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Research

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

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Communities are assembled from species that evolve or colonise a given geographic region, and persist in the face of abiotic conditions and interactions with other species. The evolutionary and colonisation histories of communities are characterised by phylogenetic diversity, while functional diversity is indicative of abiotic and biotic conditions. The relationship between functional and phylogenetic diversity infers whether species functional traits are divergent (differing between related species) or convergent (similar among distantly related species). Biotic interactions and abiotic conditions are known to influence macroecological patterns in species richness, but how functional and phylogenetic diversity of guilds vary with biotic factors, and the relative importance of biotic drivers in relation to geographic and abiotic drivers is unknown. In this study, we test whether geographic, abiotic or biotic factors drive biome-scale spatial patterns of functional and phylogenetic diversity and functional convergence in vertebrate herbivores across the Arctic tundra biome. We found that functional and phylogenetic diversity both peaked in the western North American Arctic, and that spatial patterns in both were best predicted by trophic interactions, namely vegetation

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productivity and predator diversity, as well as climatic severity. Our results show that both bottom–up and top–down trophic interactions, as well as winter temperatures, drive the functional and phylogenetic structure of Arctic vertebrate herbivore assemblages. This has implications for changing Arctic ecosystems; under future warming and northward movement of predators potential increases in phylogenetic and functional diversity in vertebrate herbivores may occur. Our study thus demonstrates that trophic interactions can determine large-scale functional and phylogenetic diversity just as strongly as abiotic conditions.

Keywords: Arctic, community structure, functional diversity, herbivory, phylogenetic diversity, trophic interactions

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Introduction

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

The combination of functional and phylogenetic characterisation of ecological communities provides complementary and synergistic information to understanding community assembly (Safi et al. 2011, Cadotte et al. 2013). The relationship between functional diversity and phylogenetic diversity across species, indicates whether functional traits are divergent (differ between closely related species) or convergent (similar in distantly related species) (Safi et al. 2011). Thus, the integration of functional ecology and phylogenetics facilitates the detection of community assembly processes across environmental gradients (Pavoine et al. 2011, Safi et al. 2011, Cadotte et al. 2013). For example, Safi et al. (2011) showed that tropical mammal assemblages had lower functional diversity than expected, suggesting higher functional redundancy and niche conservatism in tropical regions than temperate regions.

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

In this study we investigate how geographic, abiotic and biotic factors influence phylogenetic and functional diversity of vertebrate herbivores across the Arctic tundra biome (Table 1). Arctic vertebrate herbivore communities comprise species as functionally dissimilar as migratory, social grazers and solitary resident browsers, and as phylogenetically dissimilar as geese and ruminants. This broad phylogenetic and functional variation (Fig. 1) is ideal for testing hypotheses relating to mechanisms underpinning community assembly. Our objectives are to map spatial patterns in phylogenetic and functional diversity, and functional convergence (functional similarity after accounting for relatedness) of Arctic vertebrate herbivores and test three complementary hypotheses and associated predictions regarding environmental factors that drive these patterns (Table 1). We hypothesise that in Arctic vertebrate herbivores, (H1) phylogenetic diversity is driven by geographic factors affecting post-glacial colonisation, (H2) functional diversity is driven by abiotic and biotic factors affecting niche breadth, and (H3) functional convergence is mostly driven by biotic factors, in particular those relating to trophic interactions (vegetation and predator diversity). Since forage availability and predation pressure (biotic factors) modulate the abiotic environmental filtering caused by abiotic factors (Cavender-Bares et al. 2009).

Methods

Species distribution data

Analyses were based on a list of extant vertebrate herbivore species occurring in the Arctic and Subarctic (Barrio et al. 2016). This includes herbivorous species of birds with breeding and non-breeding ranges in the Arctic, as well as resident and migratory mammals. We excluded domestic livestock (i.e. domestic sheep *Ovis aries*), but included

