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Biotic interactions mediate patterns of herbivore diversity in the Arctic

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38 **ABSTRACT**

39 **Aim.** Understanding the forces shaping biodiversity patterns, particularly for groups of organisms with key
40 functional roles, will help predict ecosystem responses to environmental changes. Our aim was to evaluate the
41 relative role of different drivers in shaping diversity patterns of vertebrate herbivores, a group of organisms
42 exerting a strong trophic influence in terrestrial Arctic ecosystems. This biome, traditionally perceived as
43 homogeneous and low in biodiversity, includes wide variation in biotic and physical conditions and is currently
44 undergoing major environmental change.

45 **Location.** Arctic (including High Arctic, Low Arctic and Subarctic)

46 **Methods.** We compiled available data on vertebrate (bird and mammal) herbivore distribution at a pan-Arctic
47 scale, and used eight variables that represent the most relevant hypotheses to explain patterns of species richness.
48 We used range maps rasterized on a 100 x 100 km equal-area grid to analyse richness patterns of all vertebrate
49 herbivore species combined, and birds and mammalian herbivores separately.

50 **Results.** Overall, patterns of herbivore species richness in the Arctic were positively related to plant productivity
51 (measured with Normalized Difference Vegetation Index) and to the species richness of predators. Greater species
52 richness of herbivores was also linked to areas with higher mean annual temperature. Species richness of bird and
53 mammalian herbivores were related to the distance from the coast, with highest bird richness in coastal areas and
54 mammal richness peaking further inland.

55 **Main conclusions.** Herbivore richness in the Arctic is most strongly linked to primary productivity and the species
56 richness of predators. Our results suggest that biotic interactions, with either higher or lower trophic levels or
57 both, can drive patterns of species richness at a biome-wide scale. Rapid ongoing environmental changes in the
58 Arctic are likely to affect herbivore diversity through both impacts on primary productivity and changes in predator
59 communities via range expansion of predators from lower latitudes.

60

61 INTRODUCTION

62 Biodiversity plays a key role in maintaining the stability of ecosystems facing anthropogenic environmental
63 changes (Hautier *et al.*, 2015). In addition to the role of evolutionary processes and species dispersal, current
64 biodiversity patterns are strongly determined by environmental constraints. Understanding what shapes patterns
65 of biodiversity, particularly for groups of organisms with key functional roles in ecosystems, will improve
66 predictions about the responses of ecosystems to ongoing environmental changes. Despite recent attempts to
67 document biodiversity and to anticipate the effects of rapid and unprecedented change in the Arctic (e.g. CAFF,
68 2013), analyses of diversity patterns and especially of their drivers are still lacking for this region. Given the
69 relative simplicity of arctic food webs and the extreme abiotic conditions, the Arctic has been proposed as a model
70 for understanding the interactions between biotic and abiotic elements in ecosystem functioning. Furthermore, as
71 a temperature-limited system that is rapidly warming due to climate change, the Arctic may be regarded as a
72 bellwether for the changes to come in other systems (Post *et al.*, 2009).

73 Herbivores have a pervasive effect on the structure and dynamics of tundra ecosystems (Bråthen *et al.*, 2007;
74 Olofsson *et al.*, 2012) and can moderate the effects of climate change on plant growth (Olofsson *et al.*, 2009). The
75 composition of herbivore communities may play a crucial role in determining the impacts of herbivory on the
76 structure and dynamics of ecosystems (Ritchie & Olff, 1999) and their associated processes (Metcalf & Olofsson,
77 2015). Understanding how the diversity of herbivores varies across the Arctic can help disentangle the various
78 outcomes of plant-herbivore interactions in the tundra; something of great importance given the scope and pace
79 of change occurring in the Arctic.

80 The mechanisms behind large-scale patterns of biodiversity have been discussed by ecologists for decades, and
81 several non-exclusive hypotheses have been proposed with different levels of empirical support (**Table 1**).
82 However, the relative importance of the underlying processes may differ between specific guilds (Kissling *et al.*,
83 2012) and drivers of herbivore diversity have not been extensively investigated (but see Olff *et al.*, 2002 for
84 temperate and tropical areas). Here, we test eight explanatory variables (with their underlying hypotheses; see
85 **Table 1**) to explain large-scale geographical patterns of herbivore species richness in the Arctic. In global analyses,
86 one of the most supported hypotheses is the 'species-energy' hypothesis (Wright, 1983; Currie, 1991), which states
87 that higher energy availability, either through the amount of energy entering the system (ambient energy; 'H1a')
88 or through productivity (productive energy; 'H1b'), allows more species to coexist. Broad patterns of species
89 diversity in the Arctic, with decreasing species richness with increasing latitude, have been related to decreases in
90 primary productivity associated with lower temperatures at higher latitudes (Legagneux *et al.*, 2014). However,
91 the relative influence of ambient vs productive energy as a driver of diversity of Arctic species has not been
92 evaluated.

