly et al. 2009; Myers-Smith et al. 2011).

23 Shrubification of the Arctic is however not spatially uniform (Tape et al. 2012; Reichle et al. 2018), with
24 some areas experiencing more rapid changes in the distribution and vigour of woody vegetation than
25 others. These spatial differences have been attributed to various factors, including variation in soil
26 disturbances from natural and anthropogenic causes (Myers-Smith et al. 2011). Herbivory by large
27 ungulates is expected to be particularly important in shaping the response of shrubby vegetation to a
28 changing climate, since herbivory directly reduces shrub cover, biomass and height (Christie et al.
29 2015). In experiments, grazing by semi-domesticated reindeers has been shown to counteract the
30 effect of warming on shrub expansion (Post & Pedersen 2008; Olofsson et al. 2009; Myers-Smith et al.
31 2011), suggesting that herbivory could be used as a management tool to mitigate the impacts of
32 climate change on terrestrial Arctic ecosystems. Reindeer husbandry occurs over large parts of the
33 Eurasian Arctic and is predominantly managed by indigenous peoples (Forbes et al. 2009). Large
34 herbivore management is thus already part of socio-ecological systems in the Arctic and could

35 therefore constitute a socially and culturally acceptable climate change mitigation strategy in the
36 region (Bråthen et al. 2017). Literature assessing the extent to which large herbivores could reduce
37 shrubification over large spatial and temporal scales (i.e. several 100 square kilometres and several
38 decades) is yet currently sparse and limited to North America and Fennoscandia (Bernes et al. 2015;
39 Bråthen et al. 2017). Few studies have focused on assessing these changes within specific regions in
40 Russia. There is evidence that long-term (i.e. decades) grazing by herbivores reduces shrub cover and
41 height more than short-term grazing (Kitti et al. 2009), but it is not clear whether and how these
42 conclusions hold under rapid changes in climatic conditions.

43 To address this gap in knowledge, we used satellite remote sensing data to map changes in shrub
44 cover spanning three decades across a relatively remote study site of about 400 km² in southern
45 Yamal, Russia. The Yamal Peninsula, which extends from the Arctic circle to the high Arctic, is
46 recognised as a “hotspot of change”, being exposed to rapid changes in environmental conditions
47 (Walker et al. 2009, 2010). Other than rising temperatures, extensive grazing and trampling by
48 reindeer herds indeed heavily influence the landscape (Forbes 1999; Walker et al. 2009), with the
49 region being home to the world’s largest population of semi-domesticated reindeer managed by the
50 nomadic indigenous Nentsy (Forbes et al. 2009). Our objective was to assess the potential of intensive
51 grazing by semi-domesticated reindeer to mitigate shrub cover expansion under increasing surface
52 temperatures, to which end we compared trends of shrubification, long-term temperature change
53 and herbivore population size.

54

55 **2. Material and methods**

56 **2.1 Study Area**

57 Our study area is in southern Yamal, Russia (68.2°N, 69.1°E) and covers approximately 400 km² (Figure
58 1). The mean daily temperature ranges from -24.9°C in January to 14.45°C in July (World
59 Meteorological Organisation 2019). The area has a constant snow cover from October until June and
60 a yearly average precipitation of about 350 mm (Sokolov et al. 2012). The landscape has many rivers,
61 streams and lakes; the lowlands are flooded in the spring (Ehrich et al. 2012; Sokolov et al. 2012). The
62 study area’s topography is predominantly flat but contains scattered hills (up to 40 m in height) and
63 steep ridges along the waterbodies (Ehrich et al. 2012). The study site is situated at the border of two
64 main vegetation zones in the Yamal Peninsula: low-shrub tundra and erect dwarf shrub tundra (Walker
65 et al. 2005). Low shrub communities are common on this site and are characteristically composed of
66 a mixture of dwarf birch (*Betula nana*) and willow (*Salix* spp.) that are up to 50 cm high (Ehrich et al.
67 2012). Dense thickets of tall willows up to 2 m high are also found along water bodies (Pajunen et al.

68 2010) and on fertile slopes. Plant cover is continuous across the study area (80-100%) except for ridge
69 crests (Sokolov et al. 2012).

70

71 2.2 Temperature Data

72 Arctic warming is known to occur at a rate of 1.36 °C per century (1875–2008), which is twice as fast
73 as the Northern Hemisphere average (0.79 °C per century; Bekryaev et al. 2010). To estimate the rate
74 of warming in our study site, data on monthly air surface temperatures for the summer months
75 between June – September (which corresponds to the growing season) at a resolution of 0.5° (circa
76 55 km) latitude/longitude grid cells from 1901 – 2018 were acquired from CRU TS4.03 (Harris et al.
77 2019). Since our study site overlapped two grid cells of this dataset, we first calculated the mean
78 temperature between these two cells. For each year, we calculated the average summer season
79 temperature as the mean of monthly temperatures from June to September. To test whether average
80 summer temperatures changed over time, a linear model was fitted. Diagnostic plots indicated that a
81 linear model was appropriate for the data.

82

83 2.3 Reindeer Population Data

84 No data on reindeer populations specifically for our study area was available. However, local reindeer
85 densities are known to be relatively high compared to other parts of the Arctic, with grazing pressure
86 having been found to be universally high throughout the Yamal Peninsula (Walker et al. 2009, 2010;
87 Golovatin et al. 2012). We here assumed that overall trends in reindeer abundance were the same in
88 our study area as in the rest of Yamal, and therefore estimated this trend in reindeer population size
89 by collating abundance data for the whole Yamal Peninsula from three different studies: K. B. Klovov
90 and S. A. Khrushchev (2004), M. G. Golovatin et al. (2012) and V. D. Bogdanov and M. G. Golovatin
91 (2017). Temporal trends in abundance were assessed using the Mann-Kendall test.