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

Hypotheses	Predictions and rationale
H1 Phylogenetic diversity is driven by geographic factors	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)
	P1.2 Phylogenetic diversity differs between zoogeographical regions. Rationale: dispersal barriers limit some clades to some zoogeographic regions (Eiserhardt et al. 2013)
H2 Functional diversity is driven by both abiotic and biotic factors	P2.1 Functional diversity decreases with increasing climatic severity. Rationale: severe climates impose physiological constraints on trait expression (Reymond et al. 2013)
	P2.2 Functional diversity increases with topographic and habitat heterogeneity. Rationale: more varied environments provide greater niche space (Stark et al. 2017)
	P2.3 Functional diversity increases with vegetation productivity. Rationale: higher vegetation productivity provides greater resource availability and diversifies canopy niches (Safi et al. 2011)
	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 herbivore communities will comprise species different in functional traits) (Schmitz 2017)
H3 Functional convergence is most strongly affected by biotic factors (Cavender-Bares et al. 2009)	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)
	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)

both wild and semi-domesticated ranges of reindeer/caribou *Rangifer tarandus* since the semi-domestic herds graze the native range of reindeer in parts of Eurasia and the ecological impact of the two is comparable (Bernes et al. 2015). We included three additional species to the database of extant vertebrate herbivore species (Barrio et al. 2016) with distributions overlapping the study region: *Lagopus leucura*, *Lemmus amurensis* and *Dicrostonyx nunatakensis*. Distribution maps

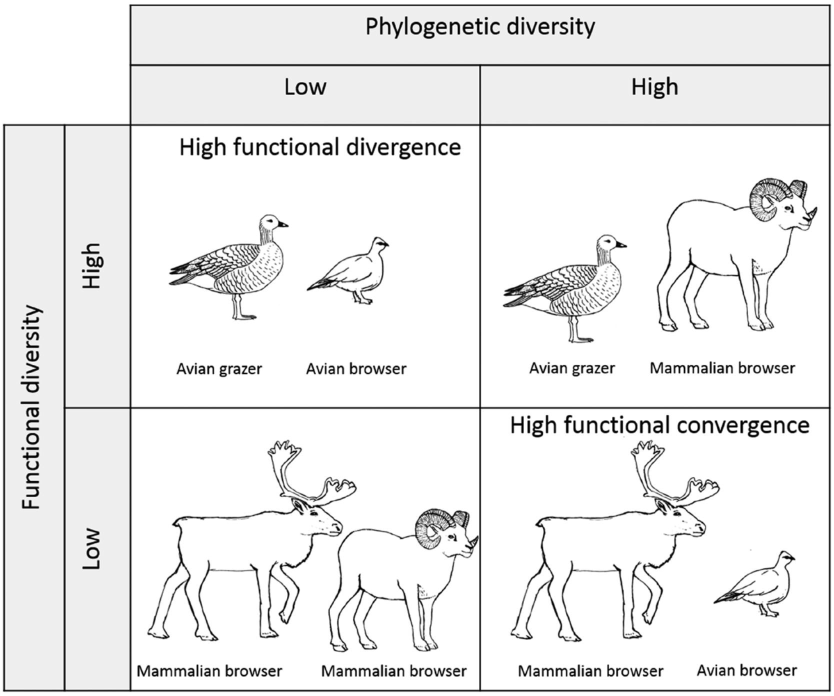

Figure 1. Hypothetical pairings of Arctic herbivores demonstrating high and low levels of functional (browsers and grazers) and phylogenetic diversity (Aves and Artiodactyla) and functional divergence to convergence (ratio of functional diversity to phylogenetic diversity). The species illustrated are (from left in the top-left panel) pink-footed goose *Anser brachyrhynchus* and ptarmigan *Lagopus muta* and (from left in the bottom-left panel) reindeer/caribou *Rangifer tarandus* and wild sheep *Ovis nivicola*. The sheep and reindeer are both Artiodactyla, and similar sized browsers. Like the reindeer and sheep, the ptarmigan is a browser, but is phylogenetically distant from Artiodactyla, hence the reindeer and ptarmigan assemblage demonstrates high functional convergence. The goose and ptarmigan have very different ecologies with the goose being a migratory grazer, but both are relatively phylogenetically similar within Aves, demonstrating low functional convergence (high functional divergence). See Supplementary material Appendix 1 Table A1, Fig. A3 for further functional and phylogenetic information on the species.

were obtained from the IUCN RedList Database (2016) and BirdLife International and Handbook of the Birds of the World (2016) following the nomenclature used by each. The semi-domesticated reindeer distribution was derived from Pravettoni (2012). Maps were rasterized to a 100 km equal-area grid. In total, 20 species of herbivorous birds and 55 species of herbivorous mammals were included (Supplementary material Appendix 1 Table A1). The majority of cells (>99%) in the study region contained at least one species of each of birds and mammals.