93 Other important drivers of species richness include environmental heterogeneity that increases the number of
94 available niches for different species to coexist and interact. Typically, two different (but potentially related)
95 aspects of environmental heterogeneity have been measured: the number of habitat types (i.e. habitat
96 heterogeneity; 'H2a', Kerr *et al.*, 2001), and the range in elevation (i.e. topographic heterogeneity; 'H2b', Kerr &
97 Packer, 1997) in an area. Topographic heterogeneity has often been used as a surrogate for microclimatic
98 conditions in broad-scale studies (Sandom *et al.*, 2013); it seems to be a strong driver of mammal species richness
99 at lower latitudes (Davies *et al.*, 2007), and may also increase local diversity of terrestrial vertebrates in the Arctic
100 (CAFF, 2013).

101 Other potential drivers of broad-scale patterns of species richness relate to historical and geographical influences,
102 edaphic factors and biotic interactions (Field *et al.*, 2009). In the Arctic, historical and geographical drivers, such as
103 colonization limitation and evolutionary effects, are likely to play a main role on patterns of species richness
104 (Davies *et al.*, 2011). Climatic oscillations in the Quaternary affected phylogeographic patterns of some arctic
105 species (Waltari & Cook, 2005) and have influenced present-day diversity patterns (Davies *et al.*, 2011). The extent
106 of ice cover since the Last Glacial Maximum (LGM) about 21,000 years ago ('H3') has influenced current patterns of
107 overall diversity (Hawkins *et al.*, 2003b) and the colonisation of particular Arctic regions (Normand *et al.*, 2013).
108 Some areas, like Beringia, acted as climatic refugia during the Quaternary and currently host the highest animal
109 and plant diversity in the Arctic. Similarly, geographical position relative to the coastline ('H4') can have an
110 influence on the distribution of terrestrial vertebrate herbivores in the Arctic, where coastal zones provide
111 important habitats for some herbivores (e.g. Ward *et al.*, 2005), but also subsidize their predators (Oksanen *et al.*,
112 2013). For example, populations of small mammalian herbivores in coastal areas can be controlled by jaegers
113 (*Stercorarius* spp.), whose populations can alternatively subsist on fish and other marine food sources (Oksanen *et al.*
114 *et al.*, 2013). Edaphic factors ('H5') can also influence the distribution of herbivore species through their effects on
115 plants. Soil pH is a main driver of vascular plant species richness in tundra (Gough *et al.*, 2000) and may thus drive
116 the diversity of its primary consumers (Jetz *et al.*, 2009).

117 The role of biotic interactions ('H6') at large spatial scales is increasingly recognized (Sandom *et al.*, 2013; Wisz *et al.*
118 *et al.*, 2013). Competition for resources and predation are the most investigated biotic interactions influencing
119 species richness, and are equally able to promote or limit herbivore diversity (Chesson & Kuang, 2008). Plant
120 productivity ('H6a') is strongly correlated to herbivore biomass and diversity in terrestrial ecosystems
121 (McNaughton *et al.*, 1989). However, more productive systems can sustain higher trophic levels that can control
122 herbivore diversity (Oksanen *et al.*, 1981). In turn, predation ('H6b') can increase herbivore species richness if it
123 reduces interspecific competition (Paine, 1966), or reduce it if predators lead to apparent competition among prey
124 (Holt, 1977). So far, the role of multi-trophic interactions in shaping broad scale patterns of herbivore diversity
125 across the Arctic has not been systematically evaluated.

