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***Rangifer* management controls a climate-sensitive tundra state transition**

Running Head: **Management controls state transition**

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23 **Abstract**

24 *Rangifer* (caribou/reindeer) management has been suggested to mitigate the temperature-
25 driven transition of arctic tundra into a shrubland state, yet how is uncertain. Here we study
26 this much focused ecosystem state transition in riparian areas, where palatable willows (*Salix*)
27 are dominant tall shrubs and highly responsive to climate change. For the state transition to
28 take place, small life stages must become tall and abundant. Therefore we predicted that the
29 performance of small life stages (potential recruits) of the tall shrubs were instrumental to the
30 focal transition, where *Rangifer* managed at high population density would keep the small-
31 stage shrubs in a “browse trap” independent of summer temperature. We used a large-scale
32 quasi-experimental study design that included real management units that spanned a wide
33 range of *Rangifer* population densities and summer temperatures in order to assess the relative
34 importance of these two driving variables. Ground-surveys provided data on density and
35 height of the small shrub life stages, while the distributional limit (shrubline) of established
36 shrublands (the tall shrub life stage) was derived from aerial photographs. Where *Rangifer*
37 densities were above a threshold of approximately 5 animals km⁻² we found, in accordance
38 with the expectation of a “browse trap”, that the small life stages of shrubs in grasslands were
39 at low height and low abundance. At *Rangifer* densities below this threshold the small life
40 stages of shrubs were taller and more abundant indicating *Rangifer* were no longer in control
41 of the grassland state. For the established shrubland state, we found that the shrubline was at a
42 100 m lower elevation in the management units where *Rangifer* have been browsing in
43 summer as opposed to the migratory ranges with no browsing in summer. In both seasonal
44 ranges the shrubline increased 100 m per 1°C increment in temperature. Our study supports
45 the proposal that *Rangifer* management within a sustainable range of animal densities can
46 mitigate the much-focused transition from grassland to shrubland in a warming arctic.

47 **Introduction**

48 Climate warming currently causes changes in the physical and biological characteristics of the
49 Arctic (Bhatt et al. 2010, Bhatt et al. 2013), with the most conspicuous earth surface change
50 being the shift towards increased shrub abundance in tundra landscapes (Walker 2000, Sturm
51 et al. 2001, Post et al. 2009, Wookey et al. 2009, Myers-Smith et al. 2011a). Increased shrub
52 abundance has the potential to induce positive climate feedback through reduced albedo,
53 increased ground temperatures and changes in a range of bio-physical processes (Chapin et al.
54 2005, Wookey et al. 2009, Myers-Smith et al. 2011a, Cohen et al. 2013, Pearson et al. 2013,
55 Menard et al. 2014) but see Blok et al. (2010). At the same time, abundant shrubs form habitat
56 that enhance species richness of a range of organism groups such as birds, insects and
57 vascular plants (Roininen et al. 2005, Ims and Henden 2012, Henden et al. 2013, Rich et al.
58 2013, Sweet et al. 2014, Bråthen and Lortie 2016). However, current predictions on the extent
59 and rate of warming-induced tundra ecosystem state shifts towards shrub dominance are
60 currently hampered by unknown context dependencies (Myers-Smith et al. 2011b, Bernes et
61 al. 2015, Swanson 2015). Here we focus on shrub increase in a particularly climate-sensitive
62 tundra ecosystem and under a particularly influential context that is often subjected to
63 management interventions, large mammalian herbivory, in order to progress the
64 understanding of what influences state shifts in the circumpolar tundra.

65 Shrub increase in tundra ecosystems is strongly linked to climate warming (Forbes et al. 2010,
66 Myers-Smith et al. 2011b, Elmendorf et al. 2012, Pearson et al. 2013, Buntgen et al. 2015).
67 However, arctic shrubs exhibit considerable intra- and interspecific heterogeneity in their
68 temperature response (Normand et al. 2013, Buntgen et al. 2015), with plant traits such as
69 longevity and size as important determinants. Strong responses to climate warming are most
70 evident among shrub species with an intrinsic capacity to grow tall in habitats with high soil

71 moisture (Elmendorf et al. 2012, Myers-Smith et al. 2015), such as *Salix* in riparian habitats
72 (Tape et al. 2012). Moreover, tall shrub species also provide the strongest climate feedbacks
73 (Kramshøj et al. 2016, Williamson et al. 2016).

74 *Salix* shrubs are palatable to many herbivores (Wolf et al. 2007, Christie et al. 2015). Thus,
75 herbivory might be a highly influential moderator to the response of shrubs to climate
76 warming. Experimental studies excluding browsing activities have shown that both small and
77 large herbivores can have strong impacts on shrubs, to the extent that they inhibit shrub
78 increase in tundra ecosystems (e.g. den Herder et al. 2008, Olofsson et al. 2009, Ravolainen et
79 al. 2014). Although conclusions from these studies have been based on extensive scales and
80 covering a range of environmental contexts, their relevance to herbivore management has
81 been unclear. Still, herbivore management has repeatedly been suggested as a way to mitigate
82 shrub expansion in the circumpolar tundra (Post and Pedersen 2008, Olofsson et al. 2009, Ims
83 and Ehrlich 2013, Biuw et al. 2014, Ravolainen et al. 2014, Väisänen et al. 2014).

84 However, tall shrubs can grow out of the physical foraging range of large herbivores and
85 thereby become invulnerable to their browsing. Hence it is the small life stages within reach
86 of the herbivores, such as saplings and ramets, that are likely to experience decrease in both
87 height and abundance (Christie et al. 2015). Moreover, this decrease is likely to be
88 exponential with increasing browsing pressure (Hegland and Rydgren 2016), causing small
89 stages of shrubs to be kept in a “browse trap” at higher herbivore densities (cf. Staver and
90 Bond 2014, Fig. 1a) and from which they are unable escape even under climate warming. In
91 riparian habitats such herbivore density-dependence can result in bimodal distributions of
92 shrub sizes (small *versus* large-stage shrubs, Fig. 1b) and ecosystem states (grassland *versus*
93 shrubland, Fig. 1c) (cf. House et al. 2003, Pajunen et al. 2010, Tape et al. 2012, Ravolainen et
94 al. 2013), where a climate warming induced ecosystem state shift may only occur at low

95 herbivore density (Fig. 1a). Further, altitudinal or latitudinal distribution limits of large stage
96 shrubs, termed *shrublines*, can only advance under climate warming where herbivore density
97 is low (Fig. 1c). Tall shrubs can however be very old (Forbes et al. 2010) causing existing
98 shrublands and shrublines to reflect effects of climate warming and herbivore control in the
99 past. Therefore, we advocate focus on small shrub life stages for studying how herbivores
100 may control ongoing and future state shifts, and a focus on tall shrub life stages for
101 understanding past events. The focal large herbivore of the present study, *Rangifer tarandus*
102 (caribou/reindeer), is the numerically dominant large herbivore species across the circumpolar
103 tundra, the tundra-forest transition zone and the northern boreal forest. In Eurasia
104 approximately 2.2 million reindeer are subject to human management (Huntington 2013).
105 Management of both wild and semi-domestic herds is considered important, exerting controls
106 on ecosystems (Ims and Ehrich 2013) such as vegetation state transitions involving shrubs
107 (van der Wal 2006, Post et al. 2009). However, the effects of *Rangifer* on shrub abundance
108 are variable, most probably because of confounding with ecological context (review in Bernes
109 et al. 2015). Moreover, as exemplified from an alpine ecosystem, shrub growth may not be
110 dependent on relaxed browsing pressure but rather the presence of a favorable hydrology
111 regime (Marshall et al. 2013). Therefore, to assess whether *Rangifer* management can exert
112 control on the ecosystem state shift scenarios outlined in our conceptual framework (Fig. 1),
113 there is a need to employ study designs that ensure non-confounding between (1) spatial
114 scales, (2) animal densities that are realistic for *Rangifer* management, (3) temperature
115 gradients and (4) habitats with an environmental context that allow for life stage transitions in
116 tall shrubs and state transitions of the ecosystem. In the present quasi-experimental study in
117 northernmost Fennoscandia we achieved this by means of field observations and aerial photos
118 of a total of 53 riparian valleys, encompassing a 4°C gradient in average summer temperature
119 and *Rangifer* management units differing between 1.8 and 16.9 animals per km² during

120 summer. This allowed us to assess if there is a threshold of managed animal densities above
121 which *Rangifer* browsing can maintain riparian grasslands within a steady state (cf. Scheffer
122 and Carpenter 2003) and prevent a shift to a shrubland state across a wide range of summer
123 temperatures. Specifically, we estimated the effects of *Rangifer* density, seasonal range use
124 indicative of past *Rangifer* density and a gradient in summer temperature on 1) the density
125 and height of small life stages of *Salix* shrub species in riparian grasslands and 2) the
126 distribution of the shrubline formed by their tall life stages.

127 **Methods**

128 *Study system*

129 Our study system is within Finnmark, the northernmost, sub-arctic and low-arctic part of the
130 Scandinavian Peninsula, spanning 150 km in latitude and 350 km in longitude (Fig. 2). The
131 geographic temperature gradients are very steep in northern Fennoscandia (Jansson et al.
132 2015) and amount to 4°C in average summer temperature (June, July and August) across the
133 study region. Average precipitation in the summer is 65, 54 and 48 mm in the west, middle,
134 and east of Finnmark, respectively (Norwegian Meteorological Institute, <http://met.no>). The
135 region is typically snow covered until early-late June. The study region is characterized by
136 variable bedrock, being mainly gabbro in the west, and slate and sandstone towards the east
137 and interior parts (Geological Survey of Norway, <http://www.ngu.no/>). The main vegetation
138 type at lower altitudes (in particular in the western part and inland sections) is sub-arctic
139 mountain birch forest (*Betula pubescens* ssp. *czerepanovii*) and at higher altitudes dwarf
140 shrub tundra (Walker et al. 2005) dominated by *Empetrum nigrum*, *Betula nana*, *Salix*
141 *herbacea*, and *Vaccinium* spp. and marshes dominated by *Eriophorum* spp. and *Carex* spp. In
142 the most eastern low-arctic section of the study region, the dwarf shrub tundra extends to the
143 sea level. Riparian grasslands are common especially in the larger valleys in the study region,
144 with presence of *Bistorta vivipara* and *Viola biflora*, *Avenella flexuosa*, *Anthoxanthum*
145 *nipponicum*, *Deschampsia cespitosa*, sedges of *Carex* spp. and shrubs of *Salix* spp. (plant
146 names follow the Pan-Arctic Flora <http://nhm2.uio.no/paf/>).