92

93 2.4 Shrub cover

94 To capture long-term changes in shrub distribution, we mapped land cover using Landsat images for
95 the years 1986, 1991, 1996, 2001, 2006 (all Landsat 4-5), 2011 (Landsat-7), 2016 and 2018 (Landsat-
96 8; all available for download at <http://earthexplorer.usgs.gov>). We used Landsat “Collection 1 Level
97 2” Surface Reflectance products (georeferenced, terrain-corrected and atmospherically corrected)
98 processed on demand by the United States Geological Survey (USGS) as these are recognised as the
99 most accurate pre-processed products (Young et al. 2017). The native cloud mask (CFMask) was
100 used to identify and eliminate pixels that were covered by clouds in all scenes. To ensure that land
101 cover classification was based on scenes from the peak-growing period, we acquired Landsat scenes

102 close to the time of maximum greenness (Pettorelli 2013). To fill any gaps created by clouds, we
103 created cloud free composite scenes for each year by selecting several overlapping satellite scenes
104 that had been acquired close together in time. We histogram-matched these scenes to standardize
105 the radiometric values before merging all overlapping scenes, resulting in cloud-free composite
106 scenes.

107

108 Six land cover classes were discerned in the landscape, namely water bodies; sand; exposed ridges;
109 shrub thickets (including willow thickets and closed canopy dwarf birch heath of 25 cm height or more,
110 as well as mixed forms); wet lowlands; and mesic tundra (see Table S1 in Supplementary materials for
111 a detailed description of these classes). Our supervised classifications were informed by a training
112 dataset composed of the following elements: 1) very high resolution (3m) imagery for the year 2011
113 (RapidEye imagery, 6th August 2011), 2016 (4-Band Planet Scope, 2nd September 2016) and 2018 (4-
114 Band Planet Scope, 13th July 2016) of the entire study site; 2) ground-truthing points consisting of
115 homogenous patches of more than 30x30 m of the defined land cover types that were
116 opportunistically sampled in July 2017 and georeferenced with hand-held GPS (these fell into 219
117 Landsat pixels); and 3) drone pictures (multispectral sensor (RGB), DJI Phantom 4, taken from a height
118 of 80m) covering an area of ca 73 ha and containing willow thickets both on slopes and on flat areas.
119 There was no available reference data to support a direct supervised classification of the scenes
120 collected by Landsat in 1986, 1991, 1996, 2001, and 2006. To overcome this limitation, we
121 opportunistically sampled pixels from the 2011 training dataset from areas identified as having stable
122 land cover; these areas were identified using a spectral Change Vector Analysis (CVA, Schulte to Bühne
123 et al. 2017). To maximise the amount of spectral information used in the CVA, we used Principal
124 Components instead of bands or single indices as input for the CVA (Schulte to Bühne et al. 2017). We
125 compared the change magnitude for each pixel to the median observed change magnitude across all
126 pixels with the same land cover. We assumed that a pixel had undergone land cover change if its
127 change magnitude was above the median change magnitude of its land cover. This threshold is
128 conservative because an exceptional amount of change in surface reflectance needs to have occurred
129 in the absence of land cover change to achieve this (Schulte to Bühne et al. 2017). This allowed us to
130 build a training dataset to inform our supervised classification for the year 1986, 1991, 1996, 2001 and
131 2006 (Xian & Homer 2010). We tested the validity of this approach by applying it to the years 2016
132 and 2018 and comparing the accuracy of the resulting map with those produced using independent
133 validation data. The maps for the years 1986, 1991, 1996, 2001 and 2006 were all internally validated
134 using the validation points created from the unchanged pixels.

135

136 Supervised land cover classifications were performed using the *Random Forest* classifier in R (Liaw &
137 Wiener 2002), which generated 500 trees using three tuning levels; *Random Forest* has been
138 demonstrated to perform robustly in different ecological settings (Belgiu & Drăguț 2016). Producer's
139 and user's accuracies were calculated for all land cover maps. Producer's accuracy quantifies the
140 probability that a given pixel will be assigned to the correct land cover class by the classification
141 algorithm. By contrast, user's accuracy estimates the probability that the assigned class of a given pixel
142 is correct. The area of each of the vegetation classes was calculated per year following the
143 recommendations of Olofsson and colleagues (2013) and the trend over time was examined using a
144 Mann-Kendall test.

145

146

147 **3. Results**

148 Average summer season temperatures (June – September) increased significantly between 1901 and
149 2018 ($F_{1, 116} = 5.72$, $p = 0.02$), with annual temperature increases of circa. 0.007°C . This means that
150 average summer season temperatures in 2018 were about 0.84°C warmer than in 1901, and circa
151 0.229°C warmer than in 1986 (Figure 1). The semi-domesticated reindeer population on the Yamal
152 Peninsula overall increased by about 75% between 1986 and 2016 ($\tau = 0.761$, $p < 0.0001$; Figure 1).
153 Semi-domesticated reindeer abundance shows a drastic increase from 1986 to 2009, peaking at
154 327,073 individuals. An important increase in reindeer numbers in our study area was thus very likely.

155

156 Land cover was classified with suitable accuracy across all years, with overall accuracies ranging from
157 approximately 82% to 91% (Table 1). Producer's and user's accuracies were relatively high in every
158 vegetation class. Our approach to generating training data for the years 1986-2006 was unlikely to
159 have inflated accuracy estimates (Table S2 in Supplementary materials). Shrub thickets showed high
160 overall accuracies (83% - 91%). Using information derived from the above land cover classifications,
161 we were unable to detect any significant change in the percentage cover of shrub thickets ($\tau = -0.50$,
162 $p = 0.11$) or mesic tundra ($\tau = -0.143$, $p = 0.71$; Figure 2).

163

164 **4. Discussion**

165 Natural vegetation distribution is both a consequence and a driver of global environmental change
166 (Foley et al. 2005; Franklin et al. 2016; Song et al. 2018). Understanding changes in vegetation cover
167 can help provide insight into ecosystem response to environmental change, and consequently support
168 effective ecosystem management strategies (Walther et al. 2002; Foley et al. 2005). With limited long-
169 term data on vegetation distribution available for the Arctic, it is however difficult to make inferences

170 about the past and understand the combined effects of climate change and herbivory on tundra
171 landscapes. Using Landsat satellite imagery over the 1986-2018 period, this study demonstrates how
172 significant increases in temperature and grazing pressures did not result in the expected change in
173 shrub cover in the Yamal Peninsula, suggesting that growing semi-domesticated reindeer numbers
174 may have counteracted the effects of rising temperatures (Figure 1) on shrub growth in the region
175 (Figure 2). These results are important as they point toward large herbivore management as being a
176 potentially efficient management strategy for maintaining open arctic landscapes in times of rapid
177 climatic changes.

