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Patterns and relationships of the distribution of arctic and boreal forest herbivores: A three-dimensional approach.

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Abstract

Biodiversity is a complex concept that presents three primary facets: genetic, species and ecological diversity. However, biodiversity is usually viewed and valued in terms of the number of discrete species present. This approach has been demonstrated to be insufficient. Therefore, three synergetic methods that function as proxies for the three facets of biodiversity, genetic, species and ecological diversity, are used in this study to provide a better understanding of biodiversity. These methods are phylogenetic diversity, species richness and functional diversity respectively. The relationship between phylogenetic or functional diversity with species richness yields information on the evolutionary history and ecological niche representation through clustering and dispersion. The arctic and boreal biomes are under great threat from climate change and land-use change and provide important ecosystems services for both, local and global communities. In order to better understand these biomes, we've focused on a group of taxa that has a wide range of functions in the ecosystem and that is composed from several genetic lineages, the vertebrate herbivores. Therefore, the aim of this study is to further our understanding of the biodiversity patterns and relationships of arctic and boreal herbivores. We found that all three biodiversity measures increased towards the south, possibly correlated to plant productivity. However functional diversity did not present such a strong gradient with the values in the north not reducing drastically as in the other measures. We have identified a "doughnut" pattern of functional dispersal in the arctic and boreal biomes with functional clustering at high and low latitudes and functional dispersion at mid-latitudes. Which indicates that at high and low altitudes herbivores are functionally similar from different environmental pressures, such as predation and abiotic conditions at low and high altitudes respectively. Furthermore, we have identified areas of a possible radiation event in south eastern Russia near the Mongolian border as well as an area of a relatively recent invasion of herbivores in the Labrador Peninsula. Our study demonstrates the importance of including trophic dynamics in biodiversity assessments and calls for future studies that explore the relationship between biodiversity measures and trophic interactions.

Acknowledgements

Table of Contents

List of Figures

List of Tables

Abbreviations

PCR	Polymerase chain reaction
16S	16s ribosomal RNA gene
12S	12s ribosomal RNA gene
COI	Cytochrome oxidase subunit 1
cytB	Cytochrome B
ND2	NADH dehydrogenase 2
MSA	Multiple sequence alignment
ML	Maximum likelihood
FAMD	Factorial Analysis of mixed data
HCPC	Hierarchical clustering of principle components

1. Introduction

Conservation biology is focused on preserving the biodiversity of the world. Biodiversity is comprised of three interrelated aspects: genetic diversity, species diversity and ecosystem diversity (Primark, 2014). Genetic diversity involves the genetic variation that occurs amongst species and individuals. Species diversity involves the diversity between species that are sympatric, and ecosystem diversity encompasses the different communities found in an ecosystem and their interactions with it, both biotic and abiotic (Primark, 2014). These three aspects of biodiversity are often segregated while conducting biodiversity research (Rodrigues & Gaston, 2002). However, increasing evidence suggests that due to the different relationships between these three aspects as well as the limitations that emerge from focusing in only one aspect (such as the commonly used species richness), it is important to consider all components of biodiversity in order to obtain a more accurate assessment of the biodiversity status of an area. (Bininda-Emonds, Vázquez, & Manne, 2000; Brooks et al., 2015; Cadotte, Dinnage, & Tilman, 2012; Devictor et al., 2010; Félix et al., 2007; Fritz & Rahbek, 2012; Li, Kraft, Yu, & Li, 2015; Rissler, Hijmans, Graham, Moritz, & Wake, 2006; Rodrigues & Gaston, 2002; Safi et al., 2011; Schipper et al., 2008; Winter, Devictor, & Schweiger, 2012). In order to account for the three facets of biodiversity and to mitigate the limitations of a single facet approach, the usage of complementary biodiversity assessment methods has been proposed (Faith, 1992; Fleishman, Noss, & Noon, 2006; Speed et al., 2019).

The first of these complementary biodiversity assessments is species richness, otherwise referred to as taxon diversity (at the species level). Species richness is the sum of species found within a geographic area, which relates directly to biodiversity via the species diversity facet (Primark, 2014). Species richness is the most common measurement of biodiversity since it requires only knowledge of the occurrence or geographical distribution of a species and because there is evidence for a correlation between species richness and functional and phylogenetic diversity (Fritz & Rahbek, 2012; Rodrigues & Gaston, 2002; Schipper et al., 2008). However, this correlation is contested, and new evidence suggests that, among other issues, it is not an adequate substitute of other biodiversity measuring methods. (Bininda-Emonds et al., 2000 ; Brooks et al., 2015; Faith, 2013; Félix et al., 2007; Petchey & Gaston, 2002; Tilman, 2001). Additionally, this method is limited in the information it can provide

(Fleishman et al., 2006). One such example is that it can't account for complex ecosystem functions, such as ecosystem resilience, defined as the capacity of an ecosystem to recuperate rapidly into a stable state after disturbance, and ecosystem resistance (Cadotte et al., 2012; Díaz & Cabido, 2001; Primark, 2014). Furthermore, species richness is unable to clearly represent the evolutionary history of an area and is unable to account for the genetic relationship amongst species (Faith & Baker, 2007; Faith, 1992).

Since species richness relies solely on the amount of species, small variations in the number of species will significantly change the values in the assessment. Furthermore, the total number of species within clades remains unresolved. Therefore, assessments based on species richness alone are susceptible to large changes in value due to taxonomic revisions. This taxonomic volatility is evidenced by cases that involve misidentified cryptic species as belonging to a single species (Lara et al., 2010), individual species that have been divided into two or more different species (Bain, Lathrop, Murphy, Orlov, & Cuc, 2003; Hundertmark & Bowyer, 2004) and taxonomic inflation, which is the recent accelerated increase in species numbers. Taxonomic inflation is generally related to low genetic variation and therefore, low genetic diversity values (Padial & De la Riva, 2006; Tattersall, 2007). This implies that an area high species richness may possess low genetic diversity. However, this area may inaccurately be considered as an area with an overall high biodiversity solely due to its high amount of species. Taxonomic inflation poses a large problem for biodiversity and conservation studies that rely on species as their sole unit of measurement. The equal value given to each species in the assessment may heavily sway the final biodiversity values if only species richness is accounted for (Padial & De la Riva, 2006). Simultaneously, species richness approaches require a stable, universal list of species. This is unrealistic due to the continuous nature of speciation and continuous taxonomic revisions (Knapp, Lughadha, & Paton, 2005; Padial & De la Riva, 2006). Therefore, in order to mitigate the limitations of species richness and ensure a better overview of biodiversity, it is important to employ other diversity assessments in tandem (Devictor et al., 2010).

Phylogenetic diversity, understood as the sum of the minimum branch lengths in a phylogenetic tree that represent a set of taxa, allows for the inclusion of the genetic diversity facet into any biodiversity assessment (Faith & Baker, 2007; Faith, 1992). This inclusion depends on the addition of molecular information that belongs to a subset of sympatric taxa. This creates a cladistic clustering of taxa (i.e. species) in which taxa with similar features (i.e. genetic

sequences) are clustered closely and taxa with more divergent features are further apart (Faith, 1992; Félix et al., 2007). This cladistic-based hierarchical clustering of taxa allows for the inclusion of molecular information into biodiversity assessments. This generates a better biodiversity analysis by accounting for the evolutionary history of the organisms (Devictor et al., 2010), the genetic diversity in a community and the promotion of ecosystem stability (Cadotte et al., 2012).

Due to the calculations of phylogenetic diversity being based on the total length of the branches in a phylogeny, the simultaneous usage of phylogenetic diversity and species richness attenuates the limitations of a species richness analysis. Since closely related species are separated by shorter spanning branch lengths (genetic distance) relative to highly divergent species, an area with a larger number of closely related species may yield lower phylogenetic diversity. On the contrary, an area with a smaller number of species but a higher level of divergence may yield higher phylogenetic diversity. Thus, an area with low phylogenetic diversity values has less genetic diversity than an area with high phylogenetic diversity values, which is not necessarily correlated to the number of species. This reduces the effect that taxonomic problems, such as taxonomic inflation, have on a diversity analysis (Bininda-Emonds et al., 2000; Faith, 2013; Félix et al., 2007; Fleishman et al., 2006; Loreau et al., 2001; Petchey & Gaston, 2002). Similarly, the evolutionary history of a community is inferred through phylogenetic diversity dispersion. This is done by comparing the phylogenetic diversity of an area with the expected phylogenetic diversity given by its recurrent linear relationship with species richness. This identifies areas of phylogenetic clustering and dispersion, which can help infer areas of radiation or invasion events as first assessed by Fritz and Rahbek (2012).

Correspondingly, the ecological facet of biodiversity must be included in a thorough biodiversity assessment. In order to do this, functional diversity may be used as a proxy to understand the effect of species on ecosystem functions in a quantifiable manner (Díaz & Cabido, 2001; Hempson, Archibald, & Bond, 2015; Loreau et al., 2001; Petchey & Gaston, 2002; Petchey & Gaston, 2006; Safi et al., 2011). The definition of functional diversity has varied over time, however it is commonly understood as "the value and the range of those species and organismal traits that influence ecosystem functioning," as defined by Tilman (2001). These organismal traits may be approached as functional traits when they describe an organism's ecological role. Functional traits are composed of three main character groupings

which are morphological (i.e. body mass), behavioural (i.e. foraging preferences) and physiological (i.e. gut efficiency) in nature (Tilman, 2001). Functional traits of high relevance for ecological studies have been proposed by Chapin et al. (1997) to be those that affect the interaction with resources, those that affect the trophic structure and as those that influence ecosystem disturbances. In essence, those traits that represent the species interaction with its ecosystem. These traits are useful for ecological studies since they allow for the generation of functional groups, such as predators, primary producers and consumers (Tilman, 2001), which permit a structured understanding of complex ecosystems. Likewise, functional traits allow for a structured and quantifiable niche evaluation. By focusing on traits that pertain a specific role of a group of taxa, (i.e. herbivores' plant predation) it is possible to assess how similar they are in their realized niche; which in turn, allows for a quantifiable analysis of the functional diversity for this subset of taxa.

Functional diversity encompasses the variation of ecological roles within a community, which allows for a community-wide ecological diversity assessment more tightly involved with the ecosystem facet of biodiversity (Laureto, Cianciaruso, & Samia, 2015; Petchey & Gaston, 2002; Tilman, 2001). Several methods have been proposed to measure functional diversity. These include indirect methods such as species richness, Shannon biodiversity index and functional groups (Díaz & Cabido, 2001; Tilman, 2001). However, these methodologies are fundamentally flawed as a proper surrogate for functional diversity. The largest problem with equating species richness as a global surrogate for functional diversity, is the 'equal value problem', similar to the limitations in equating phylogenetic diversity to species richness. Since species richness assumes the equal value of species for alternate biodiversity facets, the aforementioned taxonomic issues, as well as not accounting for the different functional value of species, become increasingly important. Employing the Shannon biodiversity index, which fundamentally assigns a diversity value relative to abundance (Primark, 2014), emulates the flaws of species richness and employing functional groups fails to account for functional differences within groups. The usage of a trait-based dendrogram approach to functional diversity allows for the identification of functional groups from a subset of taxa, as well as providing a functional diversity value calculated as the sum of the minimal branch length similar to phylogenetic diversity calculations (Díaz & Cabido, 2001; Hempson et al., 2015; Petchey & Gaston, 2002; Petchey & Gaston, 2006). A trait-based functional diversity approach relies on the characterization of functional traits of the target species consisting of traits that are relevant for an assessment of the selected species and ecosystem function.

It is important to establish that while each diversity measurement can be used as a proxy for a facet of biodiversity, they are not fully independent and should not be utilized in isolation. As previously established, the interaction between these measurements can yield complex information about the community structure, composition, evolutionary history, extinction susceptibility, resilience and ecological trends. These relationships are commonly shown as phylogenetic or functional clustering, as well as dispersion. Clustering is when either biodiversity measure presents lower values than would be expected by a null model (collapsed branch lengths). In other words, when the biodiversity measure has lower values than would be expected due to the species richness of the area. The inverse is true for dispersion, where higher values than expected are found (Safi et al., 2011). Phylogenetic dispersion and clustering shed light on the evolutionary history of the selected taxa (Fritz & Rahbek, 2012). Whilst functional dispersion and clustering demonstrate areas with functionally 'redundant' species or areas of diverse functionality more dependent on the identity of the present taxa (Safi et al., 2011). The vast amount of information obtained by a multi-diversity analysis demonstrates its value for conservation biology and natural resources management, particularly when it is employed to understand communities of species in biomes that are highly impacted by the current threats of climate and land-use changes. Hence, this study employs the previously described assessments in order to understand the biodiversity patterns of arctic and boreal herbivores.

The arctic biome is generally regarded as less productive and containing a smaller number of species than most other biomes, however its phylogenetic diversity is potentially larger than previously assumed (Skjelbred, 2017). In contrast, the boreal forest is one of the largest biomes in the world, possessing several large vertebrate species and a vast amount of fungal and plant species compared to the arctic. Within the arctic and boreal biomes, herbivores have a significant impact. Their impact extends towards the whole biome due to their interactions within the community and their central position within the trophic chain, interacting with both their predators and their prey (Hopcraft, Olff, & Sinclair, 2010). Thus, the diversity of the plant and carnivore communities vary in accordance with herbivore community composition (Hempson et al., 2015; Hopcraft et al., 2010). The largest impacts herbivores have on their ecosystem involve plant community dynamics and structure in forested areas, shrublands and grasslands, with direct impact on their succession, structure and resilience (Danell, 2006). Boreal and arctic vertebrate herbivores include mammals and birds, which are very distinct

phylogenetically. However, these two clades might converge in their ecological function (Speed et al., 2019). This functional convergence contrasts their lack of phylogenetic relatedness, further demonstrating the complexity of the two biomes. Therefore, understanding the biodiversity of herbivores in the arctic and boreal biomes is an important step in understanding a biome's biodiversity status, ecosystem and community composition.

Both the arctic and boreal biomes are significantly impacted by several biodiversity threats. The largest threats for terrestrial biodiversity in the northern biomes are land-use change (Rice, Seixas, Zaccagnini, Bedoya-Gaitán, & Valderrama, 2018; Rounsevell et al., 2018) and climate change (Rice et al., 2018; Rounsevell et al., 2018; Turetsky et al., 2017). Land use change has been proven to be the largest threat for biodiversity in northern ecosystems, which includes forestry and habitat fragmentation (Rice et al., 2018; Rounsevell et al., 2018). Simultaneously, arctic and boreal biomes are under threat from climate change, due to their latitudinal location and extreme weather variations (Turetsky et al., 2017). Climate change has the possibility of impacting northern biodiversity at several different scales, from fine spatial scales (i.e. soil and nutrients) to their larger scales (i.e. ecosystem and community). Therefore, it is important to determine how, and which climatic variables are important in explaining the distribution of arctic and boreal biodiversity. This calls for a more comprehensive understanding of arctic and boreal biodiversity and its drivers. Due to the large size of the arctic and boreal biome, macrospatial biodiversity pattern analysis can increase our current understanding of biodiversity drivers, both biotic and abiotic (Sandom et al., 2013). Since finer spatial scales the patterns of biodiversity tend to be influenced more heavily by sampling efforts, suggesting a tendency to artefact effects (Barbosa, Pautasso, & Figueiredo, 2013).

