



HAL
open science

Geochemical landscapes as drivers of wildlife reproductive success: insights from a high-Arctic ecosystem

Floris M. van Beest, Niels Martin Schmidt, Lærke Stewart, Lars H. Hansen, Anders Michelsen, Jesper Mosbacher, Hugo Gilbert, Gaël Le Roux, Sophia V. Hansson

► To cite this version:

Floris M. van Beest, Niels Martin Schmidt, Lærke Stewart, Lars H. Hansen, Anders Michelsen, et al.. Geochemical landscapes as drivers of wildlife reproductive success: insights from a high-Arctic ecosystem. *Science of the Total Environment*, 2023, 903, pp.166567. 10.1016/j.scitotenv.2023.166567 . hal-04246451

HAL Id: hal-04246451

<https://hal.science/hal-04246451>

Submitted on 17 Oct 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

1 **Geochemical landscapes as drivers of wildlife reproductive success:**
2 **insights from a high-Arctic ecosystem**

3
4 Floris M. van Beest^{a,b,*}, Niels Martin Schmidt^{a,b}, Lærke Stewart^c, Lars H. Hansen^{a,b}, Anders
5 Michelsen^d, Jesper B. Mosbacher^e, Hugo Gilbert^f, Gaël Le Roux^f, Sophia V. Hansson,^{a,f}

6
7 ^a Department of Ecoscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark

8 ^b Arctic Research Centre, Aarhus University, Ny Munkegade 116, 8000 Aarhus C, Denmark

9 ^c Department of Natural Sciences and Environmental Health, University of South-Eastern

10 Norway, Gullbringvegen 36, 3800 Bø, Norway

11 ^d Department of Biology, University of Copenhagen, Universitetsparken 15, 2100

12 Copenhagen, Denmark

13 ^e Norwegian Polar Institute, Framsenteret, 9296 Tromsø, Norway

14 ^f Laboratoire Ecologie Fonctionnelle et Environnement (UMR- 5245), CNRS, Université de

15 Toulouse, Avenue de l'Agrobiopole, 31326 Castanet Tolosan, France

16

17 **Abstract**

18 The bioavailability of essential and non-essential elements in vegetation is expected to
19 influence the performance of free-ranging terrestrial herbivores. However, attempts to relate
20 the use of geochemical landscapes by animal populations directly to reproductive output are
21 currently lacking. Here we measured concentrations of 14 essential and non-essential
22 elements in soil and vegetation samples collected in the Zackenberg valley, northeast
23 Greenland, and linked these to environmental conditions to spatially predict and map
24 geochemical landscapes. We then used long-term (1996-2021) survey data of muskoxen
25 (*Ovibos moschatus*) to quantify annual variation in the relative use of essential and non-
26 essential elements in vegetated sites and their relationship to calf recruitment the following
27 year. Results showed that the relative use of the geochemical landscape by muskoxen varied
28 substantially between years and differed among elements. Selection for vegetated sites with
29 higher levels of the essential elements N, Cu, Se, and Mo was positively linked to annual calf
30 recruitment. In contrast, selection for vegetated sites with higher concentrations of the non-
31 essential elements As and Pb was negatively correlated to annual calf recruitment. Based on
32 the concentrations measured in our study, we found no apparent associations between annual
33 calf recruitment and levels of C, Mn, Co, Zn, Cd, Ba, Hg, and C:N ratio in the vegetation. We
34 conclude that the spatial distribution and access to essential and non-essential (trace)
35 elements are important drivers of reproductive output in muskoxen, which may also apply to
36 other wildlife populations. The value of geochemical landscapes to assess habitat-
37 performance relationships is likely to increase under future environmental change.

38

39 **Keywords:** Arctic, Ecogeochemistry, Herbivores, Plant quality, Zoogeochemistry

40

41

42 **1. Introduction**

43 How free-ranging animals exploit the spatial and temporal variability in habitat and
44 resources available to them can have important implications for their survival and
45 reproduction (e.g., McLoughlin et al., 2007). Quantifying and understanding so called
46 habitat-performance relationships (Gaillard et al., 2010; Matthiopoulos et al., 2015) is critical
47 for a range of topics in environmental management including assessments of climate and
48 land-use change impacts (Verniest et al., 2022). Habitat-performance relationships can be
49 estimated by linking differences in animal performance to variation in use of resource
50 abundance or quality (Felton et al., 2020; Ofstad et al., 2020). The quality of forage resources
51 is, however, often loosely characterized e.g., by assuming a direct relationship between
52 consumer density and prey abundance (in the case of carnivores: Mosser et al., 2009) or by
53 measuring digestibility of plant material (in the case of herbivores: Proffitt et al., 2016). The
54 elemental composition of forage resources is rarely considered explicitly when estimating
55 habitat-performance relationships. This is surprising given that the quality of forage resources
56 is multidimensional and complex, and animals must balance and regulate the intake of
57 multiple essential and non-essential elements to optimize maintenance, growth, and
58 reproduction (Boersma and Elser, 2006; Sperfeld et al., 2017).

59 The fields of ecogeochemistry and ecological stoichiometry have made great progress
60 in understanding how different biochemical markers relate to the health status of animals as
61 well as ecosystem structure and stability (Elser, 2006; Trueman et al., 2016). Indeed, it is now
62 well established that a balanced intake of macro elements such as nitrogen (N) and
63 phosphorus (P) can positively affect growth (Plath and Boersma, 2001) and reproduction
64 (Durso et al., 2020) of different animal species. Similarly, micro elements i.e., elements
65 required in trace amounts for normal physiological function such as copper (Cu), selenium
66 (Se), and zinc (Zn), are critical to many biochemical pathways and thus considered essential

67 to life in most organisms (Feinberg et al., 2021; Kaspari and Powers, 2016). Adverse effects
68 may arise, however, if homeostasis is disrupted i.e., when reserves of essential elements are
69 outside required physiological ranges (Bhattacharya et al., 2016; Kabata-Pendias and Szteke,
70 2015). In addition, some trace elements, such as arsenic (As), cadmium (Cd), lead (Pb), and
71 mercury (Hg) hold no physiological function and can suppress individual health already at
72 low concentration thresholds (Burger, 2008; Massányi et al., 2020).

73 A range of processes such as weathering and atmospheric deposition combined with
74 gradients in climatic conditions and anthropogenic disturbance can cause substantial
75 heterogeneity in the bioavailability of chemical elements in natural environments (Brown et
76 al., 1999). For terrestrial herbivores, the intake of essential and non-essential elements is
77 primarily influenced by their bioavailability in vegetation, the underlying soils, and plant-
78 specific uptake rates. Thus, the way terrestrial herbivores use habitat and forage resources
79 within the heterogenous geochemical landscapes they occupy should influence the health and
80 performance of individual animals and, subsequently, population dynamics (Flueck, 1994;
81 French et al., 2017). While assessments of elemental status in free-ranging herbivores and the
82 linkages to wildlife health are rapidly increasing (Jutha et al., 2022; Mosbacher et al., 2022;
83 Rioux et al., 2022; Squadrone et al., 2022), the importance of the underlying mechanism,
84 namely variability in consumer habitat or resource use, is rarely considered. In fact, only few
85 studies have investigated how consumers' habitat use varies as a function of the
86 bioavailability of chemical elements across natural landscapes (Balluffi-Fry et al., 2020;
87 Leroux et al., 2017; Rizzuto et al., 2021; Sach et al., 2020) though the potential consequences
88 for individual or population-level performance were not quantified.

89 Our objective was to assess if spatiotemporal variation in the use of forage resources
90 within multidimensional geochemical landscapes is an important factor in habitat-
91 performance relationships of wildlife. Specifically, and using the largest herbivore roaming

92 the Arctic tundra, the muskox (*Ovibos moschatus*) as a study organism, we quantified and
93 mapped the distribution of 14 essential and non-essential elements in soils and vegetation
94 across the Zackenberg valley in northeast Greenland. We then employed long-term location
95 and demography time series of muskoxen to estimate the relative use of forage resources with
96 divergent elemental concentrations and potential linkages to annual variation in calf
97 recruitment. Given their importance in physiological function, we expected the relative use of
98 vegetated sites with increased levels of essential elements to positively correlate with annual
99 calf recruitment (Hypothesis 1), especially for trace elements Se and Cu as deficiencies of
100 these elements are known to limit reproductive success of muskoxen (Mosbacher et al., 2022;
101 Rombach et al., 2002) and other herbivores (Flueck et al., 2012; Michaluk and Kochman,
102 2007). In contrast, we expected the relative use of vegetated sites with increased
103 concentrations of contaminants (e.g., As, Cd, Hg, Pb) to have a negative effect on annual calf
104 recruitment (Hypothesis 2).

105

106 **2. Material and Methods**

107

108 *2.1 Study area*

109 All data presented here were collected in the Zackenberg valley, northeast Greenland
110 (74°28 N, 21°33 W; Fig. 1). The climate in the region is high-Arctic with a mean annual
111 ambient temperature of ca. -9°C, peaking in July with a mean of 6°C and lowest in
112 February/March with a mean of -20°C. The elevational gradient in the valley ranges from
113 sea-level to 1200m on surrounding hilltops with steep slopes (>20°) in some areas.
114 Geomorphological landforms in the valley include exposed bedrock, alluvial, fluvial and
115 glacial landforms (Cable et al., 2018). Soil water content ranges from dry conditions at
116 hilltops to wet conditions in the lower valley. Soils are dominated by non-calcareous sandy

117 sediments and are slightly acidic to neutral (pH range 5.0–7.2), with pH generally increasing
118 with soil depth (Elberling et al., 2008). Barren areas or poorly vegetated sites are common
119 above 600m in elevation, while the rest of the valley is mainly covered by a mosaic of tundra
120 vegetation types of varying productivity including *Cassiope* and *Dryas* heath, fen, grassland
121 and *Salix* snowbed (Elberling et al., 2008; Stewart et al., 2018). The growing season typically
122 extends from early June to late August and snow typically covers the ground from October to
123 May, though interannual variation in snow accumulation and duration is considerable
124 (Pedersen et al., 2016). Muskoxen are the only large herbivores in northeast Greenland and
125 are surveyed every summer (Jul-Aug) in Zackenberg valley with densities ranging between
126 0.5 and 3.0 individuals km⁻² since 1996 (Schmidt et al., 2015). The impacts of human
127 disturbance and predation by Arctic wolves (*Canis lupus arctos*) and polar bears (*Ursus*
128 *maritimus*) on muskox calf recruitment are considered negligible in this area (Schmidt et al.,
129 2015). Muskoxen at Zackenberg do exhibit anti-predator behaviors, such as forming
130 defensive circles, but this occurs at such low frequency and of such short duration that it is
131 unlikely to bias habitat use estimates.