178 In contrast to the widely accepted phenomenon of “shrubification” associated with warming and
179 documented in previous remote sensing studies (Beck & Goetz 2011; Myers-Smith et al. 2011; Naito
180 & Cairns 2011), our results highlight a lack of change in shrub cover in our study system over the past
181 30 years (Figure 2). These results echo previous findings, including those by two long-term plot-based
182 studies in south Greenland (Damgaard et al. 2016) and north-eastern Alaska (Jorgenson et al. 2015),
183 which similarly reported no trend in shrub cover despite the warming of the areas. Several reasons
184 may explain such an outcome. First, this could be a result of the relatively modest increase in summer
185 temperatures for the region (see Figure 1). Second, the lack of reported trend could be due to
186 differences in responses of shrub species to climate change coupled with our inability to differentiate
187 tall shrubs from dwarf shrubs from space. Long-term warming experiments have indeed reported that
188 tall shrubs (e.g. *Salix spp*) increase their distribution with rising temperature, while dwarf shrubs (e.g.
189 *Betula nana*) tend to respond in the opposite way (Elmendorf et al. 2012b). It is possible that taller
190 shrub species have increased over the study period, while dwarf shrub species have decreased,
191 something we would have been unable to detect given our methodological approach. Third, it could
192 be speculated that although overall shrub cover showed no significant change, shrub height and even
193 below-ground biomass have been responding positively to warming conditions (Myers-Smith et al.
194 2011), something we would have not been able to detect using Landsat imagery.

195 However, a likely hypothesis for explaining our results is that changes in herbivory pressure
196 compensated for the impacts of climate change on shrub cover (Olofsson et al. 2009). Given the
197 significant increase in reindeer population observed in the Yamal Peninsula over the period considered
198 (Figure 1), one would indeed predict shrub cover to decrease with increased herbivore abundance as
199 a result of increased grazing and trampling (Hilker et al. 2014); however, our results do not suggest
200 such a response. Again, different mechanisms could explain the observed patterns, the simplest one
201 being that reindeer grazing controlled shrub expansion through indiscriminate grazing. Bråthen et al.
202 (2017) and Ravolainen et al. (2011) both found evidence that at high densities, reindeers can prevent
203 shrubification by keeping the small stages of shrubs such as saplings in a “browse trap” independent

204 of increases in surface temperatures. However, another possibility is that reindeer grazing led to a
205 change in shrub species composition without any impact on distribution. Previous studies on reindeer
206 grazing behaviours indeed found that these large herbivores prefer willows (*Salix* spp.) over birch
207 (*Betula* spp.), due to the difference in anti-browsing defensive compounds found in the species
208 (Christie et al. 2015). As the shrub thicket land cover classification pooled both shrub species together,
209 the dissimilar influence of herbivory on the vegetation could have been overlooked. At present, it is,
210 however, difficult to isolate the impact of herbivory from the impacts of climate change on vegetation
211 distribution as reindeer husbandries in Yamal largely follow a nomadic lifestyle where migration is
212 determined by both ecological and cultural considerations (Degteva & Nellemann 2013). Because of
213 this, there are no distinct areas in Yamal where reindeers have been clearly excluded (Walker et al.
214 2009).

215 Admittedly, there are several limitations associated with our study. While this research focused on
216 the combined impacts of summer temperatures and reindeer herbivory on shrub cover on the Yamal
217 Peninsula, other variables might be important for understanding the observed lack of vegetation
218 changes in the area. For instance, a study in Alaska found that precipitation, especially snow, boosted
219 shrub expansion by providing a microclimate that insulated vegetation from extreme winter
220 temperatures (Wahren et al. 2005). In addition, the inclusion of herbivory pressures from small
221 herbivores such as voles and lemmings (Olofsson et al. 2014) could help elucidate plant-herbivore
222 interaction in the region. However, literature suggests that, compared to other regions in the Arctic
223 such as Fennoscandia, small rodent abundance has been relatively low at our study site for the last 20
224 years (Fufachev et al. 2019). The use of multispectral optical satellite imagery to map the dynamics of
225 tundra vegetation moreover limited the scope of our investigation. For example, the consideration of
226 the Landsat archives enabled us to provide a satisfactory temporal perspective on changes in
227 vegetation classes but limited our ability to explore fine scale changes in shrub distribution. As
228 previously acknowledged, changes in shrub species distribution and vertical growth could not be
229 detected using Landsat imagery.

230

231 **5. Conclusions**

232 Climate models predict that 2 – 10 °C increases in Arctic temperature could transform more than half
233 of the tundra surface into shrublands before the next century (Pearson et al. 2013); such changes in
234 shrub cover could have dramatic implications for ecosystem functioning and people while leading to
235 positive feedbacks with warming (Wookey et al. 2009; Myers-Smith et al. 2011). Here, it is likely that
236 the expected change was prevented by reindeer grazing and trampling. Thus, our study provides

237 observational evidence that semi-domesticated reindeer management within a sustainable range
238 (which will likely vary between sites based on vegetation and regional climate characteristics) could
239 be a plausible strategy for maintaining and protecting tundra landscapes from transformation in the
240 face of rapid climate changes. This study also provides further evidence that shrubification is not
241 ubiquitous across the Arctic and emphasises the importance of long-term ecological monitoring for
242 informing site-specific environmental management policies.

