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Science and Technology

Phylogenetic Diversity of Arctic Vertebrate Herbivores

Ina Åsnes Skjelbred

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Supervisor: James Speed, IBI
Co-supervisor: Michael David Martin, IBI

Norwegian University of Science and Technology
Department of Biology

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ABSTRACT

Understanding spatial diversity patterns, and factors shaping these patterns, is crucial for conservation planning, and is particularly important in areas undergoing severe climatic change. Traditionally, spatial diversity patterns have been investigated solely at the species-level, using measurement of *species richness*. However, using a phylogenetic approach to measure biodiversity can increase our understanding and give insight to both ecological and evolutionary processes shaping the diversity patterns we see today. This study has investigated patterns of *phylogenetic diversity* of arctic vertebrate herbivores relative to patterns of species richness, and further explored possible explanatory variables driving the ratio between these patterns.

The spatial diversity analyses were performed using *Biodiverse*, linking species distribution data and molecular data (a phylogeny) in order to calculate the phylogenetic diversity of vertebrate herbivores across the entire Arctic biome. Environmental data were collected from various data sources, based on evaluation of which parameters that may be important drivers shaping the patterns.

The results showed a strong correlation between the patterns of phylogenetic diversity and species richness in arctic vertebrate herbivores. In addition, phylogenetic diversity was revealed to be higher than species richness across the Arctic, suggesting arctic areas to represent a span across the phylogenetic tree of species investigated, even in species-poor areas. Further, several arctic islands were identified as areas containing an overrepresentation of phylogenetic diversity relative to species richness compared to the Arctic mainland. Seven out of nine environmental variables investigated were found to be relative important driving patterns of both phylogenetic diversity and species richness. Of these, plant productivity, glaciation history, temperature, precipitation, habitat heterogeneity, and human impact were found to have a negative effect of phylogenetic diversity relative to species richness. On the other hand, topographic heterogeneity and distance to coast were found to have a positive effect. This study illustrates that a phylogenetic approach enhances our knowledge about spatial diversity patterns, and may possibly reveal areas of special interest regarding future conservation priorities.

Key words: Phylogenetic diversity - Species richness - Vertebrate herbivores - Explanatory variables - The Arctic biome

ABSTRACT IN NORWEGIAN

Å kunne forstå romlege diversitetsmønstre og faktorar som driv desse er naudsynt for bevaringsplanlegging, og er framfor alt viktig i område utsett for store klimaendringar. Tradisjonelt har desse mønstra blitt studert ved å nytte målingar av artsdiversitet (*species richness*). Ved å derimot bruke ei fylogenetisk tilnærming i slike målingar, kan dette gi innblikk i både økologiske og evolusjonære prosessar som formar diversitetsmønstra vi ser i dag. Denne studien har undersøkt mønstre av fylogenetisk diversitet i arktiske planteetande virveldyr, samanlikna desse med mønster av artsdiversitet, og vidare utforska potensielle faktorar som driv forholdet mellom desse.

Analyseprogrammet *Biodiverse* blei nytta for kalkuleringane, kor artsdistribusjonsdata vart linka saman med molekylær data (fylogeni), for å kalkulere fylogenetisk diversitet av planteetande virveldyr på tvers av Arktis. Vidare vart miljødata henta frå ulike kjelder, basert på evalueringar av kva faktorar som kunne forventast å forme romlege diversitetsmønster.

Resultata synte sterk korrelasjon mellom mønster av fylogenetisk diversitet og arstdiversitet. I tillegg vart fylogenetisk diversitet avdekka til å vere høgare enn artsdiversitet i alle tilfelle på tvers av Arktis, noko som indikerer at artar tilstades representerar eit spenn på tvers av det fylogenetiske treet, også i meir artsfattige område. Vidare blei fleire arktiske øyer identifiserte til å halde høg overrepresentasjon av fylogenetisk diversitet relativt til artsdiversitet, samanlikna med fastlandet. Sju ut av dei ni miljøfaktorar som vart testa, synte å vere viktige drivarar av diversitetsmønstre presentert i denne studien. Av desse hadde planteproduktivitet, isbrehistorie, temperatur, nedbør, habitat-heterogenitet og menneskeleg innflytelse alle ein negativ effekt på mønstret av fylogenetisk diversitet relativt til artsdiversitet. På andre sida, synte topografisk-heterogenitet og avstand til kyst seg å ha ein positiv effekt. Denne studien illustrerer at ved å nytte ei fylogenetisk tilnærming i målingar av diversitet, aukar vår kunnskap om romlege diversitetsmønstre, og kan om mogleg avsløre område av spesiell interesse angåande framtidige bevaringsspørsmål.

Stikkord: Fylogenetisk diversitet - Artsdiversitet - Planteetande virveldyr - Forklarande faktorar - Arktis

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INTRODUCTION

In the field of Conservation Biology, the essential goal is to map and protect as much of the estimated biodiversity as possible, in order to protect possible future values (Loreau et al., 2001; Faith & Baker, 2006). Particularly important is conserving diversity in areas undergoing change, since broad variation and variability of life forms could function as a buffer (Faith & Baker, 2006) against fluctuations in the environment, and hence retain stability of ecosystem processes (Loreau et al., 2001). Therefore, spatial analysis of biodiversity is essential (Laffan, Lubarsky, & Rosauer, 2010) on the simple basis that we need to know where biodiversity is in order to protect it. Moreover, to predict possible future consequences of climate change (González-Orozco et al., 2016) it is crucial to understand spatial patterns of biodiversity (Mishler et al., 2014) and also the biotic and abiotic drivers shaping these patterns (Barrio et al., 2016).

Traditionally, spatial diversity patterns have been conducted examining species ranges across regions (Mishler et al., 2014), e.g. *species richness*. While thousands of species have been targeted and investigated individually, less is known about how spatial patterns across whole clades of species might be impacted due to climate change (González-Orozco et al., 2016; Thuiller et al., 2011). Incorporating the full tree of life in spatial diversity analysis will provide a deeper understanding of biodiversity than species richness patterns alone, and hence give more analytical power and ecological inference (Mishler et al., 2014). Such a phylogenetic approach can provide unique insights and help documenting processes that generates variation (Faith, 2008), such processes as speciation and extinction, ecosystem function and assembly rules (Mazel et al., 2015). Furthermore, a phylogenetic approach in biodiversity analyses will provide insight to how evolutionary processes may have shaped the patterns of species richness we see today (Fritz & Rahbek, 2012), as well as contribute to our understanding of what mechanisms drive patterns of species co-occurrences (Cadotte et al., 2010).

One of the pioneers of the *phylogenetic diversity* concept was Daniel Faith (1992), who described it as *'the minimum total length of all branches required to span a given set of taxa on the phylogenetic tree'* (Faith, 1992; for a discussion see Faith & Baker, 2006; Cadotte et al., 2010). When limited resources call for priority decisions, the use of phylogenetic diversity measurements in species conservation can be more effective than traditional species richness measurements alone (Faith, 1992; Faith & Baker, 2006; Mishler et al. 2014). One of the reasons is the phylogenetic diversity measurements' use of molecular data and phylogenetic analysis programs that avoid the sensitivity of conservation planning to species definitions (Isaac et al. 2004; Faith & Williams, 2006; Faith & Baker, 2006). Additionally, by weighting the cladistic hierarchy representativeness instead of only weighting the count of taxonomic units (e.g. species), phylogenetic diversity measurements aim to conserve as much information about hierarchical variation as possible (Faith, 1992). In this way, the conservation strategy that preserves the largest amount of phylogenetic diversity as the available resources permit can be considered most successful (Faith & Baker, 2006). During recent years, spatial analysis on a wide range of biodiversity indices have been made possible due to increased available data (Cadotte et al. 2010; Laffan et al. 2010; Ficetola et al., 2017). As a consequence of increased georeferenced distribution data and phylogenetic trees (Holt et al., 2013), the use of phylogenetic diversity measurements in biodiversity investigations has also increased (e.g. Faith et al., 2004; Cadotte et al., 2010; Cadotte et al., 2012; Fritz & Rahbek, 2012; Mishler et al., 2014; see Vamosi et al., 2009). This increase has also led to several proposals of new ways to calculate phylogenetic diversity (e.g. Helmus et al., 2007; Cadotte et al., 2010; Fritz & Rahbek, 2012). While each different way of calculating phylogenetic diversity has advantages, it is important to evaluate the mechanisms behind the measurement used in relation to the research question (Flynn et al., 2011).

In general, phylogenetic diversity is expected to correlate with species richness (Faith, 2008; e.g. Morlon et al., 2011; Fritz & Rahbek, 2012; González-Orozco et al., 2016) across areas, as an increase of species represented in an area hence increases the number of phylogenetic branches in the same area (Vamosi et al., 2009). However, an area where phylogenetic diversity is either over- or underrepresented compared to its associated species richness, is of special interest since this would indicate a detectable signal in existing species richness pattern left by evolutionary processes (Fritz & Rahbek, 2012). This would then reveal the significance of dispersal barriers, colonization and processes of diversification (Fritz & Rahbek, 2012).

The Arctic biome holds some of the most species-poor and least productive ecosystems worldwide (Meltofte, 2013; Turetsky et al., 2017), due to environmental conditions such as low temperatures, nitrogen limitation and short growing seasons (Schmidt et al., 2017). In addition, recent glaciation has also limited species diversification in northern ecosystems (Turetsky et al., 2017). Therefore, the Arctic has often been suggested as a model for investigating and understanding interactions between biotic and abiotic factors in ecosystems (Barrio et al., 2016). However, with the availability increase of phylogenetic and global distribution datasets, it has been revealed that arctic diversity patterns are far more complex than predicted (Meltofte, 2013). Herbivores play a central role in terrestrial ecosystems by directly and indirectly affecting the structure and dynamics in the systems (Barrio et al., 2016; Foster, Barton, & Lindenmayer, 2014; Ritchie & Olff, 1999; Van der Wal, Bardgett, Harrison, & Stien, 2004), and they have an even greater impact in the Arctic in comparison to lower latitudes (Mulder, 1999). Given the rapid climate change occurring in the Arctic (Meltofte, 2013), understanding how patterns of herbivore diversity fluctuates across the biome can help predict future interactions between plants and herbivores in tundra ecosystems (Barrio et al., 2016).

Patterns of biodiversity are strongly determined by environmental limitations, as well as evolutionary processes and species dispersal (Barrio et al., 2016). Thus, performing spatial diversity analyses on a broad scale can give insight to important drivers, of both biotic and abiotic character, shaping these diversity patterns (Sandom et al., 2013). In terrestrial ecosystems, plant productivity plays an important role in driving large scale patterns of diversity (Field et al., 2009; Meltofte, 2013), as higher net productivity might bear more individuals and hence support species coexistence (Sandom et al., 2013). Strong correlations between primary productivity and species richness has also been revealed in arctic herbivores (Barrio et al., 2016). Climate has a central role by directly or indirectly (Hawkins et al., 2003) determining large spatial patterns of species richness in terrestrial habitats (Field et al., 2009). Moreover, temperature has been demonstrated to drive biogeographical boundaries in terrestrial ecosystems (Ficetola et al., 2017). Other drivers of large spatial diversity patterns can be linked to environmental heterogeneity (Meltofte, 2013; Yang et al., 2015; Ficetola et al., 2017), as resource variety in habitats might provide more niches for species coexistence (Sandom et al., 2013) and also as topographic heterogeneity has shown to have a local effect on diversity in arctic terrestrial vertebrates (Meltofte, 2013).