132

133 2.2 Soil and vegetation sampling

134 Between 22–30 of July 2021, soil and plant material were collected from within 50
135 permanent field plots (Fig 1) that are part of a tundra vegetation monitoring study in the
136 Zackenberg valley (Stewart et al., 2018). Field plots were selected (from a total of 200 plots)
137 using a random stratified sampling approach to obtain balanced samples of material across
138 the elevation gradient (0–600m) and the five dominant vegetation types in the valley
139 (*Cassiope* and *Dryas* heath, fen, grassland, and *Salix* snowbed). In each field plot, samples of
140 the dominant plant species or, in case of fen and grassland, functional group (graminoids)
141 were collected (leaves and stems, no roots) using nitrile gloves. All vegetation was collected

142 by mimicking muskox grazing i.e., grabbing and pulling a handful of plant material. Plant
143 material (min. ~2g wet weight) was subsequently transferred into paper bags. Soil was
144 collected in each plot by mixing and homogenizing three sub-samples from the A-horizon
145 (i.e., the upper 0–10 cm layer) using nitrile gloves and a pre-cleaned stainless-steel garden
146 shovel. Soil material (~10g wet weight) was transferred into polyethylene zip-lock bags.
147 Fourteen of the 50 field plots were sampled more intensively by collecting three soil samples
148 and three plant samples from within 1 m² to assess and incorporate plot-based variability in
149 element concentrations. In total, 78 soil samples and 78 plant samples were collected from
150 within the field plots. All soil and plant material were stored frozen until sample processing
151 and chemical analyses.

152

153 *2.3 Sample processing and chemical analyses*

154 Soil samples were dried in an oven at 35°C for 5 days under constant air flow. While
155 we acknowledge that oven drying is not the ideal method, doing so was necessary due to
156 logistical constraints in the field. However, oven-drying soil samples at low temperatures
157 limits the loss of volatile elements (Roos-Barracough et al., 2002). Once dried, soil samples
158 were sieved through a 200µm nylon mesh to separate soil particles from small gravel and
159 organic matter such as root fragments. Compact samples were manually ground beforehand
160 with an agate mortar. Between each sample, all sieving material (mesh, container, mortar)
161 was rinsed twice, first with regular tap water, then with mQ H₂O (18.2 MΩ cm⁻¹) and finally
162 disinfected with 70% ethanol. Vegetation samples were lyophilized using a Christ Alpha 1–2
163 freeze-drier and ground using a laboratory mill Retsch® Mixer MILL MM 400, at 30Hz for
164 120s. All material was cleaned between each sample, i.e., rinsed under tap water then rinsed
165 with mQ H₂O and finally disinfected with 70% ethanol.

166 For wet chemistry digestion of both vegetation and soil samples, approximately
167 150mg of dried and ground sample was placed in pre-cleaned (2% HNO₃ and mQ H₂O)
168 50mL digitubes to which 3mL of ultrapure HNO₃ (Fisher Chemical, Nitric Acid HNO₃,
169 Optima Grade, 67-69%) were added. The tubes were then sealed with airtight caps and placed
170 on a hot plate at 90°C overnight (~12 hours). After allowing the digest to cool to room
171 temperature, the digested solutions were transferred to 50mL Falcon tubes and diluted with
172 mQ H₂O to reach a mother solution (MS) of 45mL. Prior to ICP-MS analysis, the MS were
173 further diluted by transferring a 5 mL aliquot to a 15mL falcon tube to which mQ H₂O were
174 added up to the 10 mL mark. For quality assurance and accuracy, blanks and certified
175 reference materials (CRMs: IAEA 336, NIST-1515, BCR 142, DORM-4, and DOLT-5) were
176 included with every 10 samples and processed the same way as the vegetation and soil
177 samples (see Table S1 for details). All blanks were >10x lower than the average of the total
178 measurement of each element, and the recovery of each element, for all five CRMs, fell
179 within ± 20 % of the certified value, with the exception of Ba in IAEA 366 (77.3% recovery)
180 and for Pb in DORM-4 (75.4 % recovery). All sample preparations were performed under
181 clean laboratory conditions (Clean room class 10000, ISO 7) using acid cleaned lab ware. All
182 concentrations (µg g⁻¹ dry weight (d.w.)) for the elements Mn, Co, Cu, Zn, As, Se, Mo, Cd,
183 Ba, Hg, Pb were above the detection limit (here set to 3 x standard deviation of blank for each
184 element, Table S1) and obtained using a Triple Quadrupole Inductively Coupled Plasma
185 Mass Spectrometer (Thermo scientific, iCap TQ-ICP-MS) at the ICP-MS platform of the
186 Observatoire Midi-Pyrenees, Toulouse, France.

187 Following the trace element analyses, soil and vegetation samples were also measured
188 for %C and %N and subsequently used to calculate C:N ratios. Subsamples were weighed
189 (soil 10–12 mg dry weight, plants 3–4 mg dry weight) and packed into tin capsules. All C
190 and N analyses were conducted at the University of Copenhagen, Denmark, using an

191 Isoprime isotope ratio mass spectrometer (Isoprime Ltd, Cheadle Hulme, Stockport, UK)
192 coupled to a CN elemental analyser (Eurovector, Milan, Italy) with continuous flow, with a
193 front furnace operating at 1050°C and a reduction furnace operating at 700°C. For quality
194 assurance, certified reference material (CRM NIST 1547 Peach leaves material, National
195 Institute of Standards & Technology) was included with every 12 samples and processed the
196 same way as the vegetation and soil samples. Certified values of the reference material had a
197 mean and standard deviation of N%: 2.965 ± 0.054 and C% 46.01 ± 1.52 and were measured
198 at N%: 2.939 ± 0.080 and C% 46.67 ± 1.89 in this study. The detection limits of the elements
199 were 0.015% for N and 0.100% for C.

200

201 *2.4 Quantifying geochemical landscapes*

202 Plot-based measurements of %C, % N and C:N ratio as well as of trace element
203 concentrations ($\mu\text{g g}^{-1}$ d.w.) (Fig. 2) were used to generate maps of their predicted
204 distribution and potential bioavailability across the soils and vegetation types of the
205 Zackenberg valley (i.e., geochemical landscapes). To do so, we used stoichiometric
206 distribution models (StDMs) as proposed by Leroux et al., (2017). StDMs generate spatially
207 explicit predictions of elemental patterns across the landscape based on statistical relationship
208 between element concentrations/ratio and environmental parameters (e.g., elevation,
209 vegetation cover, soil moisture, etc.). Such maps can then be used to link consumers'
210 distribution or habitat use to element concentrations across natural landscapes (e.g., Sach et
211 al., 2020) as described in section 2.5.

212 StDMs were computed using generalized linear models (GLMs) and constructed for
213 each element (n=14) and for both soil and vegetation samples separately (i.e., a total of 28
214 models). To improve normality of the data, concentrations of trace elements were log-
215 transformed while C, N, and C:N ratio (%) were logit-transformed, and all were fitted as

216 response variables using a Gaussian error distribution. A total of nine predictor covariates
217 were available as raster layers with a spatial resolution of 1m (Fig. S1) including soil
218 moisture (index), spring snow cover (%), ambient temperature ($^{\circ}\text{C}$) solar radiation (KWH m^{-2}),
219 elevation (m), slope ($^{\circ}$), hill shade (unitless), geomorphological landforms (7-class factor),
220 and vegetation type (7-class factor). Because the vegetation type raster layer was produced
221 using several of the candidate predictor variables (see: Stewart et al., 2018 for details), we
222 were unable to use all predictor variables in the same model. Hence, to avoid issues of
223 circularity, predictor variables for the soil analyses included: geomorphology landforms,
224 elevation, slope, spring snow cover and soil moisture. To construct geochemical landscapes
225 based on vegetation data, we considered the predictor variables: vegetation type, hill shade
226 and the element concentration or percentage in the soil. For an overview of how
227 environmental variables contribute to the clustering and spatial distribution of all elements
228 considered see Fig. S2. For the vegetation models, the percent cover of each target plant
229 species or, in cases of fen and grassland, functional group (graminoids), within the sampling
230 plots was used as a weighting variable. Sampling date (Julian day) was included as a
231 predictor variable in all StDMs to incorporate any natural changes in element concentration
232 over time. All continuous variables were included as a second order polynomial to allow for
233 non-linearity in the data.

234 To assess the predictive performance of the StDMs, we ran each element specific
235 GLM 100 times and for each iteration split the data into a new training (75%) and testing
236 (25%) set for which we calculated the MSE (using the testing data) and R^2 (using the training
237 data). We then compared the distribution of MSE and R^2 of the testing and training data to
238 those generated by 100 models where the response variable of the original data was randomly
239 resampled. We considered the performance of the StDMs to be satisfactory as the prediction
240 error was always lower and the amount of variation explained was always higher than for the

241 models based on randomized datasets (see Figs. S3 and S4). The output of the element-
242 specific StDMs (Figs. S5-S18) were used to produce spatially explicit maps of each element
243 in soil (Fig. S19) and vegetation (Fig. 3) across the study area.

244

245 *2.5 Relative use of geochemical landscapes*

246 To assess how muskoxen exploit the geochemical landscapes they inhabit, we used
247 resource selection functions (RSFs), which are statistical models that compare environmental
248 conditions encountered at used locations to those at available locations (Boyce and
249 McDonald, 1999). The output of RSFs provides estimates of the relative probability of use of
250 vegetation classes or sites along an environmental gradient and can be fitted with logistic
251 regression with used (1) and available (0) locations (Manly et al., 2002). In our RSFs, used
252 locations were geographical coordinates of muskox observations (n=3142) collected annually
253 during summer (Jun-Sep; Fig. 1C) as part of a long-term monitoring program at the
254 Zackenberg valley initiated in 1996 (Schmidt et al., 2015). Only vegetated areas were
255 considered in our analyses; thus, we excluded locations of muskoxen on barren sites or
256 exposed bedrock (n=723). Available locations were randomly generated for each year by
257 sampling locations from within the spatial domain of the geochemical landscapes (Fig. 3).
258 We used a 1:10 used:available location sampling scheme as it yielded stable model estimates
259 and adequately captured the distribution of available conditions within the landscape, which
260 are important aspects for robust model inference (Northrup et al., 2013).

261 Predicted concentrations or percentages of elements at used and available locations
262 were extracted from the vegetation-based geochemical landscape maps (Fig. 3) and fitted as
263 fixed-effect explanatory variables in the RSFs using an interaction with the categorical
264 variable Year to obtain annual coefficients of the relative probability of use of each element.
265 Because of multicollinearity among the different chemical elements at used locations

266 (Spearman rank correlations (r_s) of >0.6 and <-0.6 for some element combinations, Fig. S20),
267 separate RSFs were fitted for each element. Values of the explanatory variables were scaled
268 prior to analyses to ensure RSF coefficients across years and elements were comparable. In
269 all RSFs, we also fitted Year as a random intercept to account for unbalanced data.

270 Because no evidence exists that muskoxen, or other herbivorous animals, can sense
271 the elemental composition in plant material, they are unlikely to actively select forage
272 resources based on the bioavailability of different chemical elements. Instead, plant biomass
273 and composition and thus vegetation type is likely a more realistic driver of muskox habitat
274 use in this area as plant productivity and biomass varies between vegetation classes
275 (Tomassini et al., 2019). Therefore, and for comparative purposes, we fitted a classic RSF
276 using the interaction between vegetation type and Year as the independent variable.

277 Finally, the predictive success of all RSFs was evaluated using the k -fold cross-
278 validation procedure as proposed by Boyce et al. (2002) and Bastille-Rousseau and
279 Wittemyer (2019). For this, we calculated cross-validated Spearman rank correlations (r_s)
280 between ten RSF-bin ranks and five test-training sets. We repeated this procedure 10 times to
281 determine whether the r_s differed from random.