243

244 **Acknowledgements**

245 We would like to thank Aleksandr and Natalia Sokolov for welcoming us to work in their long-term
246 study area.

247

248 **Funding**

249 This study considered ground-based information collected by the “Yamal EcoSystem” project
250 (362259) from the Terrestrial Flagship of the High North Research Centre for Climate and the
251 Environment (Fram Centre). This research was also made possible thanks to the financial
252 support of the Russian Foundation for Basic Research (grant № 18-05-60261)

253

254 **6. References**

- Beck, P. S., & Goetz, S. J. (2011). Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: ecological variability and regional differences. *Environmental Research Letters*, 6(4), 045501. <https://doi.org/10.1088/1748-9326/7/2/029501>
- 255 Bekryaev, R. V., Polyakov, I. V., & Alexeev, V. A. (2010). Role of polar amplification in long-term
256 surface air temperature variations and modern Arctic warming. *Journal of Climate*, 23(14),
257 3888-3906. <https://doi.org/10.1175/2010JCLI3297.1>
- Belgiu, M., & Drăguț, L. (2016). Random forest in remote sensing: A review of applications and future directions. *ISPRS Journal of Photogrammetry and Remote Sensing*, 114, 24-31. <https://doi.org/10.1016/j.isprsjprs.2016.01.011>
- 258 Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J., & Gégout, J.
259 C. (2011). Changes in plant community composition lag behind climate warming in lowland
260 forests. *Nature*, 479(7374), 517. <https://doi.org/10.1038/nature10548>
- 261 Bernes, C., Jonsson, B. G., Junninen, K., Löhmus, A., Macdonald, E., Müller, J., & Sandström, J. (2015).
262 What is the impact of active management on biodiversity in boreal and temperate forests
263 set aside for conservation or restoration? A systematic map. *Environmental Evidence*, 4(1),
264 25. <https://doi.org/10.1186/s13750-015-0050-7>
- 265 Blok, D., Schaepman-Strub, G., Bartholomeus, H., Heijmans, M. M., Maximov, T. C., & Berendse, F.
266 (2011). The response of Arctic vegetation to the summer climate: relation between shrub
267 cover, NDVI, surface albedo and temperature. *Environmental Research Letters*, 6(3), 035502.
268 <https://doi.org/10.1088/1748-9326/6/3/035502>
- 269 Bogdanov, V. D., & Golovatin, M. G. (2017). Anthrax in Yamal: An ecological view on traditional
270 reindeer husbandry. *Russian Journal of Ecology*, 48(2), 95-100.
271 <https://doi.org/10.1134/S1067413617020059>

- 272 Bråthen, K. A., Ravolainen, V. T., Stien, A., Tveraa, T., & Ims, R. A. (2017). Rangifer management
 273 controls a climate-sensitive tundra state transition. *Ecological applications*, 27(8), 2416-
 274 2427. <https://doi.org/10.1002/eap.1618>
- 275 Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species
 276 associated with high levels of climate warming. *Science*, 333(6045), 1024-1026.
 277 <https://doi.org/10.1126/science.1206432>
- 278 Christie, K. S., Bryant, J. P., Gough, L., Ravolainen, V. T., Ruess, R. W., & Tape, K. D. (2015). The role of
 279 vertebrate herbivores in regulating shrub expansion in the Arctic: a
 280 synthesis. *BioScience*, 65(12), 1123-1133. <https://doi.org/10.1093/biosci/biv137>
- 281 Damgaard, C., Raundrup, K., Aastrup, P., Langen, P. L., Feilberg, J., & Nabe-Nielsen, J. (2016). Arctic
 282 resilience: no evidence of vegetation change in response to grazing and climate changes in
 283 South Greenland. *Arctic, Antarctic, and Alpine Research*, 48(3), 531-549.
 284 <https://doi.org/10.1657/AAAR0016-005>
- Degteva, A., & Nellemann, C. (2013). Nenets migration in the landscape: impacts of industrial
 development in Yamal peninsula, Russia. *Pastoralism: Research, Policy and Practice*, 3(1), 15.
<https://doi.org/10.1186/2041-7136-3-15>
- 285 Dieleman, C. M., Branfireun, B. A., McLaughlin, J. W., & Lindo, Z. (2015). Climate change drives a shift
 286 in peatland ecosystem plant community: implications for ecosystem function and
 287 stability. *Global change biology*, 21(1), 388-395. <https://doi.org/10.1111/gcb.12643>
- 288 Durán, A. P., Casalegno, S., Marquet, P. A., & Gaston, K. J. (2013). Representation of ecosystem
 289 services by terrestrial protected areas: Chile as a case study. *PLoS one*, 8(12), e82643.
 290 <https://doi.org/10.1371/journal.pone.0082643>
- 291 Ehrich, D., Henden, J. A., Ims, R. A., Doronina, L. O., Killengren, S. T., Lecomte, N., Pokrovsky, I. G.,
 292 Skogstad, G., Sokolov, A. A., Yoccoz, N. G., & Yoccoz, N. G. (2012). The importance of willow
 293 thickets for ptarmigan and hares in shrub tundra: the more the better?. *Oecologia*, 168(1),
 294 141-151. <https://doi.org/10.1007/s00442-011-2059-0>
- Elmendorf, S. C., Henry, G. H., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N., Cooper, E. J., ... &
 Gill, M. (2012). Plot-scale evidence of tundra vegetation change and links to recent summer
 warming. *Nature Climate Change*, 2(6), 453. <https://doi.org/10.1038/nclimate1465>
- Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., ... & Helkowski, J. H.
 (2005). Global consequences of land use. *science*, 309(5734), 570-574.
<https://doi.org/10.1126/science.1111772>
- 295 Forbes, B. C. (1999). Land use and climate change on the Yamal Peninsula of north-west Siberia:
 296 some ecological and socio-economic implications. *Polar Research*, 18(2), 367-373.
 297 <https://doi.org/10.3402/polar.v18i2.6597>
- 298 Forbes, B. C., Stammer, F., Kumpula, T., Meschytyb, N., Pajunen, A., & Kaarlejärvi, E. (2009). High
 299 resilience in the Yamal-Nenets social-ecological system, West Siberian Arctic,
 300 Russia. *Proceedings of the National Academy of Sciences*, 106(52), 22041-22048.
 301 <https://doi.org/10.1073/pnas.0908286106>
- Franklin, J., Serra-Diaz, J. M., Syphard, A. D., & Regan, H. M. (2016). Global change and terrestrial
 plant community dynamics. *Proceedings of the National Academy of Sciences*, 113(14), 3725-
 3734. <https://doi.org/10.1073/pnas.1519911113>
- Fufachev, I. A., Ehrich, D., Sokolova, N. A., Sokolov, V. A., & Sokolov, A. A. (2019). Flexibility in a
 changing arctic food web: can rough-legged buzzards cope with changing small rodent
 communities?. *Global change biology*. <https://doi.org/10.1111/gcb.14790>
- 302 Golovatin, M. G., Morozova, L. M., & Ektova, S. N. (2012). Effect of reindeer overgrazing on
 303 vegetation and animals of tundra ecosystems of the Yamal peninsula. *Czech Polar*
 304 *Reports*, 2(2), 80-91. <https://doi.org/10.5817/CPR2012-2-8>
- 305 Harris, I. P. D. J. (2019). Release notes for CRU TS v4.03. Retrieved on 30 March 2020 [Online]
 306 https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.03/Release_Notes_CRU_TS4.03.txt.
 307 *Dataset DOI: <http://dx.doi.org/10.5285/d6768285fdc8408bbb9b02bb0f317774>*