126 The aim of this study is to identify patterns of herbivore diversity in the Arctic biome, and to relate these patterns
127 to their potential drivers. Previous global scale analyses on herbivores focused on specific taxonomic groups
128 (birds: Kissling *et al.*, 2012; mammals: Sandom *et al.*, 2013), or explicitly excluded the Arctic region (Olf *et al.*,
129 2002). In this study, we focus on patterns of diversity of vertebrate herbivores (birds and mammals) as a cohesive
130 guild with key functional roles in arctic ecosystems. Further, we consider the Arctic as a unit; previous analyses of
131 broad-scale diversity patterns merged the Arctic with temperate regions and consequently any patterns or drivers
132 specific to the Arctic may have been masked by those observed in more diverse temperate areas. We reviewed
133 the available data on vertebrate (bird and mammal) herbivore distribution at a pan-Arctic scale, and evaluated the
134 applicability of the most relevant hypotheses that may explain patterns of species richness at regional scales to
135 herbivores across the Arctic (**Table 1**). We analysed broad-scale patterns of herbivore species richness, and
136 repeated the analysis separately for birds and mammalian herbivores. Overall we expected species richness of
137 herbivores in the Arctic to be determined mainly by energy availability, either through temperature (H1a) or plant
138 productivity (H1b). Biotic interactions (H6) with higher and lower trophic levels may also play a role in large scale
139 patterns of herbivore diversity (Wis *et al.*, 2013). We predicted that herbivore diversity would be greater in areas
140 with higher primary productivity but had no clear expectations with regards to predator diversity. We expected
141 other drivers, such as environmental heterogeneity (H2), to play a secondary role in influencing the distributions of
142 herbivores (**Table 1**). We expected different drivers of species richness for bird versus mammalian herbivores
143 because of their different life histories and divergent adaptations. For instance, while most herbivorous birds in
144 the Arctic are migratory, only some mammalian herbivores migrate seasonally (e.g. caribou/reindeer). Most
145 mammals have other strategies to cope with the most limiting winter conditions, such as hibernation in some sub-
146 Arctic mammals. Thus, the distribution and population dynamics of Arctic-breeding migratory birds might be more
147 strongly influenced by processes occurring on their wintering grounds outside the Arctic (Ward *et al.*, 2005), while
148 diversity patterns for mammalian herbivores might be more related to local conditions and historical influences
149 (H3; Davies *et al.*, 2011) in the Arctic.

150

151 **METHODS**

152 *Patterns of herbivore species and functional group richness in the Arctic*

153 The analyses presented here are based on a database of distribution maps constructed for 73 extant vertebrate
154 herbivore species occurring in the Arctic and Subarctic (CAFF, 2013). Only herbivorous species (excluding species
155 that are predominantly frugivores and granivores) of birds (20 species) and mammals (53 species) were included
156 (**Table S2.1** in Supporting Information). Distribution data for birds (Birdlife International & NatureServe, 2013)
157 included species with breeding and non-breeding ranges in the Arctic; migratory pathways and vagrant species
158 were excluded. For mammals, distribution of resident and migratory species were included (IUCN, 2013), as well

159 as introduced and reintroduced species and domestic animals that graze in uncultivated land (such as sheep and
160 semi-domestic reindeer). The original species distribution maps consisted of polygon layers that were rasterized to
161 100x100 km grid cells to accommodate the resolution of the different information layers (see **Appendix S1** for
162 details on grain size), and were overlaid to calculate species richness for all herbivores, and separately for
163 herbivorous birds and herbivorous mammals. Grid cells comprising >50% ice covered land or water were excluded,
164 resulting in 1,227 cells for our analyses (**Figure S1.3**).

165 To assess the extent of congruence in patterns of local species richness among subgroups of herbivores (birds,
166 mammals) and between subgroups and overall herbivore diversity we calculated cross-correlations (Pearson
167 correlations) between richness patterns (Kissling *et al.*, 2012).

168 *Drivers of herbivore species richness in the Arctic*

169 The explanatory variables considered in this study (**Table 1**) represent the main hypotheses that predict species
170 richness patterns at large spatial scales. To assess the species-energy hypothesis we used mean annual
171 temperature and the Normalized Difference Vegetation Index (NDVI) as measures of ambient (H1a) and productive
172 energy (H1b), respectively. NDVI correlates strongly with net primary productivity and has been widely used as a
173 productive energy metric (Evans *et al.*, 2005). In combination with energy, water availability has been well
174 established as a driver of species richness at broad spatial scales (O'Brien, 2006), particularly for plants and at
175 lower latitudes. At high latitudes, energy variables have a stronger effect on animal species richness (Hawkins *et*
176 *al.*, 2003a), and therefore water-related variables were not included in the present study.

177 We evaluated the role of environmental heterogeneity using proxies for habitat heterogeneity (number of land
178 cover types within an area; H2a) and topographic heterogeneity (range of elevation within an area; H2b). To
179 account for historic and geographic factors we included a binary variable indicating whether an area had been
180 glaciated since the Last Glacial Maximum, approximately 21,000 yrs ago (H3; Currie, 1991; Davies *et al.*, 2007), and
181 distance to coastline (H4; Currie, 1991; Kerr & Packer, 1997). Soil pH was included as a predictor to account for
182 edaphic factors (H5). NDVI and species richness of predators of terrestrial vertebrate herbivores were used to
183 account for biotic interactions (H6) with lower and higher trophic levels, respectively. NDVI represents two non-
184 exclusive hypotheses, productive energy (H1b) and biotic interactions with lower trophic levels (H6a), and can thus
185 be interpreted from a strictly energetic point of view or as a proxy for plant-herbivore interactions. More details
186 about how each explanatory variable was obtained is provided in **Appendix S1**.