147 The *Salix* shrubs, typically *Salix phylicifolia*, *S. lapponum*, *S. lanata*, and *S. hastata* and their
148 hybrids (see Ravolainen et al. 2013), have the potential to form 0.5 - 3 m tall patches
149 (thickets) that are here defined as a tall life stage. Species of tall *Salix* shrubs are long-lived
150 and highly clonal, with tall-stage stands being several decades to 100 years old (Forbes et al.

151 2010), whereas the small life stage can be saplings or ramets. There appears to be no
152 palatability differences between these *Salix* species (Speed et al. 2013), and because they
153 often mix in their canopies and hybridize we have pooled the tall shrub species of *Salix* in this
154 study.

155 *Rangifer tarandus* in Finnmark is semi-domestic and migratory. Their summer pastures are
156 located within management districts at coastal peninsulas, while the winter pastures are
157 located in the inland often close to the Finnish border (Fig. 2a). The areas between the
158 summer and winter pastures are defined as migratory ranges that are visited a few weeks
159 during migration in early spring and late fall, and are mainly snow-covered during these
160 periods. Management rules and an extensive system of fences define the borders between the
161 seasonal ranges as well as between the districts of the summer range. The fences between the
162 seasonal ranges were mostly erected in the 1970's and followed borders that the management
163 were already accustomed to. However, *Rangifer* population densities between the
164 management district are not primarily regulated by their resource base in terms of vegetation
165 (Bråthen et al. 2007, Ravolainen et al. 2010). Rather, different national management policies
166 also starting in the 1970's cause *Rangifer* population densities to vary greatly both in time
167 (Hausner et al. 2011) and spatially across different management units owing to interactions
168 between this policy and internal socio-economic affairs within and among the herding
169 districts (Hausner et al. 2012). In fact, Næss and Bårdsen (2010) concluded that individual
170 husbandry units' strategies, such as level of harvesting, have a larger effect on individual
171 husbandry units' population size than negative density-dependence. Accordingly, spatial
172 differences in population size among *Rangifer* herding units in Finnmark have been persistent
173 over many decades (Bråthen et al. 2007, Fig. S1). Co-dominant herbivores with *Rangifer* in
174 Finnmark are voles and lemming (Ims et al. 2007). In addition, moose (*Alces alces*) and
175 domestic sheep (*Ovis aries*) are common. Notably, beaver-dams that are common in many

176 riparian regions world-wide, and with high impact to *Salix* growth (Marshall et al. 2013) are
177 not present in our study region.

178 *Study design*

179 We selected management units of semi-domestic *Rangifer* to achieve a sample of riparian
180 areas for which summer temperatures and browsing intensities were non-confounded (Fig.
181 S2) according to a quasi-experimental design (Kerr et al. 2007). The management units
182 spanned the 4°C gradient in mean summer temperatures, had contrasting seasonal range use
183 (summer vs. migratory range) and had *Rangifer* population densities in the summer ranges
184 from 1.8-16.9 individuals km² (densities retrieved from official statistics at
185 www.landbruksdirektoratet.no for the years 2009-2011). We did not attempt to attribute
186 specific *Rangifer* densities to the migration ranges because the short durations of *Rangifer*
187 presence in these ranges are likely to inflict a lower browsing pressure for a given *Rangifer*
188 density. Moreover, the migration ranges are shared to differing and variable degrees between
189 several herds from different summer ranges.

190 In Finnmark, the geographic coverage of meteorological stations is scarce. Thus, to provide a
191 measure of long-term growing-season temperatures, we used modeled estimates downscaled
192 to a 100 m resolution (Pellissier et al. 2013) from WorldClim ("Warmest Quarter" Hijmans et
193 al. 2005). The full description of the downscaling procedure can be found in Dullinger et al.
194 (2012). When comparing river valleys we used estimates for the temperature at 200 m altitude
195 as our measure of the river valley temperature.

196 A total of 23 study units were selected and each represented by a study block, dominated by
197 dwarf shrub tundra and hosting riparian areas (Fig. 2). The size of the study blocks was
198 approximately 30 x 30 km but this was modified by coastline patterns, fences separating
199 summer and migration pastures, and the continuous sub-arctic birch forest that borders the

200 tundra towards the south. In the eastern parts of our study region the migration ranges are
201 smaller and in one case one block included both the migration and summer ranges. Within
202 each block we selected three river valleys that were either in a summer or in a migration
203 range, and that ascended from either the sea level or from the birch forest-line. We selected
204 the largest rivers and/or the ones running in gently sloping terrain above the treeline in order
205 to target rivers that most likely included riparian plains with sediment accumulation, as these
206 conditions provide optimal habitat for the growth of tall *Salix* shrubs (Pajunen et al. 2010,
207 Ravolainen et al. 2014). A few blocks had less than three river valleys available, in which
208 case we included all.

209 Within the river valleys we established sampling lines along which we sampled both field
210 measurements of the abundance of small-stage shrubs in grasslands and mapped presence of
211 tall shrubs from aerial photographs (Sturm et al. 2001, Lillesand et al. 2004). We made points
212 along the river valley at 100 m intervals with each point situated in the middle of the river
213 channel (Fig. 2b). The first point was placed well below the forest-line, or at sea level in the
214 mouth of the river in areas with no birch forest. The last point was placed in the high-alpine
215 vegetation zone where vegetation cover was no longer continuous, or at the source of the
216 watercourse. At each point, a 200 m sampling line was drawn perpendicular to each side of
217 the river (Fig. 2b). These lines served as sampling units for the field measurements and for the
218 analyses of the aerial photographs. In the field, the sampling lines were found using their GPS
219 coordinates.

220 In sum, the study design admitted sampling of data on shrubs along a range of river valleys,
221 each several kilometers long and including a range of potentially influential abiotic and biotic
222 contexts. Average estimates of both small and tall shrub stages per river valley then provided
223 us with robust response estimates to the specific effects of *Rangifer* density and temperature.

224 *Measurements of shrub stages*

225 Presence of tall-stage shrubs (i.e. 0.5 - 3 m tall thickets) was mapped using high-resolution
226 aerial photographs in all river valleys (53 valleys in 23 blocks), whereas measures of small-
227 stage shrubs were recorded by means of field surveys in a sub-sample of river valleys and
228 blocks (13 blocks with 1 river valley each). The tall-stage shrub mapping was used to assess
229 the shrubline per river valley, whereas the small-stage shrub measurements were used to
230 assess growth of the small-stage shrubs into tall shrub stages, averaged per river valley.

231 In the field surveys we measured the small-stage shrubs in the riparian grasslands during late
232 July and early August in 2010 (Fig. 2a). Field sampling only included areas that had a
233 minimum distance of 500 m to man-made constructions (huts, roads). Solitary birch trees
234 were accepted in the field sampling areas but areas including forest (birch >3 m, less than 30
235 m between trees) were excluded.

236 The sampling lines were first surveyed to get an overview of grassland, tall shrub patches,
237 shrubland and shrub height within each of the selected river valleys. This initial survey of
238 each river valley also provided data suitable for validation of the aerial photograph analyses
239 (see Supplementary Information and Fig. S3). For a sampling line to be included in more
240 detailed vegetation analyses it had to cross grassland or tall shrub patches on river banks.
241 Moreover, within the first 50 m of the riverbed the line had to have at least one 10 m segment
242 on level ground with at least two-thirds coverage with grassland vegetation. The final
243 vegetation analysis area was distributed among the sampling lines to include both an upper
244 and lower part of the river valleys. Where several lines were suitable, a random draw was
245 used to select between nearby lines. Sampling lines on stony or gravelly areas and on mire
246 were excluded.

247 As the vegetation analysis started at the riverbank or at the edge of a tall shrub patch if it
248 occupied the riverbank, sampling line lengths differed. Along the sampling line 10 m long
249 segments were established using a measuring tape. Within each segment a 1 m wide strip-
250 transect was surveyed by holding a 1 m long stick perpendicular to the ribbon while walking.

251 For a measurement of small shrub density, we counted the number of stems that appeared to
252 be either a ramet or a sapling, per segment. We did not dig into the soil to determine if ramets
253 were connected belowground, and counts refer to the number of small shrubs that were not
254 obviously branching from each other. When it was possible to judge without removing soil
255 that several ramets belonged to the same individual, these were counted as one small shrub.

256 For a measurement of the size of the small-stage shrubs, the height and shoot sum of the first
257 small-stage shrub at the left side of the tape was measured in every segment. If no small-stage
258 shrub was found then the right side of the ribbon was checked, and if still no small shrub was
259 found, we searched within an expanded strip-transect up to 3 m wide.

260 For each selected small-stage shrub we measured the length of the stem, which is used as a
261 primary response variable. Because small shrubs were more or less upright this is an
262 approximation of height. We also measured the length of all branches longer than 2 cm to the
263 accuracy of 1 cm. Then we calculated the average total shoot sum as the sum of the stem
264 length and the lengths of all branches. Small-stage shrub length was strongly correlated to
265 shoot sum (Fig. S4), and hence we subsequently used the latter variable in the analyses. If the
266 starting point of a sampling line was a tall shrub patch we recorded its height (± 5 cm) using a
267 ruler.

268 Using high-resolution aerial photographs from all selected river valleys (n=58) we recorded
269 the distribution of stands of *Salix* shrubs (Fig. 2). The presence or absence of tall *Salix* shrubs

270 and / or birch trees along each perpendicular line was assessed by visual inspection of the
271 aerial photographs. The probability of classifying a line as being populated by tall shrubs (0.5
272 - 3 m height) increased from 50% when the shrubs along the line were 65 cm tall to 95%
273 when shrubs were 130 cm tall (logistic regression equation $\text{logit}(p) = -2.95 + 0.046 * \text{shrub}$
274 height). This imply that mainly tall shrub life stages could be detected using the aerial
275 photographs, while small shrub life stages become indistinguishable from background
276 vegetation in these photographs. Tall shrubs were in general found at higher altitudes than
277 birch trees. As it was not possible to distinguish shrubs within lower parts of some river
278 sections with dense birch forests, tall shrubs were recorded only above the birch forest. The
279 presence-absence data on tall *Salix* shrubs were used to estimate the altitudinal distribution
280 limit (i.e. the shrubline) within each of the river valleys.

281 *Statistical analysis*

282 We analyzed the data fitting generalized linear mixed models in the R environment version
283 3.0.2 (<http://www.r-project.org>).

