

1 Trophic interactions and abiotic factors drive functional and phylogenetic structure of vertebrate
2 herbivore communities across the Arctic tundra biome

3 James D. M. Speed¹, Ina Åsnes Skjelbred¹, Isabel C. Barrio², Michael D. Martin¹, Dominique
4 Berteaux³, C. Guillermo Bueno⁴, Katie S. Christie⁵, Bruce C. Forbes⁶, Jennifer Forbey⁷, Daniel
5 Fortin⁸, John-Arvid Grytnes⁹, Katrine S. Hoset¹⁰, Nicolas Lecomte¹¹, Bryndís Marteinsdóttir¹²,
6 Jesper Bruun Mosbacher¹³, Áshild Ønvik Pedersen¹⁴, Virve Ravolainen¹⁴, Eileen C. Rees¹⁵, Anna
7 Skarin¹⁶, Natalya Sokolova¹⁷, Andrew H. Thornhill^{18,19}, Ingunn Tombre²⁰, Eeva M. Soininen²¹

8 **Affiliations**

- 9 1. Department of Natural History, NTNU University Museum, Norwegian University of
10 Science and Technology, NO7491 Trondheim, Norway
- 11 2. Department of Natural Resources and Environmental Sciences, Agricultural University of
12 Iceland, Árleyni 22, 112 Reykjavik, Iceland
- 13 3. Canada Research Chair on Northern Biodiversity and Centre for Northern Studies,
14 Université du Québec à Rimouski, Rimouski, Québec, Canada
- 15 4. Institute of Ecology and Earth Sciences, Department of Botany, University of Tartu, Lai
16 40, Tartu 51005, Estonia
- 17 5. Alaska Department of Fish and Game, 333 Raspberry Rd., Anchorage, AK, 99518
- 18 6. Arctic Centre, University of Lapland, P. O. Box 122, FI-96101 Rovaniemi, Finland
- 19 7. Department of Biological Sciences, Boise State University, Boise, ID 83725, USA
- 20 8. Centre d'Étude de la Forêt and Département de Biologie, Université Laval, 1045 avenue
21 de la Médecine, Pavillon Alexandre-Vachon, Québec, Québec, G1V 0A6, Canada
- 22 9. Department of Biological Science, University of Bergen, NO-5020 Bergen, Norway
- 23 10. Section of Ecology, Department of Biology, University of Turku, 20014 Turku, Finland
- 24 11. Canada Research Chair in Polar and Boreal Écologie and Centre for Northern Studies,
25 Département de Biologie, Université de Moncton, Moncton, New Brunswick E1A 3E9,
26 Canada
- 27 12. The Soil Conservation Service of Iceland, Gunnarsholt, 851 Hella, Iceland
- 28 13. Department of Ecosystem and Public Health, Faculty of Veterinary Medicine, University
29 of Calgary, 3280 Hospital Drive NW, Calgary, AB T2N 4Z6, Canada
- 30 14. Norwegian Polar Institute, Fram Centre, NO-9296 Tromsø, Norway
- 31 15. Wildfowl & Wetlands Trust, Martin Mere, Fish Lane, Burscough, Lancashire L40 0TA,
32 UK
- 33 16. Department of Animal Nutrition and Management, Swedish University of Agricultural
34 Sciences, 750 07 Uppsala, Sweden
- 35 17. Arctic Research Station of Institute of Plant and Animal Ecology, Ural Branch of Russian
36 Academy of Sciences, Labytnangi, Arctic Research Center of Yamal-Nenets Autonomous
37 District, Salekhard, Russia
- 38 18. Australian Tropical Herbarium, James Cook University, Cairns, Queensland, 4870,
39 Australia

40 19. University and Jepson Herbaria, and Dept. of Integrative Biology, University of
41 California, Berkeley, CA 94720-2465, USA.
42 20. Norwegian Institute for Nature Research NINA, Tromsø, Norway
43 21. Department of Arctic and Marine Biology, UiT, The Arctic University of Norway, 9037
44 Tromsø, Norway

45 **Author contributions:** JDMS, ICB, MDM & EMS conceived the ideas and designed the study.
46 MDM, IÅS & AHT developed the phylogeny. ICB, DB, KC, JF, DF, KH, NL, BM, JBM, ÅØP,
47 VR, ER, EMS, NS, JDMS & IT characterised the functional traits of the herbivores. EMS
48 developed the functional classification with input from ICB & JDMS. JDMS performed spatial
49 and statistical analyses with input from ICB, JAG, MDM, EMS & IÅS. The manuscript was
50 drafted by JDMS, IÅS, MDM, ICB & EMS with input from all co-authors.

51 **Correspondence:** James D. M. Speed, Norwegian University of Science and Technology, NTNU
52 University Museum Department of Natural History, 7491 Trondheim, Norway. Tel: +47
53 73592251. Email: james.speed@ntnu.no

54 ORCID ID: JDMS: orcid.org/0000-0002-0633-5595

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57

58 **Abstract**

59 Communities are assembled from species that evolve or colonise a given geographic region, and
60 persist in the face of abiotic conditions and interactions with other species. The evolutionary and
61 colonisation histories of communities are characterised by phylogenetic diversity, while
62 functional diversity is indicative of abiotic and biotic conditions. The relationship between
63 functional and phylogenetic diversity infers whether species functional traits are divergent
64 (differing between related species) or convergent (similar among distantly related species). Biotic
65 interactions and abiotic conditions are known to influence macroecological patterns in species
66 richness, but how functional and phylogenetic diversity of guilds vary with biotic factors, and the
67 relative importance of biotic drivers in relation to geographic and abiotic drivers is unknown. In
68 this study, we test whether geographic, abiotic or biotic factors drive biome-scale spatial patterns
69 of functional and phylogenetic diversity and functional convergence in vertebrate herbivores
70 across the Arctic tundra biome. We found that functional and phylogenetic diversity both peaked
71 in the Western North American Arctic, and that spatial patterns in both were best predicted by
72 trophic interactions, namely vegetation productivity and predator diversity, as well as climatic
73 severity. Our results show that both bottom-up and top-down trophic interactions, as well as
74 winter temperatures, drive functional and phylogenetic structure of Arctic vertebrate herbivore
75 assemblages.. This has implications for changing Arctic ecosystems; under future warming and
76 northward movement of predators potential increases in phylogenetic and functional diversity in
77 vertebrate herbivores may occur. Our study thus demonstrates that trophic interactions can
78 determine large-scale functional and phylogenetic diversity just as strongly as abiotic conditions.

79 Introduction

80 Since ecological communities comprise species co-occurring in space and time, the fields of
81 community ecology and biogeography have predominantly used species as units. However, recent
82 advances have demonstrated the importance of quantifying phylogenetic relatedness amongst
83 species to understand how diversity patterns are influenced by evolutionary history and
84 colonisation dynamics (Fritz and Rahbek 2012, Scherson et al. 2017, Thornhill et al. 2016). In
85 regions with short evolutionary history these patterns are shaped by geographical barriers to
86 dispersal and deep-time processes such as glacial-interglacial cycles (Ordonez and Svenning
87 2016). Meanwhile, the functional composition of species within communities, assessed using
88 functional response traits, has been applied to understand environmental drivers of community
89 assembly (Kraft et al. 2008, Lavorel and Garnier 2002). Abiotic and biotic elements of the
90 environment delimit niche space and are expected to relate to functional structure of communities.
91 Indeed the influence of abiotic factors on functional composition of communities has been
92 demonstrated (Hempson et al. 2015, Kraft et al. 2008). However, while the importance of biotic
93 interactions in determining species distributions and richness patterns has been acknowledged
94 (Sandom et al. 2013, Wisz et al. 2013), the role of biotic interactions in determining functional
95 and phylogenetic diversity patterns remains uncertain.