187 *Modelling approach*

188 To evaluate the relative effects of these potential drivers of herbivore diversity in the Arctic, we built Generalized
189 Least Squares (GLS) models including species richness of all herbivores, herbivorous birds and herbivorous
190 mammals as response variables. The initial (full) models included the eight explanatory variables presented above
191 as additive factors (**Table 1**): mean annual temperature (H1a), NDVI (H1b and H6a), habitat heterogeneity (H2a),

192 topographic heterogeneity (H2b), glaciation history (H3), distance to the coast (H4), soil pH (H5) and predator
193 species richness (H6b). Available raw data for each of the candidate explanatory variables were re-scaled to the
194 same grid as the species richness data (for details on sources, raw resolutions and values, and treatment of
195 explanatory variables see **Appendix S1**).

196 Univariate relationships between each explanatory variable and the responses were visually inspected for linearity
197 (**Appendix S1**). We tested for collinearity and multicollinearity among explanatory variables, using pairwise linear
198 correlations and Variance Inflation Factors (VIF). Predator species richness was correlated to NDVI ($r=0.56$);
199 therefore, to assess the relationship between predator species richness and herbivore richness, independent of
200 NDVI, we took the residuals of the regression predator richness~NDVI and included them in the models. This
201 approach assigns priority to one of the variables over the shared contribution, assuming that one variable is
202 functionally more important than the other (Graham, 2003). We checked the implications of this assumption by
203 re-running the models with the residuals of the regression NDVI~predator richness. Results were essentially the
204 same (**Appendix S3**); therefore, results presented here are from the first approach. Mean annual temperature was
205 correlated to NDVI ($r=0.42$) and soil pH ($r=-0.42$). Inclusion of mean annual temperature and NDVI in the models
206 suggested collinearity problems in the model averaging process (see below). As these variables represent different
207 aspects of the species-energy hypothesis and we were interested in assessing the relative role of each, we
208 followed the same procedure as above to statistically separate their effects, taking the residuals of the regression
209 NDVI~mean temperature. All other pairwise correlations had $r<0.4$, and VIF values for the explanatory variables
210 were <1.6 in all cases. This approach allowed us to test the direct, independent effects of the explanatory
211 variables. All explanatory variables were standardized before including them in the models, so that coefficient
212 estimates are directly comparable.

213 Spatial autocorrelation can bias estimates of environmental parameters and is of particular concern in the analyses
214 of geographical patterns of species richness when using regression models that assume independence of
215 observations (Davies *et al.*, 2007). GLS models are well suited to deal with spatially structured data, because they
216 can incorporate spatial covariance structures within the models to control for spatial autocorrelation. We fitted
217 exponential variance-covariance structures where x and y coordinates of pixel centroids were included as spatial
218 variables. Exponential structures were the best-fit choice among spatial covariance structures and including them
219 in the models effectively removed spatial autocorrelation in the residuals (**Appendix S1**).

220 Our eight explanatory variables represent non-exclusive hypotheses that have been proposed to explain species
221 richness patterns. We therefore built GLS models for all possible combinations of the 8 explanatory variables (256
222 models for each of the three response variables) and used a model averaging approach based on AIC (Akaike
223 Information Criterion) to assess the relative importance of these variables. Estimated coefficients of each variable
224 were then averaged across all models in which they were present and weighted according to the probability
225 associated to each model (see **Table S1.2** for the top-ranking models, with $\Delta AIC < 2$). Modelling assumptions,

226 including the lack of independence due to spatial autocorrelation, were checked by visually inspecting residual
227 patterns of the full models. All statistical analyses were conducted in R 3.1.2 (R Development Core Team, 2014),
228 using the libraries *AICcmodavg* and *nlme* (see **Appendix S1**).

229 Alternative analyses such as Structural Equation Modelling have been used in macroecological studies to assess
230 direct and indirect effects of different drivers of broad-scale biodiversity patterns (e.g. Kissling *et al.*, 2008; Sandom
231 *et al.*, 2013). However, these techniques cannot deal efficiently with spatial autocorrelation (e.g. coefficient shifts
232 when comparing spatial vs non-spatial models; Bini *et al.*, 2009) and in the presence of such effects (like in our
233 study, see **Appendix S4**), they can yield biased results. Our multiple regression approach using the residuals of
234 collinear variables allowed us to focus on the direct effects of explanatory variables while accounting for spatial
235 autocorrelation.