Other potential drivers of broad-scale diversity patterns in the Arctic biome can be related to historical (Meltofte, 2013; Ficetola et al., 2017) and geographical impacts (Field et al., 2009). Arctic terrestrial ecosystems are, in geological contexts, relatively young compared to other ecosystems on Earth (Meltofte, 2013) due to glaciation events during the Pleistocene. Current distribution patterns have been linked to ice-free refugia that existed under the last glacial maximum (Barrio et al., 2016), where terrestrial species were able to diverge in isolation and hence fostering arctic diversification during periods of glaciation (Meltofte, 2013). Furthermore, diversity patterns might also be associated with distance of an area to the coastline, as the Arctic harbours hold more diverse communities (Meltofte, 2013). Glacial history has also generated special characteristics associated with existing northern ecosystems soil and topography composition (Turetsky et al., 2017). One of the main drivers of richness patterns in vascular plant species is soil pH (Gough et al., 2000), and therefore it might also drive patterns of herbivores. In recent evolutionary time, drivers of biodiversity might be associated with human activity, as human-affected habitats generally contain less genetic diversity than wild areas (Miraldo et al., 2016). In arctic terrestrial systems, an increasing footprint of human activity has been observed (Meltofte, 2013), which might in turn have an impact on the genetic diversity patterns of the Arctic biome.

Recently, patterns of species richness in arctic vertebrate herbivores were outlined and drivers of these richness patterns were investigated (see Barrio et al., 2016). However, phylogenetic diversity patterns of this main trophic group and the mechanisms driving these patterns remain unknown in the Arctic biome. In this study, I investigate the spatial patterns of phylogenetic diversity of vertebrate herbivores in the Arctic biome. Additionally, I aim to identify areas of unusually high or low representation of phylogenetic diversity relative to species richness. Furthermore, I seek to identify explanatory variables driving these spatial diversity patterns in vertebrate herbivores across the Arctic, and I am specifically interested in identifying variables increasing the ratio between patterns of phylogenetic diversity and species richness in the studied group of species.

Based on previous studies (e.g. Fritz & Rahbek, 2012; González-Orozco et al., 2016) and the assumption that areas containing more species will also represent more phylogenetic branches (Vamosi et al., 2009), I expect to find a general correlation between patterns of phylogenetic diversity and patterns of species richness of vertebrate herbivores across the Arctic biome. Furthermore, due to the Arctic region generally being species-poor (Meltofte, 2013) and the studied group of herbivores including species of two distinct classes (i.e. including avian and mammalian species), I expect to find variation across areas in ratio between phylogenetic diversity and species richness. Considering potential explanatory variables, I expect to find factors driving species richness patterns also influencing patterns of phylogenetic diversity, based on the assumption of these indices being correlated. Due to few studies done investigating factors driving phylogenetic diversity patterns in terrestrial species, variables examined in this study are mainly based on previously being linked to patterns of species richness. Also, many of the examined variables has particularly been investigated driving species richness in the same group of species investigated in this study (see Barrio et al., 2016). Based on this, I expect plant productivity, climatic factors of temperature, soil pH, and environment heterogeneity (i.e. habitat heterogeneity and topographic heterogeneity) to increase phylogenetic diversity of arctic vertebrate herbivores. On the other hand, I expect increased distance to coastline and areas being affected by humans to hold less phylogenetic diversity. With that said, I am expecting glaciation history to play a greater role in driving phylogenetic diversity than of species richness, since more time since last glaciation period provides more time for speciation events. This will naturally also have an impact on species richness, but I expect 'younger' areas to hold more closely related species and 'older' areas to represent a broader span across the phylogenetic tree. Finally, I seek to identify which of these variables have the largest impact on the ratio between patterns of phylogenetic diversity and species richness in arctic vertebrate herbivores.

MATERIALS AND METHODS

Assembly of geographic data of the species

The species distribution maps in this study were collected and generated using the same data sources and methods as Barrio et al. (2016). Distribution maps of 75 arctic vertebrate herbivores were constructed based on occurrences of herbivorous species in the Arctic biome (Meltofte, 2013). Only species feeding mainly on plant material were included, resulting in 21 avian and 54 mammalian species (see Table A1, Appendix 1). The avian distribution maps were constructed using data from Birdlife International & NatureServe (2013) including both species with breeding and non-breeding ranges in the Arctic. Vagrant species or species with migratory pathways in the Arctic biome were excluded from the analyses (Birdlife International & NatureServe, 2013). Data from The International Union for Conservation of Nature (IUCN, 2013) were used to construct distribution maps of arctic mammals, including both resident and migratory species.

The original distribution maps collected from Birdlife International & NatureServe (2013) and IUCN (2013) were polygon layers. These layers were rasterized in to grid cells, each representing 100x100 km. 1581 grid cells of species distribution data remained after excluding cells consisting of >50% ice covered land or water. Within the grid cells, each species was either marked as absent or present based on their distribution ranges from the representative data sources.

The full dataset made for the main analyses consisted of all species in Table A1 (see Appendix 1), also the semi-domesticated species *Ovis aries* and the semi-domesticated ranges of *Rangifer tarandus* (including 75 species). To investigate possible impacts the semi-domesticated species would have on the diversity patterns, an additional dataset including only wild ranges of all herbivorous species was made (including 74 species). In addition, one subset of birds and one subset of mammals were made based on the assumption that different dispersal possibilities will have an impact on the overall diversity patterns. This left a total of four distribution datasets for the analyses;

(1) All herbivores (including both wild and semi-domesticated species)

(2) Avian herbivores only

(3) Mammalian herbivores only (including both wild and semi-domesticated species)

(4) All wild herbivores

Assembly of molecular data and phylogenetic analyses

The molecular data were collected in GenBank, using custom python scripts for nucleotide sequences of 18 common genetic loci of the 75 arctic vertebrate herbivores investigated. Four mitochondrial markers were identified with broad coverage across the species: cytochrome B (cytB), cytochrome oxidase subunit 1 (COI), 12S ribosomal RNA (12S), and NADH dehydrogenase subunit 4 (ND4). When available, multiple sequences for each species were compared so that a single representative sequence could be chosen for further analysis. Otherwise the longest available sequence was chosen. We were able to obtain representative sequence data for at least one marker in 71 species (see Table A2, Appendix 1). The remaining four species were excluded due to insufficient publicly available sequences data, these were: *Dicrostonyx nelsoni*, *Dicrostonyx unalascensis*, *Dicrostonyx vinogradovi*, and *Lemmus portenkoi*.

Sequences for each marker were aligned automatically using MAFFT version 7.305b (Katoh & Standley, 2013) and then manually adjusted. Large autapomorphic gaps were excised from the sequence alignments. This resulted in the final multiple sequence alignments with the following lengths: cytB, 1153 bp; COI, 657 bp; 12S, 1092 bp; ND4, 2365 bp. These were concatenated to create a final alignment of length 5267 bp.

Using PartitionFinder (Lanfear et al., 2012), hierarchical likelihood ratio tests under the Bayesian information criterion were used to determine the optimal data-partitioning scheme and substitution models. The optimal partitioning scheme contained three data subsets: COI, 12S, and combined ND4+cytB. The general time reversible nucleotide substitution model with invariant sites and Gamma-distributed among-site rate variation (GTR+I+Γ) was determined to be optimal for all three data subsets.

Independent Bayesian phylogenetic analyses were conducted on the multiple sequence alignment of each marker individually, as well as on the partitioned, concatenated dataset using MrBayes version 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck,

2003) in four chains with 4 million MCMC generations (discarding the initial 25% as burn-in), and sampling the cold chain every 1000 generations. Statistical stationarity was confirmed at the completion of the run by examining that the mean standard deviation of split frequencies was less than 1%. The reconstructed topological relationships were confirmed to be in good agreement with previously published phylogenetic analyses using the Tree of Life Web Project (Maddison & Schulz, 2007) and the TimeTree knowledge-base (Hedges et al., 2006), with a few exceptions discussed below.

We concluded that the GenBank COI sequence for *Anser canagica* (subgeneric group Chen) must have been misidentified, confirmed by performing a phylogenetic analysis with only COI. This analysis placed *Anser canagica* not only outside the genus *Anser*, but also basal to all included taxa from the superorder Neoaves. Hence, this COI sequence was removed from the multiple sequence alignment prior to the final analysis of the 5267-bp partitioned, concatenated dataset. The position of *Castor canadensis* outside the Order Rodentia disagrees with widely accepted knowledge about its evolutionary relationships to other mammals. This issue with the phylogenetic topology could not be resolved.

Biodiversity analyses

Standard indices of *species richness* and *phylogenetic diversity* were calculated in all 1581 grid cells (with equal area of 100x100km) using Biodiverse version 0.19 (Laffan et al., 2010). Species richness (Biodiverse Index 111, named: “Richness all”) was calculated by counting the number of species in cells, without the use of the phylogenetic tree. Phylogenetic diversity (Biodiverse Indices 274-277, named: “Phylogenetic Diversity”) was calculated by summing the branch lengths of the phylogenetic tree representing the species present in each cell. The phylogenetic diversity calculations in Biodiverse (Laffan et al., 2010) is calculated based on Faith´s (1992) phylogenetic diversity concept; finding the minimum total length of all phylogenetic branches represented in the investigated area (here in each grid cell), including the root of the tree. Both diversity indices in the result are presented as a proportion of total (i.e. of ‘total species’ in species richness, and of ‘total branch lengths’ in phylogenetic diversity) and are therefore on a scale from 0 to 1. The results were exported into R (R Core Team, 2016) for further statistical analyses and visualization (see description of data analyses below).

The diversity calculations were computed by importing both the four distribution data sets (see Table A1, Appendix 1) and the phylogenetic tree (Figure A1, Appendix 1) into Biodiverse (Laffan et al., 2010). Distribution data were then trimmed to match tree nodes, resulting in removing distribution data of four species (*Dicrostonyx nelsoni*, *Dicrostonyx unalascensis*, *Dicrostonyx vinogradovi*, and *Lemmus portenkoi*). In addition, *Microtus abbreviatus* was also removed by trimming the phylogenetic tree, as its distribution range was too narrow to appear in the distribution data when using 100x100 km grid cells across the Arctic. Thus, a total of 70 species remained for the analyses.

Assembly of environmental data (explanatory variables)

In total, 27 possible explanatory variables (this including 19 different bioclimatic variables) were considered in this study, in order to explain the large spatial phylogenetic diversity patterns of vertebrate herbivores in the Arctic biome. The data of all explanatory variables were resampled to grid cells of 100x100 km, in order to match the species distribution data in the response variables. Related to predictions about factors driving diversity patterns (see Introduction), the following explanatory variables were examined:

- **Plant productivity (NDVI)**

  Data representing 'Plant productivity' was collected using the normalized difference vegetation index (NDVI), which displays maximum greenness, from the data source TAGA (Alaska Geobotany Center 2012b). The original layer had a resolution of 1x1km.
- **Bioclimatic variables (temperature and precipitation)**

  Data from 19 different bioclimatic variables were collected from WorldClim (Fick & Hijmans, 2017). The original layers contained of 1x1 km grid cells. A principle components analysis (PCA) was performed to reduce dimensionality of the 19 variables. All variables were standardized before the PCA was run. Top three components axes were selected; cumulatively these axes explained 90% of the total variation. The bioclimatic variable with the strongest correlation with each axis was then selected as the best representative variable for each component. 'Annual Precipitation' (=bio12) was selected from the first component; 'Max temperature of warmest month' (=bio5) was selected for the second component and 'Annual mean temperature' (=bio1) for the third component.