96 The combination of functional and phylogenetic characterisation of ecological communities
97 provides complementary and synergistic information to understanding community assembly
98 (Cadotte et al. 2013, Safi et al. 2011). The relationship between functional diversity and
99 phylogenetic diversity across species, indicates whether functional traits are divergent (differ
100 between closely related species) or convergent (similar in distantly related species) (Safi et al.
101 2011). Thus, the integration of functional ecology and phylogenetics facilitates the detection of
102 community assembly processes across environmental gradients (Cadotte et al. 2013, Pavoine et al.
103 2011, Safi et al. 2011). For example, Safi et al. (2011) showed that tropical mammal assemblages

104 had lower functional diversity than expected, suggesting higher functional redundancy and niche
105 conservatism in tropical regions than temperate regions.

106 Functional diversity within trophic levels can shape food webs and bottom-up and top-down
107 dynamics (Gravel et al. 2016, Schmitz 2017). There is also evidence that phylogenetic diversity
108 can cascade between trophic levels (Brodersen et al. 2017). Furthermore, trophic interactions have
109 been identified as key drivers of diversity patterns at macroecological scales, with bottom-up
110 relationships being particularly important (Sandom et al. 2013). Trophic interactions underpin the
111 functioning and stability of ecosystems (Estes et al. 2011, Schmidt et al. 2017) and herbivores in
112 particular are crucial links in both community and ecosystem ecology, with the composition of
113 herbivore assemblages having dramatic impacts on the functioning of ecosystems (Bakker et al.
114 2016, Ripple et al. 2015). This further highlights the importance of simultaneously assessing
115 functional and phylogenetic diversity to understand community assembly within trophic groups,
116 rather than taxonomic groups that fail to include all relevant interactions (Wilcox et al. 2018).

117 In this study we investigate how geographic, abiotic and biotic factors influence phylogenetic and
118 functional diversity of the vertebrate herbivores across the Arctic tundra biome (**Table 1**). Arctic
119 vertebrate herbivore communities comprise species as functionally dissimilar as migratory, social
120 grazers and solitary resident browsers, and as phylogenetically dissimilar as geese and ruminants.
121 This broad phylogenetic and functional variation (**Fig. 1**) is ideal for testing hypotheses relating to
122 mechanisms underpinning community assembly. Our objectives are to map spatial patterns in
123 phylogenetic and functional diversity, and functional convergence (functional similarity after
124 accounting for relatedness) of Arctic vertebrate herbivores and test three complementary
125 hypotheses and associated predictions regarding environmental factors that drive these patterns
126 (**Table 1**). We hypothesise that in Arctic vertebrate herbivores, (**H1**) phylogenetic diversity is
127 driven by geographic factors affecting post-glacial colonisation, (**H2**) functional diversity is
128 driven by abiotic and biotic factors affecting niche breadth, and (**H3**) functional convergence is
129 mostly driven by biotic factors, in particular those relating to trophic interactions (vegetation and

130 predator diversity). since forage availability and predation pressure (biotic factors) modulate the
131 abiotic environmental filtering caused by abiotic factors (Cavender-Bares et al. 2009).

132 Methods

133 Species distribution data

134 Analyses were based on a list of extant vertebrate herbivore species occurring in the Arctic and
135 Subarctic (Barrio et al. 2016). This includes herbivorous species of birds with breeding and non-
136 breeding ranges in the Arctic, as well as resident and migratory mammals. We excluded domestic
137 livestock (i.e. domestic sheep *Ovis aries*), but included both wild and semi-domesticated ranges of
138 *Rangifer tarandus* (reindeer/caribou) since the semi-domestic herds graze the native range of
139 reindeer in parts of Eurasia and the ecological impact of the two is comparable (Bernes et al.
140 2015). We included three additional species to the database of extant vertebrate herbivore species
141 (Barrio et al. 2016) with distributions overlapping the study region: *Lagopus leucura*, *Lemmus*
142 *amurensis* and *Dicrostonyx nunatakensis*. Distribution maps were obtained from the IUCN
143 RedList Database (2016) and BirdLife International & Handbook of the Birds of the World (2016)
144 following the nomenclature used by each. The semi-domesticated reindeer distribution was
145 derived from Pravettoni (2012). Maps were rasterized to a 100 km equal-area grid. In total, 20
146 species of herbivorous birds and 55 species of herbivorous mammals were included (**Supporting**
147 **Information Table S1**). The majority of cells (>99%) in the study region contained at least one
148 species of each of birds and mammals.

149 Phylogenetic characterisation of Arctic vertebrate herbivores

150 We developed a phylogeny including all Arctic vertebrate herbivore species, at a higher
151 taxonomic resolution than published phylogenies (Cooney et al. 2017, Faurby and Svenning
152 2015). The Arctic vertebrate herbivore phylogeny was developed using nucleotide sequences
153 accessed from GenBank. We used Matrix Maker (Freyman and Thornhill 2016) to search for 18
154 common, phylogenetically-informative genetic loci. Four mitochondrial markers with broad

155 coverage across the Arctic herbivore species were identified: cytochrome B (cytB), cytochrome
156 oxidase subunit 1 (COI), a highly conserved region of the 12S ribosomal RNA (12S) (Yang et al.
157 2014) and NADH dehydrogenase subunit 4 (ND4). When available, multiple sequences for each
158 species, including across subspecies, were compared and a representative sample chosen for
159 further analysis. Otherwise the longest available sequence was chosen. Five species with very
160 restricted ranges were excluded due to insufficient publicly-available sequence data: *Dicrostonyx*
161 *nelsoni*, *D. nunatakensis*, *D. unalascensis*, *D. vinogradovi* and *Lemmus portenkoi* (**Table S1**),
162 leaving a total of 70 species.

163 Sequences for each marker were aligned automatically using MAFFT version 7.305b (Kato and
164 Standley 2013) and then manually adjusted. Large autapomorphic gaps were excised from the
165 sequence alignments. Due to saturation in the cytB and COI markers, the third codon position was
166 excluded from the nucleotide alignment. The final multiple sequence alignments had the
167 following lengths: cytB: 674 bp, COI: 438 bp, 12S: 448 bp, ND4: 2365 bp. These four alignments
168 were concatenated to create a final alignment of 3925 bp (provided here
169 <https://doi.org/10.6084/m9.figshare.6165923.v1>).

170 RAxML 8.2.11 (Stamatakis 2014) was used for maximum-likelihood (ML) phylogenetic
171 inference under the general time-reversible nucleotide substitution model with Gamma-distributed
172 among-site rate variation (GTR+ Γ ; 'GTRGAMMA') and with a separate partition for each of the
173 four markers. Since the highest-likelihood tree consistently failed to recapitulate an accepted
174 phylogeny of the 70 species, a constraint tree was used. The constraint tree enforces particular
175 relationships and then determines the maximum-likelihood tree and branch lengths conforming to
176 those constraints. The multi-furcating constraint tree was based on the TimeTree knowledge-base
177 (Hedges et al. 2006) and consisted of four nodes grouping all birds, then Artiodactyla,
178 Lagomorpha, and finally the remaining species. The rapid bootstrapping algorithm was used with
179 1000 replicate alignments to determine the node confidence in the maximum-likelihood tree. The

180 resulting phylogeny is shown in **Fig. S1**; the five main clades represent the five orders of Arctic
181 vertebrate herbivores: Anseriformes, Galliformes, Lagomorpha, Rodentia and Artiodactyla.