Phylogenetic characterisation of Arctic vertebrate herbivores

We developed a phylogeny including all Arctic vertebrate herbivore species, at a higher taxonomic resolution than published phylogenies (Faurby and Svenning 2015, Cooney et al. 2017). The Arctic vertebrate herbivore phylogeny was developed using nucleotide sequences accessed from GenBank. We used Matrix Maker (Freyman and Thornhill 2016) to search for 18 common, phylogenetically-informative genetic loci. Four mitochondrial markers with broad coverage across the Arctic herbivore species were identified: cytochrome B (cytB), cytochrome oxidase subunit 1 (COI), a highly conserved region of the 12S ribosomal RNA (12S) (Yang et al. 2014) and NADH dehydrogenase subunit 4 (ND4). When available, multiple sequences for each species, including across subspecies, were compared and a representative sample chosen for further analysis. Otherwise the longest available sequence was chosen. Five species with very restricted ranges were excluded due to insufficient publicly-available sequence data: *Dicrostonyx nelsoni*, *D. nunatakensis*, *D. unalascensis*, *D. vinogradovi* and *Lemmus portenkoi* (Supplementary material Appendix 1 Table A1), leaving a total of 70 species.

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

RAxML 8.2.11 (Stamatakis 2014) was used for maximum-likelihood (ML) phylogenetic inference under the general time-reversible nucleotide substitution model with Gamma-distributed among-site rate variation (GTR+Γ; 'GTRGAMMA') and with a separate partition for each of the four markers. Since the highest-likelihood tree consistently failed to recapitulate an accepted phylogeny of the 70 species, a constraint tree was used. The constraint tree enforces particular relationships and then determines the maximum-likelihood tree and branch lengths conforming to those constraints. The multi-furcating constraint tree was based on the TimeTree knowledge-base (Hedges et al. 2006) and consisted of four nodes grouping all birds, then Artiodactyla, Lagomorpha, and finally the remaining species. The rapid bootstrapping algorithm was used with 1000 replicate alignments to determine the node confidence in the maximum-likelihood tree. The resulting phylogeny is shown in Supplementary material Appendix 1 Fig. A1; the five main clades represent the five orders of Arctic vertebrate herbivores: Anseriformes, Galliformes, Lagomorpha, Rodentia and Artiodactyla.

Functional characterisation of Arctic vertebrate herbivores

To characterise the functional ecology of Arctic vertebrate herbivores we collated a suite of functional traits reflecting the ecology of these species, similar to the approach used by Hempson et al. (2015) to characterise African herbivores. Traits included diet, digestive system type, wintering strategy, mobility, habitat, population dynamics, litter size, group size and body size (described in Supplementary material Appendix 1 Table A2). We recorded each of the functional traits for all 75 Arctic vertebrate herbivore species (Supplementary material Appendix 1 Table A1). A functional trait database was populated by information from trait databases EltonTraits and PanTHERIA (Jones et al. 2009, Wilman et al. 2014) and supplemented by information from published literature and expert knowledge (Supplementary material Appendix 1 Table A3, Fig. A2). Average trait values across Arctic populations and subspecies were used. Most traits showed low phylogenetic conservatism (Supplementary material Appendix 1 Table A4) with the exception of digestive system type, wintering strategy and mobility and habitat type.

Following Hempson et al. (2015), we performed a hierarchical clustering of principle components on a factorial analysis of mixed data (Supplementary material Appendix 1 Table A5, Fig. A3, A4) (R package FactoMineR, Lê et al. 2008). The functional classification was based on the 70 species represented in the phylogeny, resulting in a dendrogram classifying the species by functional ecology (Supplementary material Appendix 1 Fig. A5–A8). Three main functional groups were apparent 1) limnic-habitat associated species migrating outside the Arctic for winter typified by (paragon species closest to cluster centroid) *Anser anser* 2) hindgut-fermenter, burrowing species typified by *Synaptomys borealis* and 3) large-bodied, facultative-generalist species typified by *Lepus timidus*.