284 The field survey generated data from replicated sections (n=525) within sampling lines
285 (n=152) of the river valleys. To account for dependencies in the observations within sampling
286 lines we included sampling line nested within river valley as a random factor in the analyses.
287 We used the count of ramets and /or saplings within the 10 m sampling segments as the
288 response variable in the analysis of small-stage shrub densities. To account for counts from
289 sampling lines of variable length, and to obtain density estimates at the m² scale, we included
290 log(sampling line length) as an offset variable in regression models. The residual distribution
291 of the small shrub counts was highly overdispersed. We therefore fitted models assuming a
292 negative binomial distribution and a log link function using the function `glmmadmb` in the
293 package `glmmADMB` for R (Bolker et al. 2012). First, we fitted a generalized mixed model

294 with *Rangifer* density (in the summer ranges) and average summer temperature at 200 m. a. s.
 295 l. as continuous fixed effect predictor variables, and seasonal range use (summer *versus*
 296 migration) as categorical fixed effect predictor variables. Plots of the data suggested that the
 297 effect of *Rangifer* densities within the summer ranges was non-linear with an upper limit to
 298 average small shrub densities at low *Rangifer* densities and a lower limit to average small
 299 shrub densities at high *Rangifer* densities. We therefore estimated the average small shrub
 300 density for each river valley using a generalized mixed model with river valley as a fixed
 301 factor and sampling line as random effect. To these river specific estimates of small shrub
 302 densities from the summer ranges we fitted the following 4 parameter logistic model:
 303 $\log(\text{average small shrub density}) = \beta_1 + (\beta_2 - \beta_1) / (1 + \exp((\beta_3 - \text{Rangifer density}) / \beta_4))$,
 304 with β_i being parameters estimated by the data. In this model β_1 is the asymptotic log(small
 305 shrub density) as *Rangifer* density approaches zero, β_2 is the asymptotic log as *Rangifer*
 306 density approaches infinity, β_3 is the *Rangifer* density at the inflection point and β_4 is a slope
 307 parameter. The model was fitted using weighted least squares, with weights given by the
 308 inverse of the variance of the river specific average small shrub density estimates.

309 The height of the small-stage shrub was analyzed in linear mixed models with stem length as
 310 the response variable. Seasonal range, reindeer density and average summer temperature were
 311 fitted as fixed effect predictor variables. Again, plots of the data suggested that the effect of
 312 *Rangifer* densities within the summer ranges was non-linear. We therefore proceeded with
 313 first estimating the average small-stage shrub height using a linear mixed model with river as
 314 a fixed factor and sampling line as random effect, and second, fitted a non-linear function to
 315 these river specific estimates from the summer ranges. The data did not show strong support
 316 for an upper limit to average small-stage shrub height at low reindeer densities, and we
 317 therefore used the following 3 parameter non-linear model: small-stage shrub height = $\beta_1 + (\beta_2 - \beta_1) * \exp(-\exp(\beta_3) * \text{Rangifer density})$, with β_i being parameters estimated by the
 318

319 data. In this model β_1 is the asymptotic small-stage shrub height as *Rangifer* density
320 approaches infinity, β_2 is the predicted small-stage shrub height at a *Rangifer* density of zero
321 and β_3 is a slope parameter. The model was fitted using weighted least squares, with weights
322 given by the inverse of the variance of the river specific average small-stage shrub height
323 estimates.

324 The altitudinal shrubline was estimated from the presence/absence data of the tall shrub stage
325 from the aerial photographs by fitting a logistic function of form: probability of presence = p
326 = $1/(1+\exp((\beta_1-\text{altitude}) \beta_2))$, where β_1 is the altitude at $p = 0.5$ and β_2 is the estimated slope
327 for the decrease in probability of presence with altitude, to the resulting binary data from each
328 river valley. The model was fitted to each river valley included in the study assuming a
329 binomial error distribution. In subsequent analyses, we used the estimates of β_1 as our
330 measures of the shrubline. For some river valleys furthest to the north and east of the study
331 area, neither birch nor tall shrubs were present along the river, and the shrubline was set to 0
332 m.

333 We used the estimates of β_1 as the response variable in the analysis of the spatial variation in
334 the shrubline, and included the design variable “study block” as a random factor in linear
335 mixed models. As above, the average summer temperature at 200 m asl. for each river valley,
336 and *Rangifer* seasonal range use (summer *versus* migration) were fitted as continuous and
337 categorical fixed effects, respectively. In addition, we investigated the potential effect of the
338 logarithm of the *Rangifer* density on the shrubline in the summer ranges. For model selection
339 we fitted the models using maximum likelihood and evaluated nested models using likelihood
340 ratio tests. The final statistical model for the spatial variation in the shrubline included the
341 additive fixed effects of reindeer seasonal range use (summer or migration range) and

342 temperature. There was no evidence for any interaction (i.e. different slope estimates for the
343 temperature response) between seasonal range use and temperature.

344

345 **Results**

346 *Small shrub stage*

347 Both average height and density of small-stage shrubs were non-linearly related to reindeer
348 density in the summer pastures (Fig. 3a,b) and agreed with our expectation of a browse trap
349 (Fig. 1). That is, over the range of 3-6 reindeer km⁻² the density of small shrubs decreased by
350 a factor of about 20 and their heights were on average halved. The browse trap was indicated
351 at higher reindeer densities (approximately >5-6 reindeer km⁻²), as there was no further
352 change in shrub density or height. In the migratory ranges, where reindeer are not browsing in
353 the summer, the small shrubs had the same range in heights and densities as in the summer
354 pastures with the lowest reindeer density (Figure 3). Notably, the height and density of the
355 small shrubs were not related to the temperature differences among the river valleys (Table 1,
356 Fig. S5). Small-stage shrubs were frequently present independent of altitudinal deviance from
357 the shrubline (Fig. 4), indicating a potential for transition to the tall-shrub stage and shrubland
358 in all the surveyed river valleys.

359 *Tall shrub stage*

360 The altitudinal shrubline increased with increasing mean summer temperature and was as
361 expected consistently lower where *Rangifer* browse in summer compared to migration areas.
362 The shrubline increased linearly on average by 101 m (95% CI = 65, 137) in altitude for each
363 1°C higher mean summer temperature, causing a major transition across the 4°C temperature
364 gradient of the study system (Fig. 5). The higher browsing impact in the summer ranges
365 amounted to an estimated altitudinal shrub line that was on average 104 m (95% CI = 40, 168)
366 lower altitude than in the migration ranges. The effect of *Rangifer* density on the shrubline
367 within the summer ranges was negative but not statistically significant (estimated slope = -
368 3.6, 95% CI = -12.4, 5.2).

369 **Discussion**

370 We found *Rangifer* management to represent an external mechanism (*sensu* Scheffer and
371 Carpenter 2003) that maintains riparian grasslands in a steady state across a 4°C gradient in
372 summer temperature. *Rangifer* populations managed at high densities appear to prevent
373 climate warming from pushing tundra into a shrubland state because the small life stages of
374 tall shrubs are kept in a “browse trap” (Staver and Bond 2014). In turn the browse trap
375 prevent altitudinal and latitudinal shrub lines from advancing, corresponding with the scenario
376 depicted in our conceptual framework (Fig. 1). Specifically, we found that the critical
377 browsing pressure exerted by *Rangifer* was achieved at herd densities above approximately 5
378 animals per km² and acted independently of summer temperature. This density threshold was
379 still within the lower range of *Rangifer* densities in Finnmark (ranging from 1.8 - 16.9
380 animals per km² during the study period). In management units with *Rangifer* densities below
381 the threshold we found small life stages of tall shrub species to increase in size and density,
382 indicating *Rangifer* managed at low densities cannot control the shift from grassland to
383 shrubland in a warmer climate. Thus riparian tundra may occur in two alternative states, or
384 attractors, in a warming climate (*sensu* Scheffer and Carpenter 2003) in response to variation
385 in managed *Rangifer* densities.

386 We found small-stage shrubs to be present across the entire temperature gradient reflecting
387 that our study region is currently situated within the climate envelope for *Salix* species that
388 have the potential to shift to a tall-stage (Walker et al. 2005). Within this range of 5 - 9°C in
389 summer temperatures we found *Rangifer* to control two distinct ways for small shrubs to
390 increase, i.e. in small shrub density and height, indicating the browse trap can be more than
391 just a control of height (cf. Staver and Bond 2014). In this respect our results contrast with a
392 recent study based on a mass-balance food-web modeling approach, which concluded that

393 herbivores do not regulate low-arctic tundra vegetation (Legagneux et al. 2014). For instance,
394 if regulation is specific to the small life stage of tall shrubs, herbivores can regulate a
395 vegetation state by consuming only a small proportion of the total shrub biomass production,
396 indicating that mass-balance approaches will be insensitive to such regulation. Indeed, for a
397 state variable to be a leading determinant of a state change it is beneficial that it is involved in
398 the temporal dynamics of the state transition (Bestelmeyer et al. 2011). In our study system,
399 the small life stages of the tall shrubs can be considered to be such leading determinants of the
400 focal ecosystem state shift, because the dynamics of these life stages are sensitive to both
401 herbivory and temperature.

402 Stands of tall shrubs can be old clonal structures (Forbes et al. 2010). Thus, the suppressed
403 altitudinal limit of the tall shrub state in the *Rangifer* summer ranges relative to the migration
404 ranges indicates that there have been browse traps during the last decades across all the
405 management units of the summer ranges. This is likely for two reasons. First, the geographic
406 gradients in summer temperatures as well as the contrast in browsing pressure between
407 migration and summer ranges (as determined by the migration behavior of *Rangifer*) are
408 likely to have persisted for centuries (Vorren 1962). Second, since 1950 *Rangifer* densities
409 have fluctuated below and above 5 animals km⁻² within several management units of
410 Finnmark (Tveraa et al. 2007, González et al. 2010), causing temporal variation in the
411 potential for shrubs to increase in abundance or be arrested in browse traps in most
412 management units across the summer ranges. Still, the impacts of both climate warming and
413 *Rangifer* management has been less intense in the past, when *Rangifer* numbers in the study
414 region were generally lower (González et al. 2010) and climate was colder (Førland et al.
415 2009). Hence, the current distribution of tall shrubs (i.e. the altitudinal shrubline) is likely to
416 reflect process rates at a time when the transition from grassland to shrubland was slower.
417 With the ongoing increase in temperatures there is reason to expect that processes are

418 speeding up and that even a few years of relaxed summer browsing pressure in the future may
419 trigger a rapid shift from riparian grasslands to shrublands (Marshall et al. 2014).