182 Functional characterisation of Arctic vertebrate herbivores

183 To characterise the functional ecology of Arctic vertebrate herbivores we collated a suite of
184 functional traits reflecting the ecology of these species, similar to the approach used by Hempson
185 et al. (2015) to characterise African herbivores. Traits included diet, digestive system type, group
186 size, wintering strategy, mobility, habitat, population dynamics, litter size, group size and body
187 size (described in **Table S2**). We recorded each of the functional traits for all 75 Arctic vertebrate
188 herbivore species (**Table S1**). A functional trait database was populated by information from trait
189 databases EltonTraits and PanTHERIA (Jones et al. 2009, Wilman et al. 2014) and supplemented
190 by information from published literature and expert knowledge (**Table S3, Fig. S2**). Average trait
191 values across Arctic populations and subspecies were used. Most traits showed low phylogenetic
192 conservatism (**Table S4**) with the exception of digestive system type, wintering strategy and
193 mobility and habitat type.

194 Following Hempson et al. (2015), we performed a hierarchical clustering of principle components
195 on a factorial analysis of mixed data (**Table S5, Figs. S3-S4**) (R package FactoMineR, Lê et al.
196 2008). The functional classification was based on the 70 species represented in the phylogeny,
197 resulting in a dendrogram classifying the species by functional ecology (**Figs. S5-S8**). Three main
198 functional groups were apparent (1) limnic-habitat associated species migrating outside the Arctic
199 for winter typified by (paragon species closest to cluster centroid) *Anser anser* (2) hindgut-
200 fermenter, burrowing species typified by *Synaptomys borealis* and (3) large-bodied, facultative-
201 generalist species typified by *Lepus timidus*.

202 Environmental drivers of phylogenetic and functional herbivore diversity

203 The explanatory variables considered in this study represent the hypotheses that predict patterns
204 of phylogenetic and functional diversity and functional convergence. Geographic variables

205 include landscape history and zoogeographic region. Landscape history was reflected by the time
206 since glaciation using ice-cover data at 1 000-year intervals since the Last Glacial Maximum with
207 an original resolution of 1° (Peltier 1993). This was aggregated to a 100 km resolution using the
208 modal value. We used the zoogeographic regions of Holt et al. (2013), of which the North
209 American, Eurasian and Arctico-Siberian regions cover the study region.

210 Abiotic variables included climate severity and landscape heterogeneity. As a measure of the
211 severity of the climate we used the minimum temperature of the coldest month (WorldClim
212 bioclimate variable BIO6, Fick and Hijmans 2017, O'Donnell and Ignizio 2012) as this variable
213 was assumed to be most limiting to vertebrate survival in Arctic environments. The original data
214 had a spatial resolution of 10'; these were aggregated to a 100 km grid using the mean value.

215 Landscape heterogeneity variables included habitat and topographic heterogeneity. Habitat
216 heterogeneity was calculated as the number of land cover types within the GlobCover dataset (one
217 degree resolution, Bontemps et al. 2011) present within a 100 x 100 km pixel. Topographic
218 heterogeneity was calculated based on the GLOBE digital elevation model with an original 1 km
219 spatial resolution (Hastings et al. 1999). The standard deviation of the elevation within 100 km
220 grid cells was used as a measure of heterogeneity to reflect topographical barriers to dispersal.

221 Both bottom-up and top-down trophic interactions were characterised. Vegetation productivity
222 was used as a bottom-up trophic variable and was represented using a circumpolar NDVI
223 (Normalised Vegetation Difference Index) map (CAVM Team 2003). The NDVI map had a
224 spatial resolution of 1 km and was aggregated to a 100 km resolution using the mean value. Top-
225 down trophic interactions were characterised by the species richness of predators of terrestrial
226 vertebrate herbivores, updated from Barrio *et al.* (2016) to include a total of 36 species (**Table**
227 **S6**). All explanatory variables were sampled onto the same raster grid used for the diversity
228 measures.

229 Data analysis

230 *Spatial patterns of phylogenetic and functional diversity*

231 Phylogenetic and functional diversity were calculated by summing the branch lengths represented
232 by the species present in each cell of the phylogenetic tree and functional dendrogram
233 respectively, including the root of the tree (Faith's (1992) phylogenetic diversity concept and its
234 functional equivalent (Pavoine and Bonsall 2011, Petchey and Gaston 2002)). Species richness of
235 Arctic vertebrate herbivores was investigated by Barrio et al. (2016) and is not part of the
236 hypotheses investigated in the current study; however, it is re-estimated here to complement the
237 other diversity measures since the list of included species differs. All diversity measures were
238 calculated in the 1399 100 km grid cells that are not currently more than 50% ice covered and
239 with species richness greater than one. Functional convergence was estimated as the additive-
240 inverse of the residuals of the relationship between functional diversity and log phylogenetic
241 diversity (consistent with a model of constrained functional trait evolution, Fig. 2d, Tucker et al.
242 2018). This interprets a negative residual (lower functional diversity than average for given
243 phylogenetic diversity) as a functionally converged assemblage.

244 Phylogenetic and functional diversity were estimated across the study communities using the
245 picante package (Kembel et al. 2010) running in R (v.3.4.2, R Core Team 2017). Species richness,
246 phylogenetic diversity and functional diversity are all visualised as the proportion of the total
247 (number of species, or branch lengths) present in the Arctic vertebrate herbivore data set (70
248 species).

249 *Effect size and significance*

250 Since functional and phylogenetic diversity increase with species richness (each species adds a
251 branch on the phylogenetic or functional dendrogram), we also estimated the difference between
252 observed diversity (functional and phylogenetic) and the expected diversity given the species
253 richness of each cell. Expected diversity was estimated by randomly shuffling species across the
254 phylogenetic and functional classification trees over 1000 iterations, while maintaining species

255 richness. Expected functional convergence was estimated by randomizing the species occurrence
256 matrix while maintaining species richness, and functional convergence estimated based on the
257 phylogenetic and functional diversity of each of the 1000 simulated communities. Standardised
258 effect sizes were estimated as the difference in the observed diversity and the mean expected
259 diversity, divided by the standard deviation of the expected diversity (Mishler et al. 2014, Webb et
260 al. 2008). Cells where the observed diversity was ranked in the top or bottom 2.5% of the
261 randomized values were classed as having significantly higher or lower diversity than expected
262 (two-tailed $P < 0.05$).

263 *Drivers of diversity*

264 We used generalised least square (GLS) models to evaluate the relative effects of the geographic,
265 abiotic and trophic variables on Arctic vertebrate herbivore diversity (phylogenetic diversity,
266 functional diversity and functional convergence). Global (full) models included all univariate
267 independent variables (see **Fig. S9**) with zoogeographical region included as a factorial variable.
268 Dependent variables were standardised as the residuals of the relationship with species richness
269 (linear relationship for phylogenetic diversity and functional convergence, log species richness for
270 functional diversity, **Fig. 2**). Independent variables were centred and scaled before including them
271 in the models to make coefficient estimates directly comparable. Collinearity between explanatory
272 variables was assessed using pairwise linear correlations and multicollinearity using variance
273 inflation factors (**Fig. S10, Table S7**). Predator species richness was correlated with vegetation
274 productivity ($r = 0.80$); therefore we included the residuals of the regression between predator
275 richness and vegetation productivity in the models (Barrio et al. 2016). This approach assigns
276 priority to one of the variables over the shared contribution, assuming that one variable
277 (vegetation productivity) is functionally more important than the other (Graham, 2003). All other
278 pairwise correlations had $r < 0.40$. Due to the presence of spatial autocorrelation, we incorporated
279 spatial covariance structures within the GLS models. We used exponential variance-covariance
280 structures including coordinates of cell centroids as spatial variables (**Fig. S11**), since this was

281 optimal for accounting for spatial autocorrelation in the Arctic vertebrate herbivore dataset (Barrio
282 et al. 2016).