282

283 *2.6 Temporal variation in muskox calf recruitment and the linkages to the use of geochemical* 284 *landscapes*

285 To examine whether inter-annual variation in the relative use of geochemical
286 landscapes influences calf recruitment, we related the output of the RSFs (i.e., annual
287 selection coefficients for essential and non-essential elements) to muskox demography time
288 series [updated from Schmidt et al., (2015)]. For each year during the period 1996–2021, we
289 calculated calf recruitment rates as the percentage of calves (<6 months old) per 100 adult
290 females as observed during weekly surveys in July and August (Fig. S21). Annual

291 recruitment rates were then categorized as above or below 40% as this threshold typically
292 indicates an increasing or declining population size (Reynolds, 1998; Schmidt et al., 2015).
293 We then used the multivariate ordination technique Principal Component Analysis (PCA) to
294 explore whether RSF coefficients could be used to separate calf recruitment years above and
295 below 40%. We also included spring snow cover (%) for each year as a variable in the PCA
296 as increased snow cover is known to negatively influence muskox calf recruitment (Fig. S21;
297 Schmidt et al., 2015). Muskox cows give birth to a calf in late winter if sufficient energetic
298 reserves are acquired the preceding summer (Desforges et al., 2019). Therefore, the RSF
299 coefficients acquired for year t were matched to the calf recruitment rate observed the year
300 after (year $t+1$) in all analyses. Lastly, we fitted a separate PCA using the annual coefficients
301 of the classical RSF, based on vegetation types, to assess if these could be used to separate
302 calf recruitment years above and below 40% and to compare findings to the element based
303 PCA results.

304 Because PCA is primarily used to explore patterns in multivariate data rather than to
305 test formal hypotheses (Jolliffe, 2002), which is part of our study objective (Hypotheses 1 &
306 2), we used beta regression to statistically relate annual variation in the relative use of the
307 different chemical elements to calf recruitment. Thus, muskox calf recruitment in year $t+1$
308 was the response variable, while the relative use of the various elements in year t (i.e., annual
309 RSF coefficients) as well as spring snow cover were explanatory variables. Again, separate
310 beta models were fitted for each element due to multicollinearity.

311 All statistical analyses for this study were conducted using the software package R,
312 version 4.2.3 (R Development Core Team, 2023).

313

314 **3. Results**

315

316 *3.1. Essential and non-essential elements in soil and vegetation*

317 Measurements of the elements in soil and vegetation samples collected at the Zackenberg
318 valley in northeast Greenland are presented in Fig. 2 and Table S2 and form the numerical
319 basis for the construction of the geochemical landscapes (Fig. 3).

320

321 *3.2 Relative use of geochemical landscapes and vegetation types*

322 The relative use of the geochemical landscape by muskoxen varied over time and
323 differed between elements (Fig. S22). For example, the element-based RSFs revealed that the
324 relative use of vegetated sites decreased with increasing C during the years 2014-2017, a
325 pattern that was also evident for C:N ratio and the trace elements Co and Hg (Fig. S22). The
326 relative use of vegetated sites with high levels of N, Mn, Zn, and Ba was variable across
327 years. In fact, for most elements and years, the 95% confidence intervals of the RSF
328 coefficients overlapped with 0 (Fig. S22), which indicates that the relative use of the different
329 essential and non-essential elements did not differ significantly from their availability in the
330 landscape. Nonetheless, the predictive capacity of the element-based RSFs was satisfactory
331 with a mean r_s of 0.69 (sd=0.11) across all models, which was consistently higher ($p<0.001$)
332 compared to the randomized model versions (Fig. S23).

333 Output of the classic vegetation-type based RSF also revealed considerable
334 differences and annual variation in the relative probability of use of the dominant vegetation
335 types (Fig. S24). The relative use of sites with *Cassiope* heath was higher during 2007-2014,
336 but lower before and after this period. The opposite pattern was found for sites with *Salix*
337 snowbed as the relative use was low during 2007-2014 but higher in other years, which is
338 likely influenced by annual variation in the distribution of snow cover. The relative use of fen
339 and grassland sites by muskoxen was stochastic over time as muskoxen used these vegetated
340 sites significantly more in some years but used them significantly less in other years (Fig.

341 S24). Only sites with *Dryas* heath were used proportional to their availability in the landscape
342 in all years (i.e., no statistical difference between use and availability; Fig. S24). Predictive
343 capacity of the classical RSF was also satisfactory with a mean r_s of 0.71 (sd=0.16), which
344 was significantly higher ($p<0.001$) than for a randomized model with a mean r_s of 0.03
345 (sd=0.33).

346

347 *3.3 Relating muskox calf recruitment to relative use of geochemical landscapes and* 348 *vegetation types*

349 PCA ordination on the element-specific RSF coefficients and snow cover resulted in a
350 clear separation of high and low calf recruitment years, with the first two axes explaining
351 67.5% of the between year variation (Fig. 4). C:N contributed most (13.6%) to PCA axis 1,
352 followed by Ba (13.3%), C (12.8%), and N (11.0%). Se and Mo contributed most to PCA
353 axis 2 (20.9% and 15.2% respectively), followed by As (14.5%), and Cu (11.8%). The
354 remaining variables contributed <10% to the first two PCA axes.

355 In comparison, PCA ordination on the coefficients derived from the vegetation type
356 based RSF and snow cover resulted in a slightly poorer separation of high and low calf
357 recruitment years, although the first two axes explained 78.1% of the between year variation
358 (Fig. 5). Here, the relative use of *Cassiope* heath contributed most (31.4%) to PCA axis 1,
359 followed by *Salix* snowbed (28.8%), *Dryas* heath (27.1%), and Fen areas (12.5%). Snow
360 cover contributed most (40.7%) to PCA axis 2, followed by Grasslands (39.4%), and Fen
361 areas (16.5%).

362 Output of the univariate beta regression (Fig. 6) revealed that muskox calf recruitment
363 was positively correlated to the relative use of sites with increased N content ($p=0.048$) and
364 concentrations of Cu ($p=0.0003$), Se ($p=0.031$), and Mo ($p<0.0001$). Muskox calf recruitment

365 was negatively correlated to the relative use of sites with increased concentrations of As
366 ($p=0.013$) and Pb ($p=0.045$).

367

368 **4. Discussion**

369 By coupling the relative use of geochemical landscapes to long-term variation in annual
370 calf recruitment of muskoxen, the largest herbivore roaming the Arctic tundra, this study
371 provides empirical evidence that spatial variation of multiple essential and non-essential
372 elements in vegetation and underlying soils can influence habitat-performance relationships.

373

374 *4.1 Essential elements and muskox reproduction*

375 We uncovered positive associations between annual calf recruitment of muskoxen and
376 the relative use of vegetated sites with increased concentrations of the essential elements N,
377 Cu, Se and Mo (supporting Hypothesis 1). It has long been established that deficiencies of the
378 trace elements Cu and Se can impair reproductive success in both free-ranging and captive
379 animals e.g., by reducing conception rates and increasing risks of embryonic and neonatal
380 mortality (Flueck et al., 2012; Flynn et al., 1977; Robbins, 1983). The mean Se concentration
381 across all plants sampled in our study was $0.04 \mu\text{g g}^{-1}$ d.w. and below the deficiency risk
382 threshold of $0.05 \mu\text{g g}^{-1}$ d.w. proposed for free-ranging herbivores (Flueck et al., 2012).
383 Similarly, the mean Cu concentration across all plants sampled in our study was $7.73 \mu\text{g g}^{-1}$
384 d.w. and below the deficiency risk threshold of $10 \mu\text{g g}^{-1}$ d.w. proposed for deer (Grace and
385 Wilson, 2002). It thus seems probable that poor muskox recruitment years were, at least
386 partly, influenced by a shortage of Se and Cu in the landscape, as previously suggested for
387 muskoxen in this region (Mosbacher et al., 2022). The positive association between Mo and
388 reproductive output detected here aligns with experimental work on goats that showed a
389 decline in conception and fetal survival rates reduced Mo intake (Anke et al., 2010).

390 However, the mean Mo concentration in vegetation samples collected in this study (0.98 μg
391 $\text{g}^{-1}\text{d.w.}$) is within the range required for normal plant production (Kabata-Pendias and Szteke,
392 2015) suggesting that the bioavailability of Mo in the study landscape is not limited.
393 Moreover, the bioavailability of Mo is unlikely to exceed toxicity levels of muskoxen in this
394 system, as has been reported for other herbivores (Reis et al., 2010).

395 Arctic and boreal ecosystems are characterized by strong N limitation and high C
396 stocks in soils (Liu et al., 2018). As a consequence, most ecological stoichiometry studies
397 focus on C:N ratios to assess vegetation quality and dynamics at northern latitudes
398 (Mosbacher et al., 2019; Peng et al., 2011) or to estimate linkages with consumer distribution
399 (Leroux et al., 2017; Rizzuto et al., 2021). In our study, however, we found no apparent
400 association between C:N ratio in vegetated sites used by muskoxen and annual calf
401 recruitment. Instead, muskoxen often avoided vegetated sites with high C content but selected
402 for vegetated sites with increased content of N, with the latter having a strongly positive
403 effect on annual calf recruitment. The importance of N in Arctic vegetation has previously
404 been highlighted for caribou (*Rangifer tarandus*), and N limitation was suspected to have
405 consequences for the distribution and growth of populations (Barboza et al., 2018). Our study
406 corroborates this notion by revealing that N content in Arctic plants is a major driver of
407 habitat use of muskoxen and that selection for vegetated sites with increased N content has a
408 direct positive effect on recruitment rate.

409 Overall, we interpret these results as clear indications that the concentrations,
410 distribution, and bioavailability of N and several essential trace elements in Arctic landscapes
411 play critical roles in the reproductive success of muskoxen. Moreover, results of this study
412 lend support to the notion that alternate year breeding in muskox populations in northeast
413 Greenland is driven by depletion and slow recovery of elemental and nutritional reserves
414 needed for a successful reproductive cycle (Desforges et al., 2019; Thing et al., 1987).

415 Finally, we suspect that constraints in the uptake of the essential elements N, Cu, Se, Mo in
416 poor muskox recruitment years affects the reproductive cycle through reduced conception
417 rates or increased embryonic and neonatal mortality as also observed in other herbivores
418 (Anke et al., 2010; Flueck et al., 2012).

419

420 *4.2 Non-essential elements and muskox reproduction*

421 We detected a negative association between annual calf recruitment of muskoxen and
422 the relative use of vegetated sites with higher concentrations of the non-essential elements As
423 and Pb (supporting Hypothesis 2). At first glance, these findings suggest that the
424 concentrations of these contaminants were sufficiently high to negatively affect the
425 reproductive organs of muskoxen, as has been observed for other species occupying
426 contaminated areas (Massányi et al., 2020). However, the average concentrations of Pb (0.5
427 $\mu\text{g g}^{-1}$ d.w.), As ($0.12 \mu\text{g g}^{-1}$ d.w.), and Hg ($0.02 \mu\text{g g}^{-1}$ d.w) measured in plant material
428 collected in our study area were well below those reported for plants in areas considered to be
429 (semi-) polluted with heavy metals (Kabata-Pendias and Szteke, 2015). Possible direct,
430 degenerative effects of contaminants in the vegetation on the reproductive organs of
431 muskoxen is therefore unlikely. Instead, these results may be a product of annual variation in
432 the relative use of *Cassiope* and *Dryas* heath, i.e., the vegetation types with the highest
433 concentrations of As and Pb in our study area (Figs. S12 & S18), and their negative
434 correlations with muskox calf recruitment (Fig. 5). Muskoxen generally do not select for
435 heath covered sites as forage plant productivity and biomass in those vegetation types is low
436 compared to preferred and more productive fen and grassland areas (Tomassini et al., 2019).
437 Thus, in years that muskoxen increase their use of heath vegetation, possibly because of
438 constraints in forage accessibility elsewhere due to snow cover, recruitment rates decline and
439 the relative use of sites with higher concentrations, and thus potential bioavailability, of As

440 and Pb increases. It is, of course, possible that atmospheric deposition of contaminants will
441 increase the concentrations and subsequent bioavailability of Cd, Pb, As or Hg over time, as
442 seen elsewhere in the Arctic (Aslam et al., 2019; Couture et al., 2008; Dastoor et al., 2022;
443 McConnell et al., 2019). Thus, continued monitoring of contaminant levels in Arctic
444 vegetation and their potential direct and indirect effects on resident wildlife is pertinent.