Furthermore, biodiversity patterns have been proven to depend on the environment, different evolutionary processes and the capacity to disperse (Barrio et al., 2016; Oksanen, 1992; Turetsky et al., 2017). Terrestrial herbivores have been shown to be regulated by forage abundance, forage quality and carnivory as well as depending on the environmental conditions and species-level traits (i.e. body size) (Hopcraft et al., 2010). Hence, the intimate relationship between trophic levels is an important driver for herbivore biodiversity. Plant productivity has been proven to be an important determining driver on terrestrial ecosystems (Field et al., 2009), particularly for herbivores (Hopcraft et al., 2010). Additionally, as previously described, the strong regulatory interactions between terrestrial carnivores and herbivores is an important determinant of herbivore biodiversity patterns, as well as there being a demonstrated link at

macroscales (Hopcraft et al., 2010; Sandom et al., 2013). Finally, the dynamics between three trophic levels (otherwise referred to as the three-link dynamics), including plants, herbivores and predators, has been proven to be an explanatory factor in biomass abundance amongst the three levels through the ecosystem exploitation hypothesis (Oksanen, 1992; Oksanen & Oksanen, 2000). Which states that biomass equilibrium is a result of the abiotic environmental variables as well as the interaction between the three groups, with the regulatory forces having a varying degree of importance depending mainly on the productivity of an ecosystem and the abiotic variables.

Multiple-facet biodiversity assessments have become more prevalent recently (for example see Safi et al. (2011)). However, global assessments of multiple biomes remain limited. Particularly in underrepresented ecosystems such as the arctic and the boreal biomes. Terrestrial herbivores are an important group in regulating ecosystem dynamics since they have a mid-trophic level, they aid in the regulation of both predators and plants (Schmitz, 2008). Similarly, the complex interactions in the trophic chain (Hopcraft et al., 2010), validate the benefits of focusing on a trophic guild instead of a phylogenetic clade whilst studying biodiversity. Since a trophic guild study integrates the interactions amongst guilds, which is part of the ecological facet of biodiversity. Therefore, in this study we aim describe and analyze spatial patterns of arctic and boreal herbivore biodiversity. Additionally, we attempt to identify areas that present strong differences between species richness, phylogenetic diversity and functional diversity, as well as, the differences in these metrics between the two studied biomes, the arctic and boreal forests. Furthermore, we strive to understand the environmental factors that influence the biodiversity patterns in the arctic and boreal biomes by analysing the biogeographical patterns of the three biodiversity measures and their interactions. Finally, we aim to understand the phylogenetic and functional relationships between the terrestrial vertebrate herbivores in the arctic and boreal biomes.

While determining biodiversity patterns we expect to find positive relationships between plant productivity and the three biodiversity measures. Which would appear as a latitudinal gradient due to the southern latitudes being more productive than the northern latitudes. This is because the boreal biome is richer in species than the arctic (Turetsky et al., 2017). However, we also expect that functional diversity will decrease less than phylogenetic diversity at higher latitudes due to lower productivity promoting higher ecological specialization. Furthermore, we theorize that biodiversity values will be higher in the Nearctic in relation to the Palearctic due to recent

and major biological migrations into the Americas (i.e. 'the great intercontinental exchange') (Marshall, Webb, Sepkoski, & Raup, 1982). We expect to have higher phylogenetic dispersion in the arctic rather than in the boreal biome due to the evolutionary isolation and invasion events form genetically unrelated taxa, due to glaciation events and the relatively high phylogenetic diversity generally found in the arctic (Skjelbred, 2017; Turetsky et al., 2017). Finally, we expect areas with high plant productivity to present functional clustering due to there being evidence that an over-abundance of resources leads to niche overlap and due to increased predator pressure in highly productive habitats (Wiens, 2011).

2. Materials and methods

In order to test the biodiversity patterns of terrestrial arctic and boreal herbivores, several steps were undertaken. First, the terrestrial herbivore species that inhabit the arctic and boreal biome were selected according to their consumption of vegetative plant material as well as the retrieval and handling of their spatial ranges. Secondly, the molecular data for these species was assembled, either from a repository of sequences or obtained from a laboratory extraction and subsequent sequencing. Once the sequences were assembled, they were employed in order to generate a maximum likelihood phylogenetic tree. Afterwards functional trait data was obtained from input of experts, trait databases and detailed literature review. This trait data was used to generate a functional dendrogram via a factorial analysis of mixed data and hierarchical clustering on principal components. Subsequently, the species range data, phylogenetic tree and functional dendrogram were utilized for the biodiversity patterns analysis. These analyses included the calculation of species richness, phylogenetic diversity, functional diversity, correlations between species richness and the other biodiversity measures, and both phylogenetic and functional dispersion patterns.

2.1 Species selection and geographic data assemblage

The arctic species included in this study were selected according to the methods and sources of Speed et al. (2019). Furthermore, relevant taxa were filtered according their presence or absence in the boreal biome, as defined by the World Wildlife Fund, their presence or absence in the arctic or boreal biome was identified according to the distribution data of the species found in the IUCN and Birdlife International. This was done by cross-referencing the spatial data for the original list of species with the borders of the arctic and boreal biomes obtained from the WWF, where the species that had cells inside the arctic and boreal biome's geographic distribution were selected. From the subset of all arctic and boreal animal species, the herbivores were automatically selected based on consumption of the vegetative organs in plants with a value equal or over 30% in steam and leaf consumption as found in the EltonTraits species-level foraging attributes table (Wilman et al., 2014). This excludes species which are primary frugivores and granivores. This yielded an original list of 248 species.

This species list was subsequently refined, due to possible errors in the automated selection method, by individually revising if the species met the aforementioned ≥30% plant consumption criterion and by excluding fully domesticated species, generating a list of 195 species. However, after further ecological information became available for the individual species, nine more were removed due to them not meeting the established ecological criteria. From the original list of species, *Dendrocygna bicolor* was dropped due to it not being present in arctic nor boreal biomes. The following species were excluded due to their consumption of plants being based on aquatic plants, which is not relevant to this study: *Aythya affinis, Aythya baeri, Aythya collaris, Melanitta americana, Melanitta deglandi, Melanitta stejnegeri, Netta rufina, Oxyura leucocephala*. Finally, *Allocricetulus eversmanni* was dropped due to the literature constantly referring to it as a pure granivore and no contradicting reference could be found at the time of this study. Therefore, the final species count for this study is 185 arctic and boreal herbivore species, of which 57 are birds and 129 species are mammals.

The geographical distribution maps of the species included in this study were obtained from two sources, the IUCN Red List and BirdLife International databases. These maps originally found as polygons of the species range, were rasterized into a 100 x 100km equal-area grid. The distribution for *Alces alces s.l.* was originally separated into two species, *Alces alces* and *Alces canadiensis*. The validity of these two species (in some cases more) is still debated, nevertheless molecular analysis supports a single species: *Alces alces* (Hundertmark & Bowyer, 2004). Therefore, in accordance with the IUCN, the two original distributions were merged into a single Alces alces distribution.

2.2 Molecular data and phylogenetic analysis

2.2.1 Retrieval of molecular data

The molecular data was obtained from two sources: NCBI's GenBank public sequence data repository, and via the extraction and Sanger sequencing of samples from museum specimens. First, GenBank sequences were obtained using Matrix Maker, a custom python script (Freyman & Thornhill, 2016). Five main mitochondrial markers were determined to have broad coverage across the 185 species of this study. These were cytochrome b (*cytB*), cytochrome oxidase subunit 1 (*CO1*), 12S ribosomal RNA gene (*12S*), 16S ribosomal RNA gene (*16S*), and NADH dehydrogenase 2 (*ND2*). When multiple sequences were available for a single species, the longest sequence was selected. From GenBank we were able to obtain sequences in at least one

of the relevant markers for 176 of the species. The remaining nine species were: *Allactaga major, Dicrostonyx nelsoni, Dicrostonyx nunatakensis, Dicrostonyx unalascensis, Dicrostonyx vinogradovi, Ellobius talpinus, Microtus mujanensis, Spatula querquedu*la and *Tetrao urogalloides*. For these remaining species, we attempted to obtain loans of specimens from natural history collections. However, for *M. mujanensis* we were unable to find a usable sample, it was eliminated from subsequent analyses. For the other nine species destructively sampled specimen fragments were obtained from six different museums: the Museum of Southwestern Biology (MSB), Naturmuseum Senckenberg (SMF), the Royal Ontario Museum (ROM), the Texas Tech University Museum (TTU), the University of Washington Burke Museum (UWBM) and the Yale Peabody Museum of Natural History (YPM) (see Appendix A Table S1).

DNA extraction was performed with a Qiagen DNeasy Blood & Tissue® Kit. For each sample, a bone/tissue fragment of no more than 0.25mg was cut into small pieces using a sterile razor. The manufacturers' protocol was followed as recommended, except the incubation time during the cell lysis step was increased from 13 to 18 hours. The extracted DNA was then quantified with a Qubit™ dsDNA HS assay kit and Qubit 2.0 Fluorometer. Polymerase chain reaction (PCR) was performed for the five markers 12S, 16S, CO1, cytB and ND2. Each PCR sample had a final volume of 50µL, consisting of: 5.00µL of PCR Buffer II (1X), 3.00µL of $MgCl_2$ (1.5 mM), 0.40µL of dNTPs (0.2 mM), 1.00µL of bovine serum albumin (0.4 mg/mL), 1.00µL of each primer (0.2µM), 0.25µL of AmpliTaq Gold™ polymerase (0.025 units/µL), 36.35µL of molecular grade H_2O and 2µL of the template DNA (~0.129 - ≥ 600 ng/µL). The selected primers for the cytB, 12S and 16S markers functioned for all the taxa included in this study. However, for the CO1 region, three different primer sets were utilized, and for the ND2 marker, the selected primers were only used for avian species. The PCR thermocycling protocols varied amongst primers (Table 1).

Marker	Target taxa	Source	Primer ID	PCR protocol
cytB	vertebrates	(Parson, Pegoraro, Niederstätter, Föger, & Steinlechner, 2000)	L14816-F H15173-R	10min of denaturation at 95°C; 40 cycles: 95°C 45s, 50°C 45s, 72°C 45s; final extension at 72°C 10min.
CO1	birds	(Hebert, Stoeckle, Zemlak, Francis, & Godfray, 2004)	BirdF1 BirdR1 BirdR2	5min of denaturation at 95°C; 4 cycles: 95°C 60s, 45°C 90s, 72°C 90s; 30 cycles:

				95°C 60s, 51°C 90s, 72°C 90s; final extension at 72°C 5min.
CO1	mammals	(Ivanova, Clare, & Borisenko, 2012)	AquaF2 C_VR1LRt1	10min of denaturation at 95°C; 40 cycles: 95°C 45s, 54°C 45s, 72°C 60s; final extension at 72°C 10min.
CO1	mammals	(Ivanova et al., 2012; Pfunder, Holzgang, Frey, & Pfunder, 2004)	RonM_t1 C_VR1LRt1	5min of denaturation at 95°C; 40 cycles: 95°C 45s, 54°C 45s, 72°C 1min; final extension at 72°C 10min.
ND2	birds	(Amer, Ahmed, & Shobrak, 2013)	aND2-L aND2-H	10min of denaturation at 95°C; 40 cycles: 95°C 45s, 51°C 45s, 72°C 40s; final extension at 72°C 10min.
16S	mammals, birds	(Sarri et al., 2014)	Sarri16S-F Sarri16S-R	4min of denaturation at 95°C; 45 cycles: 95°C 40s, 53°C 40s, 72°C 45s; final extension at 72°C 10min.
12S	vertebrates	(Riaz et al., 2011)	Vert01-F Vert01-R	10min of denaturation at 95°C; 40 cycles: 95°C 45s, 49°C 45s, 72°C 45s; final extension at 72°C 10min.

Table 1. The selected oligonucleotide primers and the PCR thermocycling protocols used for the amplification of the markers 12S, 16S, CO1, cytB and ND2.

The PCR products were visualized by electrophoresis in a 1.5% TAE gel stained with 9µL Invitrogen™ SYBR™. For this, 8µL of the PCR products were combined with 2µL of dense gel solution (5X). Afterwards, these prepared PCR products were compared with a 100-bp ladder. Some of the PCR reactions were not successful. Thus, they were not used in the rest of this study. The successful products were then Sanger sequenced with the forward and reverse primers by Eurofins Genomics, a commercial sequencing service. The enzymatic purification for submission and sequencing of the products was performed with illustra™ ExoProStar™ according to the manufacturer's protocol.

2.2.2 Molecular data processing and phylogenetics

Using the program Geneious (version 11.1.5), forward and reverse chromatograms of the products were inspected, edited and trimmed with a combination of automated and manual efforts, in order to keep only high-quality sequences. The forward and reverse sequences were then aligned, and the consensus nucleotide sequence for each sample was exported to text format. When more than one sample per species was available, the longest available sequence

was used. Low-quality sequences were eliminated from subsequent analysis. The automated alignment was performed with 'Geneious Alignment' in its native settings by including the generated sequences and the ones obtained from GenBank. The alignments were manually adjusted in problematic regions. These five marker alignments were then used to infer single-marker phylogenetic trees with RAxML (Stamatakis, 2014) to be individually compared against the topology of a reference phylogeny produced by TimeTree (See appendix B figure S1) (Stecher, Kumar, Hedges, & Suleski, 2017). RAxML employed a maximum-likelihood (ML) phylogenetic inference model based upon nucleotide substitution with gamma-distributed among-site variation ('GTRGAMMA'). Of the produced single-marker trees, the trees that were the least concordant to the reference were inspected further by manual re-alignment of their sequences and regenerated. Out of the five generated trees, the tree produced from the 16S marker was the tree that conformed the least to the reference tree. This, and its substantial high amount of missing data (68.5% of species missing) prompted us to remove the tree in subsequent steps and analysis. The four remaining markers (12S, CO1, cytB & ND2) were concatenated into a multiple sequence alignment (MSA) with a total length of 4608 bp via a custom Python script. Afterwards, a partitioned maximum-likelihood analysis of the generated MSA was conducted with RAxML (4 partitions, 500 bootstraps). The resulting tree was then inspected further with TimeTree as a reference. This tree did not conform to the accepted topology, and the mammalian clades were largely paraphyletic or polyphyletic. This was resolved by constraining the rodents be a monophyletic group in accordance to Speed et al. (2019). The constraint tree implements relationships between selected taxa and afterwards determines the optimal ML tree that conforms to this constraint. In this study, the constraint criterion was that all rodent genera were part of a monophyletic group. If a node had low support (<70%) but the resulting phylogeny was congruent to the reference tree, the branches were not inspected further. Geneious and FigTree (version 1.4.2) were employed to employed to visualize the dendrograms, and Geneious was used to transform the tree into a Newick file format for further analysis. The final phylogenetic tree included 189 species. The topology of the phylogenetic tree is displayed in appendix B figure S2. The five spare species were: *Alces americanus, Anas penelope, Camptorhynchus labradorius, Dendrocygna bicolor and Tetrao parvirostris*. Out of these species, the exclusion of *A. americanus, A. penelope, C. labradorius and D. bicolor* is documented previously but were unknowingly not fully dropped from the phylogenetic tree. *T. parvirostris* was considered a synonym from *Tetrao urogallides* after further revision (See Milkovsky, 2012). Therefore, it was excluded from the subsequent analysis leaving the 184 species.