Environmental drivers of phylogenetic and functional herbivore diversity

The explanatory variables considered in this study represent the hypotheses that predict patterns of phylogenetic and functional diversity and functional convergence. Geographic variables include landscape history and zoogeographic region. Landscape history was reflected by the time since glaciation using ice-cover data at 1000-year intervals since the Last Glacial Maximum with an original resolution of 1° (Peltier 1993). This was aggregated to a 100 km resolution using the modal value. We used the zoogeographic regions of Holt et al. (2013), of which the North American, Eurasian and Arctico-Siberian regions cover the study region.

Abiotic variables included climate severity and landscape heterogeneity. As a measure of the severity of the climate we used the minimum temperature of the coldest month (WorldClim bioclimate variable BIO6, O'Donnell and Ignizio 2012, Fick and Hijmans 2017) as this variable was assumed to be most limiting to vertebrate survival in Arctic environments. The original data had a spatial resolution of 10′; these were aggregated to a 100 km grid using the mean value. Landscape heterogeneity variables included habitat and topographic heterogeneity. Habitat heterogeneity was calculated as the number of land cover types within the GlobCover dataset (one degree resolution, Bontemps et al. 2011) present within a 100 × 100 km pixel. Topographic heterogeneity was calculated based on the GLOBE digital elevation model with an original 1 km spatial resolution (Hastings et al. 1999). The standard deviation of the elevation within 100 km grid cells was used as a measure of heterogeneity to reflect topographical barriers to dispersal.

Both bottom–up and top–down trophic interactions were characterised. Vegetation productivity was used as a bottom–up trophic variable and was represented using a circumpolar NDVI (normalised vegetation difference index) map (CAVM Team 2003). The NDVI map had a spatial resolution of 1 km and was aggregated to a 100 km resolution using the mean value. Top–down trophic interactions were characterised by the species richness of predators of terrestrial vertebrate herbivores, updated from Barrio et al. (2016) to include a total of 36 species (Supplementary material Appendix 1 Table A6). All explanatory variables were sampled onto the same raster grid used for the diversity measures.

Data analysis

Spatial patterns of phylogenetic and functional diversity

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

Phylogenetic and functional diversity were estimated across the study communities using the picante package (Kembel et al. 2010) running in R (ver. 3.4.2, <www.r-project.org>). Species richness, phylogenetic diversity and functional diversity are all visualised as the proportion of the total (number of species, or branch lengths) present in the Arctic vertebrate herbivore data set (70 species).

Effect size and significance

Since functional and phylogenetic diversity increase with species richness (each species adds a branch on the phylogenetic or functional dendrogram), we also estimated the difference between observed diversity (functional and phylogenetic) and the expected diversity given the species richness of each cell. Expected diversity was estimated by randomly shuffling species across the phylogenetic and functional classification trees over 1000 iterations, while maintaining species richness. Expected functional convergence was estimated by randomizing the species occurrence matrix while maintaining species richness, and functional convergence estimated based on the phylogenetic and functional diversity of each of the 1000 simulated communities. Standardised effect sizes were estimated as the difference in the observed diversity and the mean expected diversity, divided by the standard deviation of the expected diversity (Webb et al. 2008, Mishler et al. 2014). Cells where the observed diversity was ranked in the top or bottom 2.5% of the randomized values were classed as having significantly higher or lower diversity than expected (two-tailed $p < 0.05$).

Drivers of diversity

We used generalised least squares (GLS) models to evaluate the relative effects of the geographic, abiotic and trophic variables on Arctic vertebrate herbivore diversity (phylogenetic diversity, functional diversity and functional convergence). Global (full) models included all univariate independent variables (Supplementary material Appendix 1 Fig. A9) with zoogeographical region included as a factorial variable. Dependent variables were standardised as the residuals of the relationship with species richness (linear relationship for phylogenetic diversity and functional convergence, log species richness for functional diversity, Fig. 2). Independent variables were centred and scaled before including them in the models to make coefficient estimates directly comparable. Collinearity between explanatory variables was assessed using pairwise linear correlations and multicollinearity using variance inflation factors (Supplementary material Appendix 1 Fig. A10, Table A7). Predator species richness was correlated with vegetation productivity ($r = 0.80$); therefore we included the residuals of the regression between predator richness and vegetation productivity in the models (Barrio et al. 2016). This approach assigns priority to one of the variables over the shared contribution, assuming that one variable