- **Environmental heterogeneity**
    - Raw data representing 'Topographic Heterogeneity' was collected from Alaska Geobotany Center (2010), and represent the range of elevation within a given cell. The original layer had a resolution of 1x1km.
    - Raw data demonstrating 'Habitat heterogeneity' was collected from the European Space Agency´s GlobCover Project (2009), and represents the number of different habitats present in each cell.
- **History and geography:**
    - Raw data of 'Ice history' (= kya_since_ice) represents time since last ice-cover within each cell investigated. Data measured in intervals of 1 Kyr, from 0 to 21 Kyr when 0 Kyr represent cells where there is ice today. Cells not within this range were all put to be 150 Kyr in order to not lose any cells. The raw data was collected from the IGBP PAGES/World Data Center for Paleoclimatology (1993).
    - Raw data of 'Distance to coastline' was collected using The Alaskan Geobotany Center (2012a). The original data measured in meters.
- **Soil pH**

  Raw data of 'Soil pH' was collected from IGBP-DIS (1998). Data collected by measuring with a depth of 5 cm.
- **Human population densities**

  Raw data representing human population density (hereby expressed as 'Population density') was collected form the NASA Socioeconomic Data and Application Center (2004), with gridded estimates of 30 arc-seconds output resolution for the year 2000.

Data analyses (in R)

All grid cells existing of ice-on-land were removed from the analyses, reducing 1581 to 1393 grid cells. In addition, due to missing values in the variables of 'Soil pH' and 'Topographic heterogeneity', further 48 cells were excluded, leaving 1345 grid cells for the final diversity analyses.

Relationships between all explanatory variables (including the three selected Bioclimatic variables) were visually inspected using pairwise linear correlations, to detect any collinearity or multilinearity between them. All correlations with |r|>0.40, were further inspected and evaluated (Figure A2, Appendix 1). ‘Annual mean temperature’ was strongly correlated with ‘Annual precipitation’ (r=0.75) and showed some correlation with ‘Habitat heterogeneity’ (r=0.40) and ‘Soil pH’ (r=-0.42). ‘Max temperature of warmest month’ was strongly correlated with ‘Plant productivity’ (r=0.74) and ‘Distance to coast’ (r=0.71), and was moderately correlated with ‘Soil pH’ (r=-0.40). ‘Elevation’ was found to be strongly correlated with ‘Topographic Heterogeneity’ (r=0.70). In addition, ‘Plant productivity’ was found moderately correlated with ‘Distance to coast’ (r=0.49). Based on these correlations, ‘Annual mean temperature’ and ‘Elevation’ were removed as predictor variables form further analyses; all other variables were kept due to being related to specific predictions driving diversity patterns. ‘Max temperature of warmest month’ was selected above ‘Annual mean temperature’, due to its importance explaining more variation as the second component from the PCA analysis (see section above). This left the following global model of explanatory variables in the analyses; ‘Annual precipitation’, ‘Max temperature of warmest month’, ‘Plant productivity’, ‘Habitat heterogeneity’, ‘Distance to coast’, ‘Ice history’ (i.e. kya since ice), ‘soil pH’, ‘Topographic heterogeneity’ and ‘Population density’ (i.e. human population density). The explanatory variables were all standardized in order to directly compare the estimates of the coefficients.

In order to find the most parsimonious model predicting diversity of arctic vertebrate herbivores model selection was performed using Akaike´s Information Criterion (AIC), as a model averaging approach based on AIC has shown to possibly be the best approach understanding patterns of macro-ecology as it gives consistent and robust results across different methods (Diniz-Filho et al., 2008). The AIC analyses were run for three response variables for the main analyses; phylogenetic diversity of all herbivores, species richness of all herbivores and phylogenetic diversity relative to species richness of all herbivores. All potential models between the null (intercept only) and the global (all explanatory variables listed above, without any interactions) were identified using the ‘dredge’-function in the MuMIn package in R (Bartoń, 2016). Top-ranking models of ΔAIC < 3 were selected as the best-fitted models (Table A3, Appendix 1). A model averaging approach based on AIC, were used to assess the relative importance of all explanatory variables (Figure 5). For each of the nine explanatory variables, estimated coefficients were averaged across the models it was present and hence weighted to the probability related with each model (Figure 6). In addition, an extra analysis of relative variable importance driving phylogenetic diversity patterns of birds and mammals separately was computed to display any possible differences within the phylogenetic diversity pattern (see Appendix 2).

All statistical analyses were performed using the software program R version 3.3.2 (R Core Team, 2016).

RESULTS

Phylogenetic analysis

The final molecular dataset used in the phylogenetic analyses had 71 taxa, identified from four mitochondrial markers (cytB, COI, 12S, ND4). The topology of the Bayesian analysis is displayed in Figure A1 in Appendix 1. For the diversity pattern analysis (see section under) the taxa of *M. abbreviatus* was removed as the species range was too narrow to appear in the distribution maps, leaving 70 taxa for the final analyses.

Diversity patterns of arctic vertebrate herbivores

With the distribution data (Table A1, Appendix 1) and phylogenetic tree (Figure A1, Appendix 1) used in this study, the phylogenetic diversity of arctic vertebrate herbivores (measured using Faith´s (1992) calculation of phylogenetic diversity) was generally distributed across the Arctic. The highest phylogenetic diversity was found in the western and southern Nearctic, where around 70% of the total branch length was found (Figure 1a). The Arctic islands revealed generally less phylogenetic diversity than mainland with around 20-40% of all branch lengths, this including big islands such as Greenland, Iceland and the Canadian Islands. A similar pattern was shown when calculating species richness of arctic vertebrate herbivores (Figure 1b), with a peak in the same area of the western Nearctic containing around 40% of total species richness, whereas the Arctic islands contained around 5-20%. This indicated a correlation between phylogenetic diversity and species richness of this trophic group, which was supported by a correlation analysis showing a significant strong correlation ($r = 0.85$) (Figure 2).

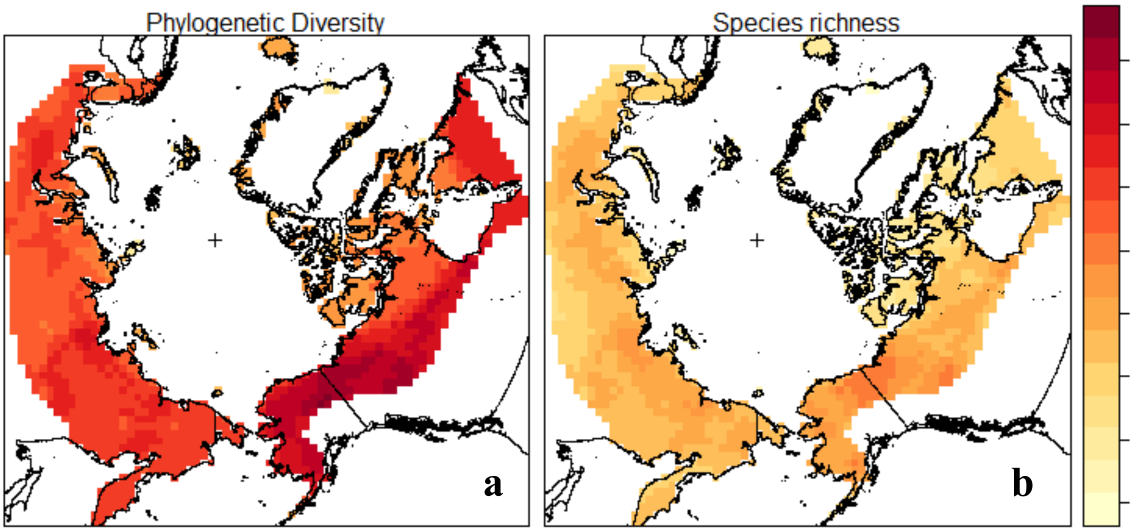

Figure 1 Distribution maps of (a) phylogenetic diversity, and (b) species richness of arctic vertebrate herbivores, both measured as a proportion of total. Using Lambert Azimuthal Equal Area Projection. In total 1345 grid cells in each map, each cell representing 100x100 km.

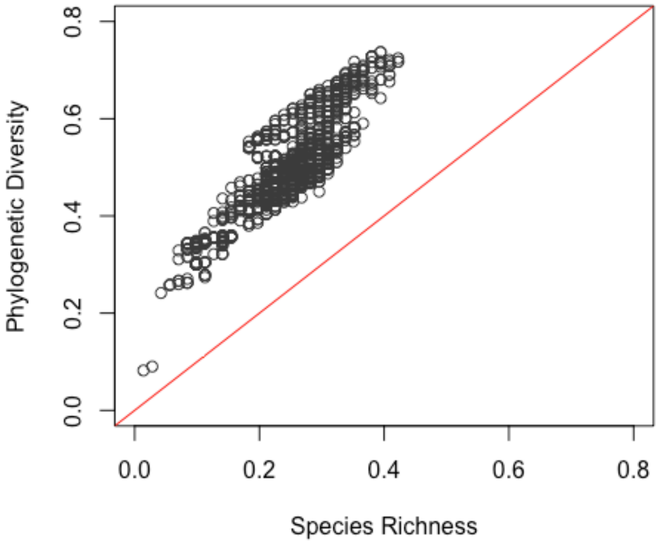

Figure 2 Correlation (r = 0.85) between phylogenetic diversity and species richness of all arctic vertebrate herbivores (both expressed as a proportion of total). The red line shows a 1:1 relationship between phylogenetic diversity and species richness with an intercept of 0 and slope of 1.

Areas of phylogenetic overrepresentation compared to species richness were identified on parts of the coastal zone of Greenland, parts of Svalbard, parts of the western and northern Canadian Islands, on Flaherty Island, on Wrangel Island, and on the Severnaya Zemlya

Islands (Figure 3). Here, the phylogenetic diversity was up to six times greater than of species richness. Other central and eastern islands in Canada revealed a phylogenetic diversity up to four times the species richness.

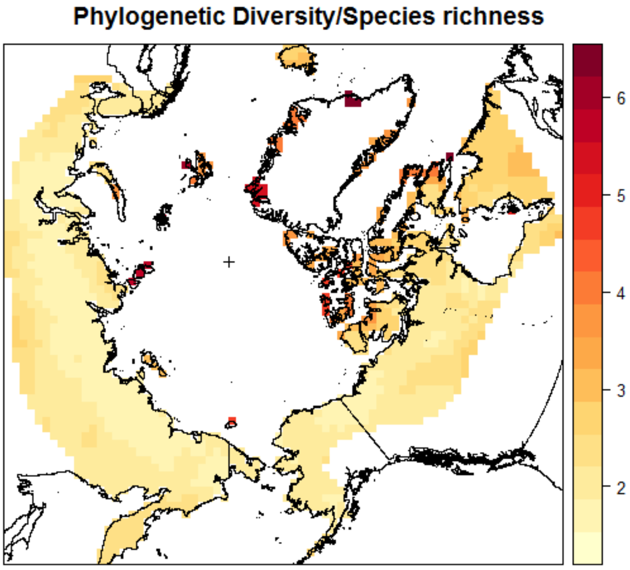

Figure 3 Distribution map showing representation of phylogenetic diversity per species richness (i.e. PD/SR) of arctic vertebrate herbivores (when both indices originally were measured as 'a proportion of total'). Using Lambert Azimuthal Equal Area Projection. In total 1345 grid cells, each cell representing 100x100 km.