236

237 **RESULTS**

238 *Patterns of herbivore species richness in the Arctic*

239 Local species richness of vertebrate herbivores in the Arctic was low and ranged between 1 and 23 species (median
240 = 14), with peaks in diversity observed in subarctic western North America (**Figure 1a; Appendix S5**). Mammalian
241 herbivores represent 72.6% of vertebrate herbivore species in the Arctic and their species richness ranged
242 between 0 and 19 (median = 8). Species richness of mammalian herbivores also peaked in subarctic western North
243 America, although over a more restricted range than overall herbivore richness; mainly in eastern Beringia (**Figure**
244 **1c**). Species richness of herbivorous birds ranged between 1 and 10 species (median = 5) and was highest in
245 Eurasia, around the Ob River, and in the Siberian low Arctic east of the Lena River (**Figure 1b**).

246 The richness of mammalian herbivores showed the highest congruence ($r=0.87$) with overall herbivore species
247 richness while the richness of birds overlapped little with overall herbivore richness ($r=0.40$). Species richness of
248 birds did not overlap with that of mammalian herbivores ($r=-0.11$; **Figure S1.6**).

249 *Drivers of herbivore species richness in the Arctic*

250 Based on the associated Akaike weights, no single model had a strong support, further justifying the use of model
251 averaging procedures. For instance, the cumulative Akaike weight for models with $\Delta AIC < 2$ (**Table S1.2**) was 0.45 in
252 the case of all herbivores, 0.50 for birds and 0.53 for mammals. The 95% credibility sets, i.e. the set of models that
253 include the best approximating model with 95% confidence (cumulative Akaike weight 0.95), included 41 models in
254 the case of all herbivores, 32 for birds and 50 for mammals. Variable importance scores consistently showed NDVI
255 and predator species richness as the most important variables across herbivore groups (**Figure 2**). Mean
256 temperature was more important in the models for all herbivores than those for birds and mammals, while
257 distance to coast was important in bird and mammal models but not in the model including all herbivores.

258 Patterns of herbivore species richness in the Arctic were consistently and positively correlated with NDVI (H1a and
259 H6a) and with species richness of predators (H6b); other explanatory variables had minimal effects or affected only
260 some subgroups of herbivores (**Figure 3**). Overall species richness of herbivores was greater in warmer areas with
261 higher NDVI and with more species of predators (**Figure 3; Figure 4**). Similar patterns were observed in our
262 separate analyses of herbivorous birds and mammals. Correlations with NDVI and predator species richness were
263 stronger for mammalian herbivores than for birds (**Figure 4b,c**). Interestingly, we found contrasting effects for
264 birds and mammalian herbivores for the only other explanatory variable that affected richness: distance to the
265 coast (H4). Mammalian species richness was positively associated with areas further from the coast, whereas bird
266 species richness was maximized closer to the coast (negative effect). Glaciation history (H3) did not have a
267 significant effect on species richness of herbivores, but mammalian herbivores tended to be more diverse in areas
268 that had not been glaciated since the LGM (95% CI interval = [-0.258, 0.033]). Environmental heterogeneity
269 (topographic or habitat; H2) and soil pH (H5) had no effect for any of the groups of herbivores considered.

270

271 **DISCUSSION**

272 Our analysis of overall patterns of herbivore species richness represents the first attempt to identify the drivers of
273 diversity of a main trophic group across the Arctic biome. We found strong support for the species-energy
274 hypothesis (productive energy) and for the role of biotic interactions in shaping herbivore diversity at a pan-Arctic
275 scale, with greater herbivore species richness in areas presenting the highest NDVI and predator richness values.

276 As predicted, overall richness of herbivore species in the Arctic was highest in subarctic regions, with higher values
277 of the energy-related variables. We detected a positive effect of mean annual temperature on species richness of
278 all herbivores, but this effect was much weaker than that of productive energy, even when the effects of both
279 variables were statistically separated. Productive energy metrics, such as NDVI, integrate the variables that
280 constrain the conversion of energy to plant biomass, i.e. water and nutrient availability, temperature and light; as a
281 composite variable, NDVI would have greater explanatory power than that of mean annual temperature alone. An
282 alternative explanation for the weak correlation between mean annual temperature and herbivore diversity is that
283 other aspects of ambient energy, such as the temperature during the different seasons, are more relevant in the
284 highly seasonal Arctic environments. Further, NDVI represents both the species-energy hypothesis (productive
285 energy; H1b) and the role of biotic interactions (H6a). NDVI has successfully been used as a predictor of
286 phytomass in the Arctic (Epstein *et al.*, 2012) and to study interactions between herbivores and plants (Olofsson *et al.*, 2012; Doiron *et al.*, 2015). These hypotheses may thus be seen as two sides of the same coin, where the
287 specific mechanisms driving the positive correlation between primary productivity and herbivore diversity cannot
288 be separated (Evans *et al.*, 2005).