283 We used a model averaging approach based on AIC (Akaike Information Criterion) to assess the
284 relative importance of each variable. Estimated coefficients of each variable were averaged across
285 all models (ranging from the null to the full model) and weighted according to the probability
286 associated with each model. Models were developed using the R packages nlme (Pinheiro et al.
287 2017) and MuMIn (Barton 2016).

288 Results

289 Spatial patterns of phylogenetic and functional diversity

290 Phylogenetic diversity increased linearly with species richness (coefficient of 1.38 ± 0.02 , **Fig.**
291 **2a**), while functional diversity saturated at intermediate levels of both species richness and
292 phylogenetic diversity (coefficient of 0.200 ± 0.002 against log species richness and 0.340 ± 0.003
293 against log phylogenetic diversity; **Fig. 2b-c**). The effect of species richness on functional
294 convergence was low (linear slope = -0.0008 ± 0.0002 , **Fig. 2d**).

295 Arctic herbivore richness, phylogenetic diversity and functional diversity (**Fig. 3**) were all highest
296 in the Western Nearctic, in particular around the Mackenzie Mountains and Interior Alaska.

297 Functional diversity was most evenly spread around the Arctic tundra biome, with a high
298 proportion (median 0.87, interquartile range 0.84-0.90) of the total functional branch lengths
299 being found across the Arctic. Species diversity was less evenly spread, any given cell having a
300 low proportion of the total species pool (median 0.21, interquartile range 0.14-0.25). The
301 distribution of phylogenetic diversity was intermediate with just under half of the phylogenetic
302 branch lengths being represented across most of the Arctic (median 0.44, interquartile range 0.41-
303 0.50). Functional convergence peaked in the Canadian Arctic archipelago and sub-Nearctic and
304 was lowest in Iceland and continental Nunavut (**Fig. 3**).

305 The phylogenetic diversity in the North American Subarctic was significantly greater than
306 expected given a random distribution of species, with standardised effect sizes between 2 and 3
307 standard deviations. In parts of the Russian low and high Arctic, the phylogenetic diversity was 1
308 to 2 standard deviations lower than expected (**Fig. 4**). Functional diversity was significantly
309 higher than expected in limited regions of the North American Arctic (65 cells in total, by around
310 1 standard deviation; **Fig. 4**). Victoria Island and subarctic Québec were both host to more
311 functionally converged herbivore communities than expected by between 2 and 3 standard
312 deviations.

313 Drivers of diversity

314 After accounting for species richness, phylogenetic diversity was best predicted by trophic
315 variables, increasing with both vegetation productivity (standardised model averaged coefficient
316 $0.007 \pm$ standard error 0.002 , **Fig 5**) and predator diversity (0.005 ± 0.001). Phylogenetic diversity
317 also decreased with milder winter temperatures (-0.020 ± 0.004). These all had relative variable
318 importance (RVI) scores of >0.98 (**Fig 5**). The geographic variable of glacial history was a less
319 important driver (RVI = 0.71) while zoogeographic region and topographic and habitat
320 heterogeneity were unimportant drivers of phylogenetic diversity (RVI <0.32 , **Fig. 5a**).

321 Trophic (vegetation productivity and predator diversity) and abiotic (climate severity and habitat
322 heterogeneity) variables were the most important predictors of functional diversity (RVI >0.70 ,
323 **Fig. 5a**). Functional diversity clearly increased with predator diversity (0.004 ± 0.002 , **Fig 5b**)
324 and habitat heterogeneity (0.003 ± 0.002) and tended to increase with vegetation productivity
325 (0.006 ± 0.003) and decrease with winter minimum temperature (-0.008 ± 0.004 , **Fig. 5b**).

326 Functional convergence was most affected by habitat heterogeneity (RVI = 0.70, **Fig. 5a**) showing
327 a negative relationship (-0.002 ± 0.001). No other variables were important predictors of
328 functional convergence (RVI <0.29)

329 Discussion

330 In this study, we tested hypothesised drivers of spatial patterns in phylogenetic and functional
331 diversity of vertebrate herbivores across the Arctic tundra biome. Our results support that bottom-
332 up (plant productivity) and top down (predation) trophic interactions regulate patterns of both
333 functional and phylogenetic diversity of Arctic vertebrate herbivores along with abiotic factors.
334 This highlights that the future functioning of Arctic tundra communities and ecosystems will be
335 dependent on changes in the regulation of trophic interactions (Legagneux et al. 2014) as well as
336 climate. Our results demonstrate the importance of biotic interactions in determining functional
337 and phylogenetic diversity at a biogeographical scale.

338 Drivers of diversity

339 The importance of abiotic variables in determining community assembly may be overstated when
340 biotic factors are omitted (Kraft et al. 2015). By focussing on the entire guild of vertebrate
341 herbivores at the biome scale, our study highlights that trophic interactions with plants and
342 predators can be important drivers of functional and phylogenetic diversity of herbivore
343 assemblages. We hypothesised that phylogenetic diversity would be driven by geographical
344 factors (**H1**). Our prediction of lower phylogenetic diversity in regions with longer post-glacial
345 history (**P1.1**) was partly supported, but we did not find evidence supporting that phylogenetic
346 diversity varies between zoogeographic regions (**P1.2**). Instead, after accounting for species
347 richness, phylogenetic diversity increased with vegetation productivity and predator diversity, and
348 increased in regions with more severe climates. Previous work has shown associations between
349 evapotranspiration (as a proxy of productivity) and mammalian phylogenetic diversity (Safi et al.
350 2011), and our results show that this pattern is also apparent for Arctic herbivores. The association
351 between herbivore phylogenetic diversity and predator species richness suggests that trophic
352 interactions can affect evolutionary history of vertebrate herbivores. This is consistent with
353 cascading diversification between herbivores and predators (Brodersen et al. 2017).

354 We found evidence to support our second hypothesis that functional diversity would be driven by
355 both abiotic and biotic variables (**H2**), although only some predictions were supported. Our
356 prediction of increasing functional diversity with habitat heterogeneity (**P2.2**) was supported,
357 while the evidence for increasing functional diversity with more productive vegetation (**P2.3**) was
358 equivocal. Functional diversity tended to increase with climate severity contrary to our
359 expectation **P2.1**. Finally, although we predicted that herbivore functional diversity would
360 decrease with predator species richness (**P2.4**), we found strong support for an increase in
361 functional diversity with predator richness. More productive ecosystems are expected to have a
362 higher number of trophic levels (Oksanen et al. 1981), however, positive relationships between
363 predator diversity and herbivore functional and phylogenetic diversity existed even though the
364 effect of vegetation productivity on predators had been removed prior to analyses. Although we
365 did not account for functional diversity of predators, the location of predator species on the
366 gradient of generalists to specialists will affect the degree of apparent competition (Holt and
367 Bonsall 2017) between functionally distinct herbivore species, as well as the ability for predators
368 to limit prey ranges (Holt and Barfield 2009). The greater impact of predators on herbivore
369 functional diversity than vegetation productivity suggests that vulnerability traits are under greater
370 selection than foraging traits (Gravel et al. 2016). Alternatively, the relationship between
371 herbivore functional diversity and predator species richness could reflect bottom up regulation
372 with a functionally diverse herbivore guild increasing niche availability for predators.