2.3 Functional traits and dendrogram

2.3.1 Retrieval of trait data

In order to conduct a functional diversity analysis, we constructed a functional trait table that reflects the ecological functionality of the arctic and boreal species. The functional data for this study was gathered by consolidating the information from databases (EltonTraits (Wilman et al., 2014), PanTHERIA (Jones et al., 2009) and the IUCN (2019) along with the information in two books The Handbook of the Mammals of the World (Lacher, Wilson, & Mittermeier, 2016, 2017; Wilson & Mittermeier, 2011) and The Handbook of the Birds of the World (Hoyo, Elliot, Sargatal, Christie, & Kirwan, 2019), as well as input from recognized experts in the included taxa, and several scientific publications (see appendix A table S2) that addressed all the different established functional traits. These traits were considered to be averages between populations across the study region. These traits were selected in accordance to their theoretical importance in determining the ecological niche of herbivores, similarly to Hempson et al. (2015) and was based on the traits defined by Speed et al. (2019) with the addition of the usage of vegetation strata. For each of the species a total of 10 traits were selected, these include: diet type, digestive system type, preference of vegetation strata, wintering strategy, mobility, habitat, population dynamics, litter size, group size and body size. When permissible traits were broken down into a more specific subset of traits that allows for a better trait description, these traits include diet, population dynamics and group size. Afterwards we constructed a table with the respective trait values. When a trait such as 'litter size' or 'body mass' were presented as an interval, the mid-point was taken. For a detailed explanation of the valuation of other traits see the appendix A table S3. Out of the 184 species in this study, there was a considerable lack of ecological and behavioural information for 6 of them. Rather than discarding these species, the missing information was inferred from a closely related species. The surrogate species for extrapolation were chosen due to a proximity in the phylogeny, a similarity of body size and geographic range (See appendix A table S4).

2.3.2 Functional dendrogram

In order to quantify the functional diversity values a functional dendrogram was created. This was done by hierarchical clustering of principle components and a factorial analysis of mixed data (FAMD) similarly to Hempson et al. (2015). Before the FAMD was conducted, the 'body

mass' trait was log transformed in order to mitigate the weight of unusually large values belonging to the large herbivore species. A FAMD was conducted since the generated trait data contained quantitative and categorical variables (See appendix B figure S3). The variables were then transformed into discrete, factor, unordered factor, continuous and binary variables. This and all data handling were conducted in R (Version 3.5.2) (R Core Team, 2019). Afterwards the hierarchical clustering on principal components (HCPC) was conducted with Wards' method to minimize the within cluster variance. This allows for the optimal number of clusters to be identified. For the HCPC to calculate the dissimilarities between observations the 'Euclidean' parameters were employed. Since this is the accepted metric of simple distance (See appendix B figure S4). This functional classification included all the 184 species in the phylogenetic assessment resulting in the functional dendrogram. For the finalized functional dendrogram see the appendix B figure S5.

2.4 Biodiversity analysis

Species richness, phylogenetic diversity and functional diversity were calculated for all 81,205 raster grid cells (equal area 100 x 100km) in R (3.5.2). Species richness was calculated as a simple sum of a raster stack, where all individual species had a presence value of one in their distribution, resulting in a numeric value indicating the number of species present per grid cell. Phylogenetic diversity and functional diversity were both calculated by utilizing the '*picante*' package (Kembel et al., 2010) in R. This package then calculates the phylogenetic diversity of an area as the sum of the total branch length for the subset of species present within each cell. Since the calculations for functional diversity are equal to those for phylogenetic diversity (via the functional dendrogram instead of the phylogenetic tree) the same method was used for functional diversity. The subsequent pair-plots to analyse the relationship between species richness, phylogenetic diversity and functional diversity were performed in R via its native '*stats*' package. Afterwards the models were manually inspected for best fit. The residuals from the pair-plot model were employed to analyses phylogenetic and functional dispersion and clustering. These were subsequently mapped with the same resolution as previously described.

3. Results

3.1 Phylogenetic analysis

The total data completeness (proportion of study species with genetic data) per marker varied. The markers with the highest completeness were COI and cytB with 79.3% and 96.7%, respectively. The coverage of 12S and ND2 was 58.7% and 32.1% respectively. The tree conformed to known topology, and the resulting clades were all monophyletic (See appendix B figures S1 & S2). The species that were not dropped before the final iteration of the phylogenetic tree, did not affect the final topology of the tree. The node support in the resulting tree ranges from 0.92 to 0.08, with lower support in shallow nodes that distinguish highly related species.

3.2 Functional trait analysis

The first two dimensions of the FAMD cumulative inertia of the trait variables captured 39.6%. Where the first dimension captured 23.923% of the inertia and the second dimension captured 15.7% of the inertia (See appendix B figure S3). Afterwards the HCPC resulted in three main clusters with minimal within-cluster distance (See appendix B figure S4). The traits that had a large importance in determining the clusters were: Habitat type, mobility and below ground feeding. This resulted in the first cluster being primarily composed of species that inhabited the limnic habitat, that were largely mobile and that fed below ground via grubbing. The second cluster was composed of species that did not feed below ground and were primarily terrestrial whilst the third cluster was composed of species that fed while burrowing, were terrestrial and were not highly mobile (See appendix B figure S5). The best representative for the three clusters were: *Mareca falcata*, *Lepus arcticus* and *Microtus xanthognathus* corresponding to the first, second and third cluster respectively. The topography of the Functional dendrogram is displayed in the appendix B figure S5.

3.3 Biodiversity pattern analysis

By employing the distribution patterns, phylogenetic tree (See appendix B figure S2) and functional dendrogram (See appendix B figure S5) that were generated in this study, three biodiversity measures maps were generated (See Figure 1). The resulting pattern maps have a total of total of 81,205 cells (excluding cells without values). Species richness (the number of

present species per cell) presents a range of values between 1-47 species per cell, with a mean of 23.7 species per cell. The areas with the highest species richness are western Canada and south eastern Russia (approaching the Mongolian border). These areas have between 19% to 25% of the species, with south eastern Russia presenting a larger area with near 25% of species coverage. Islands present the lowest amount of species coverage. The Arctic Archipelago and Greenland have lower values, whilst Iceland is one of the islands with a higher amount of species. Therefore, islands have a maximum coverage of 8.2% of the species included in this study. The map containing the absolute values of species richness is presented in the appendix figure S6.

The phylogenetic diversity patterns of the arctic and boreal herbivores (as the sum of the minimal branch length per species as established by Faith (1992) demonstrate a similar distribution pattern to species richness. However, phylogenetic diversity is more homogeneously distributed across longitudes than species richness (See figure 1 for a map with absolute values see the appendix figure S6). Once again western Canada and South Eastern Russia present the highest amount of phylogenetic diversity with them being the only areas that present cells with up to 45% of the branch lengths. However, the Scandinavian peninsula and western Canada exhibit higher amounts of phylogenetic diversity when compared to areas with a similar latitude. Equally to species richness, higher latitudes present lower branch coverage percentage. However, the lowest covered latitudes, at the Palearctic biome border, also exhibit low branch coverage (between 5% and 10%). Functional diversity presents a similar pattern to phylogenetic diversity in continental lands, with very high branch coverage around the lower latitudes near Mongolia, western Canada and in the Fennoscandian peninsula (See figure 1 for a map with absolute values see figure S6). However, functional diversity presents high values in the Arctic Archipelago and in north eastern Greenland. Whereas southern Greenland exhibit lower values of functional diversity (between 50% to 10% of branch lengths). Furthermore, Iceland also presents high values of functional diversity of approximately 55% of branch length coverage.
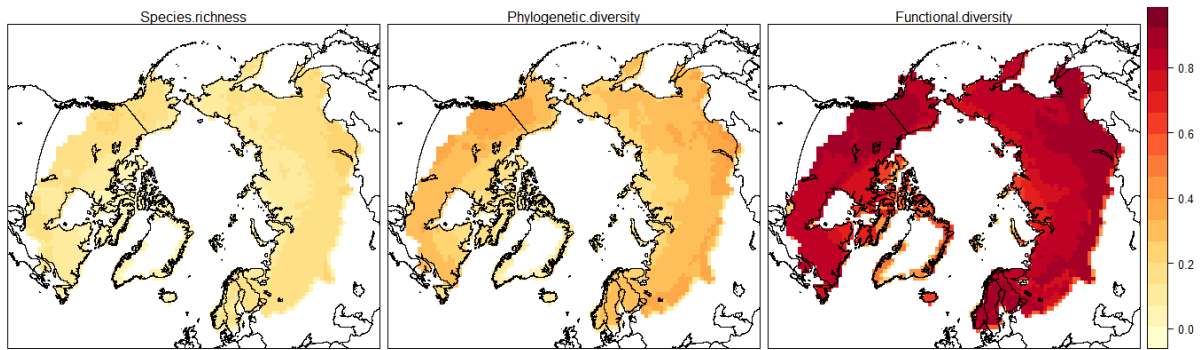
Figure 1. Distribution maps of species richness, phylogenetic diversity and functional diversity of arctic and boreal herbivores (in order). All maps are presented as a proportion of the total diversity present. These maps are projected Lambert Azimuthal Equal-Area Projection. A total of 81,205 cells with 100 x 100km dimensions.

The relationship between the three biodiversity measures was done by comparing functional or phylogenetic diversity to species richness and conducting a regression analysis for the two resulting combinations of biodiversity measures (See figure 2). The relationship between species richness and phylogenetic diversity is linear, and the relationship between species richness and functional diversity is logarithmic. Both regressions present a significant and strong relationship with an R^2 of 0.945 and 0.907, respectively. Furthermore, reduced species richness tends to increase the variance of the data, most notably in the relationship between functional diversity and species richness.
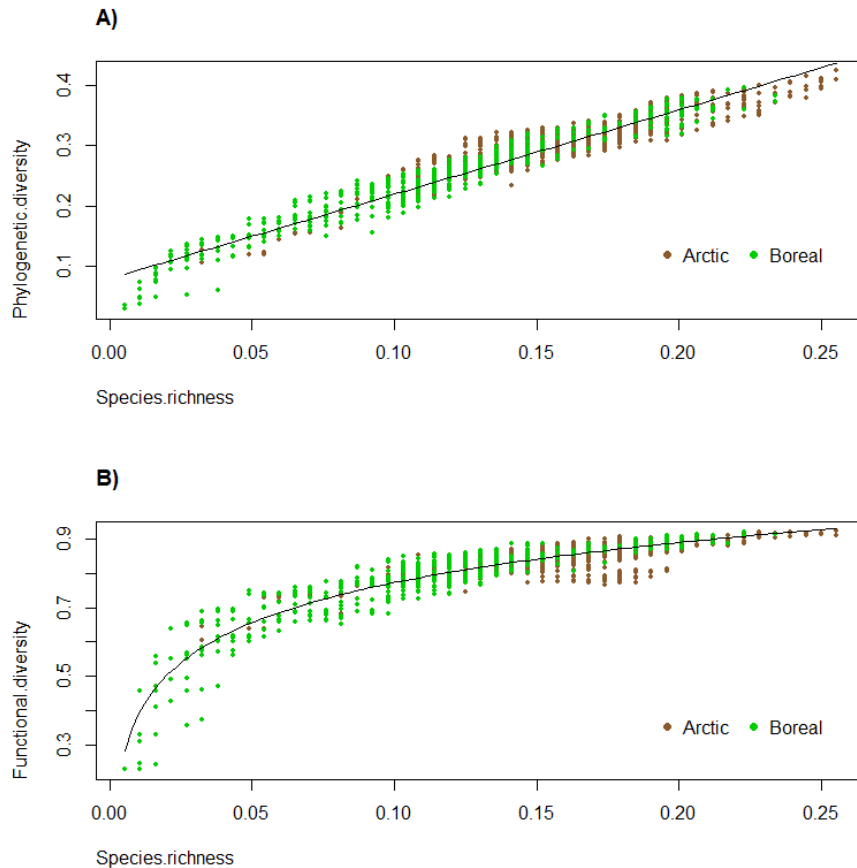
Figure 2. Pair-plots of the phylogenetic diversity and species richness (A), and functional diversity and species richness (B). The values shown are a proportion of the total for all axis. In both panels the cells belonging to arctic (brown) and boreal (green) areas are shown. The linear (A) and logarithmic (B) regression is shown. (need to add letters to the figure, possibly move to supplementary information)

The dispersion of the data from the linear model represents the cells that exhibit phylogenetic (or functional) dispersion and phylogenetic (or functional) clustering of a diversity measure. In the dispersion map between phylogenetic diversity and species richness (See figure 3), it is notable that the herbivore communities in the Labrador Peninsula and the Arctic Archipelago show substantial phylogenetic dispersal whilst western Canada, is less phylogenetically dispersed. Similarly, the Fennoscandian peninsula presents phylogenetic dispersion as do the continental landmasses near the Bering strait. South eastern Russia exhibits a large area of phylogenetic clustering near the Mongolian border, contrasting with the absolute values of the diversity measures. Eurasian arctic islands, Iceland as well as southern Greenland exhibit phylogenetic clustering.
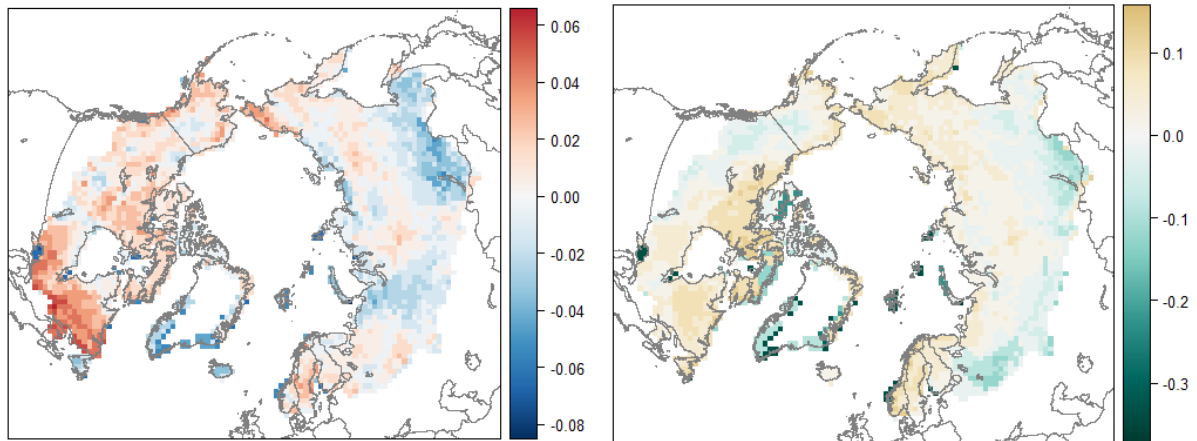
Figure 3. Distribution map of phylogenetic (Left) and functional (Right) dispersal. Phylogenetic dispersion (positive/red) and clustering (negative/blue) as well as functional dispersion (positive/brown) and clustering (negative/green), both compared to the amount of species present (species richness) per cell. This was calculated by measuring the residuals in the diversity pair-plots.