445

446 *4.3 Caveats and future prospects*

447 To link long-term (1996-2021) variation in reproductive output of muskoxen to the use of
448 geochemical landscapes, we relied on chemical analyses of plant and soil samples collected
449 during the peak-biomass period (July) of a single year (2021). An important assumption
450 underlying our work is therefore that the spatial distribution, concentrations, and
451 bioavailability of the elements considered here remained constant over time. Yet, multiple
452 processes can alter the spatiotemporal dynamics in vegetation composition and productivity
453 (Elmendorf et al., 2012), which may impact the bioavailability of chemical elements. In fact,
454 through foraging, defecating, and trampling, wildlife species themselves can alter the
455 distribution and cycling of essential and non-essential elements across landscapes (Abraham
456 et al., 2023; Schmitz et al., 2018). Further work is, therefore, recommended to assess if and
457 how the concentrations, and thus potential bioavailability, of (trace) elements in plants and
458 soils vary between years and throughout the growing season and to determine the impacts on
459 resident wildlife. Long-term herbivore exclosures provide a suitable experimental set-up to
460 address such outstanding questions.

461 Our study relied on relatively small-scale (52m²), yet long-term, survey data of muskox
462 observations and demography. However, muskoxen typically roam over larger areas
463 (Schmidt et al., 2016) with substantial individual variation in habitat use (Beumer et al.,
464 2023; van Beest et al., 2020). To further investigate the importance of geochemical

465 landscapes in wildlife ecology, we see particular value in the application of high-resolution
466 biologging data (e.g., GPS collar and 3-dimensional accelerometers). Doing so will allow for
467 the estimation of spatial and temporal variation in feeding behavior of individual animals
468 across geochemical landscapes and multiple seasons (Nunes et al., 2022). Potential
469 consequences of individual variation in habitat use and behavior on Darwinian fitness (i.e.,
470 survival and lifetime reproductive success) can then be assessed via long-term monitoring
471 data or through Dynamic Energy Budget models (Desforges et al., 2019; Sperfeld et al.,
472 2017).

473 Free-ranging animals are confronted by a myriad of environmental conditions that
474 they need to balance to optimize fitness (Gaillard et al., 2010; Stein et al., 2014; van Beest
475 and Milner, 2013). In our analyses, we focused on vegetation types, snow cover, and multiple
476 essential and non-essential elements but discounted other potential factors (e.g., ambient
477 temperature, density dependence, predation risk) influencing habitat use. We argue that this
478 analytical approach is reasonable given that habitat use of muskoxen in this low-predator
479 system is primarily influenced by snow cover, plant productivity and access to forage
480 biomass during spring and summer (Beumer et al., 2020; Tomassini et al., 2019). Indeed,
481 muskoxen use this period primarily to replenish energetic reserves to survive the upcoming
482 winter and to be able to develop a fetus (Desforges et al., 2021). This is also why we ran
483 separate RSF and PCA analyses for the chemical elements (Fig. 4) and the vegetation types
484 (Fig. 5) to facilitate comparison. The ‘classic’ PCA and RSF based on vegetation types
485 explained more variation in annual recruitment (78.1%) than the element-based analyses
486 (67.5%), which supports the idea that vegetation types are a better predictor of muskox
487 habitat use and performance. Nonetheless, the element-based RSF and PCA also showed high
488 predictive power and, moreover, provide insight into the geochemical mechanism underlying
489 linkages between habitat use and population performance.

490 The Arctic is now warming four times faster than the global average (Rantanen et al.,
491 2022). Rapid thawing of permafrost threatens to release biological, chemical, and radioactive
492 materials that have been sequestered for tens to hundreds of thousands of years. As these
493 stored compounds re-enter the environment, they have the potential to disrupt ecosystem
494 function endangering the health of humans and Arctic wildlife (Miner et al., 2021). While the
495 potential risks of leaching of trace metals following permafrost degradation have been studied
496 to some extent (Antcibor et al., 2014), little is known about possible changes in composition
497 and spatial distribution of essential trace elements following permafrost thaw. We foresee
498 great value in the application of ecogeochemical methods in combination with climate-
499 forecast models to assess shifts in the bioavailability, concentration, and distribution of
500 essential and non-essential elements over time and space. This will provide the necessary
501 foundation to assess habitat-performance relationships under contemporary and future
502 environmental change.

503

504 **5. Conclusion**

505 Our study clearly shows that the distribution and bioavailability of the essential elements
506 N, Cu, Se, and Mo in Arctic vegetation are critical to the reproductive success of muskoxen
507 and, moreover, possible contributing factors to alternate year breeding as observed in
508 populations across northeast Greenland. The distribution and bioavailability of the non-
509 essential elements As and Pb negatively correlated with calf recruitment of muskoxen, but the
510 concentrations measured were unlikely to cause degenerative impacts on reproductive organs.
511 Instead, this result likely reflects a constraint on forage accessibility in poor recruitment years
512 due to extensive snow cover, leading to an increased use of less optimal habitat with higher
513 concentrations of As and Pb and lower concentrations of the elements essential for
514 reproduction.

515 The rapid warming of the Arctic and subsequent thawing of permafrost is suspected to
516 severely alter the composition and spatial distribution of essential and non-essential elements.
517 Therefore, continued monitoring and measurements of chemical elements in Arctic soils and
518 vegetation as well as responses by resident wildlife are critical to assess habitat-performance
519 relationships under contemporary and future environmental change. While our study is
520 specific to high-Arctic muskoxen, we posit that the influence of geochemical landscapes on
521 animal performance highlighted here also affect the ecology of wildlife species living in
522 lower latitude systems.

523

524 **Funding**

525 This study was financially supported by the Danish Environmental Protection Agency (J.nr.
526 2019–7208), by ANR JCJC (ANR-21-CE34-0001 ATCAF-project), the Carlsberg foundation
527 (CF17-0097 and CF18-0279) and Independent Research Fund Denmark/ DFF Nature and
528 Universe, grant No. 0135–00140B.

529

530 **Ethics approval**

531 Not applicable.

532 **Data availability**

533 Data on concentrations and percentages of the essential and non-essential elements are
534 provided in Table S2 in the Supporting Information.

535

536 **Acknowledgements**

537 We thank Greenland Ecosystem Monitoring for access to ecosystem data, and Aarhus
538 University, Denmark, and Zackenberg Research Station, Greenland, for logistical support at
539 the study site. We also thank Laetitia Leroy for assistance in the clean room, and Camille

540 Duquenoy and Aurélie Marquet (both at the ICP-MS platform at the Observatoire Midi-
541 Pyrenees, Toulouse, France) for assistance with the ICP-MS analyses. We also thank three
542 anonymous reviewers for their extremely constructive comments that helped to improve this
543 article.

544

545 **References**

- 546 Abraham, A.J., Duvall, E., Ferraro, K., Webster, A.B., Doughty, C.E., le Roux, E., Ellis-Soto,
547 D., 2023. Understanding anthropogenic impacts on zoogeochemistry is essential for
548 ecological restoration. *Restor. Ecol.* 31, e13778. <https://doi.org/10.1111/rec.13778>
- 549 Anke, M., Seifert, M., Arnhold, W., Anke, S., Schäfer, U., 2010. The biological and
550 toxicological importance of molybdenum in the environment and in the nutrition of
551 plants, animals and man: Part V: Essentiality and toxicity of molybdenum. *Acta*
552 *Aliment.* 39, 12–26. <https://doi.org/10.1556/aalim.39.2010.1.2>
- 553 Antcibor, I., Eschenbach, A., Zubrzycki, S., Kutzbach, L., Bolshiyarov, D., Pfeiffer, E.-M.,
554 2014. Trace metal distribution in pristine permafrost-affected soils of the Lena River
555 delta and its hinterland, northern Siberia, Russia. *Biogeosciences* 11, 1–15.
556 <https://doi.org/10.5194/bg-11-1-2014>
- 557 Balluffi-Fry, J., Leroux, S.J., Wiersma, Y.F., Heckford, T.R., Rizzuto, M., Richmond, I.C.,
558 Vander Wal, E., 2020. Quantity–quality trade-offs revealed using a multiscale test of
559 herbivore resource selection on elemental landscapes. *Ecol Evol* 10, 13847–13859.
560 <https://doi.org/10.1002/ECE3.6975>
- 561 Barboza, P.S., Van Someren, L.L., Gustine, D.D., Bret-Harte, M.S., 2018. The nitrogen
562 window for arctic herbivores: plant phenology and protein gain of migratory caribou
563 (*Rangifer tarandus*). *Ecosphere* 9. <https://doi.org/10.1002/ecs2.2073>
- 564 Bastille-Rousseau, G., Wittemyer, G., 2019. Leveraging multidimensional heterogeneity in
565 resource selection to define movement tactics of animals. *Ecol. Lett.* 22, 1417–1427.
566 <https://doi.org/10.1111/ele.13327>
- 567 Beumer, L.T., Pohle, J., Schmidt, N.M., Chimienti, M., Desforges, J.-P., Hansen, L.H.,
568 Langrock, R., Pedersen, S.H., Stelvig, M., van Beest, F.M., 2020. An application of
569 upscaled optimal foraging theory using hidden Markov modelling: year-round
570 behavioural variation in a large arctic herbivore. *Mov. Ecol.* 8, 25.
571 <https://doi.org/10.1186/s40462-020-00213-x>
- 572 Beumer, L.T., Schmidt, N.M., Pohle, J., Signer, J., Chimienti, M., Desforges, J.-P., Hansen,
573 L.H., Højlund Pedersen, S., Rudd, D.A., Stelvig, M., van Beest, F.M., 2023.
574 Accounting for behaviour in fine-scale habitat selection: A case study highlighting
575 methodological intricacies. *J Anim Ecol Early View*. <https://doi.org/10.1111/1365-2656.13984>
- 576
- 577 Bhattacharya, P.T., Misra, S.R., Hussain, M., 2016. Nutritional aspects of essential trace
578 elements in oral health and disease: an extensive review. *Scientifica (Cairo)* 2016,
579 5464373. <https://doi.org/10.1155/2016/5464373>
- 580 Boersma, M., Elser, J.J., 2006. Too Much of a Good Thing: On Stoichiometrically Balanced
581 Diets and Maximal Growth. *Ecology* 87, 1325–1330. [https://doi.org/10.1890/0012-9658\(2006\)87\[1325:TMOAGT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1325:TMOAGT]2.0.CO;2)
- 582