- Hilker, T., Natsagdorj, E., Waring, R. H., Lyapustin, A., & Wang, Y. (2014). Satellite observed widespread decline in Mongolian grasslands largely due to overgrazing. *Global Change Biology*, 20(2), 418-428. <https://doi.org/10.1111/gcb.12365>
- 308 Ims, R. A., & Henden, J. A. (2012). Collapse of an arctic bird community resulting from ungulate-
309 induced loss of erect shrubs. *Biological conservation*, 149(1), 2-5.
310 <https://doi.org/10.1016/j.biocon.2012.02.008>
- 311 Joly, K., Jandt, R. R., & Klein, D. R. (2009). Decrease of lichens in Arctic ecosystems: the role of
312 wildfire, caribou, reindeer, competition and climate in north-western Alaska. *Polar*
313 *Research*, 28(3), 433-442. <https://doi.org/10.1111/j.1751-8369.2009.00113.x>
- Jorgenson, J. C., Reynolds, M. K., Reynolds, J. H., & Benson, A. M. (2015). Twenty-five year record of changes in plant cover on tundra of northeastern Alaska. *Arctic, Antarctic, and Alpine Research*, 47(4), 785-806. <https://doi.org/10.1657/AAAR0014-097>
- 314 Kitti, H., Forbes, B. C., & Oksanen, J. (2009). Long-and short-term effects of reindeer grazing on
315 tundra wetland vegetation. *Polar Biology*, 32(2), 253-261. <https://doi.org/10.1007/s00300-008-0526-9>
316
- 317 Klokov, K. B., & Khrushchev, S. A. (2004) *Reindeer Husbandry by the Indigenous Peoples of the Russian*
318 *North: an Analytical Review*. St. Petersburg: VVM
- Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R news*, 2(3), 18-22.
- Liu, D., Peñuelas, J., Ogaya, R., Estiarte, M., Tielbörger, K., Slowik, F., Yang, X., & Bilton, M. C. (2018). Species selection under long-term experimental warming and drought explained by climatic distributions. *New Phytologist*, 217(4), 1494-1506. <https://doi.org/10.1111/nph.14925>
- 319 Marsh, P., Bartlett, P., MacKay, M., Pohl, S., & Lantz, T. (2010). Snowmelt energetics at a shrub
320 tundra site in the western Canadian Arctic. *Hydrological Processes*, 24(25), 3603-3620.
321 <https://doi.org/10.1002/hyp.7786>
- 322 Myers-Smith, I. H., Forbes, B. C., Wilmsking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., Macias-
323 Fauria, M., Sass-Klaassen, U., Lévesque, E. (2011). Shrub expansion in tundra ecosystems:
324 dynamics, impacts and research priorities. *Environmental Research Letters*, 6(4), 045509.
325 <https://doi.org/10.1088/1748-9326/6/4/045509>
- 326 Naito, A. T., & Cairns, D. M. (2011). Patterns and processes of global shrub expansion. *Progress in*
327 *Physical Geography*, 35(4), 423-442. <https://doi.org/10.1177/0309133311403538>
- 328 Nooten, S. S., Andrew, N. R., & Hughes, L. (2014). Potential impacts of climate change on insect
329 communities: a transplant experiment. *PLoS One*, 9(1), e85987.
330 <https://doi.org/10.1371/journal.pone.0085987>
- 331 Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T., & Suominen, O. (2009). Herbivores
332 inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, 15(11), 2681-
333 2693. <https://doi.org/10.1111/j.1365-2486.2009.01935.x>
- 334 Olofsson, P., Foody, G. M., Stehman, S. V., & Woodcock, C. E. (2013). Making better use of accuracy
335 data in land change studies: Estimating accuracy and area and quantifying uncertainty using
336 stratified estimation. *Remote Sensing of Environment*, 129, 122-131.
337 <https://doi.org/10.1016/j.rse.2012.10.031>
- Olofsson, J., Oksanen, L., Oksanen, T., Tuomi, M., Hoset, K. S., Virtanen, R., & Kyrö, K. (2014). Long-term experiments reveal strong interactions between lemmings and plants in the Fennoscandian highland tundra. *Ecosystems*, 17(4), 606-615. <https://doi.org/10.1007/s10021-013-9740-6>
- 338 Pajunen, A. M., Kaarlejärvi, E. M., Forbes, B. C., & Virtanen, R. (2010). Compositional differentiation,
339 vegetation-environment relationships and classification of willow-characterised vegetation
340 in the western Eurasian Arctic. *Journal of Vegetation Science*, 21(1), 107-119.
341 <https://doi.org/10.1111/j.1654-1103.2009.01123.x>
- 342 Pearson, R. G., Phillips, S. J., Loranty, M. M., Beck, P. S., Damoulas, T., Knight, S. J., & Goetz, S. J.
343 (2013). Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature*
344 *Climate Change*, 3(7), 673. <https://doi.org/10.1038/nclimate1858>

345 Pettorelli, N. (2013). *The normalized difference vegetation index*. Oxford University Press.

346 Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., & Levin, S. A. (2013). Marine taxa track local
347 climate velocities. *Science*, 341(6151), 1239-1242. <https://doi.org/10.1126/science.123935>

348 Post, E., & Pedersen, C. (2008). Opposing plant community responses to warming with and without
349 herbivores. *Proceedings of the National Academy of Sciences*, 105(34), 12353-12358.
350 <https://doi.org/10.1073/pnas.0802421105>