The functional dispersion (See figure 3) map presents areas of functional clustering in the lowest and the highest latitudinal gradients, presenting a "doughnut" pattern with intermediate latitudes exhibiting functional dispersion and the high arctic and low boreal exhibiting functional clustering. Areas of higher functional dispersion include central northern Canada and the Scandinavian peninsula. The arctic islands present functional clustering with the exception of the southernmost islands in the Arctic Archipelago and the northeastern coast of Greenland.

4. Discussion

The identification of areas with dispersion and clustering of phylogenetic and functional diversity sheds light into previously unexplored community assemblage history and community interactions of arctic and boreal herbivores. This is the first study to systematically analyse the patterns of arctic and boreal herbivore biodiversity with a three-dimensional approach, which holds value for future management of these areas, and for extrapolating this methodology into areas outside the scope of this study. The approaches explored in this study demonstrates the power of including spatial phylogenetics and spatial functional analyses for better understanding evolutionary history and functional assemblage of biodiversity. This study also functions as an initial step toward understanding the evolutionary history underpinning the phylogenetic diversity patterns as well as the exploitation ecosystem hypothesis in terms of functional diversity and the regulatory forces that are involved in the determination of these patterns. Similarly, this is the first study that identifies the existence of three main functional groups of vertebrate herbivores in the arctic and boreal biomes.

4.1 Spatial analysis of biodiversity

This study is the first attempt at a worldwide assessment of functional and phylogenetic diversity across the arctic and boreal biomes. The biodiversity patterns found in this study follow similar but not identical trends amongst each other. Phylogenetic diversity and species richness in particular, have a high degree of similarity. This is due to their linear relationship, which explains the mirroring of patterns, both latitudinal and longitudinal ones. The high congruence in patterns between phylogenetic diversity and species richness is not as evident when comparing with functional diversity. Whilst there are similarities between the patterns of all three diversity measures; functional diversity presents more discrete patterns and substantially higher values in particular geographic regions in comparison with the other two biodiversity measures, such as the Scandinavian peninsula. This is possibly due to large distance between the three main functional clusters. The thee functional clusters (See Methods section 3.2 and appendix figure S4), have clear and large distinctions between them, therefore, the presence of the three clusters, in tandem, in a particular cell will automatically raise its value of the functional diversity substantially, whilst subsequent species added will increase the functional diversity value in smaller intervals. This demonstrates the non-linear, rather logarithmic, relationship between species richness and functional diversity. Ecologically, this

means that the functional diversity of the arctic and boreal vertebrate herbivores is largely dependent on the presence of the three main functional groups, described by the most representative cluster traits. This reveals the importance of ensuring the conservation of these three major functional groups for the vertebrate herbivore community in these two biomes. Finally, this is the first study to demonstrate the distribution of worldwide boreal herbivore functional diversity. It is important to state that these patterns were obtained with a $100km^2$ resolution and that these patterns might be slightly different at finer scales.

4.2 Phylogenetic and Functional dispersal

The similarities in the patterns of the three biodiversity measures indicated a relationship between species richness and the other two biodiversity measures. Whilst these relationships were corroborated for both of the biodiversity measures, they are mathematically different. As expected, there is a strong linear relationship between species richness and phylogenetic diversity (R^2 = 0.945). Similarly, there is a strong logarithmic relationship between species richness and functional diversity (R^2 = 0.907) which was expected as well (see figure 2). These two relationships support previous knowledge of strong relationships between the biodiversity measures (Faith, 1992; Safi et al., 2011; Speed et al., 2019). However, the realized values of some cells diverge from the expected values represented in the logarithmic or linear model. Cells with higher than expected values of either phylogenetic or functional diversity, indicate phylogenetic or functional dispersal. Similarly, cells with lower than expected diversity values indicate either phylogenetic or functional clustering. In the linear model, cells with either a high (>22%) or low (<3%) species coverage, present phylogenetic clustering. This suggest that in the arctic and boreal biomes, areas at either extreme of species richness tend to be phylogenetically similar. In the case of areas with high species coverage, this is likely due to several species being highly genetically related. However, an alternative explanation is that since these cells have such a small amount of species, the phylogenetic diversity that they present is drastically reduced because there are simply not enough species. Therefore, few branches are accounted for, drastically lowering the phylogenetic diversity when compared to areas of medium species richness but greater branch coverage. Alternatively, it is possible that a linear model to explain the relationship between species richness and phylogenetic diversity is not ideal. This "double-ends" pattern is not emulated in the relationship between species richness and functional diversity where the best fit was a logarithmic relationship (See figure 2). Functional diversity mainly presents functional clustering in areas with few species (<5%).

22

This is possibly due to similar reasons as the phylogenetic clustering in areas with low species coverage. Alternatively, due to the cells with functional clustering being in the boreal biome, it is possible to locate these cells by identifying the ones that that present low species richness in the boreal biome as well. These cells are primarily present near bodies of water, which possibly indicates the dominant presence of Anseriformes, which are clustered in a single functional group. This accounts for the functional clustering since these species are functionally similar. Furthermore, this functional clustering potentially indicates a regional "tipping point" in arctic and boreal herbivores functional trait diversity, as was first proposed by Faith (2015). However, this requires a more direct approach and analysis that goes beyond the scope of this study.

Since areas with phylogenetic or functional dispersion are not found at extreme values of species coverage; spatial visualization of the dispersion of values from expected values is advantageous. This comparison between expected and realized values of phylogenetic and functional diversity reveals patterns of dispersal or clustering of these biodiversity measurements. In the case of phylogenetic dispersion (see figure XX), the peninsula of Labrador in Eastern Canada as well as the south eastern area of Russia near Lake Baikal present high amounts of phylogenetic dispersion and clustering. Whilst the Fennoscandian peninsula presents lower values of phylogenetic dispersion. As discussed by Fritz and Rahbek (2012), the areas with phylogenetic dispersion suggest colonization events whilst areas of phylogenetic clustering identify areas of radiation.

This relationship in the arctic and boreal biomes can be supported further by the geographic distribution of glacial ice cover in the last glacial maximum (See appendix B figure S7). The last glacial maximum was circa 21,000 years ago and covered most of the northern regions of North America and the Fennoscandian Peninsula (Peltier, 1994). This coincides remarkably with areas that present phylogenetic dispersion, suggesting that post-glacial melt invasion events from non-ice-covered areas could explain this phylogenetic dispersion. Similarly, the areas with the highest values of phylogenetic dispersion only became ice-free circa 10,000 years ago, which suggest a correlation between ice reduction and phylogenetic dispersion for the northern biomes. The boreal biome of southwestern Russia was not covered with ice during the last glacial maximum. Therefore, it is arguable that this area has been ice-free for sufficiently long time to permit species to radiate, accounting for the phylogenetic clustering of the area. However, there are islands in the north (i.e. the Greenland and the palearctic islands)

23

that present phylogenetic clustering. In this case, it is possible that the difficulty of dispersal into islands promotes radiation from a small number of colonizer species which radiate rapidly in an island environment (Fritz & Rahbek, 2012). Alternatively, this could be caused by simply having few species that are phylogenetically similar and with similar dispersal capabilities.

The visualization of functional diversity dispersion patterns yielded an unexpected "doughnut" pattern (See figure 3). Where both, the lower latitudes in the boreal biome and high latitudes in the arctic, presented functional clustering. However, the area in the transition zone between the two biomes present functional dispersion. The lower-latitude zone potentially has functional clustering due to competitive exclusion of species that try to utilize the same resource already exploited by better competitor species (Mishra, Wieren, Heitkönig, & Prins, 2002). Simultaneously, functional clustering at the southern border of the boreal biome could happen due to predator pressure. This pressure on the herbivore community would select for endothermic herbivore species that have higher predation evasion fitness to be selected, which has a trade-offs with foraging time and nutrient requirements, thus, limiting the niche diversification capacity of the herbivore communities in these areas. We suggest these two explanations instead of a bottom-up regulation or an abiotic regulation mechanism due to the location of these cells with functional clustering, which are concentrated in the southern border of the boreal biome (See figure 2 B). This area has higher plant productivity than the arctic, as well as having climatic variables considered to be less extreme than in the arctic (i.e. reduced seasonality). On the other hand, the northern areas that present functional clustering could be an indication of abiotic environmental regulation. This is due to the reduced quantity of predators and the lower amount of plant productivity compared to the boreal biome, which mitigates their weight as regulatory forces for the vertebrate herbivore community. The areas of functional dispersal at the border between the arctic and boreal biome suggest that the values of plant productivity, predator pressure and abiotic pressure reach a point of equilibrium that maximizes functional diversity according to the amount of species present. This pattern of the dispersion of functional diversity is similar to the biomass patterns theorized in the ecosystem exploitation hypothesis (Oksanen, 1992), which states that in environments with high plant productivity and three-linked dynamics (producers, herbivores and predators), herbivore biomass is primarily regulated by predation pressure. It also states that in areas where more extreme abiotic conditions promote two-linked dynamics (herbivores and producers), the main regulatory force of herbivore biomass is environmental for both trophic levels. While this study does not look at biomass, the functional dispersion of species could potentially behave in a

similar manner. This suggest that further analysis of the drivers of these patterns, as well as an analysis of the relationship between biomass and functional dispersion could provide insight into the dynamics of the ecosystem exploitation hypothesis.

4.3 Functional and phylogenetic analysis

The topology of the final phylogenetic tree corresponds to the topology generated by the TimeTree database (see appendix B figure S7). However, the first iterations of the phylogenetic trees were incongruent with the accepted topology of the taxa included in this study. The most problematic species were: *Erethizon dorsatum* and the marmots (genus *Marmota*). *E. dorsatum* was positioned as a basal mammal causing the family Rodentia to be polyphyletic, whilst the genus *Marmota* was placed as a sister clade to Lagomorpha, causing Rodentia (Excluding *E. dorsatum*) to be paraphyletic. This is possibly due to the limited number of markers and possible absence of sequences for some of them. An alternative possibility is the contamination or miss identification of samples that results in erroneous uploads to sequence repositories. The problems with misidentification and contamination are well known problems in large sequence-repositories (Vilgalys, 2003). A possible way to mitigate the impact of these shortcomings would be to employ a larger number of markers, including markers of importance in resolving phylogenetic relationships for different clades, similarly to how Tang et al. (2018) employed the gene (GRH) to resolve the phylogenetic relationship between two rodent clades. In this study, however, these issues were resolved by constraining the tree (see Methods). In the final tree, the genus *Myodes* initially appeared as a polyphyletic group, with the genus *Alticola* nested within. The resulting position of *Myodes* coincides well with the resolved topology proposed by Tang et al. (2018), in which *Myodes rufocanus* is a basal species, and *Alticola lemminus* and *Alticola microtis* are more closely related to *Myodes* than other *Alticola*. This result supports their reassessment of taxonomic relationships between these two groups and their proposed new genera *Craseomys* and *Aschisomys* for *M. rufocanus* and the two *Alticola* species respectively. Furthermore, this congruence with the recently resolved phylogenetic relationship between *Alticola* and *Myodes*, suggests that constraining the trees for phylogenetic diversity analysis, as proposed by Speed et al. (2019), is a valuable tool for rapid analysis of problematic taxa.

This study is the first time that a functional dendrogram of arctic and boreal herbivores was constructed to assess the functional relationship of arctic and boreal herbivores. Therefore, we

were unable to compare the dendrogram topography with previous analysis. Nevertheless, the functional dendrogram yielded interesting results on the functional composition of the arctic and boreal herbivores. The three main clusters generated through the HCPC analysis suggest that the three main functional subgroups (hereafter referred to as: functional groups) are composed primarily due to differences in the habitat the species inhabits (limnic or terrestrial), the capacity of the species to move disperse for more than 100km in any two-dimensional direction and by the type of feeding below ground. This generated three different functional groups of herbivores, with the first one being composed of highly mobile species which are preferentially limnic and feed belowground by grubbing. This group of animals has the characteristic of having large impact on the biomes, due to them generally covering large amounts of land and due to them predating on plants below ground via grubbing, which has a strong impact on the plant community near bodies of water. This functional group is largely phylogenetically homogeneous as it is comprised primarily by Anseriformes, however, the brown bear (*Ursus arctos*) stands out as a member of this group. This is potentially due to its high mobility and its grubbing behaviour having substantial weight in this determination. Due to the limnic habitat this group can be defined as a highly mobile and water dependent dependant herbivore functional group. The second functional group was defined primarily due to the absence of below ground feeding and terrestrial nature of the species. This group is composed of several species that were not phylogenetically clustered, making this the most phylogenetically heterogeneous group. This includes galliform herbivores such as the capercaillie (*Tetrao urogallus*), large ungulate herbivores such as the wapiti (*Cervus canadiensis*), rodents such as the American porcupine (*Erethizon dorsatum*) and lagomorphs such as the arctic hare (*Lepus arcticus*). This group of taxa specializes in the consumption of leaves and stems of plants, resulting on this group to be constructed of important grazers, browsers and mix-feeders, as well as containing the largest herbivores in the arctic and boreal biomes. Therefore, this group is potentially extremely important for above-ground systems regulation in both biomes as well as having potentially the strongest top-down interactions with plants. This group can be seen as the browsers and grazers functional group. The third group is largely phylogenetically homogeneous where it is composed primarily of rodents. In this group was composed of species without the capacity to move beyond 100km^2 and by being burrowers and feeding below ground. This group represents taxa that have a direct impact on below ground systems via burrowing, which has a strong impact on plant dynamics and in the abiotic facet (i.e. geomorphic change) of the ecosystem (Eriksson & Eldridge, 2014; Huntly &

Reichman, 1994). It can be seen as a functional group of small burrowing herbivores in the ecosystem.