290 In our study, predator diversity was also related to patterns of herbivore diversity (Chesson & Kuang, 2008), with
291 consistently higher herbivore species richness in areas with higher predator species richness. The effect of biotic
292 interactions on species distributions has been generally assumed to prevail at a local scale, and its relevance at
293 regional or global scales has been neglected until recently (Wisz *et al.*, 2013; Belmaker *et al.*, 2015). Diversity in
294 adjacent trophic levels can be positively correlated simply because both trophic levels respond to the same
295 environmental factors in a similar way (Hawkins & Porter, 2003). This is not the sole explanation of the correlation
296 between herbivore and predator diversity in the Arctic, since the positive association between species richness of
297 herbivores and predators was evident even when the effect of NDVI on predator richness was statistically
298 removed. The greater variety of hunting strategies in a diverse predator community can favour increases in prey
299 species richness, as it provides opportunities for niche differentiation in anti-predator strategies of prey (Ruifrok *et*
300 *al.*, 2015). An alternative, non-exclusive explanation is that increased herbivore diversity is driving predator
301 species richness. Predator and prey species richness can be strongly associated at broad spatial scales, even when
302 the effects of other environmental drivers are taken into account (Sandom *et al.*, 2013). Bottom-up (prey-to-
303 predator) effects seem to be stronger than predator top-down forces at a global scale (Sandom *et al.*, 2013), but
304 the strength of bottom-up and top-down control of herbivore populations may also depend on primary
305 productivity (Oksanen *et al.*, 1981; Legagneux *et al.*, 2014).

306 When analysed separately, species richness of bird and mammalian herbivores showed contrasting patterns with
307 respect to distance to the coast. Higher values of mammal species richness were associated with areas farther
308 from the coast, while greater numbers of bird species were associated with coastal areas. These patterns were not
309 evident for the overall richness of herbivores, probably because the influence of distance to coast on each group of
310 herbivores more or less cancelled out. At continental scales in North America, higher species diversity of birds and
311 mammals are found in inland locations (Currie, 1991; Kerr & Packer, 1997). However, higher bird species richness
312 in coastal areas in the Arctic is likely related to the predominance of wetland birds among arctic herbivores.
313 Tundra swans and geese (13 of the 20 bird species analyzed) tend to congregate in lowland coastal areas during
314 breeding and moulting periods and their summer distribution may respond to specific requirements for breeding
315 (Ward *et al.*, 2005). The cooling effect along the coastline or less complex topographic landscapes in coastal areas
316 may be other factors involved. Additionally, coastal locations in the Arctic provide subsidies to predators from
317 marine ecosystems that can then maintain more abundant populations (Gauthier *et al.*, 2011; Therrien *et al.*,
318 2014).

319 Glaciation history, environmental heterogeneity and edaphic conditions (soil pH) had no detectable effect on the
320 observed patterns of herbivore richness. In the case of glaciation history, there was a non-significant trend
321 towards higher diversity of mammals in areas that remained ice-free. The fact that we did not detect a strong
322 signal of glaciation history might also be related to the coarse resolution of our grid cells (100 x 100 km), since
323 studies presenting strong support for the role of glaciation history have been conducted at finer spatial scales (e.g.

324 Normand *et al.*, 2013). Current distribution patterns of terrestrial mammals in the Arctic are linked to the
325 distribution of refugia that remained ice-free during the Last Glacial Maximum, and may reflect patterns of
326 colonization into newly forming tundra habitats as ice retreated during the Holocene (Waltari & Cook, 2005).
327 Historical influences on broad-scale species richness patterns might be masked by contemporary environmental
328 drivers and fine-scale analyses would be needed to resolve their influence (Hawkins *et al.*, 2003b). Moreover,
329 most herbivorous birds in the Arctic are migratory, so they may be less constrained by glacial history of an area as
330 they may more easily colonize newly deglaciated areas.