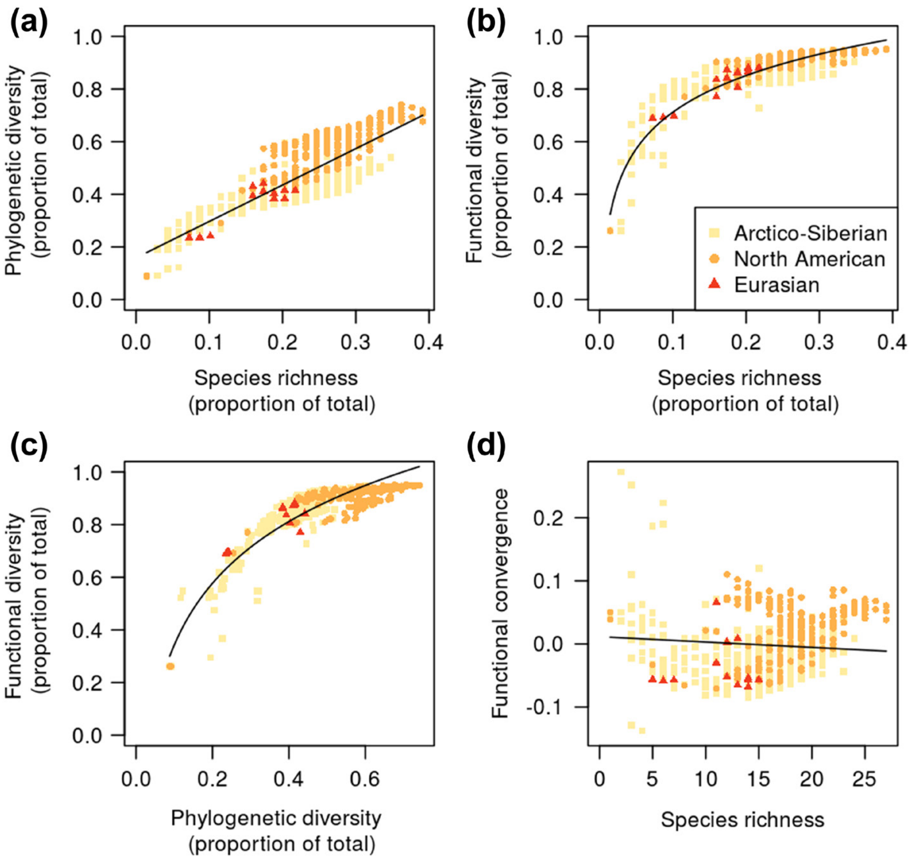

Figure 2. Pair-plots of the (a) species richness and phylogenetic diversity, (b) species richness and functional diversity and (c) phylogenetic diversity and functional diversity of Arctic vertebrate herbivores, each expressed as a proportion of the total. (d) The relationship between functional convergence (additive-inverse of the residuals from the regression shown in Fig. 3c) and species richness. In all panels, point symbols and colours represent zoogeographic regions. Linear (a, d) or log (b, d) regressions are shown.

(vegetation productivity) is functionally more important than the other (Graham 2003). All other pairwise correlations had $r < 0.40$. Due to the presence of spatial autocorrelation, we incorporated spatial covariance structures within the GLS models. We used exponential variance–covariance structures including coordinates of cell centroids as spatial variables (Supplementary material Appendix 1 Fig. A11), since this was optimal for accounting for spatial autocorrelation in the Arctic vertebrate herbivore dataset (Barrio et al. 2016).

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

Data deposition

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.4fc2591> (Speed et al. 2019).