420 While our study suggests that *Rangifer* densities above 5 animals km⁻² keep grasslands in a
421 persistent browse trap over a wide range of temperatures, there are alternative trajectories for
422 how the grassland state may be a common state in riparian areas. First, there is a high
423 uncertainty to the future role of herbivores in the Arctic because the herbivores are themselves
424 directly impacted by climate change (Ims and Fuglei 2005, Vors and Boyce 2009). *Rangifer*
425 population densities are expected to decrease due to climate warming and may gradually be
426 replaced by even more effective browsers (Ims and Ehrich 2013). Indeed, more specialized
427 ungulate browsers (i.e. moose and red deer) are already increasing within the range of
428 *Rangifer* in Fennoscandia (Austrheim et al. 2011). Under a scenario of either continuously
429 high *Rangifer* densities above 5 animals km⁻² (that already seems to be the case within certain
430 management units of Finnmark, Bernes et al. 2015) or high densities of other ungulate
431 browsers, we might expect grasslands to be in a persistent browse trap. Second, grass cover
432 promoting fire is a mechanism for stability of the grassland state for several grassland systems
433 in the world (Ratajczak et al. 2014) and may become more frequent in the future also in the
434 Arctic (Ims and Ehrich 2013). Third, there may be other environmental constraints that limit
435 the growth response of small life-stages of *Salix* to changes in browsing pressure. For
436 instance, *Salix* growth may be limited by the local hydrological regime (Marshall et al. 2013,
437 Marshall et al. 2014), with significant impact on the ability of *Salix* to respond to a decrease
438 in browsing pressure. However, whereas such environmental constraints can be common and
439 of local importance, they were not confounded with *Rangifer* densities across the larger scale
440 of our study region (see also Bråthen et al. 2007, Bråthen and Ravolainen 2015).

441 A state shift to shrubland will affect tundra ecosystem functioning (Andersen et al. 2009)
442 beyond the climate feedbacks. For instance, tundra shrublands are habitat to numerous species
443 of birds (Roininen et al. 2005, Ims and Henden 2012, Henden et al. 2013), insects (Rich et al.
444 2013) and a diversity of other plants (at least when below 40 cm, Bråthen and Lortie 2016).
445 Also, whereas *Rangifer* management can prevent the state shift from grassland to shrubland
446 from occurring, high *Rangifer* densities affect herd productivity (Tveraa et al. 2007),
447 predation rate (Tveraa et al. 2014), may deplete lichen resources in the winter ranges
448 (Tømmervik et al. 2009, Bernes et al. 2015) and reduce the abundance of forbs in the summer
449 ranges (Bråthen et al. 2007, Bernes et al. 2015). Therefore, it seems *Rangifer* management
450 needs to strike a balance between the perceived positive and negative impacts of *Rangifer*
451 densities. In particular, management needs to consider enriching the ecosystem functioning of
452 riparian tundra by having the two states co-exist, as well as considering the associated climate
453 feedbacks and the livelihood of local resource-dependent people (Huntington 2013, Ims and
454 Ehrich 2013).

455 Currently there are predictions of a 50 % increase in the shrub state across the circumpolar
456 region (Pearson et al. 2013). These predictions are based on abiotic drivers alone. Our study
457 shows that *Rangifer* management in the warmest region of the Arctic (Callaghan et al. 2004)
458 currently can control this ecosystem transition, indicating the impact of large herbivores may
459 significantly reduce the magnitude of these predictions. Notably, our study region holds
460 among the highest densities of *Rangifer* in the world (Bernes et al. 2015), and the moderate
461 *Rangifer* densities at which we found the browse trap to act are still relatively high in a
462 circumpolar comparison. Furthermore, the capacity of herbivores to prevent shrub increase is
463 dependent on the palatability of the shrubs, where for instance non-palatable tall shrubs such
464 as species of *Alnus* gain abundance even in areas of higher browsing pressures (Christie et al.
465 2015). Such non-palatable tall shrubs were not present in our study system (Pan-Arctic Flora

466 <http://nhm2.uio.no/paf/>). Nevertheless, by targeting riparian tundra that contain high quality
467 habitats, and encompassing a wide range in animal densities and thus browsing pressure, we
468 expect our results to be of relevance to other circumpolar regions where *Rangifer* are
469 managed through herding or hunting (Huntington 2013). Being the first study to demonstrate
470 how management can control a climate-sensitive ecosystem state shift in arctic tundra (cf. Ims
471 and Ehrich 2013), we also provide a case for how appropriate quasi-experimental designs can
472 be applied in studies in other terrestrial biomes with the purpose of assessing the relative
473 importance of climate change and managed large herbivores as drivers of ecosystem state
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743 **Table 1.** Parameter estimates and AIC values for different models for the effect of being in a
744 summer range (in contrast to the migration range), *Rangifer* density and average summer
745 temperature on the density and the height of small-stage shrubs. The estimates were obtained
746 using a negative binomial GLMM with a log link function (density) and a linear mixed effects
747 models and log transformed *Rangifer* density (height), both with sampling line nested within
748 river valley as random effects. Parameter estimates that differ significantly from zero
749 (P<0.05) are given in bold.

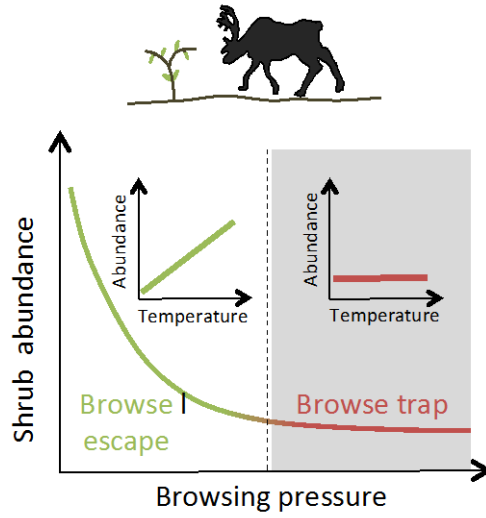
Model	Intercept	Summer range	<i>Rangifer</i> density	Temperature	AIC
Density of small-stage shrubs					
1	2.84 (3.49)	-1.21 (0.84)		-0.06 (0.48)	4042
2	2.46 (0.48)	0.69 (0.75)	-0.24 (0.06)		4032
3	-1.45 (2.47)	1.30 (0.79)	-0.28 (0.06)	0.55 (0.34)	4032
Height of small-stage shrubs					
1	29.6 (17.7)	-14.8 (4.5)		0.4 (2.8)	2718
2	13.3 (13.6)	19.3 (13.6)	-8.1 (3.1)		2711
3	1.1 (19.9)	21.8 (14.9)	-8.8 (3.5)	1.7 (2.5)	2712

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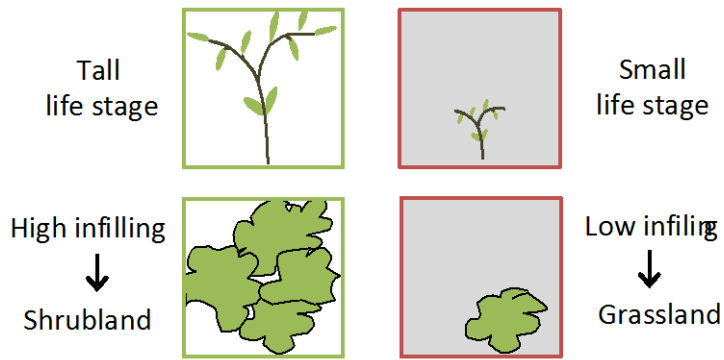
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752 **Figure 1.** A conceptual framework predicting how population density of a large herbivore can
753 influence a climate sensitive state shift from grassland to a shrubland state and in consequence
754 cause an advancing shrubline. The large herbivore density is assumed proportional to the
755 browsing pressure on palatable shrubs. **(a)** In grasslands, large herbivores readily browse
756 small life stages of palatable shrubs (saplings or small ramets) that are within their physical
757 foraging range. The abundance of small stage shrubs (i.e. their heights and/or density)
758 decreases non-linearly with browsing intensity (cf. Helgeland and Rydeng 2016) so that the
759 shrubs are kept in a browse trap independently of summer temperature when the browsing
760 pressure (and animal density) is high. At lower browsing pressures and in a warming climate
761 the small shrubs will escape the browse trap and grow into a tall life stage. In consequence,
762 shrub increase promoted by climate warming (Elmendorf et al. 2012), is only occurring in the
763 context of a low browsing pressure, i.e. for shrubs that are not in a browse trap. Overall these
764 scenarios give rise to two alternative states, either shifting towards a tall shrub state
765 (shrubland) or continuing in a grassland state **(b)**. In response to increasing temperature small
766 shrubs can grow taller. Small shrubs can also increase their shoot density, ultimately
767 determining the infilling potential of the shrubs in taking over the grassland. The temperature
768 response finally causes a state shift. **(c)** A state shift will eventually cause shrublands to
769 expand into higher latitudes and altitudes, and advance the shrubline. Such shrub increase is
770 not possible for small shrubs caught in a browse trap as they are parts of persisting grassland
771 with an arrested shrubline. The framework builds on a conceptual model of shrub increase (cf.
772 Tape et al. 2006, Myers-Smith et al. 2011b) and the concept of the browse trap (cf. Staver and
773 Bond 2014).
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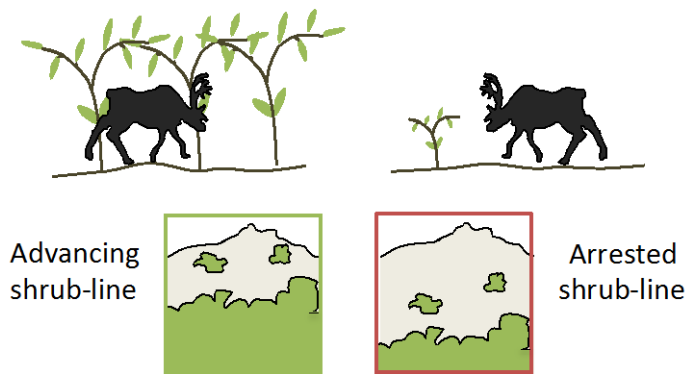
(a) BROWSING PRESSURE REGULATES POTENTIAL STATE SHIFT