331 Our results suggest the importance of considering adjacent trophic levels when investigating patterns of herbivore
332 species richness in the Arctic and the complex nature of plant-herbivore-predator interactions. The need to
333 include biotic interactions and food-web approaches to study the functioning of changing tundra ecosystems has
334 been recently highlighted (Gauthier *et al.*, 2011; Legagneux *et al.*, 2014). Including abundance data for herbivore
335 populations would increase our understanding of the relative importance of productivity and predator-prey
336 interactions as drivers of species diversity through food-webs, but reliable information is only available for some
337 species (CAFF, 2013). Further, high-quality data on the distribution of herbivores at finer temporal and spatial
338 scales will be needed to further understand the drivers of herbivore diversity in the Arctic. For example, range
339 maps represent species distribution without a temporal reference, which might limit our ability to detect
340 environmental correlates of species richness if species are shifting ranges, as predicted under ongoing global
341 change or, at a finer temporal resolution, for migratory species. It must be kept in mind that, given the coarse
342 spatial resolution of the data available, discarding pixels that encompassed more than 50% ice-covered land in
343 100x100 km pixels results in the loss of information from many High Arctic islands (e.g. Svalbard or many islands of
344 the Canadian Arctic Archipelago). Ice and snow covered land can serve as an important habitat for a number of
345 mammal and bird species (Rosvold, 2016). Rather than implying that these areas could not function as hotspots of
346 herbivore diversity, this points to the need to develop remote-sensing products and species distribution maps with
347 a resolution better tailored to the spatial attributes of Arctic ecosystems. Despite their limitations, such large scale
348 approaches are particularly needed for the Arctic, where the land area is vast, covering more than 15,000,000 km²
349 of terrain that is often difficult to access. Regional scale indices or maps of herbivore diversity based on remote
350 sensing data (e.g. NDVI or interpolated temperature data) may inform conservation priorities (e.g. WWF RACER
351 project; [http://wwf.panda.org/what we do/where we work/arctic/what we do/climate/racer/](http://wwf.panda.org/what_we_do/where_we_work/arctic/what_we_do/climate/racer/)) or guide
352 research efforts in the Arctic.

353 It is important to understand current broad-scale patterns of diversity in Arctic ecosystems so that future changes
354 under climate warming can be detected. Our approach focusing solely on the Arctic allowed us to uncover
355 patterns that are specific to this region and that had not been detected in previous studies. For example, we found
356 that the diversity of herbivorous birds was higher in coastal areas, a pattern that contrasts with what has been
357 found at broader continental scales (i.e. higher bird diversity inland; Currie, 1991). These patterns were not evident

358 in previous studies including all biomes because global patterns are largely driven by regions with higher diversity.
359 This knowledge will also help identify diversity “hotspots” that can be protected in the face of increasing
360 commercial activity in the North. Our finding that coastal regions are centres of diversity for birds highlights the
361 importance of identifying critical areas for protection before these areas are developed for oil and gas,
362 transportation, and other human activities. Recent changes in vertebrate herbivore populations in the Arctic are
363 mostly related to local increases in abundance (CAFF, 2013), but also to distribution shifts (Gilg *et al.*, 2012). Over
364 the long term, the abundance of certain herbivores may increase, but arctic specialist species may be gradually
365 replaced by range-expanding species from the south. Such changes are likely to alter the interactions among
366 herbivores that determine the structure of their communities and, ultimately, the impacts herbivores have on
367 tundra vegetation.

368

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378

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- 489
- 490

491 **BIOSKETCH**

492 The research team is part of the Herbivory Network (<http://herbivory.biology.ualberta.ca>). The aim of this
493 international research network is to investigate the role of herbivores in arctic and alpine ecosystems. The network
494 comprises more than 100 members from different countries and at different stages of their research careers, from
495 graduate and undergraduate students to well-established scientists. In several ongoing projects, the Herbivory
496 Network uses different approaches including meta-analytical, experimental and observational studies to unveil the
497 role of herbivory in northern and alpine ecosystems. A large part of the current activity of HN is focused on
498 developing standardized protocols that will enable multi-site comparisons and coordinated experiments.

499

500 **SUPPORTING INFORMATION**

501 **Appendix S1.** Extended methods

502 **Appendix S2.** List of species

503 **Appendix S3.** Extended results

504 **Appendix S4.** Results SEM

505 **Appendix S5.** KMZ file for the maps of herbivore richness

506

507 TABLES

508 **Table 1.** Explanatory variables included in the models and underlying hypotheses that have been proposed to explain broad patterns of species richness at
 509 large spatial scales. Predictions for the role of each driver are indicated.