373 Winter minimum temperature, was an important driver of phylogenetic diversity and to a lesser
374 degree functional diversity. Higher phylogenetic diversity and functional diversity were found in
375 regions with colder winters. The increase in phylogenetic diversity in regions with cold winters
376 was surprising and may relate to disparate colonisation pathways of vertebrates to high Arctic
377 regions as observed for plants (Alsos et al. 2007), or isolation by environment or dispersal barriers
378 as has been suggested at the population level for Arctic reindeer populations (Jenkins et al. 2016,
379 Yannic et al. 2017). The presence of migratory geese at high latitude breeding sites may also be

380 behind this outcome. A reduction in functional diversity in colder regions was expected (**P2.1**)
381 due to strong physiological constraints imposed on trait expression. The lack of support for this
382 (and suggestion of an increase in colder regions) indicates that multiple traits allow for persistence
383 in regions with cold winters, for example hibernation and migration. Although we characterised
384 climatic severity in terms of winter minimum temperatures, it may be that winter climate
385 variability and the occurrence of rain-on-snow events are more important drivers of Arctic
386 herbivore communities (Hansen et al. 2013).

387 Environmental heterogeneity has been linked with species richness in previous studies (Kerr and
388 Packer 1997, Stein et al. 2014). In our study, functional diversity increased with habitat
389 heterogeneity, and herbivore communities tended to become more diverged (higher functional
390 diversity for a given phylogenetic diversity) as habitat heterogeneity increased. Similar results
391 have been reported, with plant trait variation relating to environmental variation (Stark et al.
392 2017). Functional convergence was not related to biotic variables as hypothesised (**H3**). This
393 suggests that while trophic and climatic factors determine the phylogenetic and functional
394 diversity of herbivore assemblages in the Arctic, the relationship between the two is modulated by
395 environmental heterogeneity, such that in homogenous regions, herbivore communities contain
396 species tending to have convergent traits. This is also consistent with findings from plant
397 communities at biogeographical scales (Cavender-Bares et al. 2006, Freschet et al. 2011).

398 We found some evidence for functional and phylogenetic diversity differing with landscape
399 history and between zoogeographic regions. However, our results suggest that abiotic and biotic
400 environmental conditions were stronger drivers of diversity patterns. It is possible that deep-time
401 variables other than glaciation history, for example late Quaternary climatic change, may have
402 influenced Arctic herbivore diversity patterns. For example, plant functional diversity has been
403 shown to be greater in European regions with more stable climate since the Last Glacial
404 Maximum (Ordonez and Svenning 2016). Further understanding of how historical climatic

405 changes have shaped the structure of contemporary guilds will be of value given current
406 environmental changes in the Arctic.

407 Diversity patterns

408 Phylogenetic diversity and functional diversity of Arctic vertebrate herbivores were both highest
409 in the Western North American Arctic. This corresponds to the region of the Arctic tundra biome
410 with the greatest species richness of vertebrate herbivores (Fig. 2-3, Barrio et al. 2016). This
411 pattern was mostly driven by mammalian herbivores, which represented the majority of the total
412 herbivore species. Avian herbivore diversity peaked in Western Siberia (Fig. S12). When
413 accounting for species richness, large regions of the North American Subarctic had higher
414 phylogenetic diversity than expected. This implies that the species present in the warmer parts of
415 the Nearctic are phylogenetically over-dispersed (i.e. less closely related than expected by
416 chance). This is consistent the decrease in phylogenetic relatedness with temperature seen in trees
417 in North America (Ma et al. 2016). Conversely, in some parts of the Russian Arctic, phylogenetic
418 diversity of herbivores was under-dispersed (with species more closely related than expected by
419 chance) suggesting high ecological complementarity or low levels of competition (Cavender-
420 Bares et al. 2004) in the herbivore-species poor Palaeartic.

421 Functional diversity was more evenly spread across the Arctic biome than phylogenetic diversity.
422 However, some regions of the North American Arctic had higher functional diversity than
423 expected, suggesting that species in these regions are likely to exhibit more variable functional
424 traits than expected by chance. While our study includes mammalian and avian herbivores, some
425 of which are functionally convergent, to fully understand herbivore functional diversity, non-
426 vertebrate herbivores should also be considered. Invertebrate herbivory is widespread across the
427 Arctic tundra (Barrio et al. 2017) and can interact with vertebrate herbivory (Biuw et al. 2014,
428 Olofsson et al. 2013). Patterns of trophic functional diversity may only be fully understood by
429 including both invertebrate and vertebrate herbivores in the same analysis.

430 Together, functional and phylogenetic diversity can increase our understanding of large scale
431 biodiversity patterns (Cadotte et al. 2013, Pavoine et al. 2011). Our results show that herbivore
432 assemblages are functionally convergent in Subarctic Québec and on Victoria Island, with
433 herbivore assemblages functionally more similar than expected from their evolutionary history.
434 The herbivore communities in these regions may show high convergence if assembled as a result
435 of weak environmental limitation, relaxed competition or low habitat heterogeneity (Safi et al.
436 2011).

437 Trophic interactions can influence species' ranges (Holt and Barfield 2009) and have been linked
438 to macroecological patterns in species richness (Barrio et al. 2016, Sandom et al. 2013). It has
439 been suggested that top-down trophic interactions can shape the phylogenetic structure of
440 communities by the amplification of environmental limitation, particularly where abiotic
441 conditions are more harsh (Cavender-Bares et al. 2009). In this study, we have shown that trophic
442 interactions drive both the phylogenetic and functional structure of communities across a whole
443 guild and biome.

444 Implications and summary

445 High latitude ecosystems are susceptible to environmental changes (Post et al. 2009), as climatic
446 warming, shrub advance and an influx of boreal species are driving changes in trophic dynamics
447 (Gilg et al. 2012, Legagneux et al. 2014). The observed relationships between top-down (predator
448 diversity) and bottom-up (vegetation productivity) trophic interactions and the functional and
449 phylogenetic structure of Arctic vertebrate herbivore assemblages seen in our results are
450 noteworthy. Vegetation productivity is increasing in many regions of the Arctic, characterised by
451 both northward distribution shifts and height growth of woody plants (Macias-Fauria et al. 2012,
452 Myers-Smith et al. 2015, Sturm et al. 2001). Increases in shrub cover and height will have
453 important implications for vertebrate communities and herbivory in the Arctic (Wheeler et al.
454 2017, Zhou et al. 2017). Furthermore, northward range expansions of both boreal herbivores (e.g.
455 moose, Tape et al. 2016) and predators (e.g. red fox; Elmhagen et al. 2017) are also occurring.

456 Taken together, these top-down and bottom-up changes are likely to increase the functional and
457 phylogenetic diversity of herbivore assemblages.

458 The interface of community ecology and biogeography has facilitated efforts to understand the
459 environmental drivers of the phylogenetic and functional structure of communities at large spatial
460 scales (Hempson et al. 2015, Thornhill et al. 2017, Violle et al. 2014). These efforts have largely
461 focussed on abiotic variables, and climatic factors in particular (Safi et al. 2011, Voskamp et al.
462 2017). However, our findings propose that trophic interactions can drive both phylogenetic and
463 functional structure of trophic guilds just as strongly as abiotic conditions. Thus, our study calls
464 for inclusion of biotic interactions in empirical studies of functional and phylogenetic structure of
465 communities.