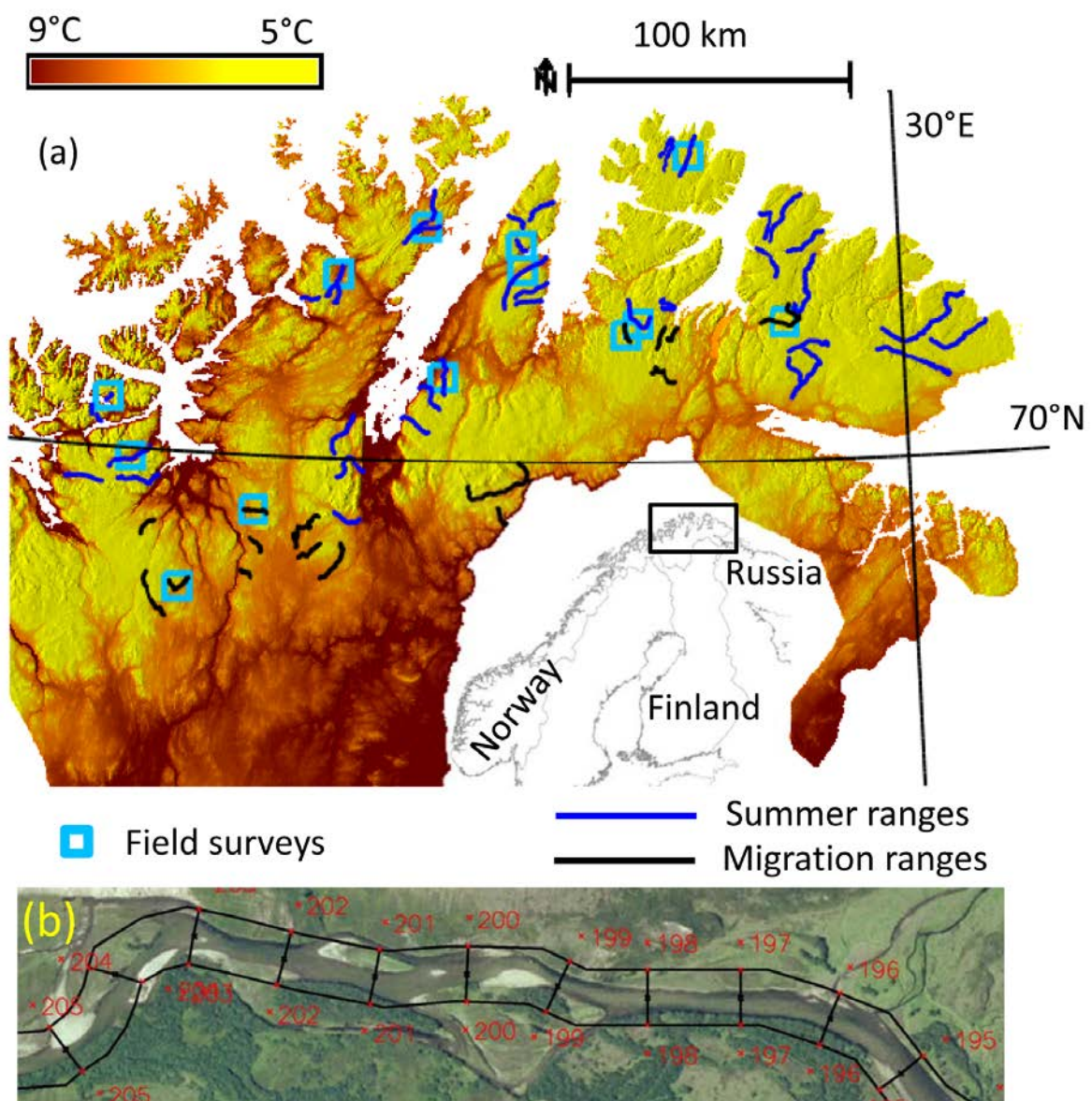
(b) STATE SHIFT NO STATE SHIFT



(c) SHRUBLAND STATE GRASSLAND STATE

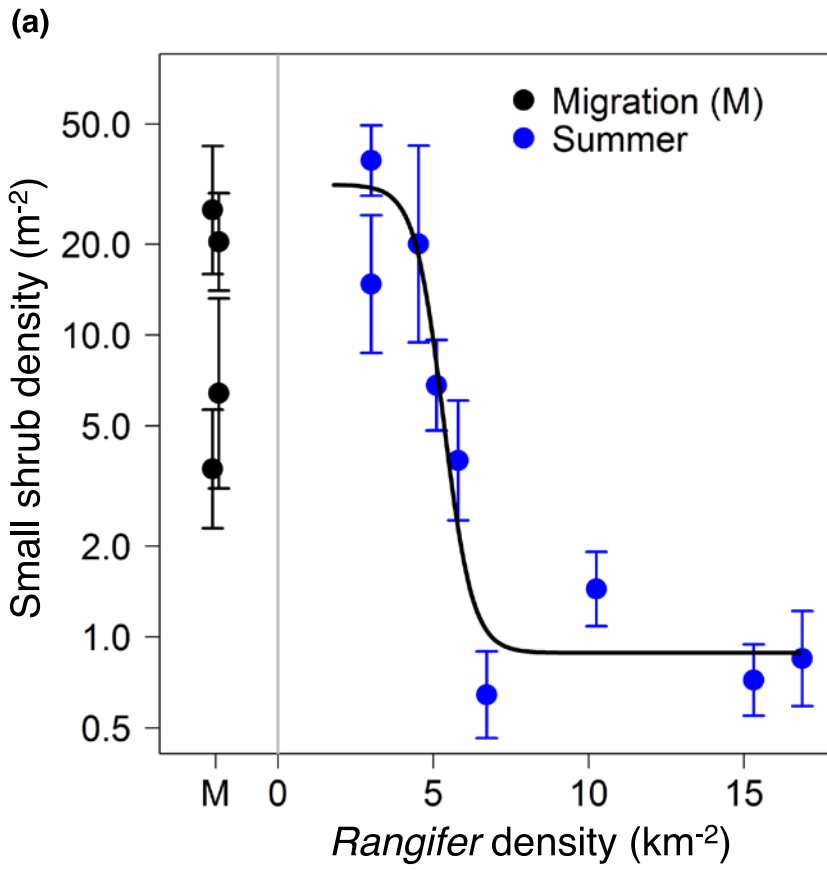


776 **Figure 2.** Study design. (a) Finnmark is partly mountainous, with peaks up to 1200 m asl in
 777 its western part and 500 m asl in its eastern part causing temperature variations across the
 778 whole region. River valleys in *Rangifer* summer ranges (blue lines) or in migration ranges
 779 (black lines) were sampled for variables describing the shrubland state (all rivers) and the
 780 grassland state (field surveys depicted with blue squares). (b) Data collection of target
 781 vegetation states was carried out along sampling lines perpendicular to the river course for
 782 each 100 m down the river.

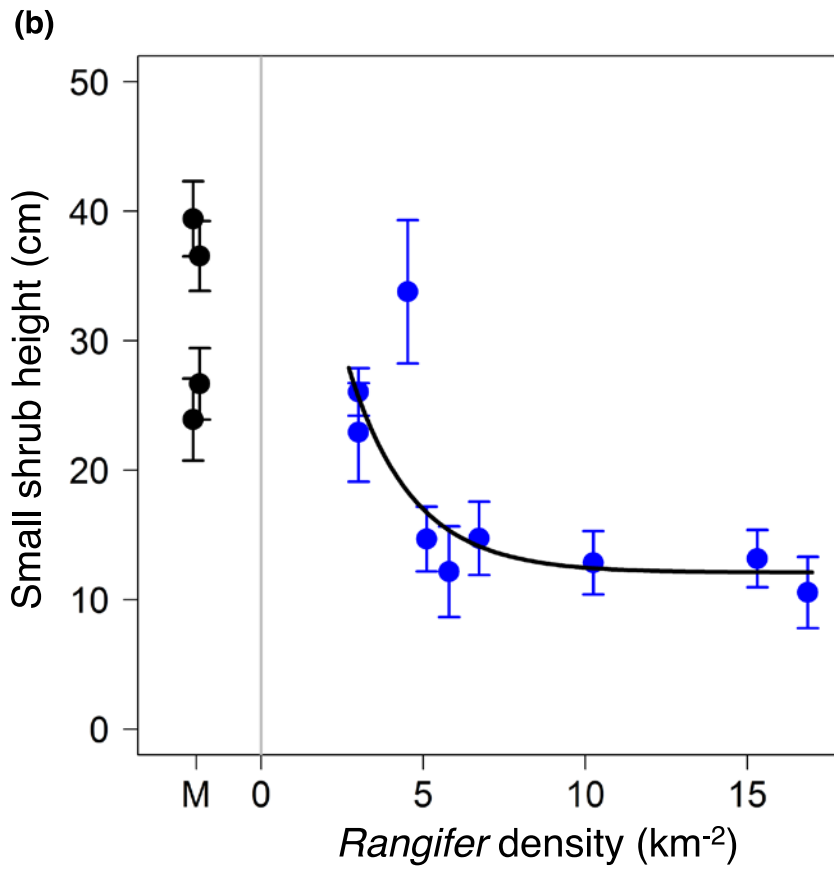


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784 **Figure 3.** The average (± 1 SE) **(a)** small shrub density (m^{-2}) and **(b)** small shrub height (cm)
785 estimated for river valleys in *Rangifer* summer ranges (n=9) and migration ranges (M, n=4)
786 included in the field surveys (light blue polygons in Figure 2a). Non-linear regression lines
787 indicate the relationship between small shrub performance and *Rangifer* density in the
788 summer ranges (regression equations for **(a)** small shrub density in summer ranges = $\beta_1 + (\beta_2 -$
789 $\beta_1) / (1 + \exp((\beta_3 - \text{Rangifer density}) / \beta_4))$, with $\beta_1 = 3.45$, SE = 0.36, $\beta_2 = -0.12$, SE = 0.23, $\beta_3 =$
790 5.32 , SE = 0.26, $\beta_4 = 0.46$, SE = 0.27; and for **(b)** small shrub height in summer ranges = $\beta_1 +$
791 $(\beta_2 - \beta_1) * \exp(-\exp(\beta_3) * \text{Rangifer density})$, with $\beta_1 = 12.1$, SE = 2.0, $\beta_2 = 74.7$, SE = 56.4, $\beta_3 = -$
792 0.67 , SE = 0.59).