Results

Spatial patterns of phylogenetic and functional diversity

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

Arctic herbivore richness, phylogenetic diversity and functional diversity (Fig. 3) were all highest in the Western Nearctic, in particular around the Mackenzie Mountains and Interior Alaska. Functional diversity was most evenly spread around the Arctic tundra biome, with a high proportion (median 0.87, interquartile range 0.84–0.90) of the total functional branch lengths being found across the Arctic. Species diversity was less evenly spread, any given cell having a low proportion of the total species pool (median 0.21, interquartile range 0.14–0.25). The distribution of phylogenetic diversity was intermediate with just under half

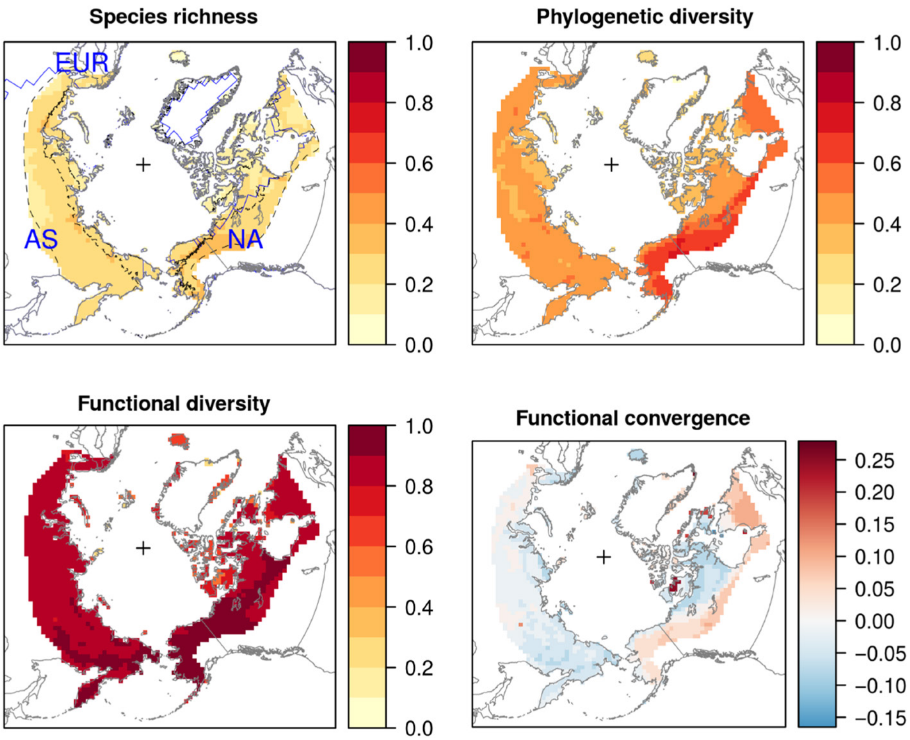

Figure 3. Spatial patterns in diversity in terms of species richness, phylogenetic diversity, functional diversity and functional convergence. Note species, phylogenetic and functional diversity are plotted on the same colour scale. Arctic zones and zoogeographical regions are shown in the species richness panel. Arctic zones (Conservation of Arctic Flora and Fauna Working Group 2010) are delimited by dotted black lines, from south to north Subarctic, low Arctic and high Arctic. Zoogeographical regions (Holt et al. 2013) are delimited by solid blue lines AS – Arctico-Siberian, NA – North American, EUR – Eurasian. Lambert azimuthal equal area projection. Raster GIS layers of these maps are provided at <https://doi.org/10.6084/m9.figshare.6165923.v2> and separate analyses for mammals and birds are shown in Supplementary material Appendix 1 Fig. A12.

of the phylogenetic branch lengths being represented across most of the Arctic (median 0.44, interquartile range 0.41–0.50). Functional convergence peaked in the Canadian Arctic archipelago and sub-Nearctic and was lowest in Iceland and continental Nunavut (Fig. 3).

The phylogenetic diversity in the North American Subarctic was significantly greater than expected given a random distribution of species, with standardised effect sizes between 2 and 3 standard deviations. In parts of the Russian low and high Arctic, the phylogenetic diversity was 1–2 standard deviations lower than expected (Fig. 4). Functional diversity was significantly higher than expected in limited regions of the North American Arctic (65 cells in total, by around 1 standard deviation; Fig. 4). Victoria Island and