Maps of phylogenetic diversity of arctic herbivorous mammals and birds separately, are shown in Figure 4a-b. Birds represented 30% of total species investigated, whereas mammals represented 70%. The phylogenetic diversity of mammalian herbivores showed a parallel pattern as of phylogenetic diversity of all herbivores (Figure 1b) with a peak in the west- and southern areas of the Nearctic, containing around 65% of the total branch length considering mammals only. Phylogenetic diversity of herbivorous birds was generally high across the entire Arctic (80-100% of total branch length considering birds only), with some areas of lower representation in Greenland, and other arctic islands (around 60%). Further analysis (Figure A3, Appendix 1) showed that phylogenetic diversity of mammals had an almost perfect correlation with phylogenetic diversity of all herbivores (r = 0.99), while phylogenetic diversity of birds had a weak correlation (r = 0.37) with all herbivores. There was also a weak correlation between phylogenetic diversity of birds and mammals (r = 0.28).

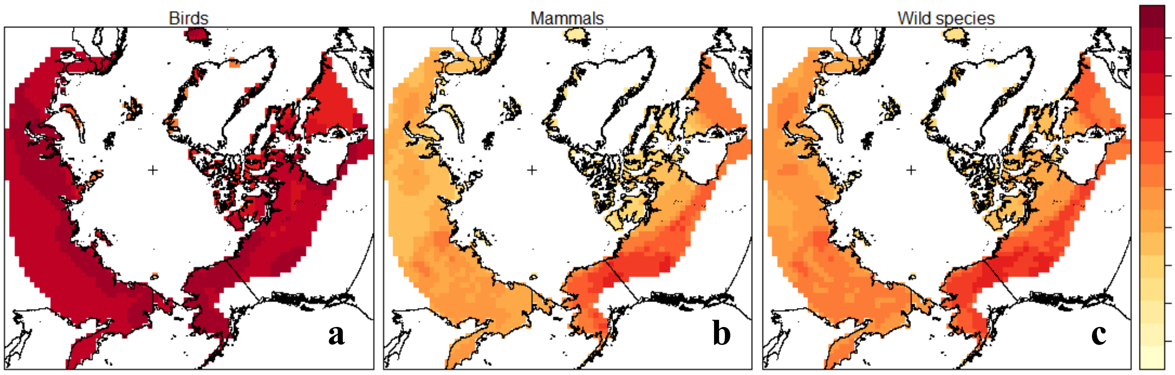

Figure 4 Distribution maps of phylogenetic diversity of (a) Arctic herbivorous birds, (b) Arctic herbivorous mammals, and (c) all wild herbivores. All three maps measured as a proportion of total. Using Lambert Azimuthal Equal Area Projection. In total 1345 grid cells in each map, each cell representing 100x100 km.

Phylogenetic distribution of all arctic vertebrate herbivores when only distribution maps of wild species were included (Figure 4c) showed similar patterns as the phylogenetic diversity when also including semi-domesticated species (i.e *Rangifer tarandus* and *Ovis aries*). This was supported by a correlation analysis (Figure A3, Appendix 1), revealing a complete correlation between the two distribution maps ($r = 1.00$).

Diversity drivers of arctic vertebrate herbivores

Possible explanatory variables driving the diversity patterns presented in Figure 1a-b and Figure 3 were analysed using model selection based on the Akaike Information Criterion. No single model had strong support based on the Akaike weights from the AIC model selection. The cumulative Akaike weight for the best-fitted models with ΔAIC < 3 (Table A3, Appendix 1) was 0.88 (five models) for phylogenetic diversity of all herbivorous species, 0.99 (two models) for species richness of all herbivores, and 1.00 (four models) for phylogenetic diversity relative to species richness (i.e. PD/SR) of all herbivores.

Variable importance scores (Figure 5) revealed the explanatory variables ‘Population density’, ‘Max temperature of warmest month’ (= bio5), ‘Annual precipitation’ (= bio 12), ‘Topographic heterogeneity’, ‘Habitat heterogeneity’ and ‘Distance to coast’ to be the most important variables (with a score around 100% of the cumulative AIC weight) driving all three diversity patterns of all herbivores across the Arctic (i.e. patterns of phylogenetic diversity, species richness, and phylogenetic diversity relative to species richness). Secondly, 'Ice history' (= kya since ice) was also found to be one of the most important variables driving patterns of species richness and phylogenetic diversity relative to species richness (both with a score around 100%). Considering the phylogenetic diversity pattern, 'Ice history' showed to be slightly less important than of the two other patterns, while still having a score around 90%. 'Plant productivity' (=NDVI) was the variable revealing most variance in the result across the three diversity patterns investigated, with a score around 35% for phylogenetic diversity, around 55% for phylogenetic diversity relative to species richness, and 100% importance for species richness. 'Soil pH' revealed to be the least important variable across all three groups (a score around 25% for all).

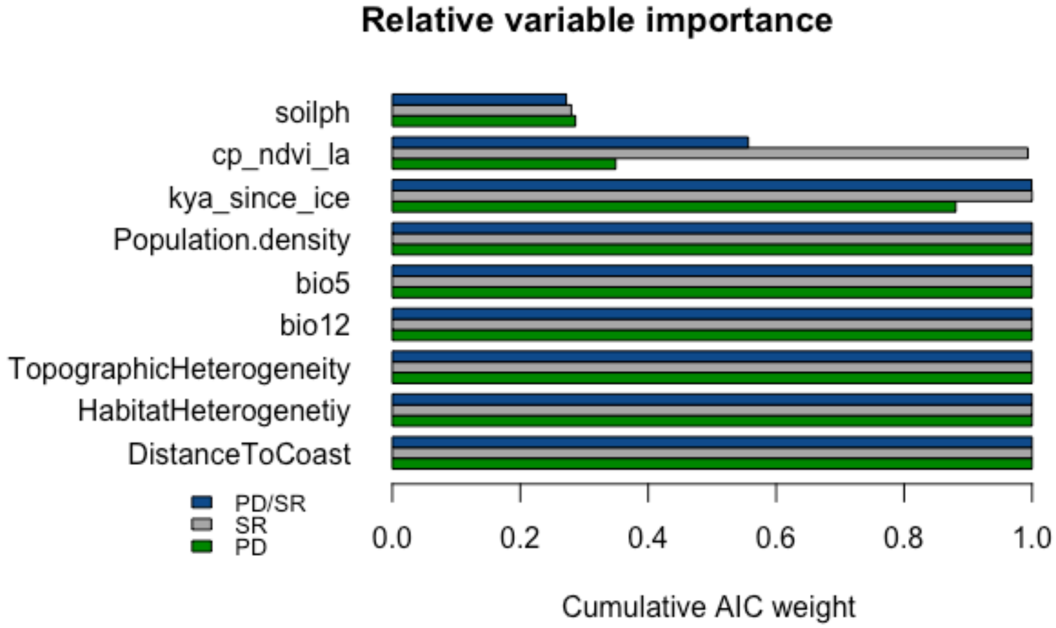

Figure 5 Variable importance scores for diversity patterns of all herbivores across the Arctic; Phylogenetic diversity (PD; green), species richness (SR; grey), and phylogenetic diversity relative to species richness (PD/SR; blue). For each variable, the AIC weight for all models in which it appears is summed to represent the relative importance of the variable. The cumulative weight can be used to set order of importance of each variable, thus it can be understood as the probability of the variable being present in the best-fitted model. Cp_ndvi_la is 'Plant productivity', kya_since_ice is 'Ice history', bio5 is the 'Max temperature of the warmest month', and bio12 is the 'Annual precipitation'.

The model-averaged coefficient estimates for all variables tested to explain patterns of phylogenetic diversity, species richness, and phylogenetic diversity relative to species richness of arctic vertebrate herbivores, are shown in Figure 6. The coefficient estimates reveal that the most important variables of phylogenetic diversity and species richness (shown in Figure 5) have an effect driving these patterns in the same direction (i.e. both indices either have a positive or a negative effect). This includes the variables; 'Distance to coast', 'Habitat heterogeneity', 'Population density', 'Topographic heterogeneity', 'Annual precipitation', 'Max temperature of warmest month', and to some degree 'Plant productivity'. Interestingly, the estimated coefficient of 'Ice history' (= kya since ice) reveals a positive effect considering phylogenetic diversity of herbivores (0.02) and a slightly negative effect considering species richness of herbivores (-0.005).

Considering the estimated coefficients of variables explaining patterns of phylogenetic diversity relative to species richness (i.e. PD/SR), several coefficient estimates for important variables (see Figure 5) have the opposite effect (i.e. negative or positive) compared to the coefficient estimates of both phylogenetic diversity and species richness. The estimated coefficient of 'Distance to coast' was around 0.025 for phylogenetic diversity relative to species richness, whereas it was around -0.03 for both phylogenetic diversity and species richness. The estimated coefficient of 'Habitat heterogeneity' was around -0.01 for phylogenetic diversity relative to species richness, while it was around 0.025 for phylogenetic diversity and around 0.05 for species richness. The estimated coefficient of 'Max temperature of the warmest month' was around -0.025 for phylogenetic diversity relative to species richness, whereas it was in the range of 0.05-0.06 for both phylogenetic diversity and species richness. The estimated coefficient of 'Ice history' for phylogenetic diversity relative to species richness was similar to that of species richness (around -0.005). Considering 'Plant productivity' the estimated coefficients were somewhat positive for phylogenetic diversity (around 0.01) and close to 0.00 for species richness, whereas it was slightly negative for phylogenetic diversity relative to species richness (around -0.015). The other variables had estimated coefficients quite similar between the three patterns (i.e. being either all negative or all positive), including the variables 'Topographic heterogeneity', 'Population density', and 'Annual precipitation'. The standard errors for all investigated variables had very small range (< 0.005).

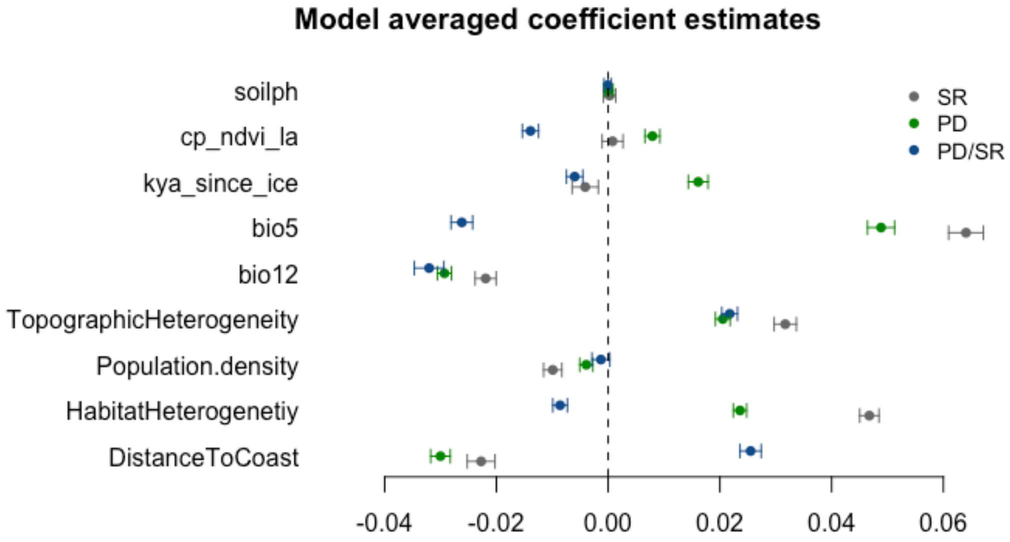

Figure 6 Model averaged coefficients for drivers of phylogenetic diversity (PD; green), species richness (SR; grey), and phylogenetic diversity relative to species richness (PD/SR; blue) of all arctic vertebrate herbivores. All predictor variables were standardized. Coefficients of a variable overlapping the vertical dashed line, means the variable had different effect (i.e. positive or negative effect) on the indices (i.e. phylogenetic diversity, species richness and phylogenetic diversity relative to species richness). Variable coefficients not overlapping the dashed line, means it had a similar affect driving value of the indices in the same direction. Standard errors for each point are all marked with arrows. Cp_ndvi_la is 'Plant productivity', kya_since_ice is 'Ice history', bio5 is 'Max temperature of the warmest month', and bio12 is 'Annual precipitation'.