These three functional groups shed light on the important niche classification of the arctic and boreal biomes, due to the way they were constructed, it is possible to argument that the three most important broad niches for herbivores in the arctic and boreal biomes are: 1) limnic and highly mobile species, 2) browsers and grazers and 3) small burrowers. The presence or absence of these three large niche groups could aid in a rapid assessment of the functional composition of an area of interest within the arctic and boreal biomes. This could have implications in monitoring important natural areas rapidly. However, insight on the possibility of using these three niches as a tool for a rapid initial assessment is needed. This could be tested further by analysing the relationship between functional dispersion and its drivers at different geographical locations as well as by investigating the relationship, if any, between biomass and functional dispersion.

5. Conclusion

To conclude, this study is the first study to analyse the relationship amongst three different biodiversity measures for the arctic and boreal vertebrate herbivores. Making this the first study to assess the biodiversity of a trophic guild across biomes. Similarly, this study illustrates that the synergetic integration of these three biodiversity measures reveals different biodiversity patterns and dynamics of vertebrate herbivores in the arctic and boreal biome. Furthermore, this study determines that species richness and phylogenetic diversity present an apparently latitudinal pattern with increased values of biodiversity towards the southern border of the boreal biome. The boreal biome is generally more phylogenetically diverse and has a higher number of species than the arctic. Functional diversity does not present a strong latitudinal gradient of increased diversity, with high functional diversity values found repeatedly in the arctic as well.

The geographical patterns of phylogenetic dispersion and clustering match with areas that were covered in ice and those that were not in the last glacial maximum, respectively. This demonstrates the possibility of radiation events for vertebrate herbivores in south-eastern Russia. Similarly, in the Labrador Peninsula, the presence of ice during the last glacial maximum period (between 21,000 and 10,000 years ago) as well as the phylogenetic dispersion indicate a possible northward invasion event from vertebrate herbivores. The geographical patterns of functional clustering and dispersion generate a "doughnut" of functional dispersion at mid latitudes. The functional clustering present at low latitudes is potentially due to predation pressure, competitive exclusion or both forces in tandem. Furthermore, the functional clustering at high latitudes is possibly due to bottom-up regulation due to lower productivity and more environmental heterogeneity. The mid-latitude functional dispersion "doughnut" is possibly due to lower predator pressure (compared to the south) but higher plant productivity (compared to the north) maximizing functional diversity relative to species richness. These patterns of functional dispersion are similar to the biomass patterns predicted in the ecosystem exploitation hypothesis, which calls for further investigation on the relationship of functional dispersion and the ecosystem exploitation hypothesis. This study corroborates recently known phylogenetic relationships between the genera *Alticola* and *Myodes*, which in turn supports the value of constraining phylogenetic trees for phylogenetic diversity analysis where there is limited data for reconstructing the phylogenetic tree. Finally, this study identified three vertebrate herbivore functional groups, which could aid in rapid assessment of arctic and boreal

areas of interest. These findings support our expectations of increased absolute value of the biodiversity measures being positively correlated to the plant productivity. Similarly, our findings agree with our hypothesis that stated that the values for functional diversity would be higher than the values of phylogenetic diversity in the arctic. Whilst we can't state with complete certainty that this is due to the plant productivity, further investigations assessing the relationship of plant productivity and biodiversity directly, may resolve this relationship more adequately. Our hypothesis regarding higher values of the three biodiversity measures in the Nearctic when compared to the Palearctic lacks sufficient evidence to be supported, since there wasn't a substantial difference between the two in terms of absolute values from these measures. Furthermore, our expectations of high phylogenetic dispersal in the arctic due to evolutionary isolation or invasion events is partially supported since it is more likely that this is due to the glaciation events. Additionally, areas with high plant productivity did present functional clustering. Whilst we cannot state with absolute certainty that this is due to niche overlap and predator pressure, the prominent resemblance of the realized patterns of functional clustering and dispersion coincide with expected patterns of biomass due to the ecosystem exploitation hypothesis. Therefore, we recommend that this congruency in the patterns be investigated further to identify the possible relationship between functional dispersion and the ecosystem exploitation hypothesis. Finally, our study demonstrates the importance of employing a multi-dimensional analysis of biodiversity to better understand it and all its facets, which will aid in improving our global conservation and management efforts.

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7. Appendices

Appendix A

Museum Samples Table

Species Name	Species key	Date collected	Country of origin	Museum of origin	Institution code	Catalog number	Preservation method
Allactaga major	2439483L	1991	US	Museum of Southwestern Biology	MSB	67486	skin; skull
Aythya baeri	2498260L	2011	US	Yale Peabody Museum of Natural History	YPM	YPM ORN 084748	skeleton; tissue frozen
Dicrostonyx nelsoni 2438390L		1967	US	University of Washington Burke Museum	UWBM	39681	Skeleton
		1962	US	University of Washington Burke Museum	UWBM	82860	skeleton
		1989	US	Museum of Southwestern Biology	MSB	280304	skull; skeleton, postcranial
Dicrostonyx nunatakensis	2438387L	2011	CA	Royal Ontario Museum	ROM	121084	kidney tissue in ethanol
Dicrostonyx unalascensis	2438385L	1967	US	University of Washington Burke Museum	UWBM	39679	skeletal
Dicrostonyx vinogradovi 2438388L		1975	US	Texas Tech University Museum	TTU	39015	SS, skin, skull
		1975	US	Texas Tech University Museum	TTU	39016	SS, skin, skull
Ellobius talpinus	2438760L	1991	US	Museum of Southwestern Biology	MSB	67504	Skin; Skull
Melanitta deglandi 2498238L		2014	US	Yale Peabody Museum of Natural History	YPM	YPM ORN 84583	tissue ethanol
		2014	US	Yale Peabody Museum of Natural History	YPM	YPM ORN 150076	tissue ethanol
Sicista caudata	2439445L	1964	DE	Forschungsinstitut und Natur-	SMF	49401	No info

				Museum Senckenberg			
Spatula querquedula			US	University of Washington Burke Museum	UWBM	47172	tissue ethanol
Tetrao urogalloides	7915745L	1980	US	University of Washington Burke Museum	UWBM	60001	tissue ethanol

Table S1. This table describes the in detail the received museum samples that were used to extract the DNA of species not found in GenBank.

Functional Trait Table

Binomial	EPO	BM	GT	GSS	GSW	LCS	PD	HT	BGF	M	DT	DIF	DIG	DIS	DIM	DIL	WS	UOV
Aix galericulata	30	567.04	undifferentiated	small_groups	large_group	10.5	noncyclic	limnic	none	yes	facultative_generalist	0	2	1	0	0	not_present	ground_vegetation
Aix sponsa	50	657.59	undifferentiated	small_groups	large_group	12	noncyclic	limnic	none	yes	facultative_generalist	1	2	1	0	0	not_present	ground_vegetation
Alces alces	100	35699.8.16	ruminant	solitary	solitary	1.25	cyclic_noncyclic	terrestrial	none	yes	facultative_specialist	2	1	3	0	0	active_above_snow	understory
Alces americanus	100	54146.0.44	ruminant	solitary	solitary	1	noncyclic	terrestrial	none	yes	facultative_generalist	2	2	3	1	1	active_above_snow	understory
Alectoris chukar	70	502.10	hindgut_fermenter	solitary	small_group	10.5	noncyclic	terrestrial	none	no	facultative_generalist	1	3	1	0	0	active_above_snow	ground_vegetation
Allactaga major	30	350.00	hindgut_fermenter	solitary	solitary	5.9	noncyclic	terrestrial	burrowing	no	obligatory_generalist	2	3	1	0	0	hibernation	ground_vegetation
Allactaga sibirica	30	97.50	hindgut_fermenter	solitary	solitary	3.5	noncyclic	terrestrial	burrowing	no	facultative_specialist	2	1	1	0	0	hibernation	ground_vegetation
Alticola lemminus	100	33.56	hindgut_fermenter	solitary	solitary	6.17	noncyclic	terrestrial	burrowing	no	facultative_generalist	1	1	1	2	2	active_below_snow	ground_vegetation
Alticola macrotis	100	36.00	hindgut_fermenter	solitary	solitary	6.17	cyclic	terrestrial	burrowing	no	facultative_generalist	1	1	1	2	2	active_below_snow	ground_vegetation
Alticola olchonensis	100	36.96	hindgut_fermenter	solitary	solitary	6.17	cyclic	terrestrial	burrowing	no	facultative_generalist	1	1	1	2	2	active_below_snow	ground_vegetation
Alticola semicanus	100	33.39	hingut_fermenter	solitary	solitary	6.5	cyclic	terrestrial	none	no	facultative_generalist	0	3	0	0	0	active_below_snow	ground_vegetation
Alticola tuvinicus	100	33.32	hingut_fermenter	solitary	solitary	4.5	cyclic	terrestrial	burrowing	no	obligatory_generalist	3	2	0	0	0	active_below_snow	ground_vegetation
Anas acuta	50	944.62	undifferentiated	small_groups	large_group	8	noncyclic	limnic	grubbing	yes	facultative_generalist	2	3	1	0	0	not_present	ground_vegetation
Anas crecca	50	341.89	undifferentiated	small_groups	large_group	9.5	noncyclic	limnic	none	yes	facultative_generalist	3	3	2	0	0	not_present	ground_vegetation
Anas platyrhynchos	20	843.42	undifferentiated	small_groups	large_group	11	noncyclic	limnic	none	yes	facultative_generalist	1	3	0	0	0	not_present	ground_vegetation
Anas rubripes	30	1240.96	undifferentiated	small_groups	large_group	9.5	noncyclic	limnic	none	yes	facultative_generalist	1	3	1	0	0	not_present	ground_vegetation
Anas zonorhyncha	HBofW	1017.50	undifferentiated	small_groups	large_group	8	noncyclic	limnic	none	yes	facultative_generalist	2	3	0	0	0	not_present	ground_vegetation
Anser albifrons	90	2506.39	undifferentiated	large_group	large_group	5	noncyclic	limnic	grubbing	yes	facultative_generalist	2	3	2	1	0	not_present	ground_vegetation
Anser anser	80	3302.41	undifferentiated	large_group	large_group	5	noncyclic	limnic	grubbing	yes	facultative_generalist	1	3	1	0	0	not_present	ground_vegetation

Species																		
Anser brachyrhynchus	90	2642.04	undifferentiated	large_group	large_group	4	noncyclic	limnic	grubbing	yes	facultative_generalist	3	3	1	1	0	not_present	ground_vegetation
Anser caerulescens	90	2636.15	undifferentiated	large_group	large_group	4	noncyclic	limnic	grubbing	yes	facultative_generalist	2	3	1	1	0	not_present	ground_vegetation
Anser canagica	70	2136.49	undifferentiated	large_group	large_group	4.9	noncyclic	limnic	none	yes	facultative_specialist	1	3	1	0	0	not_present	ground_vegetation
Anser cygnoid	70	3511.94	undifferentiated	small_groups	large_group	5.5	noncyclic	limnic	grubbing	yes	facultative_generalist	1	3	0	0	0	not_present	ground_vegetation
Anser erythropus	100	1755.50	undifferentiated	large_group	large_group	5	noncyclic	limnic	none	yes	facultative_generalist	1	3	1	0	0	not_present	ground_vegetation
Anser fabalis	80	2754.73	undifferentiated	large_group	large_group	4	noncyclic	limnic	grubbing	yes	facultative_generalist	3	3	2	1	0	not_present	ground_vegetation
Anser rossii	100	1635.99	undifferentiated	large_group	large_group	4	noncyclic	limnic	none	yes	facultative_generalist	2	3	1	2	0	not_present	ground_vegetation
Apodemus agrarius	40	23.30	hindgut_fermenter	solitary	solitary	5.5	cyclic	terrestrial	burrowing	no	obligatory_generalist	1	2	0	0	0	active_below_snow	ground_vegetation
Apodemus flavicollis	40	26.70	hindgut_fermenter	solitary	solitary	6.5	noncyclic	terrestrial	burrowing	no	obligatory_generalist	2	3	1	0	0	active_below_snow	ground_vegetation
Apodemus peninsulae	40	32.90	hindgut_fermenter	solitary	solitary	4.41	noncyclic	terrestrial	burrowing	no	obligatory_generalist	1	2	0	0	0	active_below_snow	ground_vegetation
Apodemus sylvaticus	40	30.45	hindgut_fermenter	solitary	solitary	5.16	noncyclic	terrestrial	burrowing	no	obligatory_generalist	2	3	3	0	0	active_below_snow	ground_vegetation
Apodemus uralensis	40	17.10	hindgut_fermenter	solitary	solitary	5	noncyclic	terrestrial	burrowing	no	obligatory_generalist	1	2	0	0	0	active_below_snow	ground_vegetation
Arvicola amphibius	80	120.00	hindgut_fermenter	solitary	solitary	4.76	cyclic_noncyclic	terrestrial	burrowing	no	obligatory_generalist	3	3	1	0	0	active_below_snow	ground_vegetation
Aythya americana	70	1075.69	undifferentiated	small_group	large_group	9	noncyclic	limnic	none	yes	facultative_generalist	1	2	0	0	0	not_present	ground_vegetation
Aythya ferina	50	822.99	undifferentiated	small_group	large_group	9	noncyclic	limnic	grubbing	yes	facultative_generalist	1	1	0	0	0	not_present	ground_vegetation
Aythya nyroca	50	574.00	undifferentiated	small_group	large_group	9	noncyclic	limnic	grubbing	yes	facultative_generalist	1	2	0	0	0	not_present	ground_vegetation
Aythya valisineria	60	1202.00	undifferentiated	small_group	large_group	9.5	noncyclic	limnic	grubbing	yes	facultative_generalist	0	2	0	0	0	not_present	ground_vegetation
Bison bison	100	710000.00	ruminant	large_group	large_group	0.98	noncyclic	terrestrial	none	yes	facultative_generalist	2	3	1	0	1	active_above_snow	ground_vegetation
Bonasa bonasia	70	429.00	hindgut_fermenter	solitary	solitary	8.5	cyclic_noncyclic	terrestrial	none	no	facultative_generalist	2	0	3	0	0	active_above_snow	ground_vegetation
Bonasa umbellus	70	530.91	hindgut_fermenter	solitary	solitary	11	cyclic	terrestrial	none	no	facultative_generalist	1	0	3	0	0	active_above_snow	ground_vegetation
Branta bernicla	100	1277.91	undifferentiated	large_group	large_group	5	noncyclic	limnic	none	yes	facultative_generalist	3	1	0	3	0	not_present	ground_vegetation
Branta canadensis	90	2811.68	undifferentiated	large_group	large_group	4	noncyclic	limnic	grubbing	yes	facultative_generalist	2	3	1	0	0	not_present	ground_vegetation
Branta hutchinsii	90	2050.00	undifferentiated	large_group	large_group	4	noncyclic	limnic	grubbing	yes	facultative_generalist	2	3	1	0	0	not_present	ground_vegetation