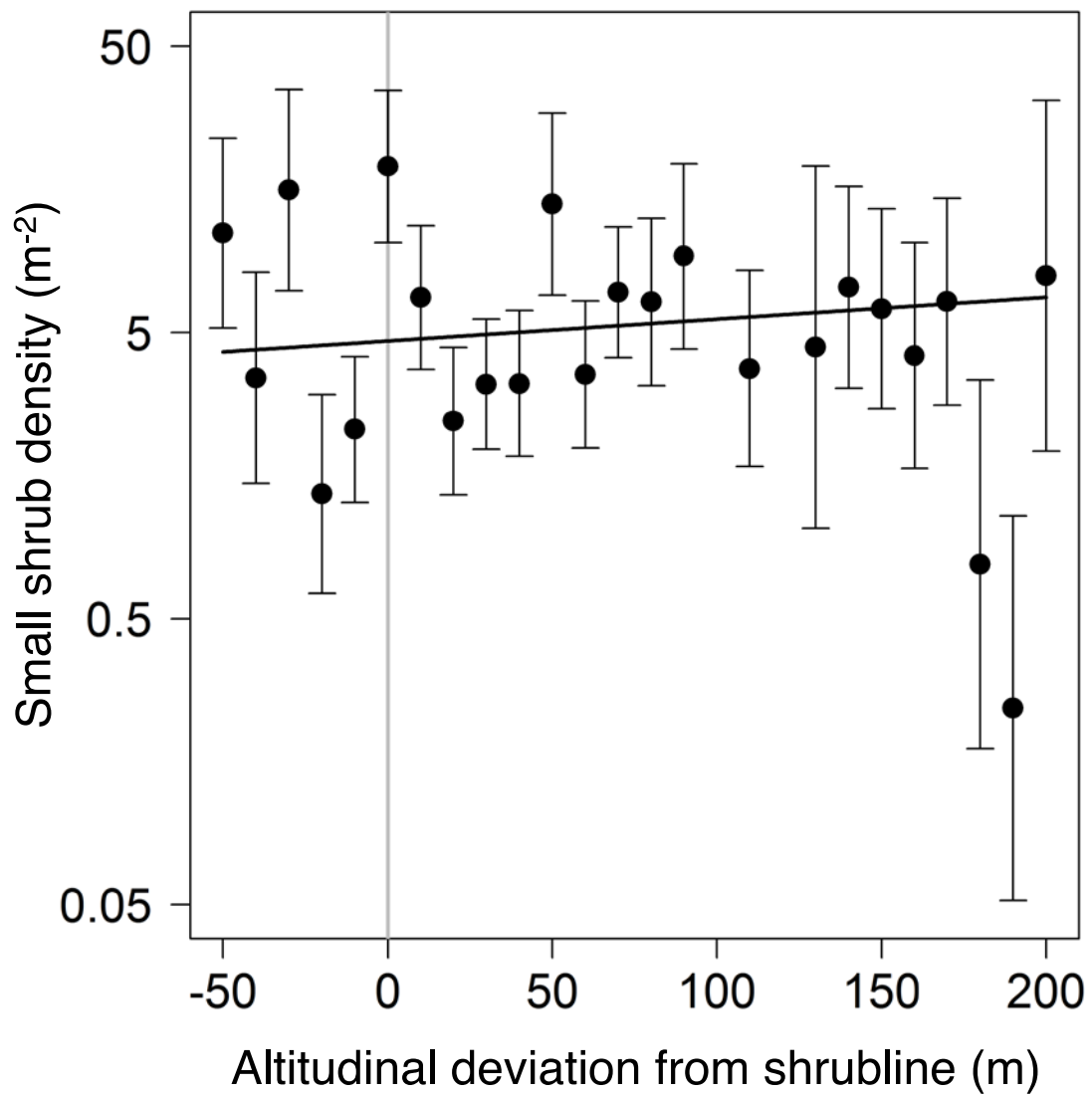


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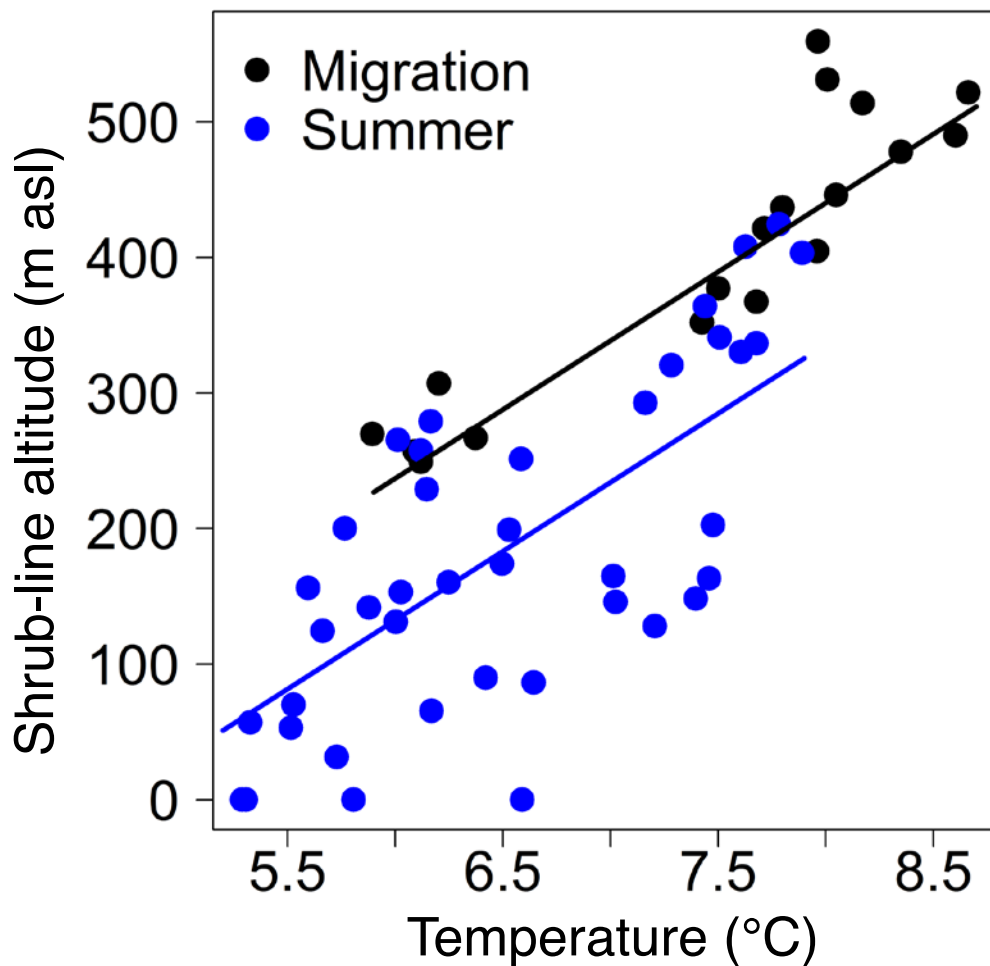
795 **Figure 4.** Average small-stage shrub densities (± 1 SE) in riparian grasslands plotted against
796 the deviance between the altitude of sampling lines along river valleys and the estimated
797 shrubline. The small-stage shrub density was modelled using a log linear model. The
798 regression line is given by $y = \exp(\beta_0 + \beta_1 * x)$, with $\beta_0 = 1.54$ (95% CI = [0.70, 2.38]) and $\beta_1 =$
799 0.0018 (95% CI = [-0.0040, 0.0076]).



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802 **Figure 5.** The altitudinal shrubline of the shrubland state was estimated for each sampled
803 river valley (points), from records of stands of tall willow (*Salix*) shrubs along the sampling
804 lines using aerial photographs. The regression lines indicate the average pattern of variation in
805 the shrubline with temperature for the *Rangifer* summer (n = 40, blue line and points) and
806 migration ranges (n = 18, black line and points) (shrubline = $-372 (\pm 134) + 102 (\pm 18) *$
807 temperature - $104 (\pm 32) * \text{summer range}$, with ± 1 SE of estimates given in brackets).
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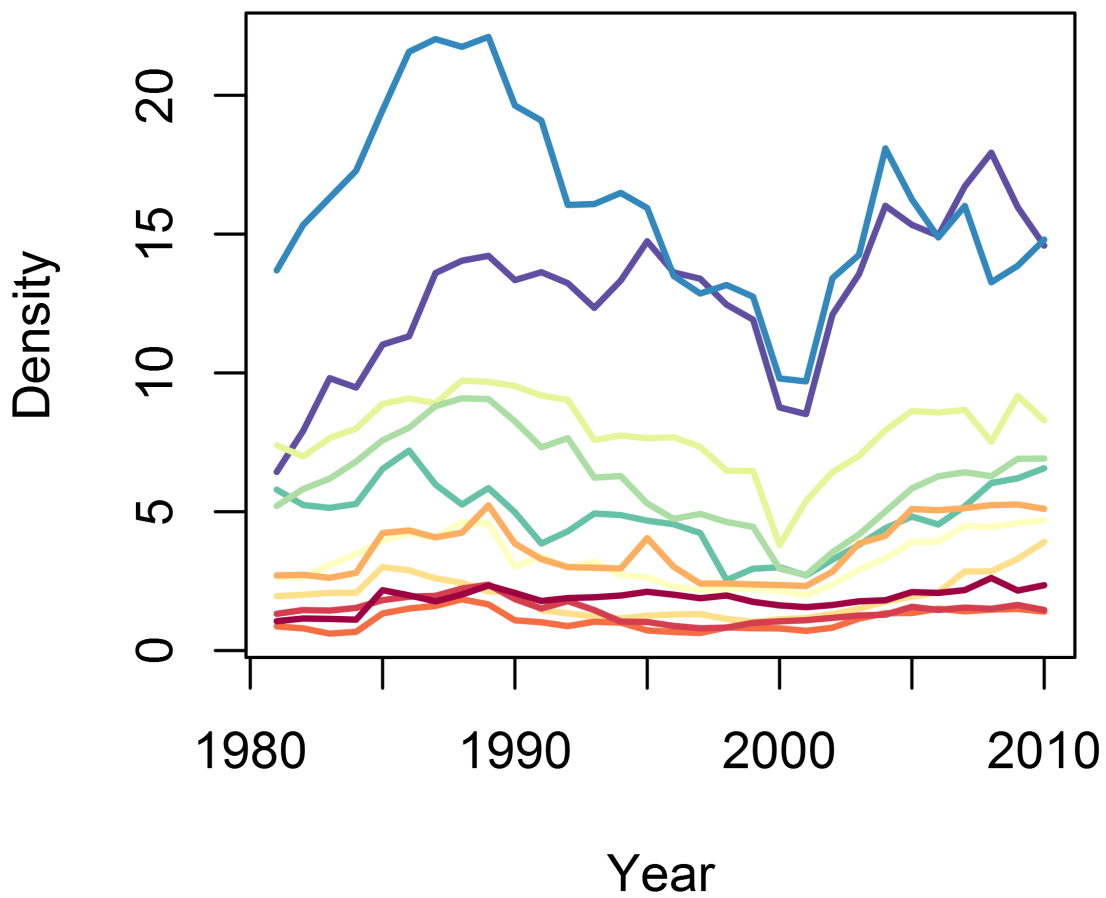
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1 **Supplementary Information**

2 **Figure 1S.** *Rangifer* densities per *Rangifer* management unit (animals per km²) at the summer
3 ranges included in this study. *Rangifer* densities show temporal variability over the three
4 decades preceding our survey (a). Average *Rangifer* densities over these decades correlate
5 strongly with those measured over the last three years preceding our survey (b), indicating a
6 consistency between the *Rangifer* management units in their managed animal densities.