DISCUSSION

Relationship between patterns of phylogenetic diversity and species richness

By incorporating phylogenetic analysis and distribution data, this study has made a first attempt to reveal spatial phylogenetic diversity patterns across vertebrate herbivores in the Arctic biome. As expected, a strong correlation (r = 0.85) was found between phylogenetic diversity and species richness. This confirms previous findings of strong correlations between measures of phylogenetic diversity and species richness (e.g. Morlon et al., 2011; Fritz & Rahbek, 2012).

However, due to the analysis not revealing a complete correlation, the data highlights the presence of areas with either over- or underrepresentation of phylogenetic diversity in relation to species richness in arctic vertebrate herbivores. In other words, it suggests areas of phylogenetic clumping or dispersion (Faith, 2008). By incorporating a 1:1 line in the correlation plot (Figure 2), it shows clearly that phylogenetic diversity overall has a trend of being higher than of species richness in the investigated group of species. This suggests that even though arctic terrestrial communities generally hold few species (Meltofte, 2013), the species present span the phylogenetic tree, and generally are distantly related (Vamosi et al., 2009). Stated differently, it implies that arctic areas in general support species not restricted to small mono- or paraphyletic groups, but rather contain polyphyletic groups of vertebrate herbivorous species. It should be added that while this study has investigated patterns on a macro-scale with grid cells of 100x100 km, the findings might appear differently investigating diversity patterns of arctic vertebrate herbivores on a finer scale. As earlier outlined, *C. canadensis*' placement in the phylogeny used for the analyses in this study (see Figure A1, Appendix 1), disagrees with commonly accepted knowledge placing this taxon within the clade of Rodentia, and may therefore have impacted the result of the phylogenetic diversity patterns.

Considering the results found in this study, one possible explanation for the overall higher phylogenetic diversity compared to species richness (Figure 2) may be due to different dispersal and migration possibilities of birds and mammals (Cáceres et al., 2014). Herbivorous birds have high phylogenetic diversity throughout the Arctic, including arctic islands (areas representing 60-90% of total avian phylogenetic diversity, see Figure 4a). In comparison, phylogenetic diversity in herbivorous mammals (Figure 4b) is lower across the Arctic overall and is less evenly distributed than that of birds (areas representing 10-80% of total mammalian phylogenetic diversity). However, the mammalian species represent a larger percentage (70%) than avian species (30%) of total species investigated, and will therefore naturally have a greater influence on the overall phylogenetic diversity pattern including all vertebrate herbivores. Simple correlations (Figure A3, Appendix 1) between all three groups (all herbivores, birds, and mammals) reveal that the pattern of mammals and all herbivores have an almost total correlation (r=0.99), whereas the avian pattern has a weak correlation to all herbivores (r=0.37). In addition, there is an even weaker correlation between birds and mammals (r=0.28). This can be interpreted as the mammalian distribution having an effect that is more than 2.5 times that of the avian distribution, on the phylogenetic diversity pattern of all herbivores. However, the even distribution of birds will have an overall impact when looking at phylogenetic diversity pattern in relation to species richness. If both mammalian and avian species are present across the entire Arctic, then all areas will represent a large span across the phylogenetic tree (i.e. have high phylogenetic diversity), even if there are few species present, as shown in Figure 2. Viewed differently, the results can be interpreted that no arctic area withholds phylogenetic clumping of arctic vertebrate herbivores, since no data points showed higher species richness than of phylogenetic diversity in Figure 2. It is also important to be aware of the removal of five species (i.e. *D. nelsoni*, *D. unalascensis*, *D. vinogradovi*, *L. portenkoi* and *M. abbreviatus*), as described earlier, may have impacted the final diversity patterns outlined in this study.

Even though the result in this study suggests a general overrepresentation of phylogenetic diversity relative to species richness across arctic vertebrate herbivores, it is even more interesting to ask another question: If there are any areas where phylogenetic diversity is either significantly lower or higher than that of a null hypothesis (Mishler et al., 2014) in which all branches are collapsed to zero length (i.e. value of species richness). In other words, does the observed pattern of phylogenetic diversity reveal higher or lower values than what one could expect if values were only based on counting the taxonomic units (i.e. species)? This is interesting because areas that show a noteworthy over- or underrepresentation of phylogenetic diversity in comparison to a null hypothesis might reflect ecological processes and biogeographic history (Mishler et al., 2014), such as dispersal barriers and processes of colonization and diversification (Fritz & Rahbek, 2012). In this study, areas with high overrepresentation of phylogenetic diversity relative to species richness were identified on several arctic islands, including parts of Greenland, the Canadian islands, Svalbard, Flaherty Island, Wrangel Island and Severnaya Zemlya Islands (Figure 3). On these islands, the phylogenetic diversity of arctic vertebrate herbivores was as much as six times the species richness (both measured as a proportion). In comparison, the Arctic mainland overall revealed phylogenetic diversity less than three times the species richness. Figure 3 then indicates that the identified arctic islands have a high overrepresentation of long branches from the phylogeny (Figure A1, Appendix 1) considering the amount of taxonomic units (i.e. species) present, compared to the rest of the Arctic.

This pattern of high overrepresentation of phylogenetic diversity relative to species richness on arctic islands could be linked to both historical (i.e. evolutionary) and contemporary (i.e. ecological) factors (see Mishler et al., 2014). Considering historical factors, the areas might be refugial (Barrio et al., 2016) and hence have supported speciation events over a longer period of time compared to the rest of the Arctic (Meltofte, 2013). This statement is supported by previous research exploring historical glaciation of the Arctic islands, revealing several of the identified islands being completely ice-free or to have had ice-free nunataks during the last glacial maximum (Alsos et al., 2009). Furthermore, investigations of zoogeographical boundaries have identified the existence of an intermediate boundary between the Nearctic islands (i.e. the Canadian islands and Greenland) and the rest of the Nearctic (Holt et al., 2013; see Ficetola et al., 2017), placing the northeastern Neartic islands to be more phylogenetic similar to species in the Palearctic than the rest of the Neartic region (Holt et al., 2013). This might insinuate that species present on the arctic islands have either migrated from the Eurasian continent to the Nearctic islands or that species between these areas have been separated by historical vicariance events (Lomolino et al., 2010). If additional species from the Nearctic mainland also have migrated to the islands, this then might impact the phylogenetic diversity in the Nearctic islands since the species present then will be phylogenetic distantly related. Taking the different phylogenetic diversity patterns of birds and mammals into consideration, Figure 4a-b reveals low phylogenetic diversity of mammals and intermediate phylogenetic diversity of birds in the arctic islands, which implies that a large span across the phylogenetic tree will be present in these areas. At the same time, the species richness pattern (Figure 1b) reveals that the same areas of the arctic islands are some of the most species poor in relation to the overall vertebrate herbivore species. These two factors will therefore result in the high overrepresentation of phylogenetic diversity in relation to species richness.

In an ecological context, the areas of significantly high overrepresentation of phylogenetic diversity relative to species richness might be affected by interspecific competition between close relatives that prevent co-occurrence between these species and hence promotes existence of more distant related species due to low niche overlap (Webb et al., 2002). Taking into consideration that the areas of significantly high overrepresentation of phylogenetic diversity are islands, it is also natural to assume that factors such as island size and degree of isolation will impact the species composition in these areas (Lomolino et al., 2010).

Explanatory variables driving diversity patterns

When considering potential factors driving the investigated diversity patterns of arctic vertebrate herbivores seen in Figure 1a-b and Figure 3 (i.e. patterns of phylogenetic diversity, species richness, and patterns of phylogenetic diversity relative to species richness), the variables 'Population density' (i.e. human population density), 'Annual precipitation', 'Max temperature of warmest month', environmental heterogeneity (i.e. 'Habitat heterogeneity' and 'Topographic heterogeneity'), and 'Distance to coast' revealed a great importance (i.e. relative to variables tested) across all three patterns (see Figure 5). In addition, the variable of 'Ice history' was found to have great importance relative to the other variables, driving patterns of species richness and phylogenetic diversity relative to species richness (scores around 100%), whereas it had a somewhat less importance, but was still strong, driving patterns of phylogenetic diversity (score around 90%). `Plant productivity' showed most variation in relative importance scores across the three diversity patterns investigated. The variable revealed a strong importance, relative to the other variables, driving species richness patterns (around 100%), which confirms previous findings of plant productivity being one of the main drivers of species richness in arctic vertebrate herbivores (see Barrio et al., 2016). Whereas it revealed a medium or weak importance relative to the other variables considering the two other diversity patterns, suggesting the variable not being important relative to other variables tested driving phylogenetic diversity in this group of species. 'Soil pH' was the only variable revealing a weak importance driving all three diversity patterns having a score around 25% for all. This also confirming previous findings regarding ‘Soil pH’ not being important, relative to other variables tested, driving species richness patterns in arctic vertebrate herbivores (see Barrio et al., 2016). Shortly summarized, the variable importance scores (Figure 5) implies that all explanatory variables investigated, except for ‘Soil pH’, ‘Plant productivity’, and to some extent ‘Ice history’, have an equally strong support being important factors (i.e. relative to variables tested) driving patterns of phylogenetic diversity, species richness and phylogenetic diversity relative to species richness in arctic vertebrate herbivores. Considering the result revealing most of the variables tested to be highly important relative to each other, this result may also support previous findings suggesting arctic communities being far more complex than former assumed (Meltofte, 2013).

Furthermore, considering seven out of nine variables revealing almost identical scores of importance across all patterns investigated (Figure 5) and additionally patterns of phylogenetic diversity and species richness generally being strongly correlated (Figure 2), this makes it difficult to interpret whether these variables are driving phylogenetic diversity patterns directly, or if the variables instead have an indirect effect driving patterns of species richness in areas where there is high correlation between these indices. Therefore, more information may be provided examining estimated coefficients for all important variables, as this will give indications if there are variables affecting the relationship between patterns of phylogenetic diversity and species richness (i.e. in this case looking at estimated coefficients of variables driving the pattern of phylogenetic diversity relative to species richness).

As expected based on previous studies mostly identifying factors driving species richness, variables having a positive impact driving phylogenetic diversity in this study were; ‘Plant productivity’ (Sandom et al., 2013; Barrio et al., 2016), the climatic factor ‘Max temperature of warmest month’ (Hawkins et al., 2003), ‘Habitat heterogeneity’ (Sandom et al., 2013), and ‘Topographic heterogeneity’ (Meltofte, 2013). It was also expected that ‘Soil pH’ possibly could have a positive impact driving patterns of phylogenetic diversity of arctic herbivores, on the basis of being one of the main drivers of vascular plants (Gough et al., 2000), but as earlier mentioned this variable were not found important driving the diversity patterns in this study. As expected, both ‘Distance to coast’ and ‘Population density’ (i.e. human population density) had a negative impact on patterns of phylogenetic diversity, as well as for patterns of species richness. Interestingly, as predicted ‘Ice history’ was the only variable showing a positive trend driving phylogenetic diversity whereas it was slightly negative for species richness. This indicates that areas which has been ice-free for a longer time period holds more phylogenetic diversity, but are not necessarily more species rich. As previous mentioned, this may be due areas previously being refugial where species has been isolated for a longer period of time, hence have had more time supporting speciation events (Waltari & Cook, 2005; Meltofte, 2013). With results discussed above, it is still important to acknowledge the possible influence different classes of species (i.e. avian and mammalian) might have on the overall result of explanatory variables driving phylogenetic diversity patterns in this study. Therefore, additional analyses testing the explanatory variables driving phylogenetic diversity patterns of birds and mammals separately were computed in order to briefly display possible differences between them (see Appendix 2).