351 Ravolainen, V. T., Bråthen, K. A., Ims, R. A., Yoccoz, N. G., Henden, J. A., & Killengreen, S. T. (2011).
352 Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and
353 large mammalian herbivores. *Basic and Applied Ecology*, 12(8), 643-653.
354 <https://doi.org/10.1016/j.baae.2011.09.009>

355 Reichle, L. M., Epstein, H. E., Bhatt, U. S., Reynolds, M. K., & Walker, D. A. (2018). Spatial
356 heterogeneity of the temporal dynamics of arctic tundra vegetation. *Geophysical Research*
357 *Letters*, 45(17), 9206-9215. <https://doi.org/10.1029/2018GL078820>

358 Rixen, C., Schwoerer, C., & Wipf, S. (2010). Winter climate change at different temporal scales in
359 *Vaccinium myrtillus*, an Arctic and alpine dwarf shrub. *Polar Research*, 29(1), 85-94.
360 <https://doi.org/10.1111/j.1751-8369.2010.00155.x>

361 Roxy, M. K., Modi, A., Murtugudde, R., Valsala, V., Panickal, S., Prasanna Kumar, S., ... & Lévy, M.
362 (2016). A reduction in marine primary productivity driven by rapid warming over the tropical
363 Indian Ocean. *Geophysical Research Letters*, 43(2), 826-833.
364 <https://doi.org/10.1002/2015GL066979>

365 Schulte to Bühne, H., Wegmann, M., Durant, S. M., Ransom, C., de Ornellas, P., Grange, S., &
366 Pettorelli, N. (2017). Protection status and national socio-economic context shape land
367 conversion in and around a key transboundary protected area complex in West
368 Africa. *Remote Sensing in Ecology and Conservation*, 3(4), 190-201.
369 <https://doi.org/10.1002/rse2.47>

370 Schuur, E. A., Bockheim, J., Canadell, J. G., Euskirchen, E., Field, C. B., Goryachkin, S. V., ... &
371 Mazhitova, G. (2008). Vulnerability of permafrost carbon to climate change: Implications for
372 the global carbon cycle. *BioScience*, 58(8), 701-714. <https://doi.org/10.1641/B580807>

373 Sokolov, V., Ehrich, D., Yoccoz, N. G., Sokolov, A., & Lecomte, N. (2012). Bird communities of the
374 Arctic shrub tundra of Yamal: habitat specialists and generalists. *PLoS One*, 7(12), e50335.
375 <https://doi.org/10.1371/journal.pone.0050335>

Song, X. P., Hansen, M. C., Stehman, S. V., Potapov, P. V., Tyukavina, A., Vermote, E. F., &
Townshend, J. R. (2018). Global land change from 1982 to 2016. *Nature*, 560(7720), 639.
<https://doi.org/10.1038/s41586-018-0411-9>

376 Sturm, M., Douglas, T., Racine, C., & Liston, G. E. (2005). Changing snow and shrub conditions affect
377 albedo with global implications. *Journal of Geophysical Research:*
378 *Biogeosciences*, 110(G1). <https://doi.org/10.1029/2005JG000013>

379 Tape, K. D., Hallinger, M., Welker, J. M., & Ruess, R. W. (2012). Landscape heterogeneity of shrub
380 expansion in Arctic Alaska. *Ecosystems*, 15(5), 711-724. [https://doi.org/10.1007/s10021-](https://doi.org/10.1007/s10021-012-9540-4)
381 [012-9540-4](https://doi.org/10.1007/s10021-012-9540-4)

382 Walker, D. A., Reynolds, M. K., Daniëls, F. J., Einarsson, E., Elvebakk, A., Gould, W. A., ... &
383 Moskalenko, N. G. (2005). The circumpolar Arctic vegetation map. *Journal of Vegetation*
384 *Science*, 16(3), 267-282. <https://doi.org/10.1111/j.1654-1103.2005.tb02365.x>

385 Walker, D. A., Leibman, M. O., Epstein, H. E., Forbes, B. C., Bhatt, U. S., Reynolds, M. K., ... &
386 Kaarlejärvi, E. (2009). Spatial and temporal patterns of greenness on the Yamal Peninsula,
387 Russia: interactions of ecological and social factors affecting the Arctic normalized difference
388 vegetation index. *Environmental Research Letters*, 4(4), 045004.
389 <https://doi.org/10.1088/1748-9326/4/4/045004>

390 Walker, D. A., Forbes, B. C., Leibman, M. O., Epstein, H. E., Bhatt, U. S., Comiso, J. C., Drozdov, D. S.,
391 Gubarkov, A. A., Jia, G. J., Kaarlejärvi, E. (2010). Cumulative effects of rapid land-cover and

392 land-use changes on the Yamal Peninsula, Russia. In *Eurasian Arctic land cover and land use*
393 *in a changing climate*. Springer, Dordrecht.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., & Bairlein, F. (2002).
Ecological responses to recent climate change. *Nature*, *416*(6879), 389.
<https://doi.org/10.1038/416389a>

Wahren, C. H., Walker, M. D., & Bret-Harte, M. S. (2005). Vegetation responses in Alaskan arctic
tundra after 8 years of a summer warming and winter snow manipulation
experiment. *Global Change Biology*, *11*(4), 537-552. <https://doi.org/10.1111/j.1365-2486.2005.00927.x>

World Meteorological Organisation. (2019). World Meteorological Organisation. Available from
<http://worldweather.wmo.int/en/home.html> (accessed 26 July 2019).