- 583 Boyce, M.S., McDonald, L.L., 1999. Relating populations to habitats using resource selection
584 functions. *Trends Ecol. Evol.* 14, 268–272.
- 585 Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource
586 selection functions. *Ecol Model* 157, 281–300.
- 587 Brown, G.E., Foster, A.L., Ostergren, J.D., 1999. Mineral surfaces and bioavailability of
588 heavy metals: A molecular-scale perspective. *Proc. Natl. Acad. Sci. U.S.A.* 96, 3388–
589 3395. <https://doi.org/10.1073/pnas.96.7.3388>
- 590 Burger, J., 2008. Assessment and management of risk to wildlife from cadmium. *Sci. Total*
591 *Environ.* 389, 37–45. <https://doi.org/10.1016/j.scitotenv.2007.08.037>
- 592 Cable, S., Christiansen, H.H., Westergaard-Nielsen, A., Kroon, A., Elberling, B., 2018.
593 Geomorphological and cryostratigraphical analyses of the Zackenberg Valley, NE
594 Greenland and significance of Holocene alluvial fans. *Geomorphology* 303, 504–523.
595 <https://doi.org/10.1016/J.GEOMORPH.2017.11.003>
- 596 Desforges, J.-P., Gonçalo, |, Marques, M., Beumer, L.T., Chimienti, M., Hansen, L.H., Stine,
597 |, Pedersen, H., Schmidt, N.M., Van Beest, F.M., 2021. Environment and physiology
598 shape Arctic ungulate population dynamics. *Glob Change Biol* 27, 1755–1771.
599 <https://doi.org/10.1111/gcb.15484>
- 600 Desforges, J.P., Marques, G.M., Beumer, L.T., Chimienti, M., Blake, J., Rowell, J.E.,
601 Adamczewski, J., Schmidt, N.M., van Beest, F.M., 2019. Quantification of the full
602 lifecycle bioenergetics of a large mammal in the high Arctic. *Ecol Model* 401, 27–39.
603 <https://doi.org/10.1016/J.ECOLMODEL.2019.03.013>
- 604 Durso, A.M., Smith, G.D., Hudson, S.B., French, S.S., 2020. Stoichiometric and stable
605 isotope ratios of wild lizards in an urban landscape vary with reproduction,
606 physiology, space and time. *Conserv Physiol* 8, coaa001.
607 <https://doi.org/10.1093/conphys/coaa001>
- 608 Elberling, B., Tamstorf, M.P., Michelsen, A., Arndal, M.F., Sigsgaard, C., Illeris, L., Bay, C.,
609 Hansen, B.U., Christensen, T.R., Hansen, E.S., Jakobsen, B.H., Beyens, L., 2008. Soil
610 and Plant Community-Characteristics and Dynamics at Zackenberg. *Adv. Ecol. Res.*
611 40, 223–248. [https://doi.org/10.1016/S0065-2504\(07\)00010-4](https://doi.org/10.1016/S0065-2504(07)00010-4)
- 612 Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Bjorkman, A.D., Callaghan,
613 T.V., Collier, L.S., Cooper, E.J., Cornelissen, J.H.C., Day, T.A., Fosaa, A.M., Gould,
614 W.A., Grétarsdóttir, J., Harte, J., Hermanutz, L., Hik, D.S., Hofgaard, A., Jarrad, F.,
615 Jónsdóttir, I.S., Keuper, F., Klanderud, K., Klein, J.A., Koh, S., Kudo, G., Lang, S.I.,
616 Loewen, V., May, J.L., Mercado, J., Michelsen, A., Molau, U., Myers-Smith, I.H.,
617 Oberbauer, S.F., Pieper, S., Post, E., Rixen, C., Robinson, C.H., Schmidt, N.M.,
618 Shaver, G.R., Stenström, A., Tolvanen, A., Totland, Ø., Troxler, T., Wahren, C.H.,
619 Webber, P.J., Welker, J.M., Wookey, P.A., 2012. Global assessment of experimental
620 climate warming on tundra vegetation: Heterogeneity over space and time. *Ecol Lett*
621 15, 164–175. <https://doi.org/10.1111/j.1461-0248.2011.01716.x>
- 622 Elser, J., 2006. Biological stoichiometry: a chemical bridge between ecosystem ecology and
623 evolutionary biology. *Am. Nat.* 168 Suppl, S25-35. <https://doi.org/10.1086/509048>
- 624 Feinberg, A., Stenke, A., Peter, T., Hinckley, E.-L.S., Driscoll, C.T., Winkel, L.H.E., 2021.
625 Reductions in the deposition of sulfur and selenium to agricultural soils pose risk of
626 future nutrient deficiencies. *Commun Earth Environ* 2, 1–8.
627 <https://doi.org/10.1038/s43247-021-00172-0>
- 628 Felton, A.M., Holmström, E., Malmsten, J., Felton, A., Cromsigt, J.P.G.M., Edenius, L.,
629 Ericsson, G., Widemo, F., Wam, H.K., 2020. Varied diets, including broadleaved
630 forage, are important for a large herbivore species inhabiting highly modified
631 landscapes. *Sci Rep* 10, 1904. <https://doi.org/10.1038/s41598-020-58673-5>

632 Flueck, W.T., 1994. Effect of trace elements on population dynamics: Selenium deficiency in
633 free-ranging black-tailed deer. *Ecology* 75, 807–812. <https://doi.org/10.2307/1941736>

634 Flueck, W.T., Smith-Flueck, J.M., Mionczynski, J., Mincher, B.J., 2012. The implications of
635 selenium deficiency for wild herbivore conservation: a review. *Eur J Wildl Res* 58,
636 761–780. <https://doi.org/10.1007/S10344-012-0645-Z>

637 Flynn, A., Franzmann, A.W., Arneson, P.D., Oldemeyer, J.L., 1977. Indications of Copper
638 Deficiency in a Subpopulation of Alaskan Moose. *J Nutr* 107, 1182–1189.
639 <https://doi.org/10.1093/jn/107.7.1182>

640 French, A.S., Shaw, D., Gibb, S.W., Taggart, M.A., 2017. Geochemical landscapes as drivers
641 of trace and toxic element profiles in wild red deer (*Cervus elaphus*). *Sci. Total*
642 *Environ.* 601–602, 1606–1618. <https://doi.org/10.1016/J.SCITOTENV.2017.05.210>

643 Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M., van
644 Moorter, B., 2010. Habitat-performance relationships: finding the right metric at a
645 given spatial scale. *Philos Trans R Soc Lond B Biol Sci* 365, 2255–2265.
646 <https://doi.org/10.1098/rstb.2010.0085>

647 Grace, N.D., Wilson, P.R., 2002. Trace element metabolism, dietary requirements, diagnosis
648 and prevention of deficiencies in deer. *New Zealand Veterinary Journal* 50, 252–259.
649 <https://doi.org/10.1080/00480169.2002.36321>

650 Jolliffe, I.T. (Ed.), 2002. Principal Component Analysis for Special Types of Data, in:
651 Principal Component Analysis, Springer Series in Statistics. Springer, New York,
652 NY, pp. 338–372. https://doi.org/10.1007/0-387-22440-8_13

653 Jutha, N., Jardine, C., Schwantje, H., Mosbacher, J., Kinniburgh, D., Kutz, S., 2022.
654 Evaluating the use of hair as a non-invasive indicator of trace mineral status in
655 woodland caribou (*Rangifer tarandus caribou*). *PLOS ONE* 17, e0269441.
656 <https://doi.org/10.1371/JOURNAL.PONE.0269441>

657 Kabata-Pendias, A., Szeke, B., 2015. Trace Elements in Abiotic and Biotic Environments.
658 CRC Press, Boca Raton. <https://doi.org/10.1201/b18198>

659 Kaspari, M., Powers, J.S., 2016. Biogeochemistry and geographical ecology: Embracing all
660 twenty-five elements required to build organisms. *Am. Nat.* 188, S62–S73.
661 <https://doi.org/10.1086/687576/ASSET/IMAGES/LARGE/FG4.JPEG>

662 Leroux, S.J., Wal, E.V., Wiersma, Y.F., Charron, L., Ebel, J.D., Ellis, N.M., Hart, C., Kissler,
663 E., Saunders, P.W., Moudrá, L., Tanner, A.L., Yalcin, S., 2017. Stoichiometric
664 distribution models: ecological stoichiometry at the landscape extent. *Ecol Lett* 20,
665 1495–1506. <https://doi.org/10.1111/ELE.12859>

666 Liu, X.-Y., Koba, K., Koyama, L.A., Hobbie, S.E., Weiss, M.S., Inagaki, Y., Shaver, G.R.,
667 Giblin, A.E., Hobara, S., Nadelhoffer, K.J., Sommerkorn, M., Rastetter, E.B., Kling,
668 G.W., Laundre, J.A., Yano, Y., Makabe, A., Yano, M., Liu, C.-Q., 2018. Nitrate is an
669 important nitrogen source for Arctic tundra plants. *Proc. Natl. Acad. Sci. U.S.A.* 115,
670 3398–3403. <https://doi.org/10.1073/pnas.1715382115>

671 Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002.
672 Resource selection by animals: Statistical analysis and design for field studies.
673 Kluwer Academic Publishers, Dordrecht, The Netherlands.

674 Massányi, P., Massányi, M., Madeddu, R., Stawarz, R., Lukáč, N., 2020. Effects of
675 Cadmium, Lead, and Mercury on the Structure and Function of Reproductive Organs.
676 *Toxics* 8, 94. <https://doi.org/10.3390/toxics8040094>

677 Matthiopoulos, J., Fieberg, J., Aarts, G., Beyer, H.L., Morales, J.M., Haydon, D.T., 2015.
678 Establishing the link between habitat selection and animal population dynamics. *Ecol.*
679 *Monogr.* 85, 413–436. <https://doi.org/10.1890/14-2244.1>

680 McLoughlin, P.D., Gaillard, J.M., Boyce, M.S., Bonenfant, C., Messier, F., Duncan, P.,
681 Delorme, D., Van Moorter, B., Saïd, S., Klein, F., 2007. Lifetime reproductive

682 success and composition of the home range in a large herbivore. *Ecology* 88, 3192–
683 3201.