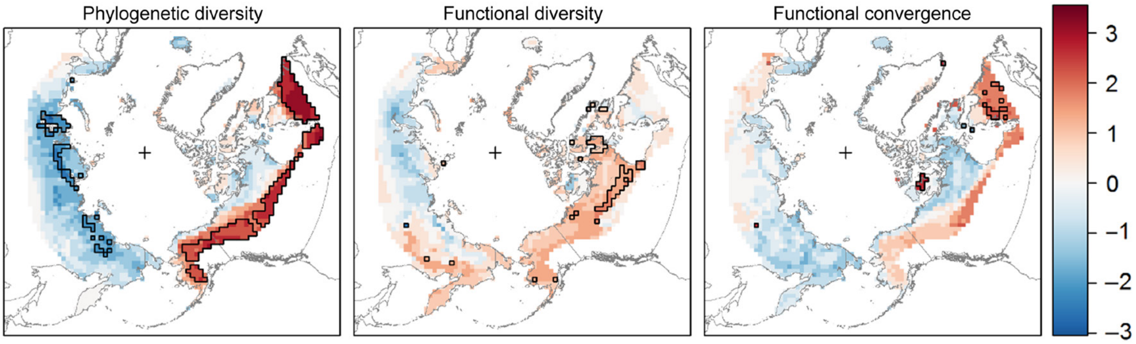

Figure 4. Standardised effect sizes of phylogenetic and functional diversity and functional convergence. Effect sizes were estimated as the difference in observed diversity with the mean expected diversity, divided by the standard deviation expected diversity. Red colours show higher diversity (or higher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

subarctic Québec were both host to more functionally converged herbivore communities than expected by between 2 and 3 standard deviations.

Drivers of diversity

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

Trophic (vegetation productivity and predator diversity) and abiotic (climate severity and habitat heterogeneity) variables were the most important predictors of functional diversity (RVI >0.70, Fig. 5a). Functional diversity clearly increased with predator diversity (0.004 ± 0.002, Fig. 5b) and habitat heterogeneity (0.003 ± 0.002) and tended to increase with vegetation productivity (0.006 ± 0.003) and decrease with winter minimum temperature (−0.008 ± 0.004, Fig. 5b). Functional convergence was most affected by habitat heterogeneity (RVI = 0.70, Fig. 5a) showing a negative relationship (−0.002 ± 0.001). No other variables were important predictors of functional convergence (RVI <0.29).

Discussion

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

Drivers of diversity

The importance of abiotic variables in determining community assembly may be overstated when biotic factors are omitted (Kraft et al. 2015). By focussing on the entire guild