394 Wookey, P. A., Aerts, R., Bardgett, R. D., Baptist, F., Bråthen, K. A., Cornelissen, J. H., ... & Shaver, G.
395 R. (2009). Ecosystem feedbacks and cascade processes: understanding their role in the
396 responses of Arctic and alpine ecosystems to environmental change. *Global Change*
397 *Biology*, *15*(5), 1153-1172. <https://doi.org/10.1111/j.1365-2486.2008.01801.x>

Xian, G., & Homer, C. (2010). Updating the 2001 National Land Cover Database impervious surface
products to 2006 using Landsat imagery change detection methods. *Remote Sensing of*
Environment, *114*(8), 1676-1686. <https://doi.org/10.1016/j.rse.2010.02.018>

398 Young, N. E., Anderson, R. S., Chignell, S. M., Vorster, A. G., Lawrence, R., & Evangelista, P. H. (2017).
399 A survival guide to Landsat preprocessing. *Ecology*, *98*(4), 920-932.
400 <https://doi.org/10.1002/ecy.1730>

401

402

403
404
405
406
407
408
409
410
411
412

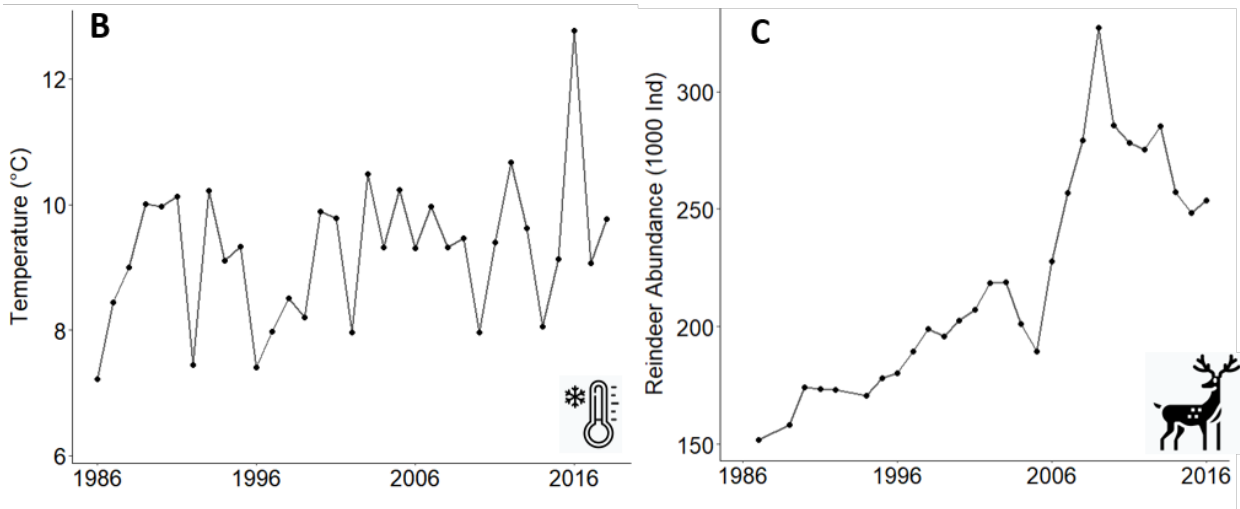
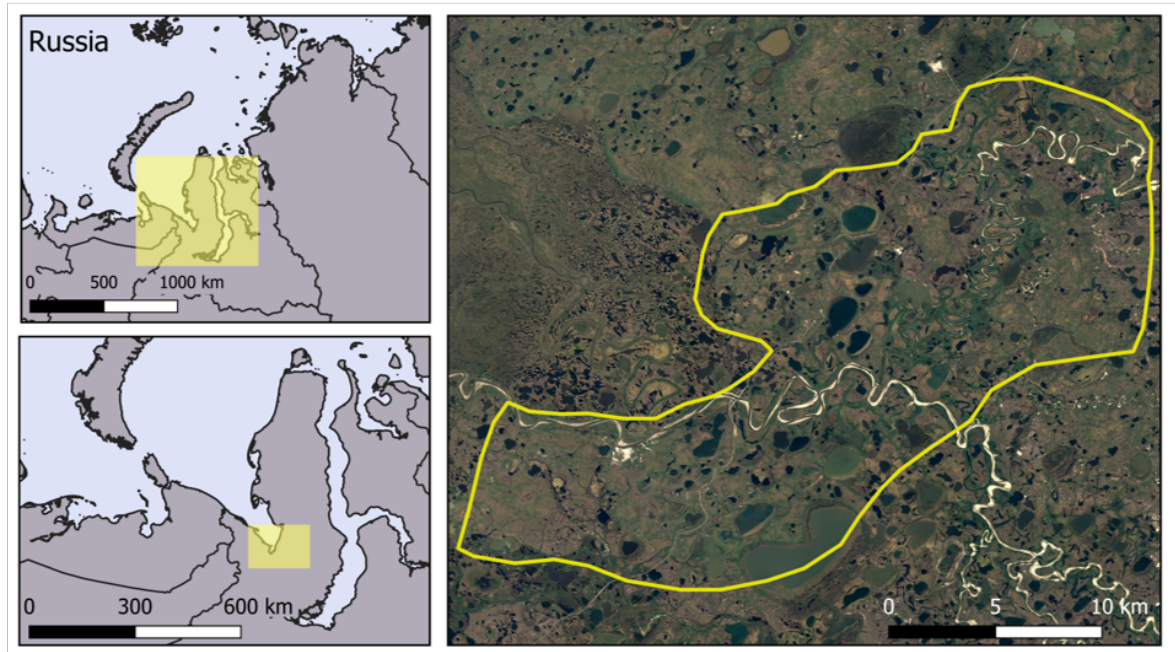
TABLES AND FIGURES

Table 1: Area-adjusted user and producer accuracies for shrub thickets, as well as overall area-adjusted accuracy of the land cover maps generated for the years 1986-2018. Confidence intervals at 95% confidence levels given in brackets were calculated based on the methodology proposed by Olofsson et al. (2013). Producer’s accuracy quantifies the probability that a given pixel will be assigned to the correct land cover class by the classification algorithm. By contrast, user’s accuracy estimates the probability that the assigned class of a given pixel is correct. Overall accuracy corresponds to the percentage of correctly identified pixels across the entire study site.