684 Michaluk, A., Kochman, K., 2007. Involvement of copper in female reproduction. *Reprod*
685 *Biol* 7, 193–205.

686 Miner, K.R., D’Andrilli, J., Mackelprang, R., Edwards, A., Malaska, M.J., Waldrop, M.P.,
687 Miller, C.E., 2021. Emergent biogeochemical risks from Arctic permafrost
688 degradation. *Nat. Clim. Chang.* 11, 809–819. [https://doi.org/10.1038/s41558-021-](https://doi.org/10.1038/s41558-021-01162-y)
689 [01162-y](https://doi.org/10.1038/s41558-021-01162-y)

690 Mosbacher, J.B., Desforges, J.-P., Michelsen, A., Hansson, S.V., Stelvig, M., Eulaers, I.,
691 Sonne, C., Dietz, R., Jenssen, B.M., Ciesielski, T.M., Lierhagen, S., Flaten, T.P.,
692 Roux, G.L., Aggerbeck, M.R., Schmidt, N.M., 2022. Hair mineral levels as indicator
693 of wildlife demographics?—a pilot study of muskoxen. *Polar Res.* 41.
694 <https://doi.org/10.33265/polar.v41.8543>

695 Mosbacher, J.B., Michelsen, A., Stelvig, M., Hjermstad-Sollerud, H., Schmidt, N.M., 2019.
696 Muskoxen modify plant abundance, phenology, and nitrogen dynamics in a high
697 Arctic fen. *Ecosystems* 22, 1095–1107. <https://doi.org/10.1007/s10021-018-0323-4>

698 Mosser, A., Fryxell, J.M., Eberly, L., Packer, C., 2009. Serengeti real estate: density vs.
699 fitness-based indicators of lion habitat quality. *Ecol. Lett.* 12, 1050–1060.
700 <https://doi.org/10.1111/j.1461-0248.2009.01359.x>

701 Northrup, J.M., Hooten, M.B., Anderson, C.R., Wittemyer, G., 2013. Practical guidance on
702 characterizing availability in resource selection functions under a use–availability
703 design. *Ecology* 94, 1456–1463. <https://doi.org/10.1890/12-1688.1>

704 Nunes, G.T., Efe, M.A., Barreto, C.T., Gaiotto, J.V., Silva, A.B., Vilela, F., Roy, A.,
705 Bertrand, S., Costa, P.G., Bianchini, A., Bugoni, L., 2022. Ecological trap for seabirds
706 due to the contamination caused by the Fundão dam collapse, Brazil. *Sci. Total*
707 *Environ.* 807, 151486. <https://doi.org/10.1016/j.scitotenv.2021.151486>

708 Ofstad, E.G., Markussen, S.S., Saether, B.-E., Solberg, E.J., Heim, M., Haanes, H., Røed,
709 K.H., Herfindal, I., 2020. Opposing fitness consequences of habitat use in a harvested
710 moose population. *J Anim Ecol.* <https://doi.org/10.1111/1365-2656.13221>

711 Pedersen, S.H., Tamstorf, M.P., Abermann, J., Westergaard-Nielsen, A., Lund, M., Skov, K.,
712 Sigsgaard, C., Mylius, M.R., Hansen, B.U., Liston, G.E., Schmidt, N.M., 2016.
713 Spatiotemporal characteristics of seasonal snow cover in northeast Greenland from in
714 situ observations. *Arct. Antarct. Alp. Res* 48, 653–671.
715 <https://doi.org/10.1657/AAAR0016-028>

716 Peng, Y., Niklas, K.J., Sun, S., 2011. The relationship between relative growth rate and
717 whole-plant C : N : P stoichiometry in plant seedlings grown under nutrient-enriched
718 conditions. *J Plant Ecol* 4, 147–156. <https://doi.org/10.1093/jpe/rtq026>

719 Plath, K., Boersma, M., 2001. Mineral Limitation of Zooplankton: Stoichiometric Constraints
720 and Optimal Foraging. *Ecology* 82, 1260–1269. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9658(2001)082[1260:MLOZSC]2.0.CO;2)
721 [9658\(2001\)082\[1260:MLOZSC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1260:MLOZSC]2.0.CO;2)

722 Proffitt, K.M., Hebblewhite, M., Peters, W., Hupp, N., Shamhart, J., 2016. Linking
723 landscape-scale differences in forage to ungulate nutritional ecology. *Ecol. Appl.* 26,
724 2156–2174.

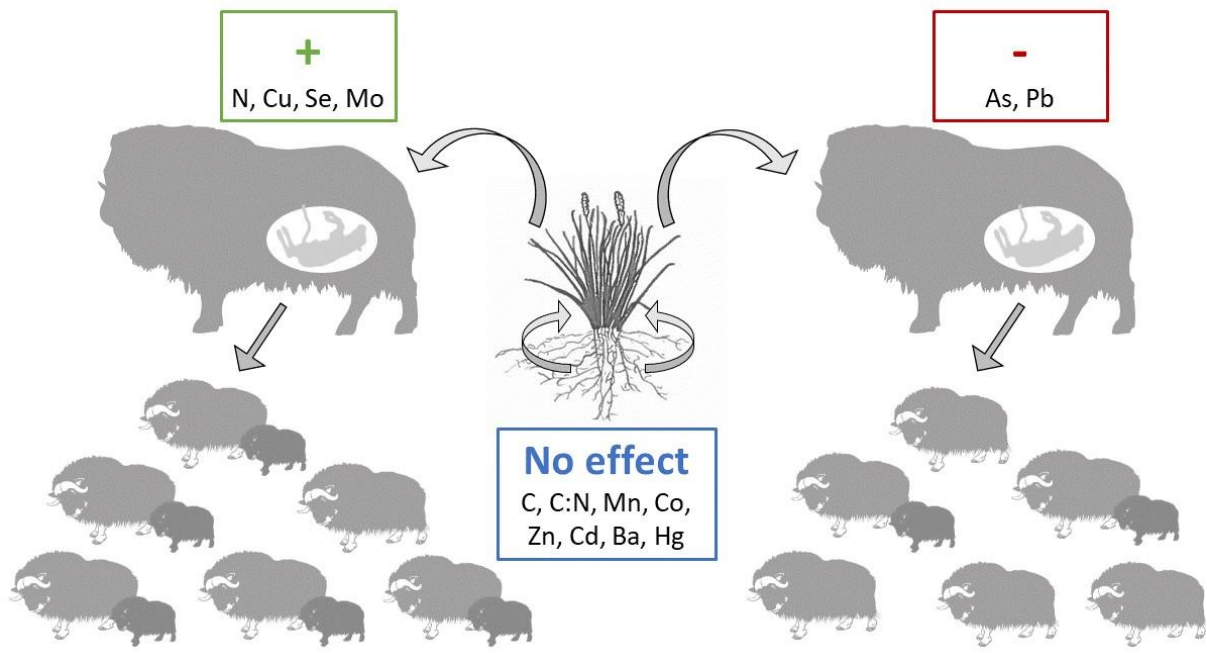
725 R Development Core Team, 2023. R: A language and environment for statistical computing.

726 Rantanen, M., Karpechko, A.Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruostenoja, K.,
727 Vihma, T., Laaksonen, A., 2022. The Arctic has warmed nearly four times faster than
728 the globe since 1979. *Commun Earth Environ* 3, 1–10.
729 <https://doi.org/10.1038/s43247-022-00498-3>

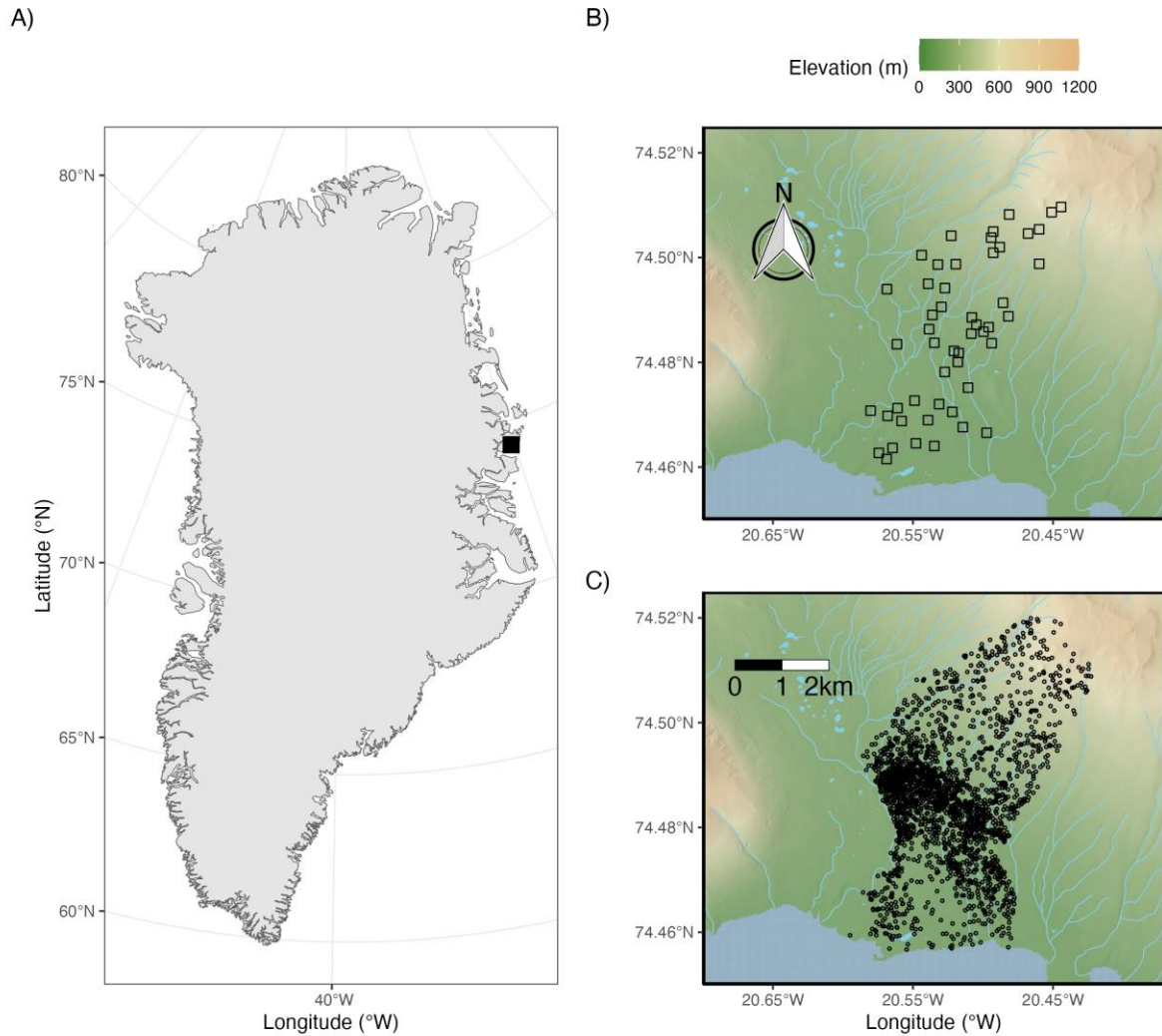
730 Reis, L.S.L.S., Pardo, P.E., Camargos, A.S., Oba, E., 2010. Mineral element and heavy metal
731 poisoning in animals. *J Medicine & Med. Sci.* 1, 560–579.