Species																		
Branta leucopsis	90	1683.97	undifferentiated	large_group	large_group	4	noncyclic	limnic	none	yes	facultative_generalist	2	3	0	2	0	not_present	ground_vegetation
Branta ruficollis	100	1226.47	undifferentiated	large_group	large_group	5	noncyclic	limnic	none	yes	facultative_specialist	3	2	2	0	0	not_present	ground_vegetation
Capreolus capreolus	100	22500.00	ruminant	family_group	family_group	1.79	cyclic_noncyclic	terrestrial	none	no	facultative_generalist	3	1	3	0	0	active_above_ground	gound_vegetation
Capreolus pygargus	100	43752.21	ruminant	solitary	family_group	2	noncyclic	terrestrial	none	yes	facultative_specialist	3	1	3	2	2	active_above_ground	gound_vegetation
Castor canadensis	100	21820.00	hindgut_fermenter	small_group	small_group	3.6	noncyclic	limnic	none	no	obligatory_generalist	1	1	3	0	0	active_above_snow	understory
Castor fiber	100	19000.00	hindgut_fermenter	family_group	family_group	2.95	noncyclic	limnic	none	no	obligatory_generalist	1	1	3	0	0	active_above_ground	understory
Cervus canadensis	100		ruminant	large_group	large_group	1.09	noncyclic	terrestrial	none	yes	facultative_generalist	2	2	3	0	0	active_above_snow	groun_vegetation
Cervus elaphus	100	165015.85	ruminant	family_group	family_group	1.09	cyclic_noncyclic	terrestrial	none	no	obligatory_generalist	2	2	3	0	0	active_above_snow	gound_vegetation
Coturnix japonica	70	94.78	hindgut_fermenter	solitary	solitary	7	cyclic_noncyclic	terrestrial	none	yes	facultative_generalist	1	3	0	0	0	not_present	ground_vegetation
Cricetulus barabensis	50	22.85	hindgut_fermenter	solitary	solitary	7.7	noncyclic	terrestrial	burrowing	no	facultative_generalist	2	3	0	0	0		ground_vegetation
Cricetulus longicaudatus	50	22.10	hindgut_fermenter	solitary	solitary	6.5	noncyclic	terrestrial	burrowing	no	obligatory_generalist	2	3	1	0	0	hibernating	ground_vegetation
Cricetus cricetus	80	510.00	hindgut_fermenter	solitary	solitary	9	cyclic_noncyclic	terrestrial	burrowing	no	obligatory_generalist	3	3	2	0	0	hibernating	ground_vegetation
Cygnus buccinator	70	11071.13	undifferentiated	large_group	large_group	5	noncyclic	limnic	grubbing	yes	facultative_generalist	3	3	2	2	0	not_present	ground_vegetation
Cygnus columbianus	100	6298.81	undifferentiated	large_group	large_group	3.85	noncyclic	limnic	grubbing	yes	facultative_generalist	3	3	2	2	0	not_present	ground_vegetation
Cygnus cygnus	100	9349.99	undifferentiated	large_group	large_group	4.47	noncyclic	limnic	grubbing	yes	facultative_generalist	3	3	1	1	0	not_present	ground_vegetation
Cygnus olor	80	10682.04	undifferentiated	family_group	family_group	6	noncyclic	limnic	grubbing	yes	facultative_generalist	1	2	0	0	0	not_present	ground_vegetation
Dama dama	100	52375.00	ruminant	large_group	large_group	1	cyclic_noncyclic	terrestrial	none	no	obligatory_generalist	3	3	2	0	0	active_above_snow	ground_vegetation
Dendragapus fuliginosus	80	1047.31	hindgut_fermenter	solitary	solitary	8	cyclic	terrestrial	none	no	facultative_specialist	2	1	3	0	0	active_above_snow	canopy
Dendragapus obscurus	80	1047.31	hindgut_fermenter	small_group	large_group	8	noncyclic	terrestrial	none	no	facultative_specialist	2	1	3	0	0	active_above_snow	canopy
Dicrostonyx groenlandicus	80	54.40	hindgut_fermenter	solitary	solitary	3.78	cyclic	terrestrial	burrowing	no	obligatory_generalist	3	2	3	1	1	active_below_snow	ground_vegetation
Dicrostonyx hudsonius	80	57.00	hindgut_fermenter	solitary	solitary	3.49	cyclic	terrestrial	burrowing	no	obligatory_generalist	2	2	2	1	0	active_below_snow	ground_vegetation
Dicrostonyx nelsoni	80	60.85	hindgut_fermenter	solitary	solitary	3.5	cyclic	terrestrial	burrowing	no	obligatory_generalist	2	2	3	1	0	active_below_snow	ground_vegetation
Dicrostonyx nunatakensis	80	60.82	hindgut_fermenter	solitary	solitary	3	cyclic	terrestrial	burrowing	no	obligatory_generalist	2	2	3	1	0	active_below_snow	ground_vegetation

Species																		
Dicrostonyx richardsoni	80	55.00	hindgut_fermenter	small_group	solitary	3.5	cyclic	terrestrial	burrowing	no	obligatory_generalist	3	3	3	0	0	active_below_snow	ground_vegetation
Dicrostonyx torquatus	80	85.00	hindgut_fermenter	solitary	solitary	3.85	cyclic	terrestrial	burrowing	no	obligatory_generalist	2	2	3	0	0	active_below_snow	ground_vegetation
Dicrostonyx unalascensis	80	60.84	hindgut_fermenter	solitary	solitary	2.79	cyclic	terrestrial	burrowing	no	obligatory_generalist	3	2	3	1	0	active_below_snow	ground_vegetation
Dicrostonyx vinogradovi	80	60.78	hindgut_fermenter	solitary	solitary	6.15	cyclic	terrestrial	burrowing	no	obligatory_generalist	2	2	3	0	0	active_below_snow	ground_vegetation
Ellobius talpinus	100	40.00	hindgut_fermenter	family_group	family_group	4.9	cyclic	terrestrial	burrowing	no	obligatory_generalist	3	2	0	0	0	active_above_snow	ground_vegetation
Erethizon dorsatum	70	7085.33	hindgut_fermenter	solitary	solitary	1	cyclic_noncyclic	terrestrial	none	no	facultative_specialist	1	1	3	0	0	active_above_snow	ground_vegetation
Falcipennis canadensis	90	473.65	hindgut_fermenter	solitary	solitary	6	noncyclic	terrestrial	none	no	facultative_specialist	2	1	3	0	0	active_above_snow	ground_vegetation
Falcipennis falcipennis	80	685.61	hindgut_fermenter	solitary	large_group	5	noncyclic	terrestrial	none	no	facultative_specialist	0	0	3	0	1	active_above_snow	canopy
Falcipennis franklinii			hindgut_fermenter	solitary	solitary	5.5	noncyclic	terrestrial	none	no	facultative_specialist	3	0	3	0	0	active_above_snow	ground_vegetation
Glaucomys sabrinus	30	166.00	hindgut_fermenter	solitary	solitary	3	noncyclic	terrestrial	none	no	facultative_generalist	0	0	1	0	3	active_above_snow	canopy
Lagopus lagopus	90	566.86	hindgut_fermenter	solitary	large_group	9	cyclic_noncyclic	terrestrial	none	yes	facultative_generalist	1	1	3	1	0	active_above_snow	ground_vegetation
Lagopus leucura	100	354.97	hindgut_fermenter	solitary	large_group	5.5	cyclic_noncyclic	terrestrial	none	yes	facultative_generalist	1	1	3	0	0	active_above_snow	ground_vegetation
Lagopus muta	70	535.30	hindgut_fermenter	solitary	large_group	9	cyclic_noncyclic	terrestrial	none	yes	facultative_specialist	1	1	3	1	0	active_above_snow	ground_vegetation
Lagurus lagurus	100	20.03	hindgut_fermenter	family_group	family_group	8.9	cyclic_noncyclic	terrestrial	burrowing	no	facultative_generalist	3	2	2	1	1	active_below_snow	ground_vegetation
Lasiopodomys brandtii	100	93.82	hindgut_fermenter	family_group	family_group	9.8	cyclic	terrestrial	burrowing	no	facultative_generalist	3	2	2	0	0	active_below_snow	ground_vegetation
Lasiopodomys mandarinus	100	47.48	hindgut_fermenter	family_group	family_group	5.7	noncyclic	terrestrial	burrowing	no	facultative_specialist	3	0	0	0	0	active_below_snow	ground_vegetation
Lemmus amurensis	90	43.70	hindgut_fermenter	solitary	solitary	5.5	cyclic	terrestrial	burrowing	no	obligatory_specialist	1	1	0	3	0	active_below_snow	ground_vegetation
Lemmus lemmus	90	47.50	hindgut_fermenter	solitary	solitary	5.1	cyclic	terrestrial	burrowing	no	facultative_generalist	1	3	1	3	0	active_below_snow	ground_vegetation
Lemmus portenkoi	90	55.76	hindgut_fermenter	solitary	solitary	5.75	cyclic	terrestrial	burrowing	no	facultative_specialist	2	2	0	3	0	active_below_snow	ground_vegetation
Lemmus sibiricus	90	52.27	hindgut_fermenter	solitary	solitary	6.39	cyclic	terrestrial	burrowing	no	facultative_generalist	2	3	1	0	0	active_below_snow	ground_vegetation
Lemmus trimucronatus	90	69.82	hindgut_fermenter	solitary	solitary	6.86	cyclic	terrestrial	burrowing	no	facultative_generalist	1	3	1	3	0	active_below_snow	ground_vegetation
Lepus americanus	70	120.00	hindgut_fermenter	solitary	solitary	3.02	noncyclic	terrestrial	none	no	facultative_generalist	2	1	2	0	1	active_below_snow	ground_vegetation
Lepus arcticus	100	142.15	hindgut_fermenter	solitary	solitary	3.4	noncyclic	terrestrial	none	no	facultative_generalist	2	1	2	0	1	active_below_snow	ground_vegetation

Species																		
Lepus europaeus	100	129.00	hindgut_fermenter	solitary	solitary	3.35	noncyclic	terrestrial	none	no	facultative_generalist	1	3	3	1	1	active_below_snow	ground_vegetation
Lepus mandshuricus	100	1710.02	hindgut_fermenter	solitary	solitary	3.54	cyclic_noncyclic	terrestrial	none	no	facultative_generalist	2	1	3	0	0	active_above_snow	ground_vegetation
Lepus othus	100	4405.04	hindgut_fermenter	solitary	solitary	5.62	noncyclic	terrestrial	none	no	facultative_generalist	1	1	3	1	1	active_above_snow	ground_vegetation
Lepus timidus	100	4805.96	hindgut_fermenter	solitary	solitary	6.15	noncyclic	terrestrial	none	no	facultative_generalist	1	2	3	0	0	active_above_snow	ground_vegetation
Lepus tolai	100	3048.00	hindgut_fermenter	solitary	solitary	3.16	noncyclic	terrestrial	none	no	facultative_generalist	2	2	3	1	1	active_above_snow	ground_vegetation
Lepus townsendii	100	3740.00	hindgut_fermenter	family_groups	solitary	4.49	noncyclic	terrestrial	none	no	facultative_generalist	3	3	1	0	0	active_above_snow	ground_vegetation
Lyrurus tetrix	70	1068.66	hindgut_fermenter	large_group	small_group	8.2	cyclic_noncyclic	terrestrial	none	no	facultative_generalist	2	2	3	0	0	active_above_snow	ground_vegetation
Mareca americana	100	754.61	undifferentiated	small_groups	large_group	8	noncyclic	limnic	none	yes	facultative_generalist	3	3	0	0	0	not_present	ground_vegetation
Mareca falcata	80	645.83	undifferentiated	small_group	large_group	7.5	noncyclic	limnic	none	yes	facultative_generalist	2	3	0	0	0	not_present	ground_vegetation
Mareca penelope	80	770.03	undifferentiated	small_groups	large_group	8	noncyclic	limnic	none	yes	facultative_generalist	3	3	0	0	0	not_present	ground_vegetation
Mareca strepera	60	915.58	undifferentiated	small_group	large_group	10	noncyclic	limnic	grubbing	yes	facultative_generalist	0	2	0	0	0	not_present	ground_vegetation
Marmota broweri	40	3405.00	hindgut_fermenter	large_group	family_group	4.5	noncyclic	terrestrial	burrowing	no	facultative_generalist	3	3	1	1	1	not_present	ground_vegetation
Marmota caligata	40	4900.00	hindgut_fermenter	large_group	family_group	3.9	noncyclic	terrestrial	burrowing	no	facultative_generalist	3	3	1	1	1	not_present	ground_vegetation
Marmota camtschatica	40	3500.00	hindgut_fermenter	large_group	family_group	4.99	noncyclic	terrestrial	burrowing	no	facultative_generalist	3	3	1	1	1	not_present	ground_vegetation
Marmota monax	40	3801.72	hindgut_fermenter	solitary	family_group	4.1	noncyclic	terrestrial	burrowing	no	facultative_generalist	3	3	2	1	1	not_present	ground_vegetation
Marmota sibirica	40	8000.00	hindgut_fermenter	small_group	small_group	4.5	noncyclic	terrestrial	burrowing	no	facultative_generalist	2	3	0	0	0	not_present	ground_vegetation
Meleagris gallopavo	40	5791.37	hindgut_fermenter	large_group	small_group	11.5	cyclic_noncyclic	terrestrial	none	yes	facultative_generalist	2	1	2	0	0	active_above_snow	ground_vegetation
Meriones unguiculatus	50	53.30	hindgut_fermenter	family_group	family_group	5.5	noncyclic	terrestrial	burrowing	no	facultative_generalist	3	3	1	0	0	active_below_snow	ground_vegetation
Micromys minutus	30	6.00	hindgut_fermenter	solitary	small_group	5.5	cyclic	terrestrial	burrowing	no	obligatory_generalist	2	3	1	0	0	active_above_snow	ground_vegetation
Microtus abbreviatus	80	62.00	hindgut_fermenter	solitary	family_group	3	cyclic	terrestrial	burrowing	no	obligatory_generalist	2	2	2	1	1	active_below_snow	ground_vegetation
Microtus agrestis	80	42.50	hindgut_fermenter	solitary	solitary	7.4	cyclic	terrestrial	burrowing	no	facultative_generalist	3	1	1	0	0	active_below_snow	ground_vegetation
Microtus arvalis	80	28.00	hindgut_fermenter	family_group	family_group	6.8		terrestrial	burrowing	no	obligatory_generalist	3	3	0	0	2	active_above_snow	ground_vegetation
Microtus chrotorrhinus	80	39.00	hindgut_fermenter	solitary	solitary	3.58	noncyclic	terrestrial	burrowing	no	obligatory_generalist	2	1	2	1	0	active_below_snow	ground_vegetation