All but two of the variables showing great relative importance explaining the diversity patterns, reveals having a negative effect on the pattern of phylogenetic diversity relative to species richness (Figure 6). This includes; ‘Habitat heterogeneity’, ‘Annual precipitation’, ‘Max temperature of warmest month’, ‘Ice history’, and somewhat ‘Population density’. This result suggests that an increase in either of these variables will decrease the ratio between phylogenetic diversity and species richness, since all arctic areas revealed to have an higher representation of phylogenetic diversity than of species richness (Figure 2). In other words, an increase in either of these variables mentioned will drive areas to either become more species rich or less phylogenetically diverse considered in relation to each other. Interestingly, the results reveal positive coefficient estimates for the variables ‘Distance to coast’ and ‘Topographic heterogeneity’ in the pattern of phylogenetic diversity relative to species richness. Considering ‘Distance to coast’, the estimated coefficients of both phylogenetic diversity and species richness are negative, confirming expectations decreasing phylogenetic diversity and species richness when moving further from the coast. However, moving further inland also increases the ratio between these measurements, suggesting an areas distance to coastline being more important driving phylogenetic diversity patterns than of species richness patterns in the investigated group of species. When considering ‘Topographic heterogeneity’, the result shows positive coefficients for both phylogenetic diversity and species richness, supporting expectations of areas consisting of more heterogeneous topography to be more phylogenetic diverse and species rich (Meltofte, 2013). Additionally, ‘Topographic heterogeneity’ will also increase the ratio of phylogenetic diversity relative to species richness, suggesting this variable being more important driving patterns of phylogenetic diversity than of species richness in arctic vertebrate herbivores. Put together, these results suggest a greater difference between measures of phylogenetic diversity and species richness in arctic vertebrate herbivores in areas that are more topographically heterogeneous and further inland. In the end, one must also acknowledge that the actual ratio between the indices of arctic vertebrate herbivores will also be dependent on the value of other important variables found in the same area, which includes other variables yet to be investigated in addition to the variables investigated in this study.

Concluding remarks

To summarize, this study has illustrated that incorporation of phylogenetic diversity measurements in biodiversity analyses provides new insights of diversity patterns and mechanisms driving these patterns in arctic vertebrate herbivores. A strong correlation was found between patterns of phylogenetic diversity and species richness on this studied group of species. Further, correlation analyses revealed phylogenetic diversity overall being higher than of species richness across the Arctic. Several arctic islands were identified having a high overrepresentation of phylogenetic diversity relative to species richness, suggesting these areas representing a span across the phylogenetic tree even though being quite species-poor compared to the Arctic mainland. Finally, several explanatory variables were identified as important, relative to each other, driving the ratio between the patterns of phylogenetic diversity and species richness in vertebrate herbivores across the Arctic. The variables of ‘Plant productivity’, ‘Ice history’, ‘Max temperature of warmest month’, ‘Annual precipitation’, ‘Habitat heterogeneity’ and to some extent ‘Population density’ were found to have a negative effect on the pattern of phylogenetic diversity relative to species richness. On the other hand, the variables ‘Topographic heterogeneity’ and ‘Distance to coast’ was revealed to have a positive effect, increasing the ratio between the patterns of phylogenetic diversity and species richness of arctic vertebrate herbivores.

When further considering the Arctic being particularly vulnerable to climate change and other environmental changes (Meltofte, 2013; Turetsky et al., 2017), incorporation of phylogenetic diversity measurements in conservation challenges (Faith, 2008) in this region can provide new information. The measurement offers a more objective approach (Hartmann & André, 2013) to avoid debating conservation priorities solely on a species-level, because when using phylogenetic diversity measurements, you aim to conserve as much hierarchical variation as the available resources permit (Faith, 1992; Faith & Baker, 2006). In other words, using phylogenetic diversity in conservation assessments takes into account the relationship between species, and therefore ancestral branches between the existing species are also considered in the calculations (Faith, 2008). This study has focused on investigating the total branch length of the vertebrate herbivorous species present in areas across the Arctic, also investigated relative to species richness patterns. As formerly discussed, areas of the northwestern Nearctic were found to be the most phylogenetic diverse (i.e. have representation of the longest total branch length of the phylogenetic tree) (Figure 1a), whereas several arctic islands were found to have the highest overrepresentation of phylogenetic diversity relative to species richness (i.e. have representation of the longest total branch length of the phylogenetic tree per species present) (Figure 3). These results can be used to motivate further research, such as investigating phylogenetic endemism (Faith, 2008) of arctic vertebrate herbivores at a level of features-within-areas rather than species-within-areas, in order to reveal if there are any branches or whole clades restricted to certain areas of the Arctic.

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APPENDIX

Appendix 1

Table A1 List of investigated species, all vertebrate herbivores present in the Arctic region (including the Subarctic region). Species removed from the analysis due to missing molecular data in the phylogenetic analysis or due to too small range to occur in the grid cells (when each cell were 100x100 km) are marked in red. For the analyses, four species distribution datasets were made: (1) all herbivores also including the semi-domesticated species *Ovis aries* and *Rangifer tarandus*. (2) All avian species. (3) All mammalian species, including semi-domesticated species. (4) All herbivores excluding the semi-domesticated species (i.e. only wild species).

Class	**Order**	**Family**	**Species**	**Common name**
Mammalia	Lagomorpha	Leporidae	*Lepus americanus*	Snowshoe hare
Mammalia	Lagomorpha	Leporidae	*Lepus arcticus*	Arctic hare
Mammalia	Lagomorpha	Leporidae	*Lepus othus*	Alaskan hare
Mammalia	Lagomorpha	Leporidae	*Lepus timidus*	Mountain hare
Mammalia	Lagomorpha	Ochotonidae	*Ochotona collaris*	Collared pika
Mammalia	Lagomorpha	Ochotonidae	*Ochotona hyperborea*	Northern pika
Mammalia	Lagomorpha	Ochotonidae	*Ochotona turuchanensis*	Turuchan pika
Mammalia	Rodentia	Castoridae	*Castor canadensis*	American bever
Mammalia	Rodentia	Cricetidae	*Arvicola amphibius*	Water vole
Mammalia	Rodentia	Cricetidae	*Alticola lemminus*	Mountain vole
Mammalia	Rodentia	Cricetidae	*Microtus abbreviatus*	Insular vole
Mammalia	Rodentia	Cricetidae	*Microtus chrotorrhinus*	Rock vole
Mammalia	Rodentia	Cricetidae	*Microtus gregalis*	Narrow-headed vole
Mammalia	Rodentia	Cricetidae	*Microtus hyperboreus*	North Siberian vole
Mammalia	Rodentia	Cricetidae	*Microtus levis*	East European vole
Mammalia	Rodentia	Cricetidae	*Microtus longicaudus*	Long-tailed vole
Mammalia	Rodentia	Cricetidae	*Microtus middendorffii*	Middendorff's vole
Mammalia	Rodentia	Cricetidae	*Microtus miurus*	Singing vole
Mammalia	Rodentia	Cricetidae	*Microtus oeconomus*	Tundra vole
Mammalia	Rodentia	Cricetidae	*Microtus pennsylvanicus*	Meadow vole
Mammalia	Rodentia	Cricetidae	*Microtus xanthognathus*	Taiga vole
Mammalia	Rodentia	Cricetidae	*Myodes gapperi*	Southern red-backed vole
Mammalia	Rodentia	Cricetidae	*Myodes rufocanus*	Grey red-backed vole
Mammalia	Rodentia	Cricetidae	*Myodes rutilus*	Northern red-backed vole

Mammalia	Rodentia	Cricetidae	*Dicrostonyx hudsonius*	Ungava collared lemming
Mammalia	Rodentia	Cricetidae	*Dicrostonyx groenlandicus*	Nearctic collared lemming
Mammalia	Rodentia	Cricetidae	*Dicrostonyx nelsoni*	Nelson's collared lemming
Mammalia	Rodentia	Cricetidae	*Dicrostonyx richardsoni*	Richardson's collared lemming
Mammalia	Rodentia	Cricetidae	*Dicrostonyx torquatus*	Palearctic collared lemming
Mammalia	Rodentia	Cricetidae	*Dicrostonyx unalascensis*	Umnak Island collared lemming
Mammalia	Rodentia	Cricetidae	*Dicrostonyx vinogradovi*	Wrangel Island collared lemming
Mammalia	Rodentia	Cricetidae	*Lemmus amurensis*	Amur lemming
Mammalia	Rodentia	Cricetidae	*Lemmus lemmus*	Norway lemming
Mammalia	Rodentia	Cricetidae	*Lemmus portenkoi*	Wrangel Island brown lemming
Mammalia	Rodentia	Cricetidae	*Lemmus sibiricus*	Siberian brown lemming
Mammalia	Rodentia	Cricetidae	*Lemmus trimucronatus*	Nearctic brown lemming
Mammalia	Rodentia	Cricetidae	*Synaptomus borealis*	Northern bog lemming
Mammalia	Rodentia	Cricetidae	*Ondarta zibethicus*	Muskrat
Mammalia	Rodentia	Dipodidae	*Sicista betulina*	Boreal birch mouse
Mammalia	Rodentia	Erethizontidae	*Erethizon dorsatum*	North American porcupine
Mammalia	Rodentia	Muridae	*Apodemus sylvaticus*	Long-tailed field mouse
Mammalia	Rodentia	Sciuridae	*Marmota broweri*	Alaskan marmot
Mammalia	Rodentia	Sciuridae	*Marmota caligata*	Hoary marmot
Mammalia	Rodentia	Sciuridae	*Marmota camtschatica*	Black-capped marmot
Mammalia	Rodentia	Sciuridae	*Marmota monax*	Woodchuck
Mammalia	Rodentia	Sciuridae	*Spermophilus parryii*	Arctic ground squirrel
Mammalia	Ungulata	Bovidae	*Bison bison*	American bison
Mammalia	Ungulata	Bovidae	*Ovibos moschatus*	Muskox
Mammalia	Ungulata	Bovidae	*Ovis aries*	Domestic sheep
Mammalia	Ungulata	Bovidae	*Ovis dalli*	Dall's sheep
Mammalia	Ungulata	Bovidae	*Ovis nivicola*	Snow sheep
Mammalia	Ungulata	Cervidae	*Alces alces*	Eurasian elk
Mammalia	Ungulata	Cervidae	*Alces americanus*	Moose
Mammalia	Ungulata	Cervidae	*Rangifer tarandus*	Caribou/reindeer

Aves	Anseriformes	Anatidae	*Anas americana*	American Wigeon
Aves	Anseriformes	Anatidae	*Anas penelope*	Eurasian Wigeon
Aves	Anseriformes	Anatidae	*Anser albifrons*	Greater white-fronted goose
Aves	Anseriformes	Anatidae	*Anser anser*	Greylag goose
Aves	Anseriformes	Anatidae	*Anser brachyrhynchus*	Pink footed goose
Aves	Anseriformes	Anatidae	*Anser erythropus*	Lesser white-fronted goose
Aves	Anseriformes	Anatidae	*Anser fabalis*	Bean goose
Aves	Anseriformes	Anatidae	*Branta bernicla*	Brent goose
Aves	Anseriformes	Anatidae	*Branta canadensis*	Canada goose
Aves	Anseriformes	Anatidae	*Branta hutchinsii*	Crackling goose
Aves	Anseriformes	Anatidae	*Branta leucopsis*	Russian barnacle goose
Aves	Anseriformes	Anatidae	*Branta ruficollis*	Red-breasted goose
Aves	Anseriformes	Anatidae	*Chen caerulescens*	Snow goose
Aves	Anseriformes	Anatidae	*Chen canagica*	Emperor goose
Aves	Anseriformes	Anatidae	*Chen rossii*	Ross's goose
Aves	Anseriformes	Anatidae	*Cygnus buccinator*	Trumpeter swan
Aves	Anseriformes	Anatidae	*Cygnus columbianus*	Tundra swan
Aves	Anseriformes	Anatidae	*Cygnus cygnus*	Whooper swan
Aves	Galliformes	Phasianidae	*Lagopus lagopus*	Willow ptarmigan
Aves	Galliformes	Phasianidae	*Lagopus leucura*	White-tailed ptarmigan
Aves	Galliformes	Phasianidae	*Lagopus muta*	Rock ptarmigan

Table A2 List of accession numbers for each taxon (i.e. species) used in the Bayesian phylogenetic analyses (see Figure A1). Four mitochondrial markers were used when available; cytochrome B – cytB; cytochrome oxidase subunit 1 – COI; 12S ribosomal RNA; 12S; NADH dehydrogenase subunit 4 – ND4.