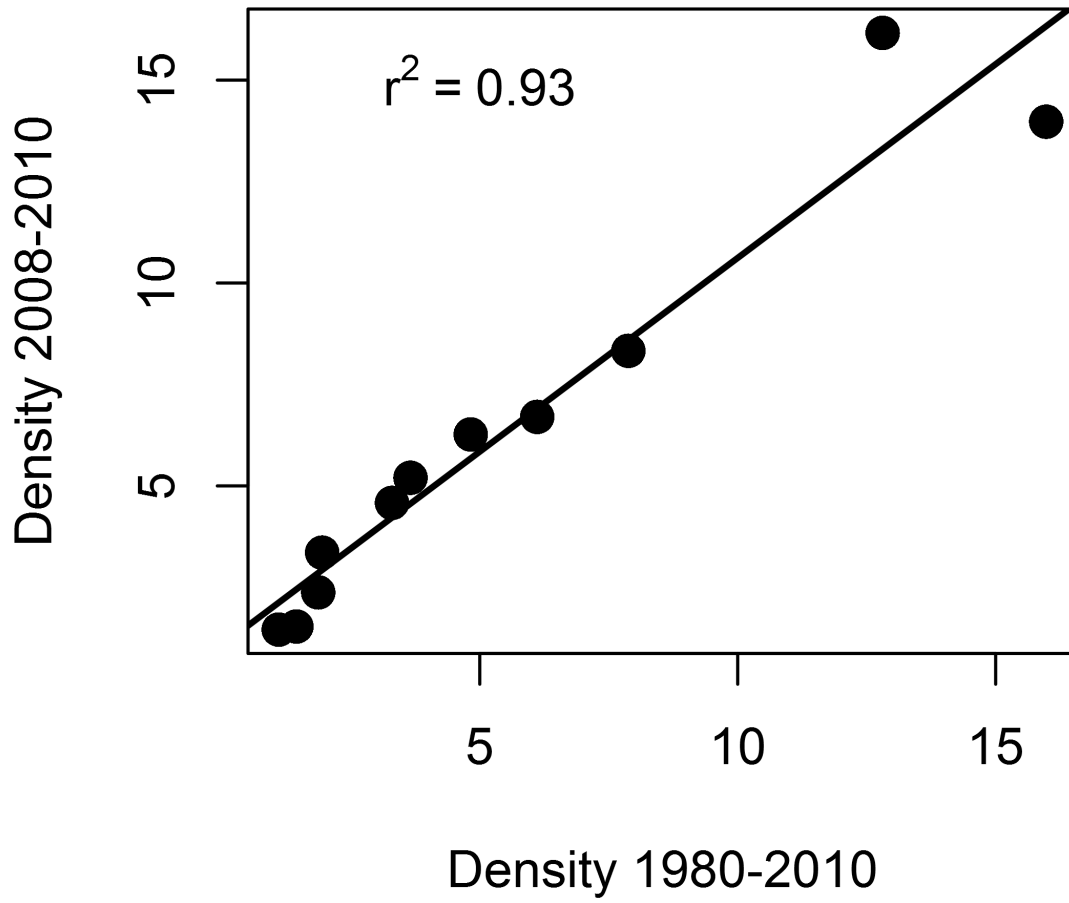
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8 (a)



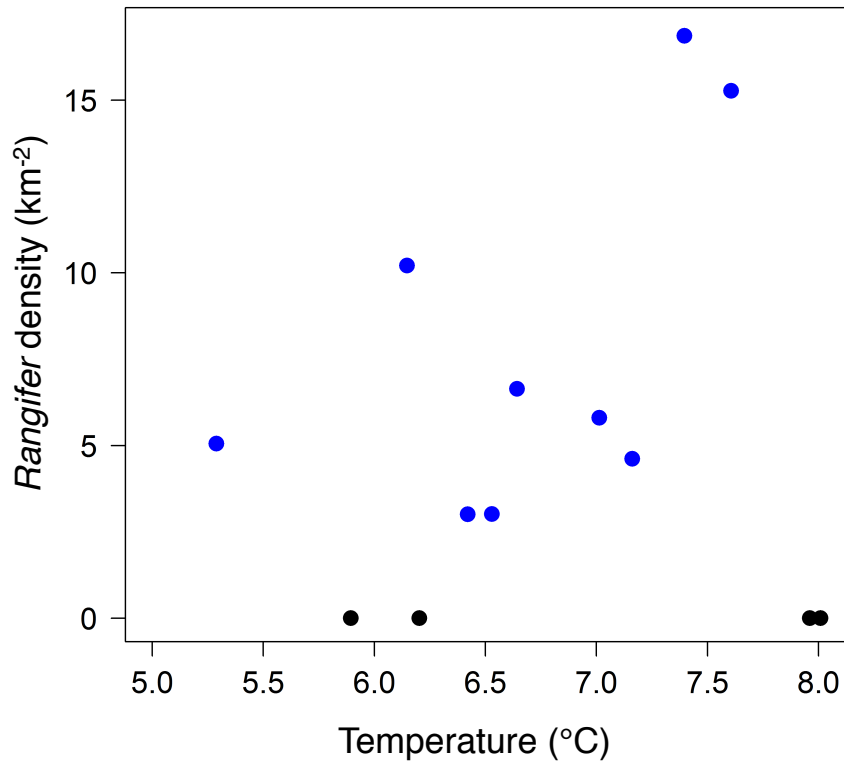
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11 (b)



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14 **Figure S2.** The estimated average summer temperature at 200 m asl for the river valleys
15 selected for the survey of small-stage shrubs, plotted against *Rangifer* density for river valleys
16 within the summer ranges (blue), and plotted along the x-axis (*Rangifer* density = 0) for river
17 valleys in the migration ranges (black).



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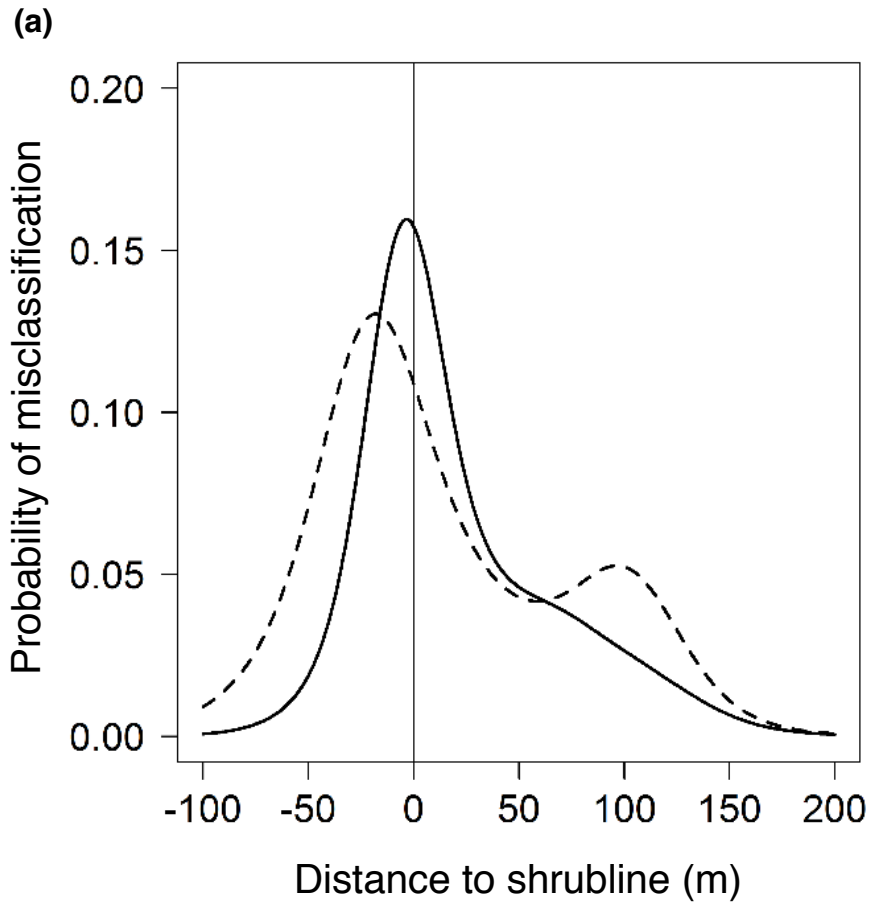
20 **Appendix**

21 *Validation of shrub mapping from photographs*

22 To validate the accuracy of the presence/absence records of tall shrubs mapped from the
23 photographs, matching field data on tall shrubs (>50 cm height) obtained from 675 survey
24 lines was compared to the photography classification of the same lines. In the field, 509 lines
25 were classified as not having tall shrubs of which 44 were classified as having shrubs using
26 the photographs (discrepancy = 8.6 %). In the field 166 lines were found to have tall shrubs,
27 whereas in the analysis of the photographs 44 were classified as not having shrubs
28 (discrepancy = 26.5 %). There was a clear peak in discrepancy around the estimated shrubline
29 (Fig. S2a) and at sites where there were a low number of tall shrubs along the line (Fig S2b).

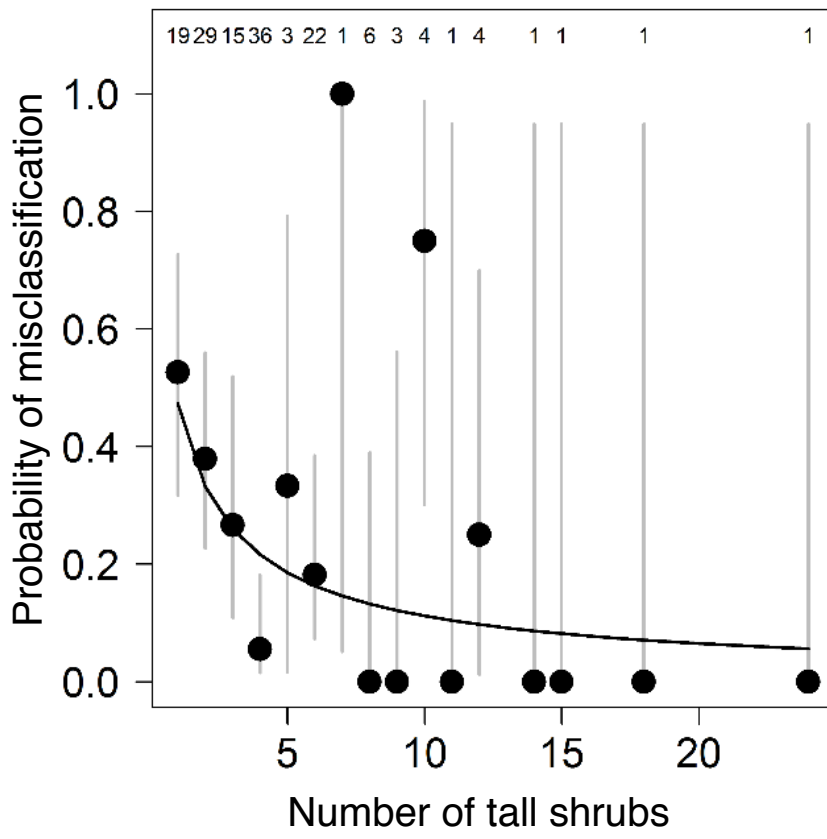
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31 **Figure S3.** Patterns in the misclassification of tall shrub presence in photographs as compared
32 with observed presence in the field. **(a)** The distribution of misclassification probabilities in
33 relation to the estimated shrubline as estimated by a smoothing spline fit to observed patterns
34 of misclassification. The dotted line gives the error distribution for the presence of tall shrubs
35 and the full line the error distribution for the absence of tall shrubs. **(b)** The probability of
36 misclassification of tall shrub presence in photographs in relation to the number of tall shrubs
37 found along the transect lines in the field (\pm 95% CI). Sample sizes are given along the top of
38 the figure. The logistic regression line is given by: $\text{logit}(\text{misclassification probability}) = -0.11$
39 $(\pm 0.36) - 0.85 (\pm 0.29) * \log(\text{number of shrubs}) (\pm 1 \text{ SE})$.