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475 Supporting Information

- 476 • Appendix S1 Supplementary methods and results
- 477 • Appendix S2 Multiple sequence alignment of markers COI, cytB, 12S, and ND4. The file
478 is in FASTA format. Provided here <https://doi.org/10.6084/m9.figshare.6165923.v2>
- 479 • Appendix S3 Herbivore diversity maps as GIS layers. Provided here
480 <https://doi.org/10.6084/m9.figshare.6165923.v2>

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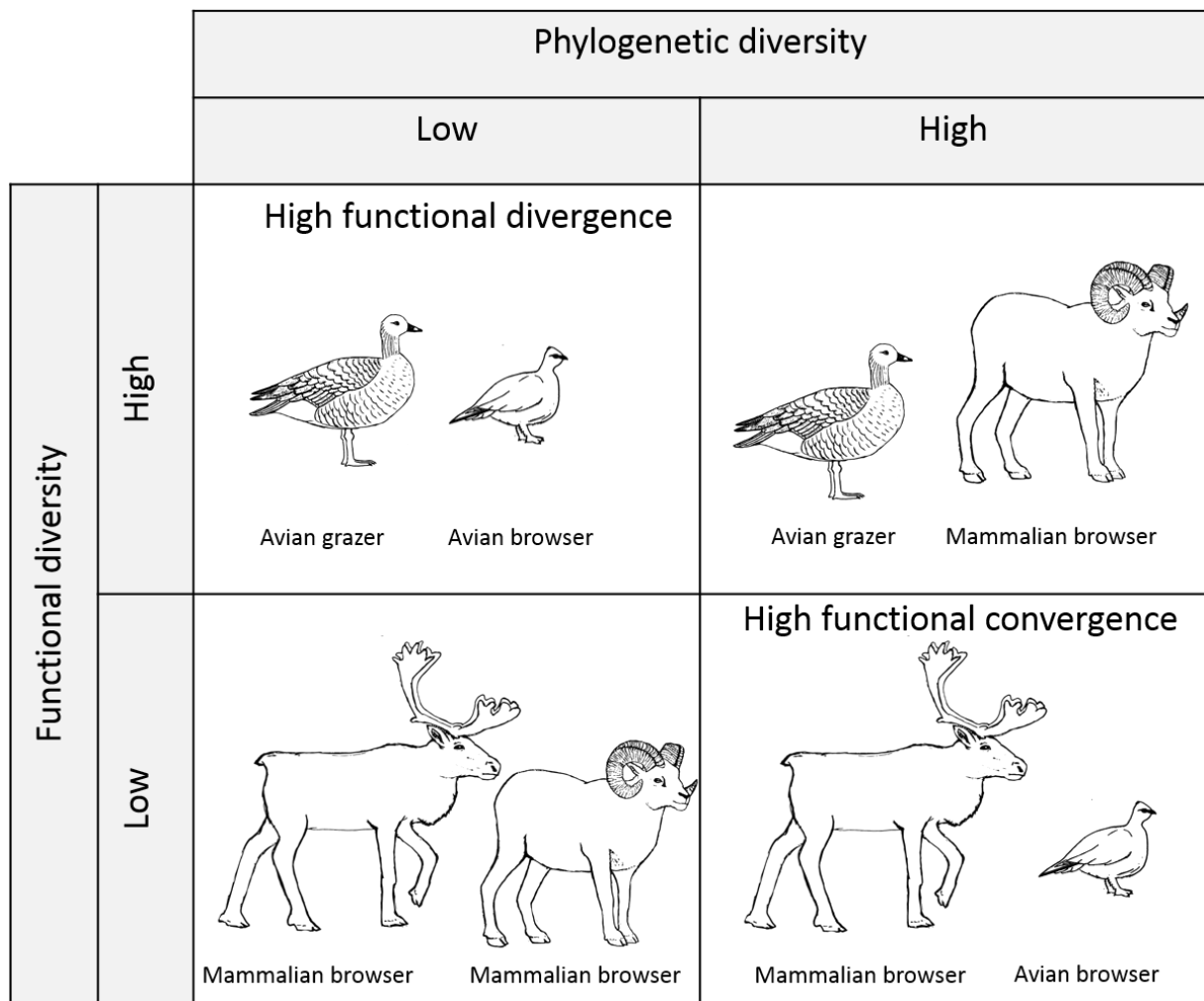
661 Table 1. Hypotheses and predictions for environmental drivers of vertebrate herbivore diversity
 662 across the Arctic tundra biome

Hypotheses	Predictions and rationale
<p>H1 Phylogenetic diversity is driven by geographic factors</p>	<p>P1.1 Phylogenetic diversity is lower in regions with shorter post-glacial history. Rationale: Lower recolonization of more recently de-glaciated regions (Voskamp et al. 2017)</p> <p>P1.2 Phylogenetic diversity differs between zoogeographical regions. Rationale: Dispersal barriers limit some clades to some zoogeographic regions (Eiserhardt et al. 2013)</p>
<p>H2 Functional diversity is driven by both abiotic and biotic factors</p>	<p>P2.1 Functional diversity decreases with increasing climatic severity. Rationale: Severe climates impose physiological constraints on trait expression (Reymond et al. 2013)</p> <p>P2.2 Functional diversity increases with topographic and habitat heterogeneity. Rationale: More varied environments provide greater niche space (Stark et al. 2017)</p> <p>P2.3 Functional diversity increases with vegetation productivity. Rationale: Higher vegetation productivity provides greater resource availability and diversifies canopy niches (Safi et al. 2011)</p> <p>P2.4 Functional diversity decreases with predator diversity. Rationale: Predation drives ecological overlap between herbivore species by constraining herbivore diet and body size (in the absence of predators herbivores communities will comprise species different in functional traits) (Schmitz 2017)</p>