Year	Shrub Thickets		Overall Accuracy (%)
	User’s Accuracy (%)	Producer’s Accuracy (%)	
1986	86.7 (±4.6)	65.4 (±7.8)	83.9 (±2.5)
1991	94.4 (±2.9)	55.3 (±7.8)	87.2 (±2.5)
1996	94.5 (±2.9)	77.7 (±7.1)	86.9 (±2.2)
2001	94.4 (±3.4)	86.1 (±8.1)	85.7 (±2.6)
2006	97.0 (±2.3)	78.0 (±8.0)	91.4 (±1.9)
2011	94.6 (±2.3)	97.3 (±3.0)	89.9 (±1.8)
2016	94.1 (±5.0)	70.9 (±15.7)	84.1 (±4.3)
2018	91.9 (±4.1)	84.9 (±7.4)	88.1 (±2.1)

413
414
415

A



416

417 **Figure 1.** (A) Overview of the study site located in Southern Yamal Peninsula, Russia. The two small
418 insets show the position of our study site within Russia and then the Yamal Peninsula (yellow square).

419 The larger inset shows the boundary of our study site in yellow outlined over the base scene from

420 Google Earth Engine, which has a spatial resolution of 3 m. (B) Average monthly summer temperature
421 for the months June – September from 1986 to 2018. The data was acquired from CRU TS3.10 (Harris

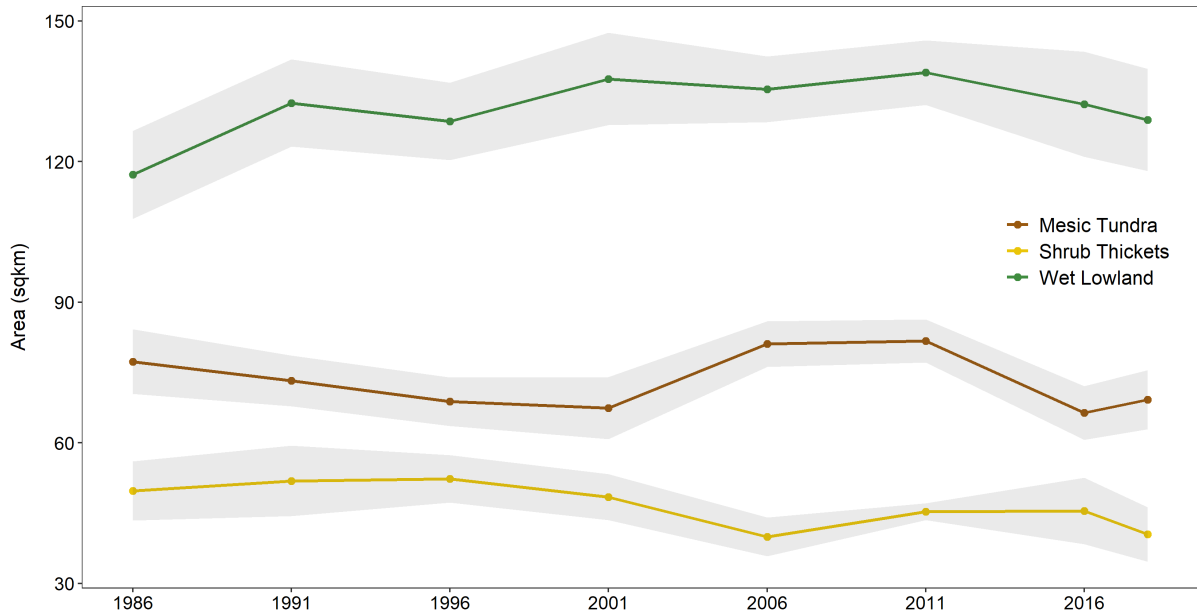
422 et al. 2019). (C) Semi-domesticated reindeer abundance (1000 individuals) per year for the period

423 1986 – 2016 for the entire Yamal Peninsula region collated from three different studies (and averaged

424 in the case of disagreement): Klokov and Khrushchev (2004); Golovatin et al. (2012); and Bogdanov

425 and Golovatin (2017).

426



427

428

429 **Figure 2.** Cover of the different vegetation classes at the study site from 1986 to 2018, based on land
 430 cover classifications from 1986 to 2016. The shaded areas indicate the margin of error with a 95%
 431 confidence interval (calculated based on the methodology suggested by Olofsson et al. 2013).

432

433

434

435

436 **Supplementary Materials**

437

438

439 **Table S1.** Description of land cover classes used in this study.

440

Type	Class	Description
Non-Vegetation	Water Bodies	River and Lakes
	Sand	Loose sand and gravel found close to riverbanks and exposed hills.
	Exposed Ridges	Limited plant cover with more than 25% of the area covered by biological soil crust. Vegetation composed of graminoids, lichens and prostrate dwarf shrubs less than 5 cm high.
Vegetation	Shrub Thickets	Dominated by <i>Betula nana</i> shrubs and <i>Salix spp.</i> more than 25 cm high, growing near water bodies, river valleys and on hillsides. Forbs and graminoid plants are abundant in the understory.
	Wet Lowlands	Occurs primarily in areas of flat topography with poor drainage, often close to lakes and rivers where flooding occurs. Characterized by a continuous layer of <i>Sphagnum</i> mosses more than 10 cm thick, and abundant graminoids with a few dwarf shrubs.
	Mesic Tundra	Characterized by tussocks of <i>Eriophorum vaginatum L.</i> and other graminoids. Dwarf shrubs and lichens are also abundant in these areas, and forbs occur at lower abundance. A thick, sometimes discontinuous, moss layer could also be found across hilltops, depending on microrelief and drainage.

441

442

443

444

445

446

447

448

449

450

451

452

453

454

455

456

457

458

459

460

461

462 **Table S2.** Internal validation accuracies (%) calculated with the validation points created from
 463 unchanged validation pixels using the CVA methodology and external validation accuracies (%)
 464 calculated independently with high resolution imagery. Confidence intervals at 95% confidence levels
 465 are given in brackets.

466
 467

Year	Internal Validation			External Validation		
	UA	PA	OA	UA	OA	PA
2016	95.0 (±2.5)	59.9 (±9.1)	82.8 (±2.9)	94.1 (±5.0)	70.9 (±15.7)	84.1 (±4.3)
2018	98.0 (±1.6)	77.9 (±10.9)	86.9 (±2.9)	91.9 (±4.1)	84.9 (±7.4)	88.1 (±2.1)

468

469 * UA – Area-adjusted User’s Accuracy; PA – Area-adjusted Producer’s Accuracy; OA – Overall Accuracy

470