Taxon	**cytB**	**COI**	**12S**	**ND4**
Alces_alces	KC337273.1	KX859263.1		
Alces_americanus	M98484.1	JF443170.1		
Alticola_lemminus	KJ556633.1			
Anas_americana	AF059103.1	DQ433309.1		
Anas_penelope	AF059107.1	GU571239.1	AY164518.1	
Anser_albifrons	EU585612.1	DQ433314.1	AY164531.1	
Anser_anser	AY427814.1	GU571242.1	AY164530.1	DQ468124.1
Anser_brachyrhynchus	EU585614.1	GU571244.1		
Anser_erythropus	EU585617.1	GU571729.1		
Anser_fabalis	EU585618.1	FJ808625.1	AY164514.1	
Apodemus_sylvaticus	KM582049.1	KP869163.1	AJ311131.1	
Arvicola_amphibius	KM005047.1	AY332681.1		AF128938.1
Bison_bison	AF036273.1	JF443195.1		
Branta_bernicla	HM063580.1	GU571279.1	HM063557.1	
Branta_canadensis	EU585629.1	DQ434443.1	AF173715.1	
Branta_hutchinsii	AY072593.1	DQ434479.1		
Branta_leucopsis	EU585630.1	GU571283.1		
Branta_ruficollis	EU585631.1			
Castor_canadensis	KY321562.1	LC144616.1	AY012111.1	JQ663965.1
Chen_caerulescens	X77190.1	DQ434537.1		
Chen_canagica	EU585615.1		AF173714.1	
Chen_rossii	EU914156.1	DQ434538.1	U83734.1	
Cygnus_buccinator	AY509690.1	AY666404.1	U59667.1	
Cygnus_columbianus	EU585642.1	DQ433560.1		
Cygnus_cygnus	EU585643.1	GU571360.1	AY164523.1	
Dicrostonyx_groenlandicus	KJ556713.1	JF456464.1		AF128937.1
Dicrostonyx_hudsonius	AJ238436.1	JF456491.1		
Dicrostonyx_richardsoni	AJ238435.1	JF443818.1		
Dicrostonyx_torquatus	KT867537.1			
Erethizon_dorsatum	KC463889.1	JF456596.1	AY012118.1	
Lagopus_lagopus	EF571187.1	GU571438.1	AF222583.1	
Lagopus_leucura	AF230171.1	DQ433716.1	AF222584.1	
Lagopus_muta	AY156346.1	DQ433738.1	KC785614.1	
Lemmus_amurensis	FJ025979.1			
Lemmus_lemmus	JX483908.1			
Lemmus_sibiricus	AY219144.1			
Lemmus_trimucronatus	AF119276.1	JF456714.1		AF128943.1
Lepus_americanus	KM261475.1		U58923.1	
Lepus_arcticus	HQ596461.1	JF443819.1		
Lepus_othus	HQ596479.1			
Lepus_timidus	DQ882959.1		AB058610.1	HM232960.1
Marmota_broweri	JN024621.1			
Marmota_caligata	KJ458055.1			JF313275.1
Marmota_camtschatica	AF100715.1			JF313276.1

Marmota_monax	AF157953.1	JF456717.1	AY227529.1	JF313286.1
Microtus_abbreviatus	AF163890.1			
Microtus_chrotorrhinus	AF163893.1			
Microtus_gregalis	KP190244.1	KP190315.1		
Microtus_hyperboreus		HM137736.1		
Microtus_levis	FJ641161.1	EF608582.1	FJ619947.1	EF608583.1
Microtus_longicaudus	KF964344.1	JF456725.1		AF128936.1
Microtus_middendorffii	AF163898.1	HM137740.1		
Microtus_miurus	EF608581.1			
Microtus_oeconomus	KP190237.1	KP190307.1	AJ616853.1	
Microtus_pennsylvanicus	KF948531.1	KM189812.1	JN393216.1	U83806.1
Microtus_xanthognathus	AF163907.1			
Myodes_gapperi	DQ323950.1	JQ350489.1		U83808.1
Myodes_rufocanus	KR059903.1	JF693313.1		
Myodes_rutilus	JX477342.1	HM165297.1		
Ochotona_collaris	KP411020.1			EU549753.1
Ochotona_hyperborea	KR076823.1	DQ347441.1	AY012127.1	EU549756.1
Ochotona_turuchanensis	EF567056.1	DQ347468.1		
Ondatra_zibethicus	KT376465.1	JF456977.1	JN315625.1	U83809.1
Ovibos_moschatus	U17862.1	JF443354.1	AY670662.1	
Ovis_aries	KU253486.1	KT750039.1		
Ovis_dalli	AF034728.1	JF443359.1	AY670664.1	
Ovis_nivicola	AJ867265.1		Y09259.1	
Rangifer_tarandus	KJ138217.1	JF443494.1	AY184438.1	
Sicista_betulina	KP715861.1			
Spermophilus_parryii	AF157931.1	KM537933.1		
Synaptomys_borealis	AF119259.1	JF457125.1		AF128932.1

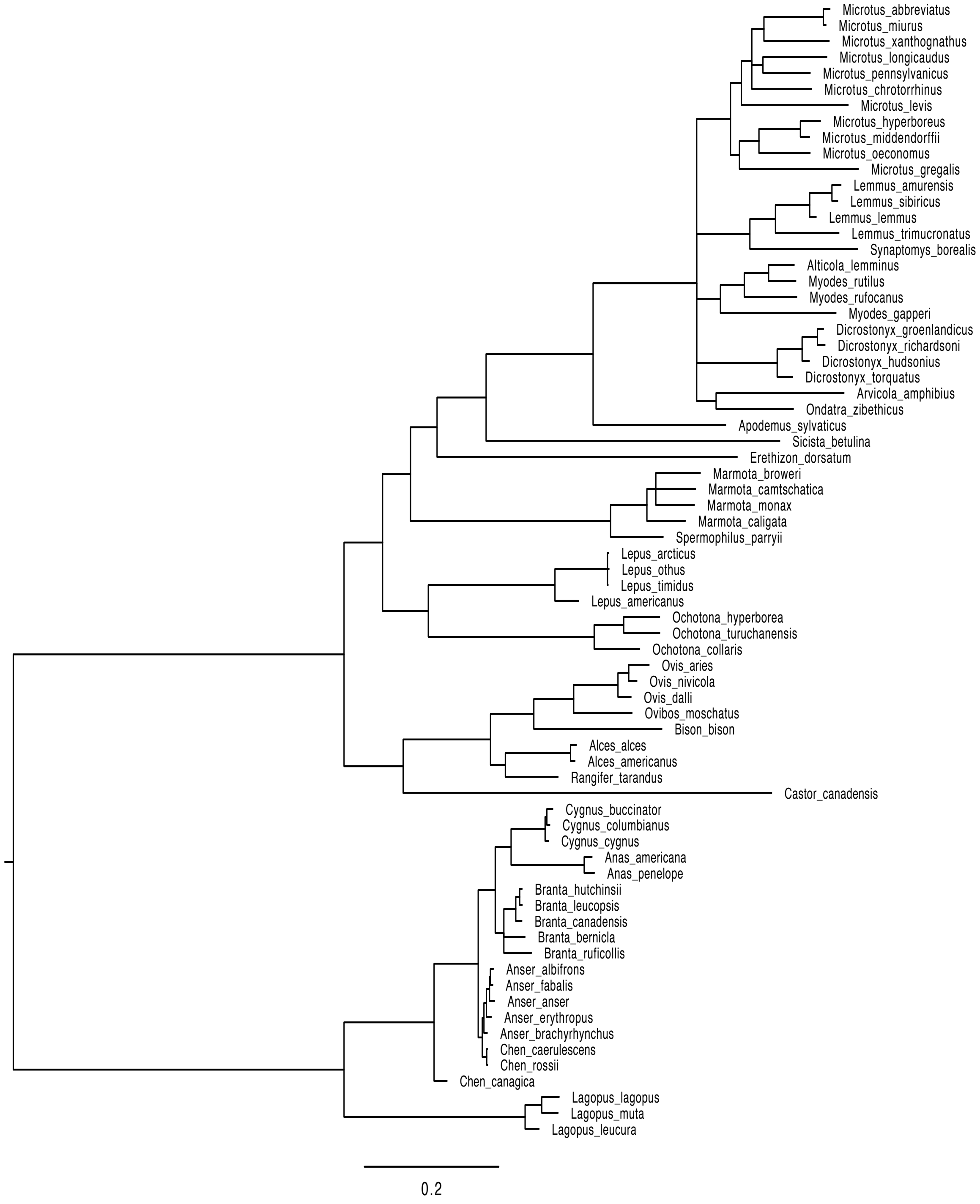

Figure A1 Topology of the phylogenetic Bayesian analysis consisting of 71 taxa (including *Castor canadensis*). Four mitochondrial markers were included in the analysis; cytB, COI, 12S, ND4. In the diversity analysis performed in Biodiverse (Laffan et al., 2010) the tree was trimmed to match distribution data, resulting in the removal of Microtus Abbreviatus as the species range were too narrow to appear in the grid cells (consisting of 100x100 km). Therefore, 70 taxa from this topology were left for the diversity analysis. The topology is displayed using FigTree version 1.4.3[1].

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[1] http://tree.bio.ed.ac.uk/software/figtree/

Figure A2 Relationship between the different explanatory variables investigated. All moderate and strong correlations with |r| >0.40 are marked in red. Based on these correlations, ‘Annual mean temperature’ (= Bio1) and ‘Elevation’ were removed in the analysis due to strong correlations with other variables. All other variables were included in further analysis, despite revealing some correlations, since these were linked to specific hypotheses. Bio1 is ‘Annual mean temperature’, Bio5 is ‘max temperature of the warmest month’, Bio12 is ‘Annual precipitation’, cp_ndvi_la is ‘plant productivity’, population.density is ‘human population density’, kya_since_ice is ‘Ice history’.