- 732 Reynolds, P.E., 1998. Dynamics and range expansion of a re-established muskox population.
733 J Wildl Manage 62, 734–744. <https://doi.org/10.2307/3802350>
- 734 Rioux, È., Pelletier, F., Mosbacher, J.B., Lesmerises, F., St-Louis, R., Kutz, S., St-Laurent,
735 M.-H., 2022. Links between individual performance, trace elements and stable
736 isotopes in an endangered caribou population. Glob. Ecol. Conserv. 38, e02234.
737 <https://doi.org/10.1016/j.gecco.2022.e02234>
- 738 Rizzuto, M., Leroux, S.J., Wal, E.V., Richmond, I.C., Heckford, T.R., Balluffi-Fry, J.,
739 Wiersma, Y.F., 2021. Forage stoichiometry predicts the home range size of a small
740 terrestrial herbivore. Oecologia 1, 327–338. [https://doi.org/10.1007/s00442-021-](https://doi.org/10.1007/s00442-021-04965-0)
741 04965-0
- 742 Robbins, C.T., 1983. Wildlife feeding and nutrition. Academic Press Inc, New York, USA.
- 743 Rombach, E.P., Barboza, P.S., Blake, J.E., 2002. Utilization of copper during lactation and
744 neonatal development in muskoxen. Can. J. Zool. 80, 1460–1469.
745 <https://doi.org/10.1139/Z02-139>
- 746 Roos-Barraclough, F., Givelet, N., Martinez-Cortizas, A., Goodsite, M.E., Biester, H.,
747 Shotyk, W., 2002. An analytical protocol for the determination of total mercury
748 concentrations in solid peat samples. Sci Total Environ 292, 129–139.
749 [https://doi.org/10.1016/s0048-9697\(02\)00035-9](https://doi.org/10.1016/s0048-9697(02)00035-9)
- 750 Sach, F., Yon, L., Henley, M.D., Bedetti, A., Buss, P., de Boer, W.F., Dierenfeld, E.S.,
751 Gardner, A., Langley-Evans, S.C., Hamilton, E., Lark, R.M., Prins, H.H.T.,
752 Swemmer, A.M., Watts, M.J., 2020. Spatial geochemistry influences the home range
753 of elephants. Sci Total Environ 729, 139066.
754 <https://doi.org/10.1016/J.SCITOTENV.2020.139066>
- 755 Schmidt, N.M., Pedersen, S.H., Mosbacher, J.B., Hansen, L.H., 2015. Long-term patterns of
756 muskox (*Ovibos moschatus*) demographics in high arctic Greenland. Polar Biol. 38,
757 1667–1675. <https://doi.org/10.1007/s00300-015-1733-9>
- 758 Schmidt, N.M., van Beest, F.M., Mosbacher, J.B., Stelvig, M., Hansen, L.H., Nabe-Nielsen,
759 J., Grøndahl, C., 2016. Ungulate movement in an extreme seasonal environment:
760 year-round movement patterns of high-arctic muskoxen. Wildlife Biol 22, 253–267.
761 <https://doi.org/10.2981/wlb.00219>
- 762 Schmitz, O.J., Wilmers, C.C., Leroux, S.J., Doughty, C.E., Atwood, T.B., Galetti, M.,
763 Davies, A.B., Goetz, S.J., 2018. Animals and the zoogeochemistry of the carbon
764 cycle. Science 362, eaar3213. <https://doi.org/10.1126/science.aar3213>
- 765 Sperfeld, E., Wagner, N.D., Halvorson, H.M., Malishev, M., Raubenheimer, D., 2017.
766 Bridging Ecological Stoichiometry and Nutritional Geometry with homeostasis
767 concepts and integrative models of organism nutrition. Funct. Ecol. 31, 286–296.
768 <https://doi.org/10.1111/1365-2435.12707>
- 769 Squadrone, S., Robetto, S., Orusa, R., Griglione, A., Falsetti, S., Paola, B., Abete, M.C.,
770 2022. Wildlife hair as bioindicators of metal exposure. Biol. Trace Elem. Res.
771 <https://doi.org/10.1007/s12011-021-03074-6>
- 772 Stein, A., Gerstner, K., Kreft, H., 2014. Environmental heterogeneity as a universal driver of
773 species richness across taxa, biomes and spatial scales. Ecol. Lett. 17, 866–880.
774 <https://doi.org/10.1111/ele.12277>
- 775 Stewart, L., Simonsen, C.E., Svenning, J.C., Schmidt, N.M., Pellissier, L., 2018. Forecasted
776 homogenization of high Arctic vegetation communities under climate change. J.
777 Biogeogr. 45, 2576–2587. <https://doi.org/10.1111/JBI.13434>
- 778 Thing, H., Klein, D.R., Jingfors, K., Holt, S., 1987. Ecology of Muskoxen in Jameson Land,
779 Northeast Greenland. Holarctic Ecol. 10, 95–103.

780 Tomassini, O., van Beest, F.M., Schmidt, N.M., 2019. Density, snow and seasonality lead to
781 variation in muskox habitat selection during summer. *Can. J. Zool.* 97, 997–1003.
782 <https://doi.org/10.1139/cjz-2018-0292>
783 Trueman, C.N., Chung, M.-T., Shores, D., 2016. Ecogeochemistry potential in deep time
784 biodiversity illustrated using a modern deep-water case study. *Philos Trans R Soc*
785 *Lond B Biol Sci* 371, 20150223. <https://doi.org/10.1098/rstb.2015.0223>
786 van Beest, F.M., Beumer, L.T., Chimienti, M., Desforges, J.-P., Huffeldt, N.P., Pedersen,
787 S.H., Schmidt, N.M., 2020. Environmental conditions alter behavioural organization
788 and rhythmicity of a large Arctic ruminant across the annual cycle. *R. Soc. Open Sci.*
789 7, 201614. <https://doi.org/10.1098/rsos.201614>
790 van Beest, F.M.M., Milner, J.M.M., 2013. Behavioural responses to thermal conditions affect
791 seasonal mass change in a heat-sensitive northern ungulate. *PLOS ONE* 8, e65972.
792 <https://doi.org/10.1371/journal.pone.0065972>
793 Verniest, F., Galewski, T., Julliard, R., Guelmami, A., Le Viol, I., 2022. Coupling future
794 climate and land-use projections reveals where to strengthen the protection of
795 Mediterranean Key Biodiversity Areas. *Conserv. sci. pract* 4, e12807.
796 <https://doi.org/10.1111/csp2.12807>
797



802



803

804 **Fig. 1:** A) Map of Greenland with Zackenberg valley indicated by the black square. B)

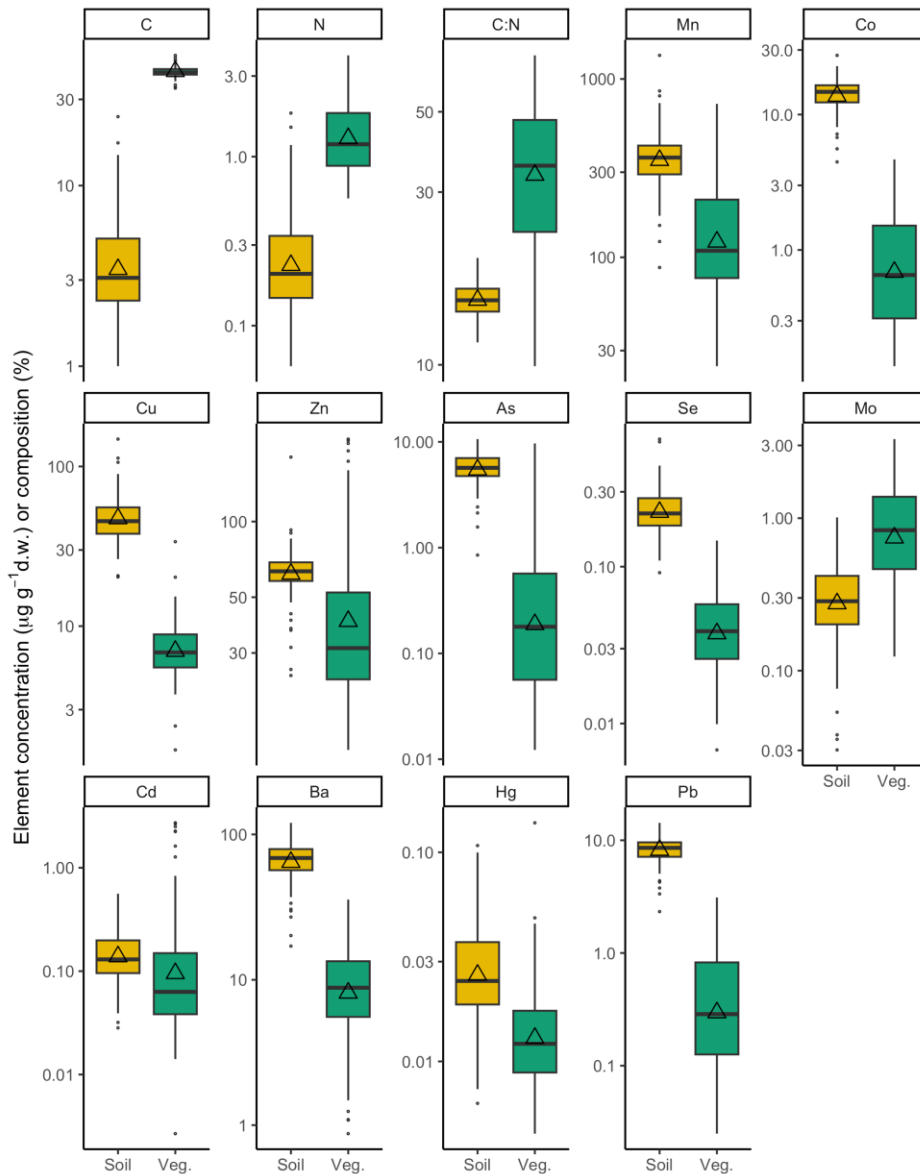
805 Elevation map of the Zackenberg valley with the locations of the 50 field plots used in this

806 study to sample plant and soil material. C) Elevation map of the Zackenberg valley with the

807 locations of muskox observations (n=3142) during summer (Jun-Sep) for the years

808 1996–2021.

809



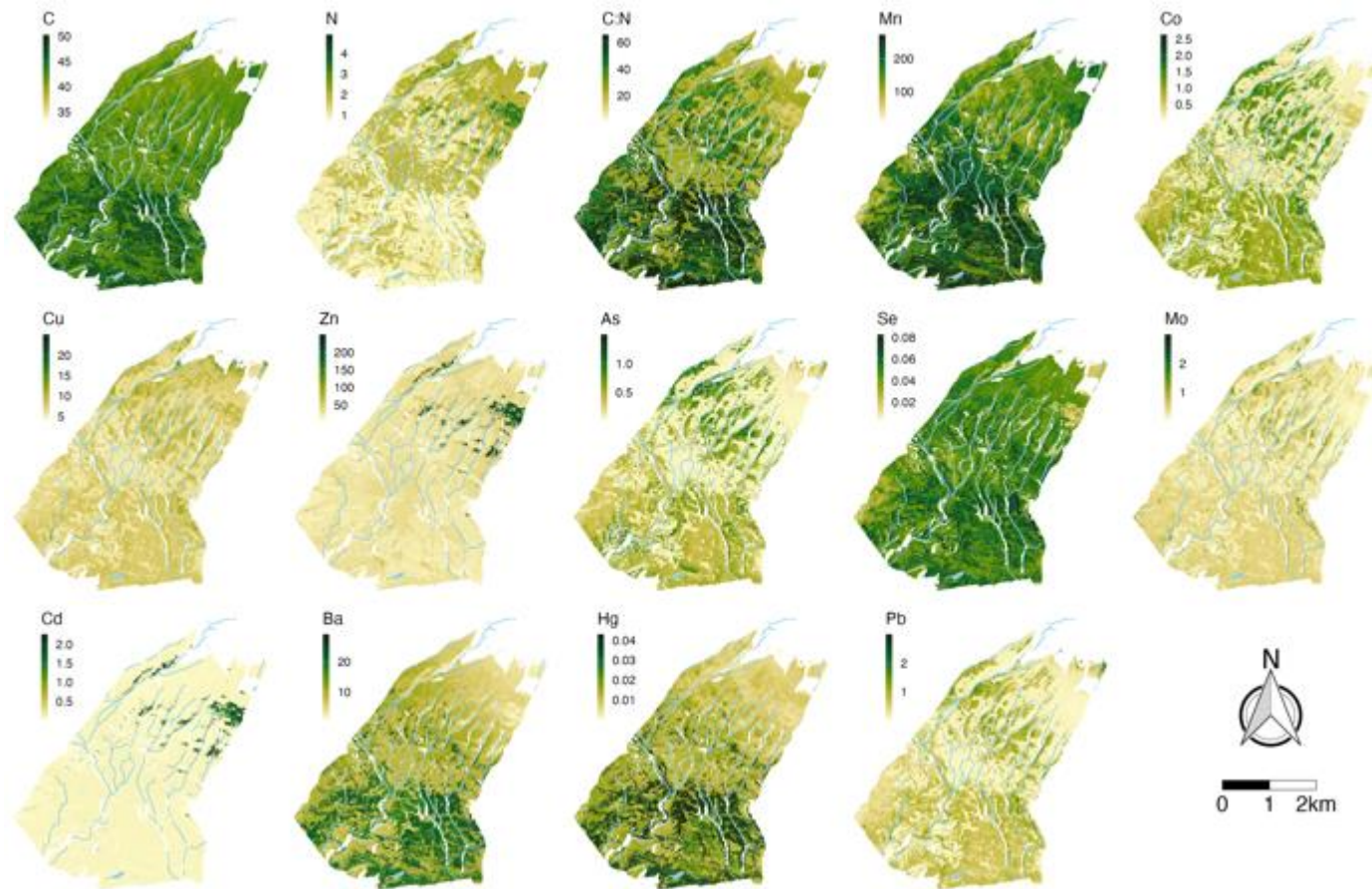
810

811 **Fig. 2:** Boxplots showing measurements of chemical elements in soil (yellow) and vegetation

812 (green) samples collected during July 2021 in the Zackenberg valley, northeast Greenland.