Species																		
Microtus evoronensis	80	41.42	hindgut_fermenter	solitary	family_group	3.89	cyclic_noncyclic	terrestrial	burrowing	no	obligatory_generalist	2	2	2	1	1	active_below_snow	ground_vegetation
Microtus fortis	80	63.00	hindgut_fermenter	solitary	solitary	5.34	cyclic_noncyclic	limnic	burrowing	no	facultative_generalist	1	3	1	0	0	active_below_snow	ground_vegetation
Microtus gregalis	80	47.50	hindgut_fermenter	family_group	solitary	9	cyclic	terrestrial	burrowing	no	obligatory_generalist	3	3	2	0	0	active_below_snow	ground_vegetation
Microtus hyperboreus		36.00	hindgut_fermenter	solitary	solitary	5.49	cyclic	terrestrial	burrowing	no	facultative_generalist	2	3	2	0	0	active_below_snow	ground_vegetation
Microtus levis	80	35.49	hindgut_fermenter	solitary	solitary	5.2	cyclic	terrestrial	burrowing	no	obligatory_generalist	3	3	0	0	0	active_below_snow	ground_vegetation
Microtus longicaudus	80	46.71	hindgut_fermenter	solitary	solitary	4.73	cyclic	terrestrial	burrowing	no	obligatory_generalist	2	1	1	0	0	active_below_snow	ground_vegetation
Microtus maximowiczii	80	41.49	hindgut_fermenter	solitary	family_group	6.8	cyclic	terrestrial	burrowing	no	obligatory_generalist	2	2	2	1	1	active_below_snow	ground_vegetation
Microtus middendorffii	80	36.49	hindgut_fermenter	solitary	solitary	5.49	cyclic	terrestrial	burrowing	no	facultative_generalist	2	3	2	0	0	active_below_snow	ground_vegetation
Microtus miurus	80	41.00	hindgut_fermenter	solitary	family_group	3.89	cyclic_noncyclic	terrestrial	burrowing	no	obligatory_generalist	2	2	2	1	1	active_below_snow	ground_vegetation
Microtus mongolicus	80	27.50	hindgut_fermenter	solitary	solitary	6.8	cyclic	terrestrial	burrowing	no	obligatory_generalist	2	3	0	0	0	active_below_snow	ground_vegetation
Microtus ochrogaster	80	38.01	hindgut_fermenter	solitary	solitary	3.87	cyclic	terrestrial	burrowing	no	facultative_generalist	3	3	2	0	0	active_above_snow	ground_vegetation
Microtus oeconomus	80	34.38	hindgut_fermenter	solitary	solitary	5.62	cyclic	terrestrial	burrowing	no	obligatory_generalist	1	3	2	1	1	active_below_snow	ground_vegetation
Microtus pennsylvanicus	80	36.75	hindgut_fermenter	solitary	solitary	5.16	cyclic	terrestrial	burrowing	no	obligatory_generalist	2	2	1	0	0	active_below_snow	ground_vegetation
Microtus sachalinensis	80	36.33	hindgut_fermented	solitary	solitary	7.89	cyclic	terrestrial	burrowing	no	facultative_generalist	2	3	2	0	0	active_below_snow	ground_vegetation
Microtus subterraneus	80	19.50	hindgut_fermenter	small_group	small_group	4.5	noncyclic	terrestrial	burrowing	no	facultative_generalist	3	1	0	1	0	active_below_snow	ground_vegetation
Microtus xanthognathus	80	125.75	hindgut_fermenter	solitary	solitary	8.1	noncyclic	terrestrial	burrowing	no	obligatory_generalist	2	3	1	0	1	active_below_snow	ground_vegetation
Moschus moschiferus	100	13000.00	ruminant	family_group	family_group	1.74	noncyclic	terrestrial	none	no	facultative_generalist	2	1	1	1	3	active_above_snow	ground_vegetation
Mus musculus	60	16.25	hindgut_fermenter	family_group	family_group	7.5	noncyclic	terrestrial	burrowing	no	obligatory_generalist	2	2	2	1	0	active_above_snow	ground_vegetation
Myodes gapperi	50	19.83	hindgut_fermenter	solitary	solitary	5.37	noncyclic	terrestrial	burrowing	no	facultative_generalist	1	1	2	1	1	active_below_snow	ground_vegetation
Myodes glareolus	50	20.73	hindgut_fermenter	solitary	solitary	5	cyclic	terrestrial	burrowing	no	obligatory_generalist	2	3	1	0	0	active_below_snow	ground_vegetation
Myodes rufocanus	50	36.43	hindgut_fermenter	solitary	solitary	5.01	cyclic	terrestrial	burrowing	no	obligatory_generalist	3	3	3	1	0	active_below_snow	ground_vegetation
Myodes rutilus	50	19.94	hindgut_fermenter	solitary	family_group	5.6	cyclic_noncyclic	terrestrial	none	no	facultative_generalist	1	1	2	1	2	active_below_snow	ground_vegetation
Myopus schisticolor	100	25.00	hindgut_fermenter	solitary	solitary	7	cyclic	terrestrial	none	no	facultative_generalist	1	1	1	3	0	active_below_snow	ground_vegetation

Species																		
Myospalax aspalax	50	237.75	hindgut_fermenter	solitary	solitary	4.5	noncyclic	terrestrial	burrowing	no	facultative_generalist	2	3	1	0	0	active_below_snow	ground_vegetation
Myospalax psilurus	50	259.21	hindgut_fermenter	solitary	solitary	3.11	noncyclic	terrestrial	burrowing	no	facultative_generalist	2	3	0	0	0	active_below_snow	ground_vegetation
Napaeozapus insignis	30	22.30	hindgut_fermenter	solitary	solitary	4.5	cyclic	terrestrial	burrowing	no	facultative_specialist	2	1	2	0	0	hibernating	ground_vegetation
Neotoma cinerea	70	299.15	hindgut_fermenter	solitary	solitary	4	cyclic	terrestrial	none	no	obligatory_generalist	2	3	1	0	0	active_below_snow	ground_vegetation
Ochotona alpina	100	1800.00	hindgut_fermenter	solitary	solitary	3.07	cyclic_noncyclic	terrestrial	none	no	facultative_specialist	2	0	2	0	0	active_above_ground	ground_vegetation
Ochotona collaris	100	1589.00	hindgut_fermenter	solitary	solitary	3.35	cyclic_noncyclic	terrestrial	grubbing	no	facultative_generalist	1	3	1	0	1	active_above_ground	ground_vegetation
Ochotona dauurica	100	1555.00	hindgut_fermenter	family_group	solitary	5.91	cyclic	terrestrial	none	no	facultative_generalist	3	3	2	0	0	active_above_ground	ground_vegetation
Ochotona hoffmanni	100	150.00	hindgut_fermenter	solitary	solitary	3.07	noncyclic	terrestrial	none	no	facultative_generalist	2	3	0	0	1	active_above_snow	ground_vegetation
Ochotona hyperborea	100	109.00	hindgut_fermenter	solitary	solitary	3.02	noncyclic	terrestrial	none	no	facultative_specialist	3	3	0	0	0	active above_ground	ground_vegetation
Ochotona pusilla	100	142.15	hindgut_fermenter	family_group	family_group	8.59	cyclic_noncyclic	terrestrial	none	no	facuktative_generalist	1	3	0	0	0	active above_ground	ground_vegetation
Ochotona turuchanensis	100	142.50	hindgut_fermenter	soliary	solitary	3.07	cyclic_noncyclic	terrestrial	none	no	facultative_generalist	3	2	3	0	0	active_above_snow	ground_vegetation
Odocoileus hemionus	90	54212.57	ruminant	family_group	large_group	1.61	cyclic	terrestrial	none	no	facultative_generalist	2	1	3	0	0	active_above_snow	ground_vegetation
Odocoileus virginianus	90	55508.56	ruminant	family_group	family_group	1.57	cyclic_noncyclic	terrestrial	none	no	obligatory_generalist	2	1	2	1	1	active_above_snow	ground_vegetation
Ondatra zibethicus	90	1065.75	hindgut_fermenter	large_group	family_group	6.55	cyclic	limnic	burrowing	no	facultative_generalist	2	3	0	0	0	active_below_snow	ground_vegetation
Oreamnos americanus	100	72500.33	ruminant	family_group	family_group	1.4	noncyclic	terrestrial	none	no	facultative_generalist	3	3	3	2	2	active_above_snow	ground_vegetation
Ovibos moschatus	90	340501.06	ruminant	large_group	large_group	1.01	noncyclic	terrestrial	none	yes	facultative_generalist	2	3	2	0	0	active_above_snow	ground_vegetation
Ovis dalli	100	55650.62	ruminant	family_group	large_group	1.22	noncyclic	terrestrial	none	yes	obligatory_generalist	2	3	2	0	1	active_above_snow	ground_vegetation
Ovis nivicola	100	90000.00	ruminant	large_group	large_group	1	noncyclic	terrestrial	none	yes	facultative_generalist	1	3	2	1	2	active_above_snow	ground_vegetation
Perdix perdix	40	405.30	hindgut_fermenter	small_group	large_group	15	noncyclic	terrestrial	none	yes	facultative_generalist	1	2	0	0	0	active_above_snow	ground_vegetation
Phasianus colchicus	30	1120.31	hindgut_fermenter	family_group	small_group	11	cyclic_noncyclic	terrestrial	none	yes	facultative_generalist	2	2	2	0	0	active_above_snow	ground_vegetation
Phenacomys intermedius	60	25.20	hindgut_fermenter	solitary	solitary	4.4	cyclic	terrestrial	burrowing	no	facultative_generalist	2	0	3	0	1	active_below_snow	ground_vegetation
Phenacomys ungava	60	32.50	hindgut_fermenter	solitary	solitary	5	noncyclic	terrestrial	burrowing	no	facultative_generalist	3	0	2	0	0	active_below_snow	ground_vegetation
Phodopus campbelli	30	23.40	hindgut_fermenter	solitary	solitary	7.5	noncyclic	terrestrial	burrowing	no	facultative_generalist	2	3	0	0	0	active_below_snow	ground_vegetation

Species																		
Phodopus sungorus	30	33.75	hindgut_fer menter	solitary	solitary	6.4	cyclic	terrest rial	burro wing	n o	facultative_ge neralist	1	3	0	0	0	active_below snow	ground_veg etation
Procapra gutturosa	100	27750.00	ruminant	large_gro up	large_gr oup	1.41	noncylcic	terrest rial	grubbi ng	y es	facultative_ge neralist	3	2	0	0	0	active_above_ snow	ground_veg etation
Pteromys volans	30	143.75	hindgut_fer menter	solitary	solitary	2.5	noncyclic	terrest rial	none	n o	facultative_ge neralist	0	0	2	0	1	active_above_ snow	understory
Rangifer tarandus	100	86033.98	ruminant	large_gro up	large_gr oup	1	noncyclic	terrest rial	none	y es	facultative_ge neralist	2	2	2	1	3	active_above_ snow	ground_veg etation
Sciurus carolinensis	30	506.50	hindgut_fer menter	family_g roup	family_g roup	2.98	noncyclic	terrest rial	burro wing	n o	facultative_ge neralis	1	0	1	0	0	active_aboveg round	canopy
Sciurus vulgaris	30	333.00	hindgut_fer menter	solitary	small_gr oup	4.5	noncyclic	terrest rial	none	n o	facultative_ge neralist	1	0	1	0	0	active_aboveg round	canopy
Sibirionetta formosa	70	433.98	undifferenti ated	small_gr oups	large_gr oup	7.5	noncyclic	limnic	none	y es	facultative_ge neralist	1	3	0	0	0	not_present	ground_veg etation
Spatula discors	60	359.44	undifferenti ated	small_gr oups	large_gr oup	9.5	noncyclic	limnic	grubbi ng	y es	facultative_ge neralist	2	3	0	0	0	not_present	ground_veg etation
Spatula querquedula	30	325.60	undifferenti ated	small_gr oups	large_gr oup	8.5	noncyclic	limnic	grubbi ng	y es	facultative_ge neralist	0	2	0	2	0	not_present	ground_veg etation
Spermophilus dauricus	40	161.30	hindgut_fer menter	solitary	solitary	5.62	noncyclic	terrest rial	none	n o	facultative_ge neralist	2	0	1	0	0	active_aboveg round	ground_veg etation
Spermophilus franklinii	40	363.00	hindgut_fer menter	solitary	solitary	8.69	noncyclic	terrest rial	burro wing	n o	facultative_ge neralist	2	3	1	0	0	hibernating	ground_veg etation
Spermophilus major	40	269.07	hindgut_fer menter	family_g roup	family_g roup	9.8	noncyclic	terrest rial	burro wing	n o	facultative_ge neralist	3	3	1	0	0	active_bellow groud	ground_veg etation
Spermophilus richardsonii	40	406.00	hindgut_fer menter	family_g roup	solitary	7.59	noncyclic	terrest rial	burro wing	n o	facultative_ge neralist	3	2	0	0	0	hibernating	ground_veg etation
Spermophilus tridecemlineatus	40	131.67	hindgut_fer menter	small_gr oup	solitary	8.08	noncyclic	terrest rial	burro wing	n o	facultative_ge neralist	2	2	0	0	0	hibernating	ground_veg etation
Spermophilus undulatus	40	840.00	hindgut_fer menter	large_gro up	large_gr oups	7.77	noncyclic	terrest rial	burro wing	n o	facultative_ge neralist	2	2	1	0	0	hibernating	ground_veg etation
Sus scrofa	60	96118.09	undifferenti ated	family_g roup	family_g roup	4.52	cyclic_non cyclic	terrest rial	grubbi ng	n o	facultative_ge neralist	3	3	2	1	1	active_above_ snow	ground_veg etation
Sylvilagus floridanus	100	1172.79	hindgut_fer menter	family_g roup	family_g roup	4.62	noncyclic	terrest rial	none	n o	facultative_ge neralist	3	2	2	0	0	active_above_ snow	ground_veg etation
Synaptomys borealis	80	21.30	hindgut_fer menter	solitary	solitary	4.27	cyclic_non cyclic	terrest rial	burro wing	n o	facultative_ge neralist	2	3	1	0	0	active_below snow	ground_veg etation
Synaptomys cooperi	80	31.92	hindgut_fer menter	small_gr oup	small_gr oup	3.09	noncyclic	terrest rial	burro wing	n o	facultative_ge neralist	2	2	0	1	1	active_below _snow	ground_veg etation
Tadorna ferruginea	60	1235.03	undifferenti ated	small_gr oups	large_gr oup	8.5	noncyclic	limnic	none	y es	facultative_ge neralist	1	3	0	0	0	not_present	ground_veg etation
Tamias striatus	30	111.91	hindgut_fer mented	solitary	solitary	4.5	noncyclic	terrest rial	burro wing	n o	facultative_ge neralist	1	0	1	0	1	hibernating	canopy
Tetrao urogalloides	80	2752.29	hindgut_fer menter	solitary	solitary	6.5	noncyclic	terrest rial	none	n o	obligatory_ge neralist	2	0	3	1	0	active_above_ snow	canopy
Tetrao urogallus	90	2716.61	hindgut_fer menter	solitary	solitary	8.5	cyclic	terrest rial	none	y es	facultative_sp ecialist	2	1	3	1	0	active_above_ snow	ground_veg etation