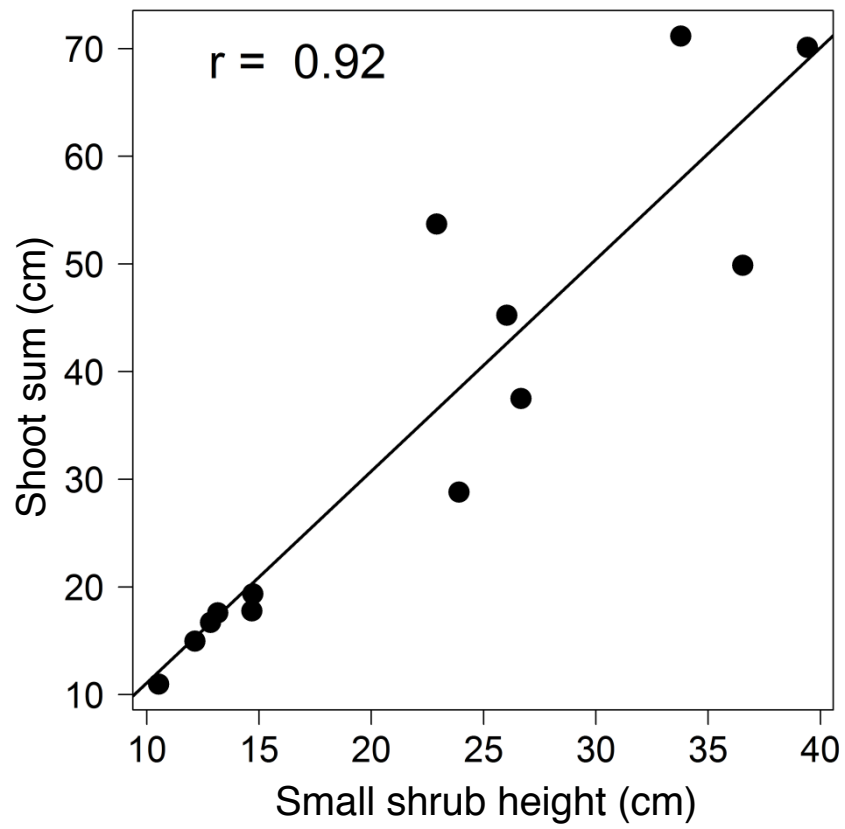
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(b)



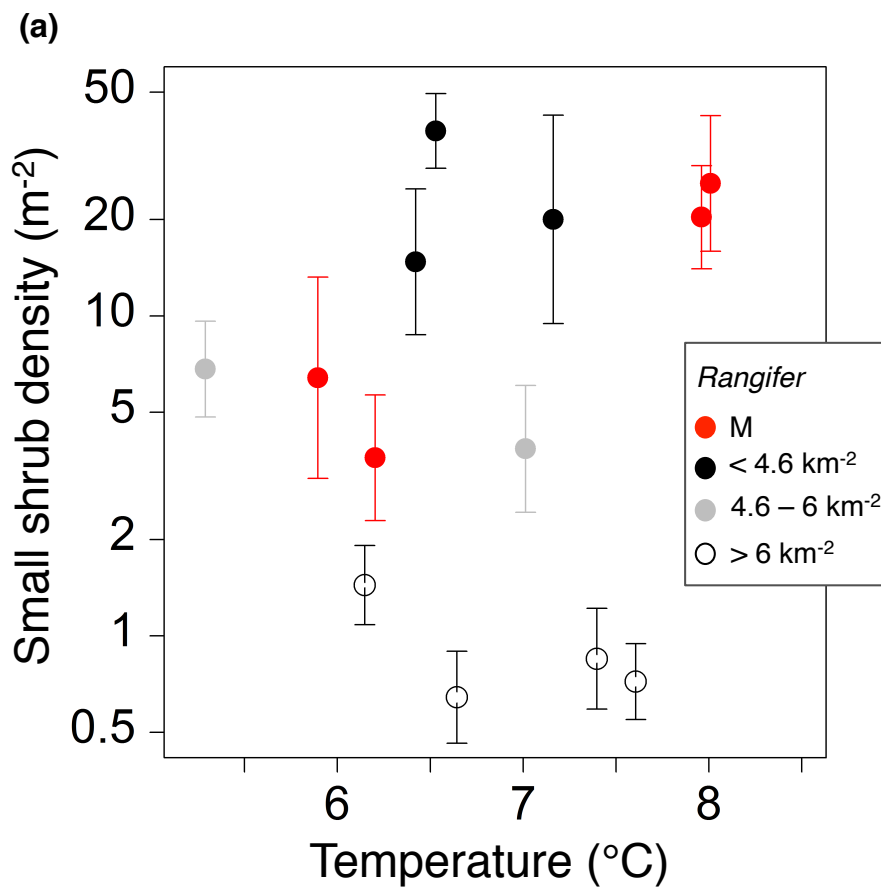
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43 **Figure S4.** Correlation between the height and the sum of all shoots (stem and branches) of
44 small-stage shrubs. Points represent the river valley specific estimates based on field
45 measurements.

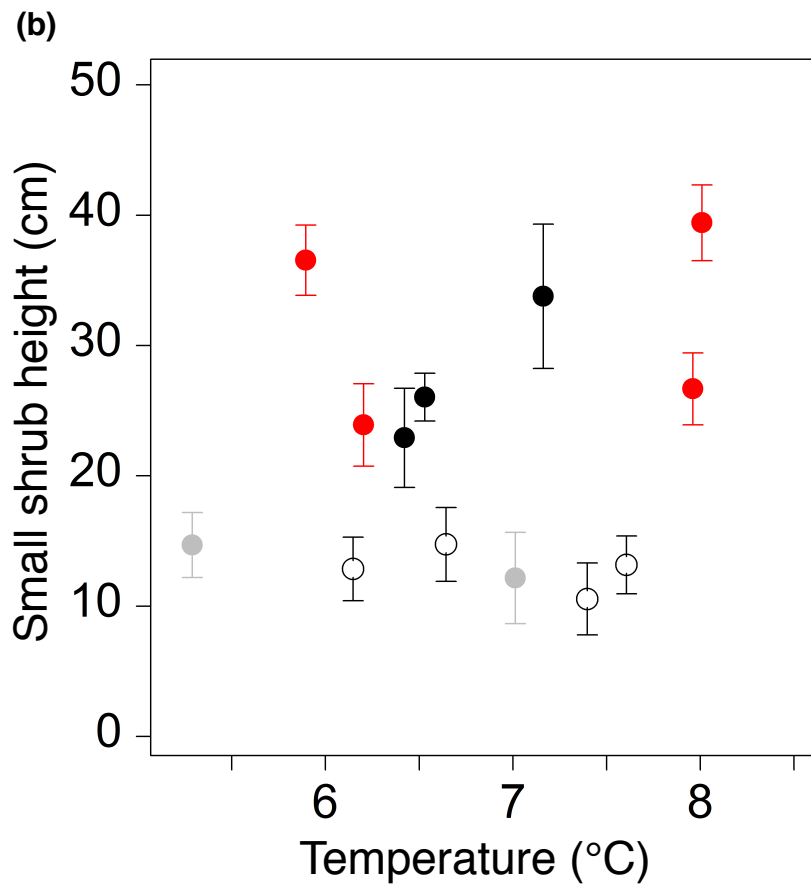


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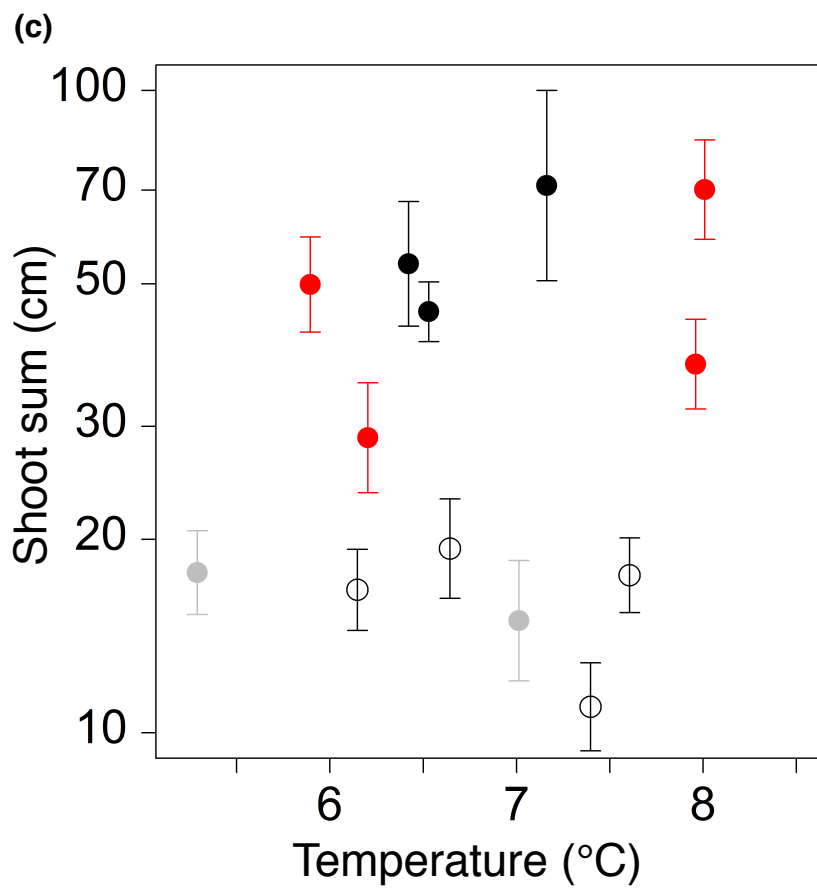
47 **Figure S5.** River specific estimates (± 1 SE) of (a) small-stage shrub densities, (b) height of
48 small shrubs, and (c) shoot sum of small shrubs, each plotted against average summer
49 temperature. The symbols distinguish between rivers in the migration (no browsing during
50 summer, red circles) and summer ranges with low reindeer densities (< 4.6 *Rangifer* km^{-2} ,
51 black circles), medium *Rangifer* densities (4.6 - 6 *Rangifer* km^{-2} , gray circles) and high
52 densities (>6 *Rangifer* km^{-2} , open circles).



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