Table A3 Top-ranking models (ΔAIC < 3) for possible explanatory variables for diversity patterns of arctic vertebrate herbivores: (a) Phylogenetic diversity (PD) for all herbivores. (b) Species richness (SR) for all herbivores. (c) Phylogenetic diversity relative to species richness (PD/SR) for all herbivores. The global model of explanatory variables used for all five analyses included these variables: 'Annual precipitation', 'Max temperature of warmest month', 'NDVI', 'Habitat heterogeneity', 'Distance to coast', 'Ice history' (=kya since ice), 'soil pH', 'Topographic heterogeneity' and 'Population density' (i.e. human population density). For each model the explanatory variables included are specified as well as the number of parameters (k). The ΔAIC value shows the AIC value increase for a model relative to the top-ranking one of ΔAIC = 0.0. AIC weights (AIC wt) shows, given the data, the probability of each model being the single best of all the models. In addition are the cumulative weight (Cum wt) and the LogLikelihood for each model also presented here. Coast – effect of 'Distance to coast'; HbH – effect of 'Habitat heterogeneity'; Pop.dens – effect of 'Human population density'; TpH – effect of 'Topographic heterogeneity'; Bio12 – effect of 'Annual temperature'; Bio5 – effect of 'Max temperature of warmest month'; NDVI – effect of 'Plant productivity'; Ice – effect of 'Ice history'; Soil – effect of 'Soil pH'.

	k	**ΔAIC**	**AIC wt**	**Cum wt**	**LogLikelihood**
a) PD of all herbivores					
~Coast+HbH+Pop.dens +TpH+Bio12+Bio5+Ice	7	0.00	0.403	0.403	1913.016
~Coast+HbH+Pop.dens+TpH+Bio12+Bio5+NDVI+Ice	8	1.17	0.225	0.628	1913.447
~Coast+HbH+Pop.dens+TpH+Bio12+Bio5+Ice+Soil	8	1.81	0.163	0.791	1913.127
~Coast+HbH+Pop.dens+TpH+Bio12+Bio5+NDVI+Ice+Soil	9	2.99	0.090	0.881	1913.554
b) SR of all herbivores					
~Coast+HbH+Pop.dens+TpH+Bio12+Bio5+NDVI+Soil	8	0.00	0.716	0.716	2402.918
~Coast+HbH+Pop.dens+TpH+Bio12+Bio5+NDVI+Ice+Soil	9	1.89	0.278	0.994	2402.989
(c) PD/SR of all herbivores					
~Coast+HbH +TpH+Bio12+Bio5+NDVI+Ice+Soil	8	0.00	0.405	0.405	2302.366
~Coast+HbH+Bio12+Bio5+NDVI+Ice+Soil	7	0.45	0.323	0.728	2301.126
~Coast+HbH+Pop.dens+TpH+Bio12+Bio5+NDVI+Ice+Soil	9	1.97	0.151	0.879	2302.398
~Coast+HbH+Pop.dens +Bio12+Bio5+NDVI+Ice+Soil	8	2.42	0.121	1.00	2301.155

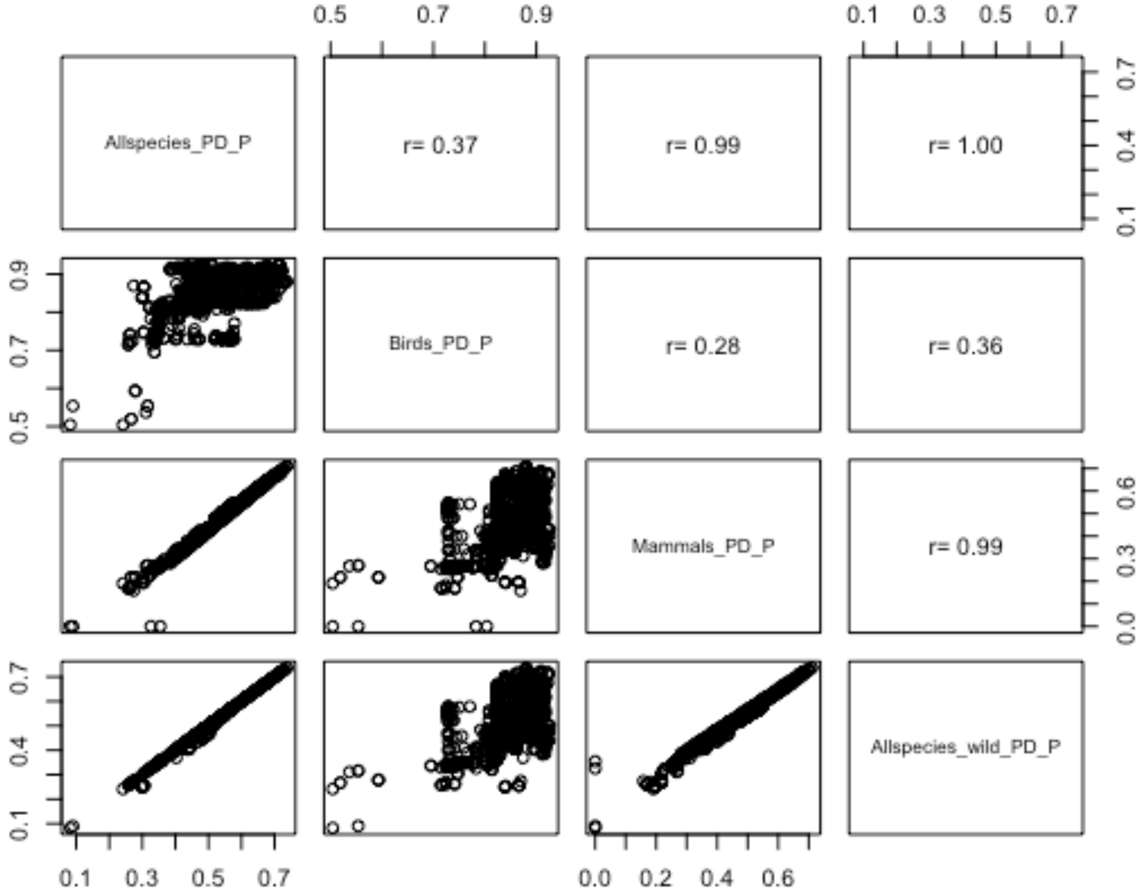

Figure A3 Correlations between phylogenetic diversity between different groups investigated: Allspecies_PD_P is phylogenetic diversity of all herbivores, including the semi-domesticated species *Ovis aries* and *Rangifer tarandus*. Birds_PD_P is phylogenetic diversity including all herbivorious birds investigated. Mammals_PD_P is phylogenetic diversity including all herbivorious mammals investigated. Allspecies_wild_PD_P is all herbivores excluding the semi-domesticated species.

Appendix 2

Additional results revealing relative importance scores of variables when investigating patterns of phylogenetic diversity in birds (see Figure 4a) and mammals (see Figure 4b) separately. Same procedure used as in the main analyses (see section of Materials and Methods).

Table A4 Top-ranking models (ΔAIC < 3) for possible explanatory variables for diversity patterns of Arctic vertebrate herbivores: (i) Phylogenetic diversity (PD) for all herbivores. (ii) Phylogenetic diversity (PD) for all birds. (iii) Phylogenetic diversity (PD) for all mammals. The global model of explanatory variables used for all three analyses included these variables: 'Annual precipitation', 'Max temperature of warmest month', 'NDVI', 'Habitat heterogeneity', 'Distance to coast', 'Ice history' (=kya since ice), 'soil pH', 'Topographic heterogeneity' and 'Population density' (i.e. human population density). For each model the explanatory variables included are specified as well as the number of parameters (k). The ΔAIC value shows the AIC value increase for a model relative to the top-ranking one of ΔAIC = 0.0. AIC weights (AIC wt) shows, given the data, the probability of each model being the single best of all the models. In addition are the cumulative weight (Cum wt) and the LogLikelihood for each model also presented here. Coast – effect of 'Distance to coast'; HbH – effect of 'Habitat heterogeneity'; Pop.dens – effect of 'Human population density'; TpH – effect of 'Topographic heterogeneity'; Bio12 – effect of 'Annual temperature'; Bio5 – effect of 'Max temperature of warmest month'; NDVI – effect of 'plant productivity'; Ice – effect of 'Ice history'; Soil – effect of 'Soil pH'.

	k	**ΔAIC**	**AIC wt**	**Cum wt**	**LogLikelihood**
i) PD of all herbivores					
~Coast+HbH+Pop.dens +TpH+Bio12+Bio5+Ice	7	0.00	0.403	0.403	1913.016
~Coast+HbH+Pop.dens+TpH+Bio12+Bio5+NDVI+Ice	8	1.17	0.225	0.628	1913.447
~Coast+HbH+Pop.dens+TpH+Bio12+Bio5+Ice+Soil	8	1.81	0.163	0.791	1913.127
~Coast+HbH+Pop.dens+TpH+Bio12+Bio5+NDVI+Ice+Soil	9	2.99	0.090	0.881	1913.554
ii) PD of herbivorous birds					
~Coast+HbH+TpH+Bio12+Bio5+NDVI+Ice+Soil	8	0.00	0.447	0.447	2254.670
~Coast+HbH+Pop.dens+TpH+Bio12+Bio5+NDVI+Ice+Soil	9	0.52	0.344	0.791	2255.425
iii) PD of herbivorous mammals					
~Coast+HbH+Pop.dens+TpH+Bio12+Bio5+Ice	7	0.00	0.508	0.508	1665.260
~Coast+HbH+Pop.dens+TpH+Bio12+Bio5+NDVI+Ice	8	1.89	0.197	0.705	1665.329
~Coast+HbH+Pop.dens+TpH+Bio12+Bio5+Ice+Soil	8	1.92	0.194	0.899	1665.315

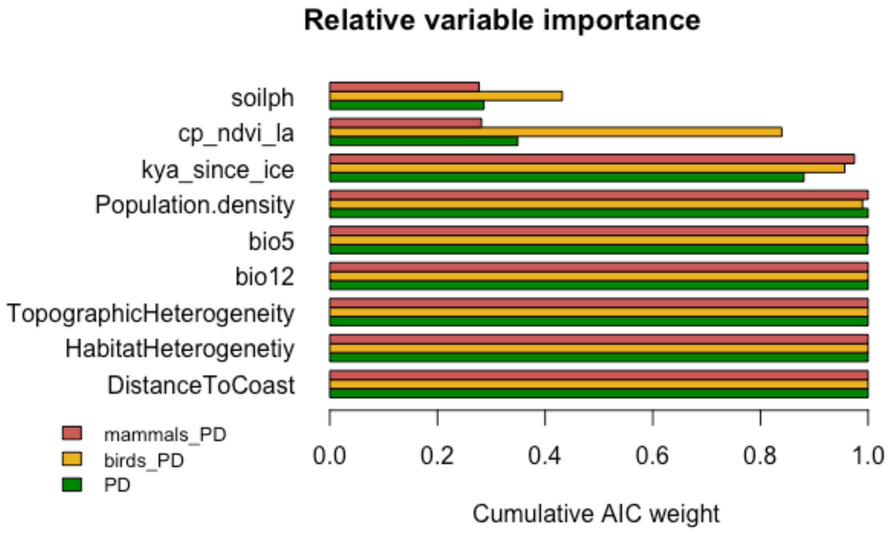

Figure A4 Variable importance scores for phylogenetic diversity of all herbivores (PD; green), herbivores mammals (mammals_PD; red) and herbivores birds (birds_PD; yellow). For each variable, the AIC weight for all models in which it appears is summed to represent the relative importance of the variable. The cumulative weight can be used to set order of importance of each variable, thus it can be understood as the probability of the variable being present in the best-fitted model. Cp_ndvi_la is ‘Plant productivity’, kya_since_ice is ‘Ice history’, bio5 is the ‘max temperature of the warmest month’, and bio12 is the ‘annual precipitation’.