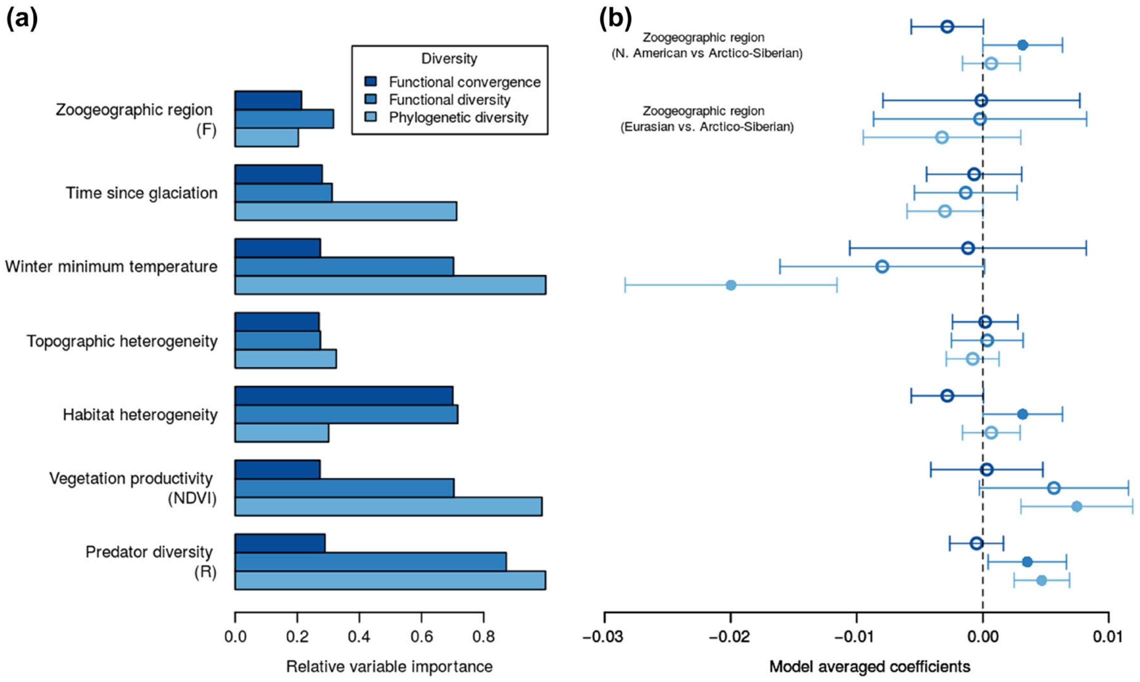

Figure 5. (a) Relative variable importance for environmental variables as predictors of different aspects of Arctic vertebrate herbivore diversity. Variable importance is interpreted as the probability of that variable being a component of the best model, and can be used to rank the predictors in order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

of vertebrate herbivores at the biome scale, our study highlights that trophic interactions with plants and predators can be important drivers of functional and phylogenetic diversity of herbivore assemblages. We hypothesised that phylogenetic diversity would be driven by geographical factors (H1). Our prediction of lower phylogenetic diversity in regions with longer post-glacial history (P1.1) was partly supported, but we did not find evidence supporting that phylogenetic diversity varies between zoogeographic regions (P1.2). Instead, after accounting for species richness, phylogenetic diversity increased with vegetation productivity and predator diversity, and increased in regions with more severe climates. Previous work has shown associations between evapotranspiration (as a proxy of productivity) and mammalian phylogenetic diversity (Safi et al. 2011), and our results show that this pattern is also apparent for Arctic herbivores. The association between herbivore phylogenetic diversity and predator species richness suggests that trophic interactions can affect evolutionary history of vertebrate herbivores. This is consistent with cascading diversification between herbivores and predators (Brodersen et al. 2017).

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

Winter minimum temperature, was an important driver of phylogenetic diversity and to a lesser degree functional diversity. Higher phylogenetic diversity and functional diversity were found in regions with colder winters. The increase in phylogenetic diversity in regions with cold winters was surprising and may relate to disparate colonisation pathways of vertebrates to high Arctic regions as observed for plants (Alsos et al. 2007), or isolation by environment or dispersal barriers as has been suggested at the population level for Arctic reindeer populations (Jenkins et al. 2016, Yannic et al. 2018). The presence of migratory geese at high latitude breeding sites may also be behind this outcome. A reduction in functional diversity in colder regions was expected (P2.1) due to strong physiological constraints imposed on trait expression. The lack of support for this (and suggestion of an increase in colder regions) indicates that multiple traits allow for persistence in regions with cold winters, for example hibernation and migration. Although we characterised climatic severity in terms of winter minimum temperatures, it may be that winter climate variability and the occurrence of rain-on-snow events are more important drivers of Arctic herbivore communities (Hansen et al. 2013).

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

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

Diversity patterns

Phylogenetic diversity and functional diversity of Arctic vertebrate herbivores were both highest in the western North American Arctic. This corresponds to the region of the Arctic tundra biome with the greatest species richness of vertebrate herbivores (Fig. 2, 3, Barrio et al. 2016). This pattern was mostly driven by mammalian herbivores, which represented the majority of the total herbivore species. Avian herbivore diversity peaked in western Siberia (Supplementary material Appendix 1 Fig. A12). When accounting for species richness, large regions of the North American Subarctic had higher phylogenetic diversity than expected. This implies that the species present in the warmer parts of the Nearctic are phylogenetically over-dispersed (i.e. less closely related than expected by chance). This is consistent the decrease in phylogenetic relatedness with temperature seen in trees in North America (Ma et al. 2016). Conversely, in some parts of the Russian Arctic, phylogenetic diversity of herbivores was under-dispersed (with species more closely related than expected by chance) suggesting high ecological complementarity or low levels of competition (Cavender-Bares et al. 2004) in the herbivore-species poor Palaearctic.

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

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

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

Implications and summary

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

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

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

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Supplementary material (available online as Appendix ecog-04347 at <www.ecography.org/appendix/ecog-04347>). Appendix 1–3.