<p>H3 Functional convergence is most strongly affected by biotic factors (Cavender-Bares et al. 2009)</p>	<p>P3.1 Functional convergence of herbivores decreases with vegetation productivity. Rationale: Higher resource availability and forage diversity promote herbivore niche differentiation (when foraging traits are not phylogenetically conserved, e.g. geese and ptarmigan are grazers and browsers, Fig. 1)</p> <p>P3.2 Functional convergence of herbivores increases with predator diversity. Rationale: Traits determining vulnerability to predators are phylogenetically conserved (for example, all rodents are vulnerable to many predator species).</p>
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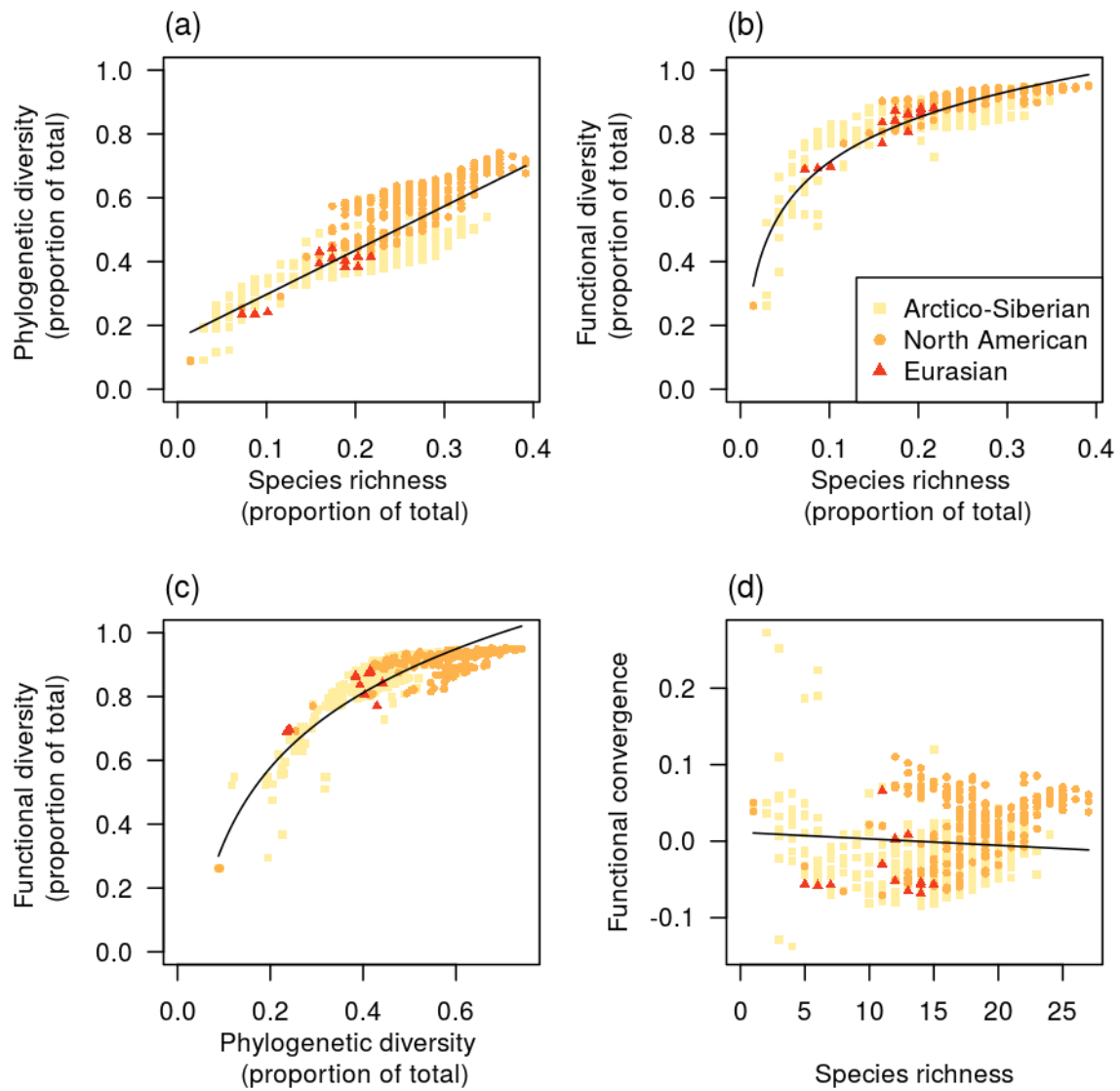
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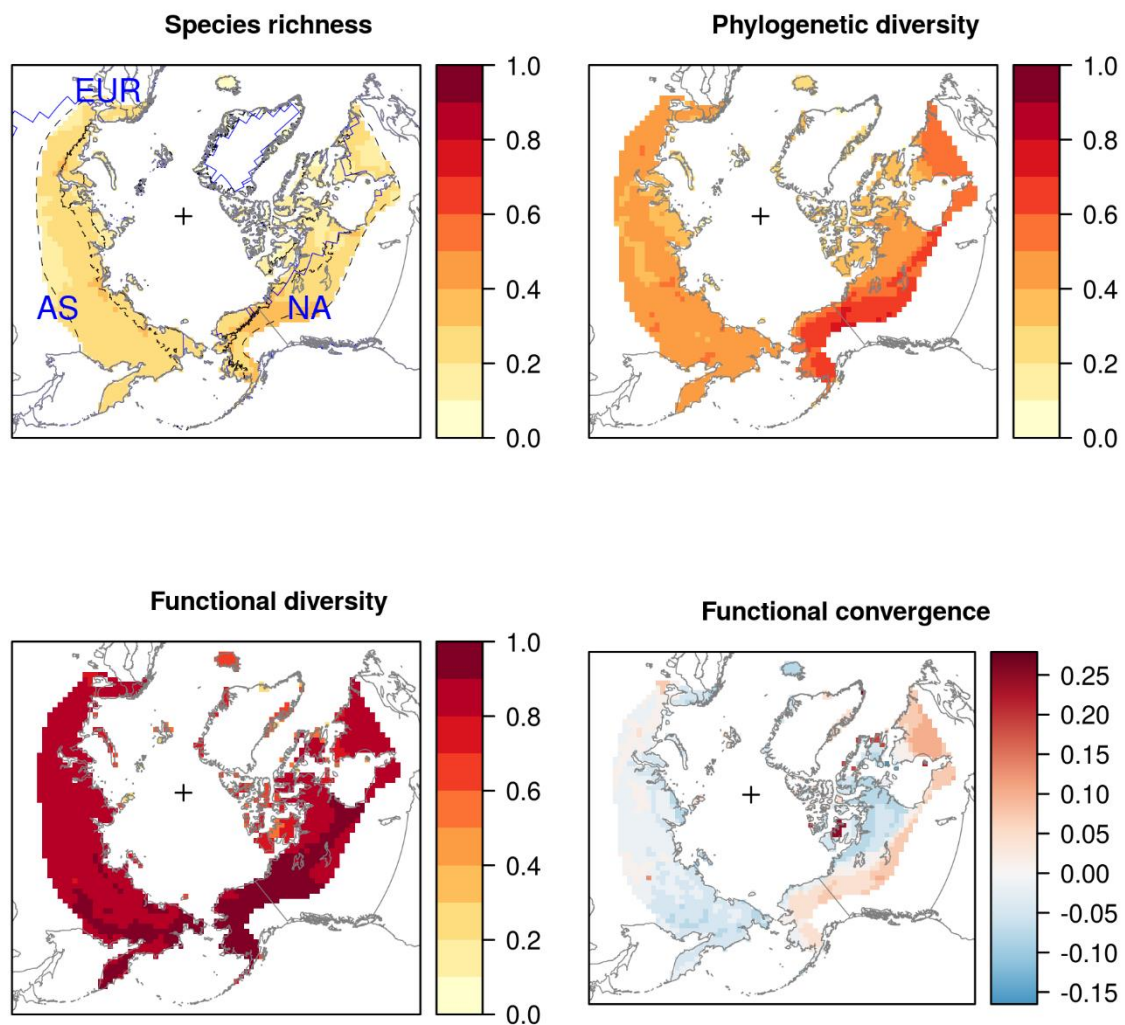
667 **Fig. 1** Hypothetical pairings of Arctic herbivores demonstrating high and low levels of functional
668 (browsers and grazers) and phylogenetic diversity (Aves and Artiodactyla) and functional
669 divergence to convergence (ratio of functional diversity to phylogenetic diversity). The species
670 illustrated are (from left in the top-left panel) *Anser brachyrhynchus* (pink-footed goose) and
671 *Lagopus muta* (ptarmigan) and (from left in the bottom-left panel) *Rangifer tarandus*
672 (reindeer/caribou) and *Ovis nivicola* (wild sheep). The sheep and reindeer are both Artiodactyla,
673 and similar sized browsers. Like the reindeer and sheep, the ptarmigan is a browser, but is
674 phylogenetically distant from Artiodactyla, hence the reindeer and ptarmigan assemblage
675 demonstrates high functional convergence. The goose and ptarmigan have very different ecologies
676 with the goose being a migratory grazer, but both are relatively phylogenetically similar within

677 Aves, demonstrating low functional convergence (high functional divergence). See Table S1 and
678 Fig. S3 for further functional and phylogenetic information on the species.