Hypothesis		Explanatory variables	Justification	Predictions
Energy				
	Ambient energy	Mean annual temperature (H1a)	Physiological constraints limit species richness ¹ . As mean annual temperature increases, climatic conditions are within the physiological tolerance range of more species, leading to greater species richness.	Ambient energy variables at high latitudes will dominate species richness of herbivores over productive energy ² . The effect of ambient energy at high latitudes might be stronger for mammals than birds, as shown at continental scales ³
	Productive energy	Normalized Difference Vegetation Index (NDVI) (H1b)	Limits to species richness are set by the energy flowing through food webs; herbivore diversity is limited by net primary production of plants ⁴ .	Correlates of net primary productivity may better represent the energy available to heterotrophs ^{2,5}
Environmental heterogeneity				
	Habitat heterogeneity	Number of different habitat types (H2a)	Greater habitat diversity provides increased available niche space that can be used by a greater number of coexisting species ⁶ .	Environmental heterogeneity is predicted to have a positive impact on species richness of herbivores ⁷ , probably more so in the case of non-migratory Arctic herbivores (i.e. most mammals). Topographic heterogeneity will increase local diversity of terrestrial vertebrates in the Arctic ⁸ .
	Topographic heterogeneity	Altitudinal range (i.e. difference between maximum and minimum elevation; H2b)	High rate of change in habitats along elevational gradients produces high between-habitat diversity in areas with greater topographic variability, increasing the potential for species coexistence ⁹ .	
History/geography				
		Glaciation (H3)	More time since an area has been glaciated allows for colonization by more species and speciation ¹ .	We expect mammal species richness to be constrained by glaciation history. Birds (mostly migratory) are less likely to be affected by glaciation history.
		Distance to coastline (H4)	In the Arctic distance to the coastline may play an important role in the functioning of ecosystems through the potential influence of productive marine ecosystems through subsidies on predators ¹⁰ , their lower topographic complexity and oceanicity.	Coastal areas will host lower species richness of herbivores ^{1,9} . This effect will be stronger for mammals, as many Arctic birds are wetland birds and may be positively associated to coastal areas.
	Edaphics	Soil pH (H5)	Soil pH is a main driver of vascular plant species richness in tundra ¹¹	Higher herbivore species richness is expected in less acidic substrates that host greater plant diversity. This effect will be stronger for birds than for mammals as has been shown at global scale ¹² .
Biotic interactions				

	Plant-herbivore	Primary productivity (NDVI; H6a)	Primary productivity can determine the structure and abundance of herbivores and predators, increasing resource availability ¹³	At a pan-Arctic scale more productive areas will host higher diversity of herbivores.
	Predator-herbivore	Predator species richness (H6b)	Species diversity of prey can increase as a result of predation, if predators reduce the strength of inter-specific competition ¹⁴ . Alternatively, in simple food webs, predation can reduce species diversity via apparent competition ¹⁵	Predator diversity can enhance the diversity of prey ¹⁶ . This effect might be related to diversity of body sizes ¹⁷ and we predict it will be stronger for mammalian herbivores, which represent a wider range in body sizes.

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529

530 **FIGURE LEGENDS**

531 **Figure 1.** Distribution maps of species richness of all herbivores (A), richness of herbivorous birds (B) and mammals
532 (C). Grid cells are 100x100 km in size.

533 **Figure 2.** Variable importance scores for all herbivores (green), birds (purple) and mammals (orange). The relative
534 importance of each variable is calculated summing the Akaike weights for all models in which that variable
535 appears. Variable weight can be interpreted as the probability of that variable being a component of the best
536 model, and can be used to rank the predictors in order of importance.

537 **Figure 3.** Model averaged coefficients for drivers of species richness of all herbivores (green), and bird (purple) and
538 mammalian (orange) herbivores. All predictors were standardized, so coefficients are directly comparable.
539 Coefficients were averaged across all models, and means and 95% CI are shown. Coefficients different from zero
540 (i.e. not overlapping the vertical dashed line) had a significant effect on species richness of herbivores. NDVI (R):
541 effect of NDVI independent of mean annual temperature. Predator species richness (R): effect of predator species
542 richness independent of NDVI.

543 **Figure 4.** Predicted relationship between species richness of all herbivores (a), herbivorous birds (b) and
544 mammalian herbivores (c) in the Arctic, and plant productivity (NDVI, standardized residuals; left) and species
545 richness of predators (standardized residuals; right) based on the multi-model average. Fitted lines for the partial
546 effects (with all other predictor variables set to their means) are shown; points indicate observed values with
547 random noise added to improve visualization.

548