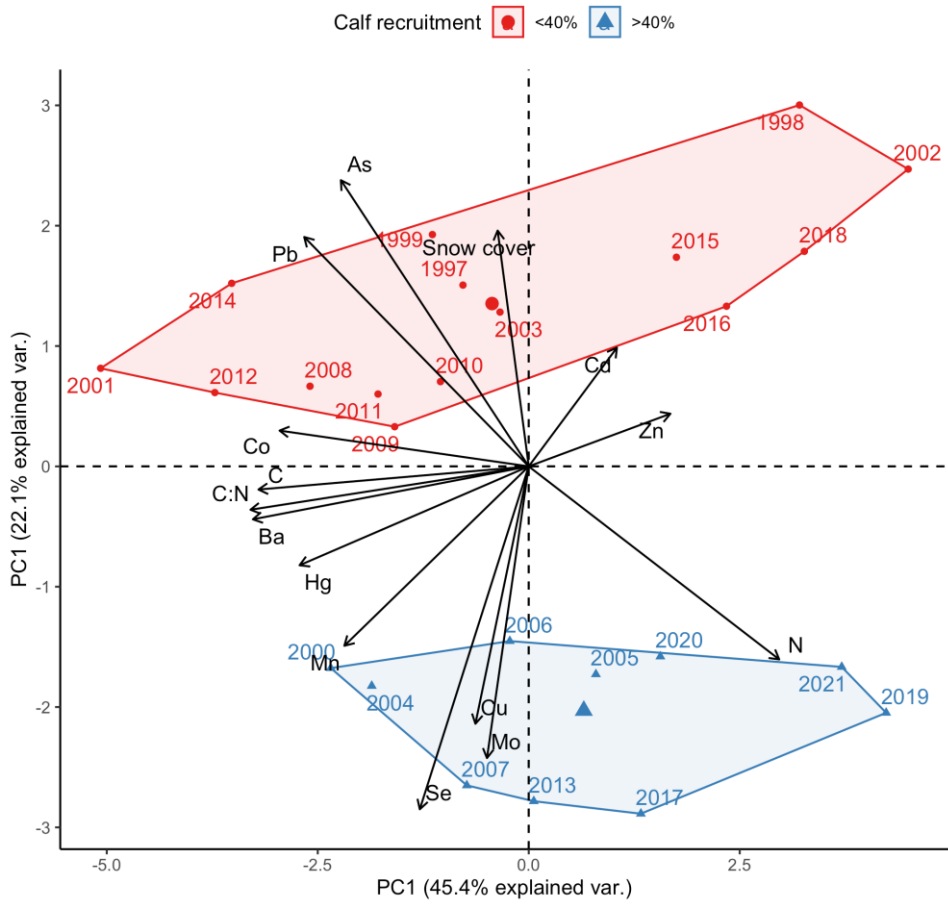
813 The triangle plotted within the box shows the mean value. Note that elements are arranged

814 based on their position in the periodic table (atomic number).



815

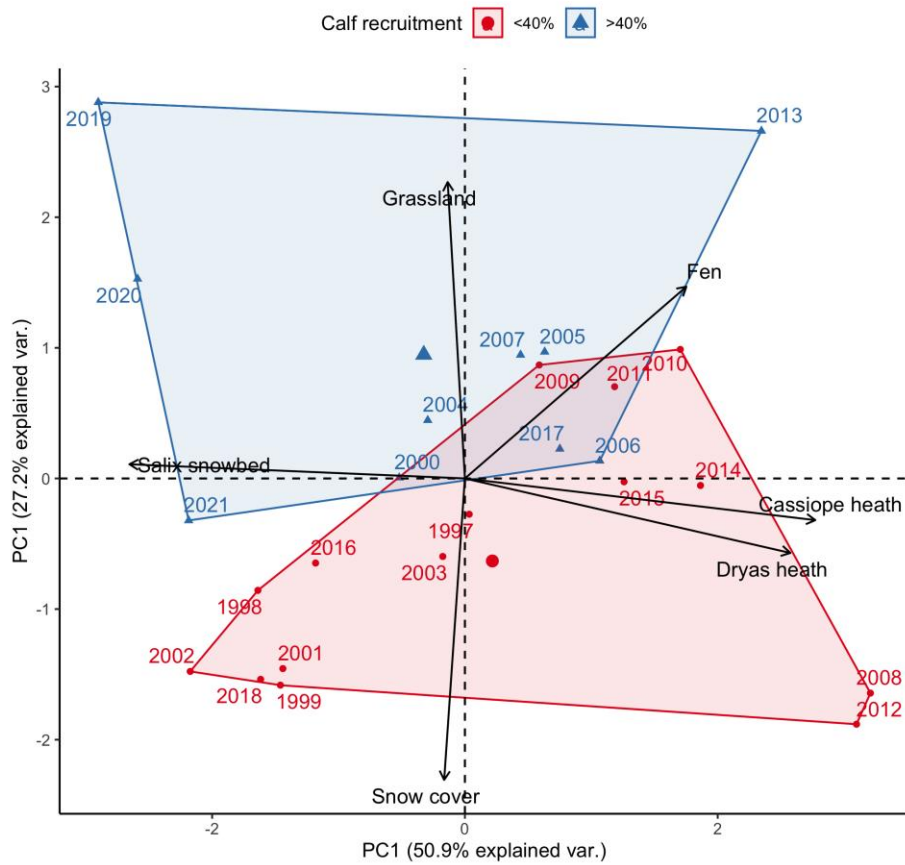
816 **Fig. 3:** Predicted spatial distribution of chemical elements in vegetation across the Zackenberg valley in northeast Greenland. The unit for C, N
 817 and C:N are in percentages while the remaining elements are in $\mu\text{g g}^{-1}$ d.w.



818

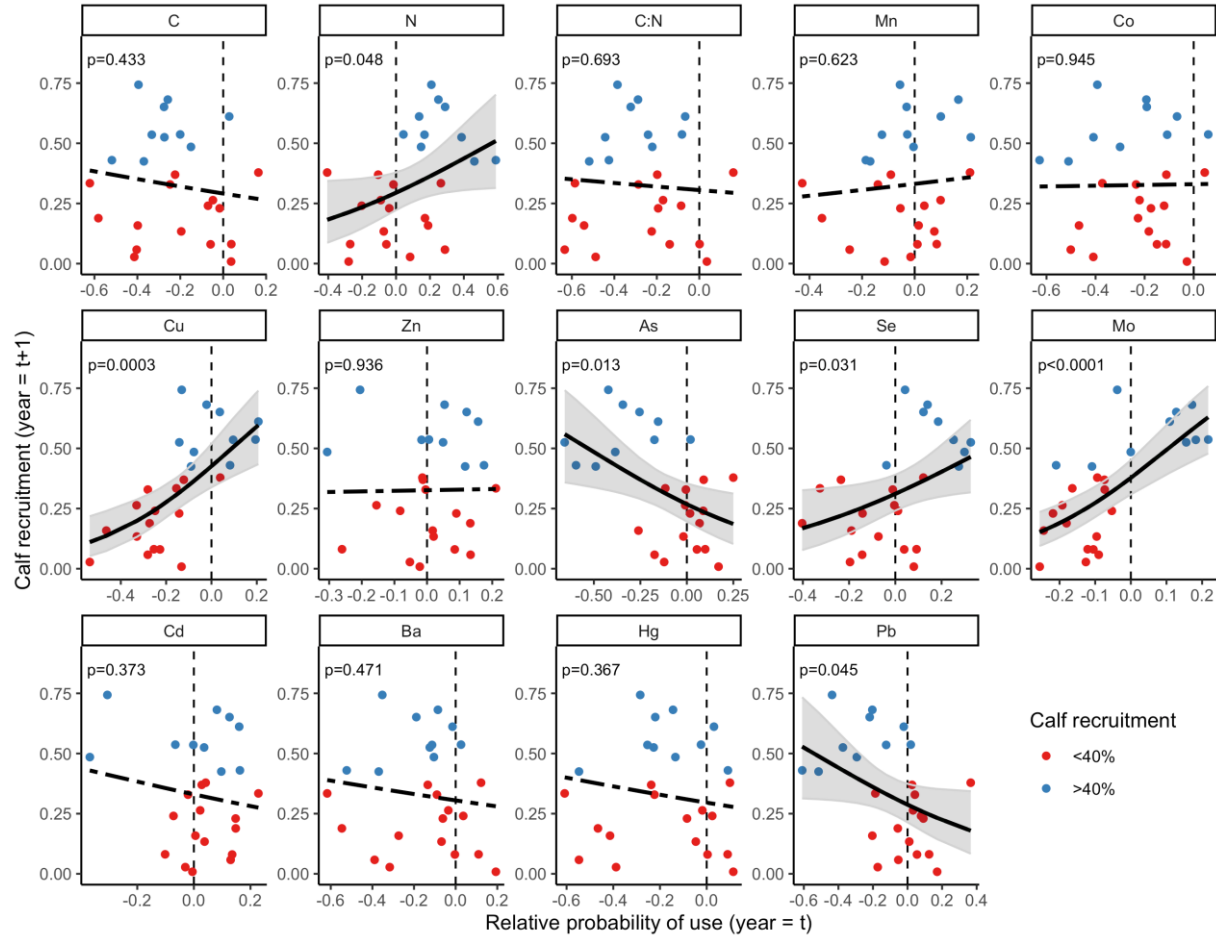
819 **Fig. 4:** Biplot showing how spring snow cover and the relative use of chemical elements in
 820 vegetated sites during summer (vectors) relate to muskox calf recruitment years in the
 821 Zackenberg valley, northeast Greenland.

822



823

824 **Fig. 5:** Biplot showing how spring snow cover and the relative use of vegetation types during
 825 summer (vectors) relate to muskox calf recruitment years in the Zackenberg valley, northeast
 826 Greenland.



827

828 **Fig. 6:** Effects of the relative probability of use of chemical elements in vegetated sites during summer (in year t) and calf recruitment (in year t
 829 $+1$) of muskoxen in the Zackenberg valley, northeast Greenland (1996-2021). Panels with solid black lines (predicted mean) and shaded areas
 830 (95% confidence intervals) indicate statistically significant relationships ($p < 0.05$), while dashed lines indicate no statistical relationships.