679

680 **Fig. 2** Pair-plots of the (a) species richness and phylogenetic diversity, (b) species richness and
 681 functional diversity and (c) phylogenetic diversity and functional diversity of Arctic vertebrate
 682 herbivores, each expressed as a proportion of the total. (d) The relationship between functional
 683 convergence (additive-inverse of the residuals from the regression shown in Fig3c) and species
 684 richness. In all panels, point symbols and colours represent zoogeographic regions. Linear (a, d)
 685 or log (b, d) regressions are shown.



686

687 **Fig. 3** Spatial patterns in diversity in terms of species richness, phylogenetic diversity, functional

688 diversity and functional convergence. Note species, phylogenetic and functional diversity are

689 plotted on the same colour scale. Arctic zones and zoogeographical regions are shown in the

690 species richness panel. Arctic zones (Conservation of Arctic Flora and Fauna Working Group

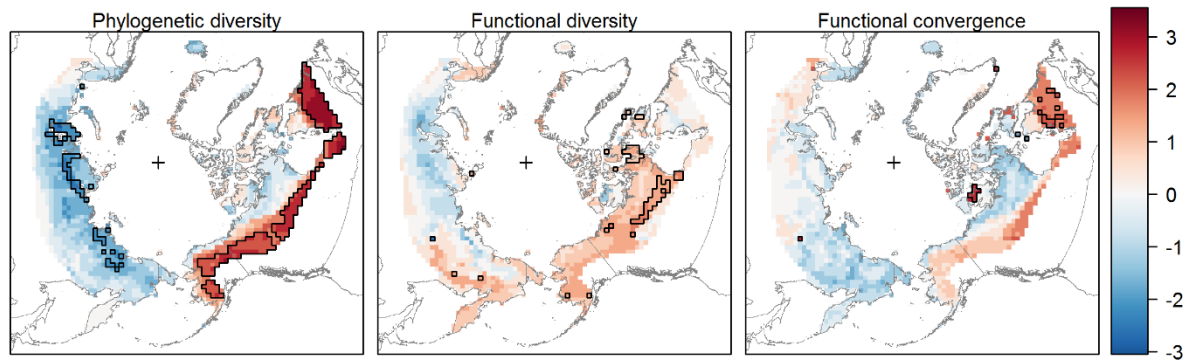
691 2010) are delimited by dotted black lines, from south to north Subarctic, low Arctic and high

692 Arctic. Zoogeographical regions (Holt et al. 2013) are delimited by solid blue lines AS – Arctico-

693 Siberian, NA – North American, EUR – Eurasian. Lambert azimuthal equal area projection.

694 Raster GIS layers of these maps are provided <https://doi.org/10.6084/m9.figshare.6165923.v2> and

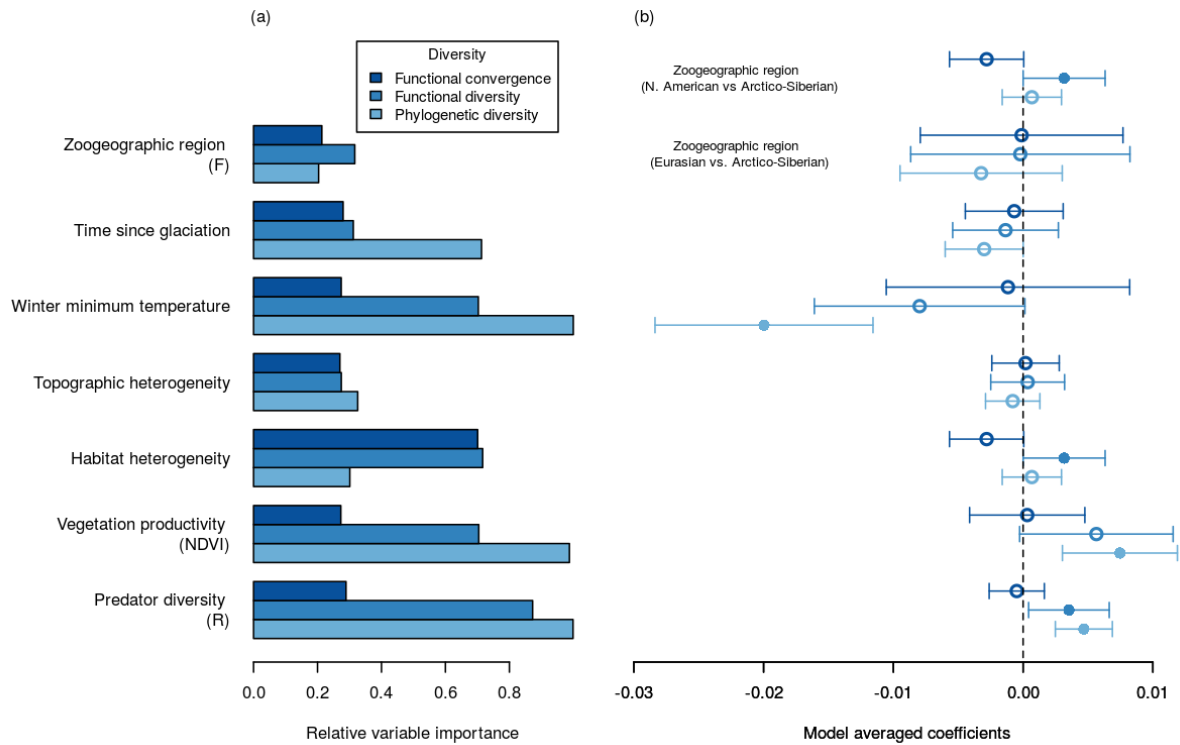
695 separate analyses for mammals and birds are shown in **Fig S12**.



696

697 **Fig. 4** Standardised effect sizes of phylogenetic and functional diversity and functional
 698 convergence. Effect sizes were estimated as the difference in observed diversity with the mean
 699 expected diversity, divided by the standard deviation expected diversity. Red colours show higher
 700 diversity (or higher convergence) than expected, while blue colours show lower diversity (or
 701 higher divergence) than expected. Outlined cells show where the effect size significantly differs
 702 from expected (two-tailed alpha = 0.05) estimated as where the observed value ranks within the
 703 top or bottom 2.5% quantiles across randomisations for each cell.

704



705

706 **Fig. 5** (a) Relative variable importance for environmental variables as predictors of different
 707 aspects of Arctic vertebrate herbivore diversity. Variable importance is interpreted as the
 708 probability of that variable being a component of the best model, and can be used to rank the
 709 predictors in order of importance. (b) Model averaged coefficients for drivers of phylogenetic
 710 diversity, functional diversity and functional convergence. All dependent variables are
 711 standardised as the residuals of the relationships with species richness (**Fig 2**). All predictors were
 712 centred and scaled so coefficients are directly comparable. Coefficients were averaged across all
 713 models, and means and 95% confidence intervals are shown. Coefficients with 95% confidence
 714 intervals not overlapping zero are shown with solid symbols and those with overlapping
 715 confidence intervals with open symbols. F indicates factorial variables, and R that the variable is
 716 the residuals of a model to reduce collinearity among pairs of variables (here between predator
 717 diversity and vegetation productivity).