Species	EPO	BM	GT	GSS	GSW	LCS	PD	HT	BGF	M	DT	DIF	DIG	DIS	DIM	DIL	WS	SOV
Tetraogallus altaicus	50	2760.43	hindgut_fermenter	solitary	solitary	8	cyclic	terrestrial	grubbing	no	facultative_generalist	0	2	3	0	0	active_above_snow	ground_vegetation
Thomomys talpoides	100	130.08	hindgut_fermenter	solitary	solitary	4.86	noncyclic	terrestrial	burrowing	no	facultative_generalist	3	2	1	0	0	active_below_ground	ground_vegetation
Tympanuchus phasianellus	70	882.38	hindgut_fermenter	small_group	small_group	12	cyclic	terrestrial	none	yes	facultative_generalist	2	1	2	0	0	active_above_snow	grpund_vegetation
Urocitellus parryii	40	759.99	hindgut_fermenter	large_group	family_group	6.5	noncyclic	terrestrial	burrowing	no	facultative_generalist	3	3	2	1	1	not_present	ground_vegetation
Ursus arctos	60	########	undifferentiated	solitary	solitary	2.24	noncyclic	terrestrial	grubbing	yes	facultative_generalist	3	2	0	0	0	hibernating	ground_vegetation

Table S2. Trait table with all the realized values for each trait. For further explanation on the traits outlined in this table see table S3. The headers are acronyms for the traits as follows: Plant consumption value in EltonTraits (EPO), Body Mass (BM), Gut Type (GT), Group size in the Summer (GSS), Group Size in the Winter (GSW), Litter-Clutch Size (LCS), Population Dynamics (PD), Habitat Type (HT), Below Ground Feeding (BGF), Mobility (M), Diet Type (DT), Diet Item Forbes (DIF), Diet Item Graminoid (DIG), Diet Item Shrubs (DIS), Diet Item Moss (DIM), Diet Item Lichen (DIL), Winter Strategy (WS) and Use of Vegetation (SOV). For information on how this data was gathered see Methods 2.3.1 and for references see the bottom of the table.

Table of Trait Overview

Trait		Trait function	Trait quantification	Variable type
Importance of main arctic functional groups of plants in the herbivore's diet	Forbs	If the herbivore species feeds mainly on forbs, it will likely have a large impact on this plant functional group	Scored 0-3 depending on the frequency in diet. 0; non-existing 1; low importance, (0-10% of an average diet or known usage from only some populations; diet proportions above 0.5 should be infrequent) 2; medium importance (10-50% of an average diet or used by most populations during most seasons; proportions can vary from low to high) 3; high importance (>50% of an average diet or known usage of medium to high proportions from all populations and seasons)	Discrete, ordered from low to high importance in diet
	Graminoids	If the herbivore species feeds mainly on graminoids, it will likely have a large impact on this plant functional group		
	Woody plants	If the herbivore species feeds mainly on woody plants, it will likely have a large impact on this plant functional group		
	Mosses	If the herbivore species feeds mainly on mosses, it will likely have a large impact on this plant functional group		
	Lichens	If the herbivore species feeds mainly on lichens, it will likely have a large impact on this plant functional group		
Diet type		How selective or generalist a herbivore species is will determine if its impacts affect only certain plant species, or the effects spread across several plant species	According to Shipley et al 2009: Obligatory generalist (OG, 1) Facultative generalist (FG, 2) Facultative specialist (FS, 3)	Factor, ordered from generalist to specialist

			Obligatory specialist (OS, 4)	
Gut type		Gut morphology will determine what plants or plant parts can be eaten by the herbivore	Type of gut: undifferentiated (U, 1) hindgut fermenter (HF, 2) ruminant (R, 3)	Factor, ordered from inefficient to efficient
Belowground feeding		Belowground feeding by herbivores can have distinct impacts on vegetation	Type of belowground feeding: Burrowing (B) Grubbing (G) None (N)	Unordered factor
Body mass		Key variable in trophic ecology, reflecting both feeding and predation ecology.	Body mass (grams)	Continuous
Mobility		Wide ranging herbivores will have an impact on vegetation over larger spatial scales than herbivores with reduced mobility	Ability to move between the 100x100 km pixels used in analyses: Yes (1) No (0)	Binary
Group size	summer	Larger groups of herbivores foraging together will have a more intense effect on vegetation and behaviour in relation to predation	Group size categories: solitary (S, 1) small group (SG, 2) family group (FG, 3) large group (LG, 4)	Factor, ordered from solitary to large groups
	winter	Larger groups of herbivores foraging together will ha e a more intense effect on vegetation and behaviour in relation to predation		
Population dynamics (cyclicity)		The effects of herbivores can also vary over time, from variable (cyclic) impacts when herbivores have peaks in abundance, to uniform (noncyclic). These affect trophic dynamics in relation to vegetation and plants.	Prevalence of cyclic populations: non-cyclic (NC, 1) cyclic/non-cyclic (C/NC, 2); when some populations of a species cycle and others do not.	Factor, ordered from low to high degree of temporal variation in population size

		Cyclic (C, 3)	
Litter/clutch size	Larger litter/clutch sizes underlie population dynamics, notably growth rates, with impacts on trophic dynamics.	Litter size, number of offspring per year.	Continuous
Wintering strategy	Winter strategy controls trophic interactions in the Arctic during winter. Several species migrate out of the Arctic during winter.	Wintering strategy: Not present in during winter (NP, 1) Active below ground (BS, 2) Active above ground (AAS, 3) Hibernating (H, 2?)	Factor, ordered from not present to active above snow
Habitat	Main habitat affects the type of trophic interactions	Habitat class: Terrestrial (T) Limnic (L)	Factor
Usage of vegetation	Main strata selection affects community composition on trophic interactions	Vegetation strata: Ground Vegetation (GV, 1) Understory (U, 2) Canopy (C, 3)	Factor, ordered from Ground vegetation to canopy

Table S3. Description of the functional traits used to develop the functional classification of Arctic & Boreal vertebrate herbivores. Abbreviations for trait categories in the column Trait quantification refer to abbreviations used in Appendix S4. Numeric values for factors refer to the order for ordered factors this table was created by Speed et al. (2019). In this study we added the trait named "Vegetation use".

Surrogate Species Table

Species with a lack of information	Surrogate species
Alticola macrotis	Alticola lemminus
Alticola olchonensis	
Microtus evoronensis	Microtus miurus
Microtus maximowiczii	
Microtus mujanensis	
Microtus sachalinensis	Microtus middendorffii

Table S4. This table describes which surrogate species were chosen in order to reduce the information gap for understudied species
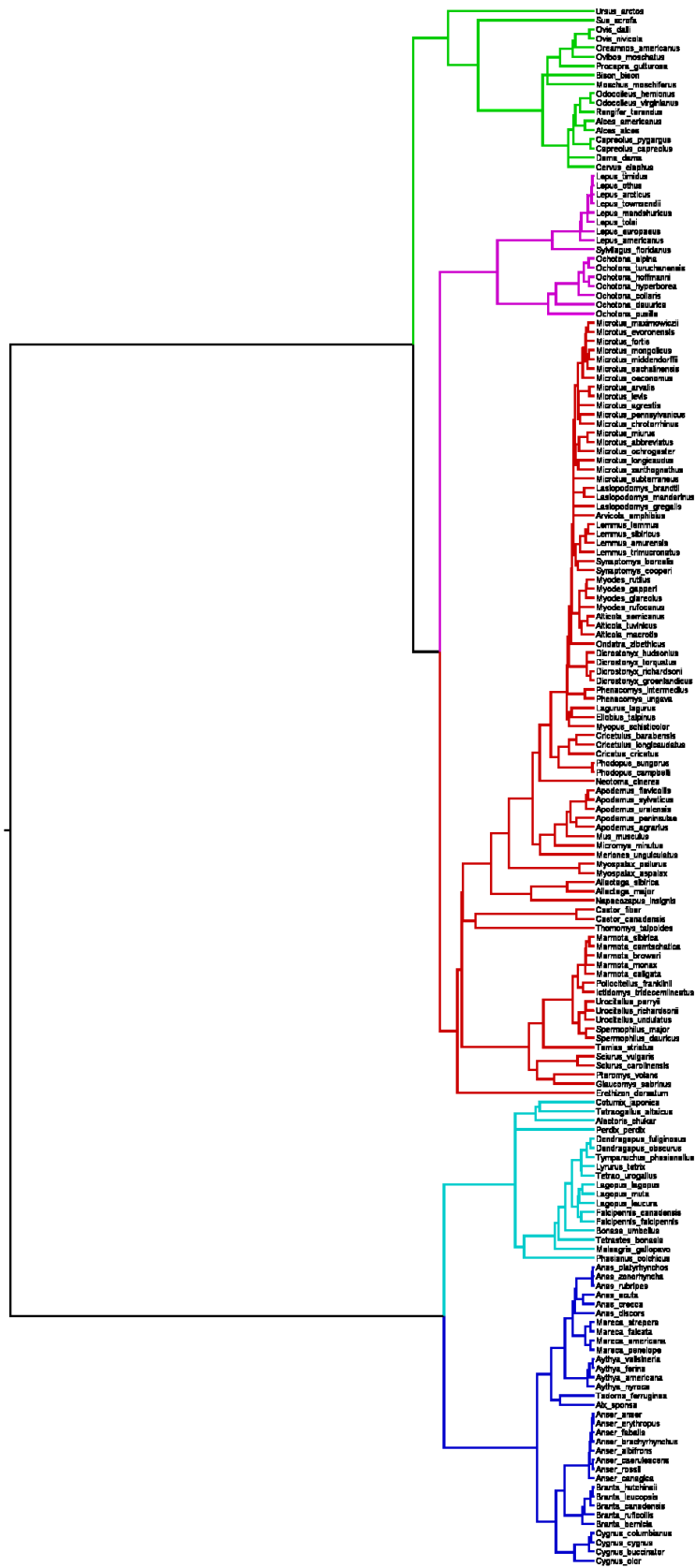
Appendix B

TimeTree Dendrogram

Figure S1. This phylogenetic tree was obtained from the TimeTee database to compare the topology of our constructed phylogenetic tree. The colors correspond to mayor clades Artiodactyla and *Ursus arctos* (Green), Lagomorpha (Pink), Rodentia (Red), Galliformes (Cyan), Anseriformes (Blue).

Phylogenetic Dendrogram

Figure S2. The topology of the phylogenetic tree consisting of 189 taxa (including: *Alces americanus, Anas penelope, Camptorhynchus labradorius, Dendrocygna bicolor and Tetrao parvirostris*). The four mitochondrial markers used in this ML tree were 12S, COI, cytB and ND2. Only 184 species from this tree were used for the analysis, excluding only the aforementioned species. The colors correspond to mayor clades Artiodactyla and *Ursus arctos* (Green), Lagomorpha (Pink), Rodentia (Red), Galliformes (Cyan), Anseriformes (Blue).

Factorial Analysis of Mixed Data

A)
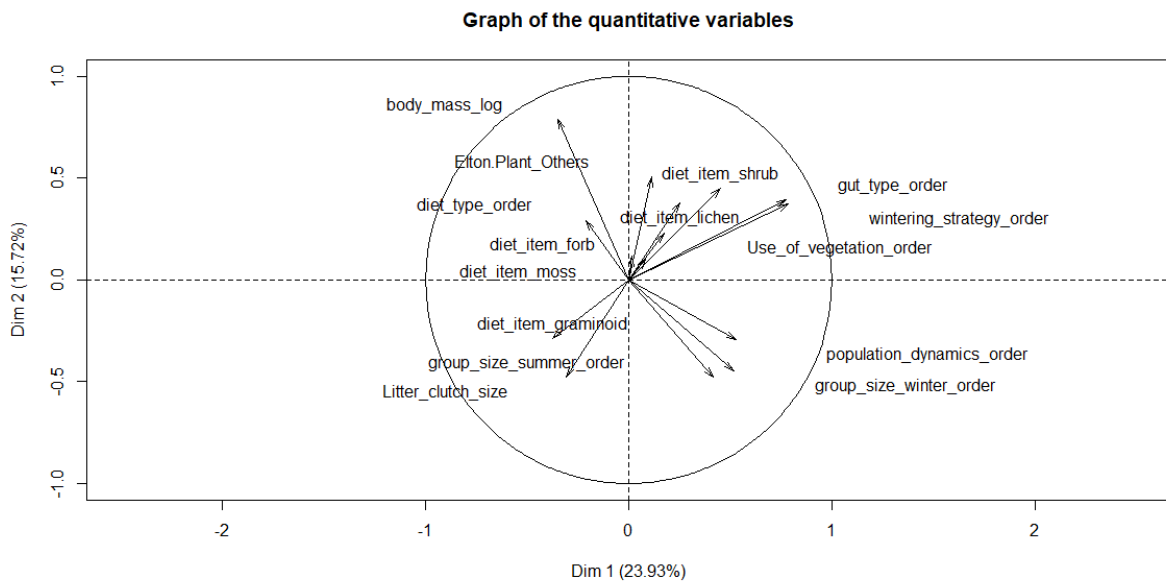
B)
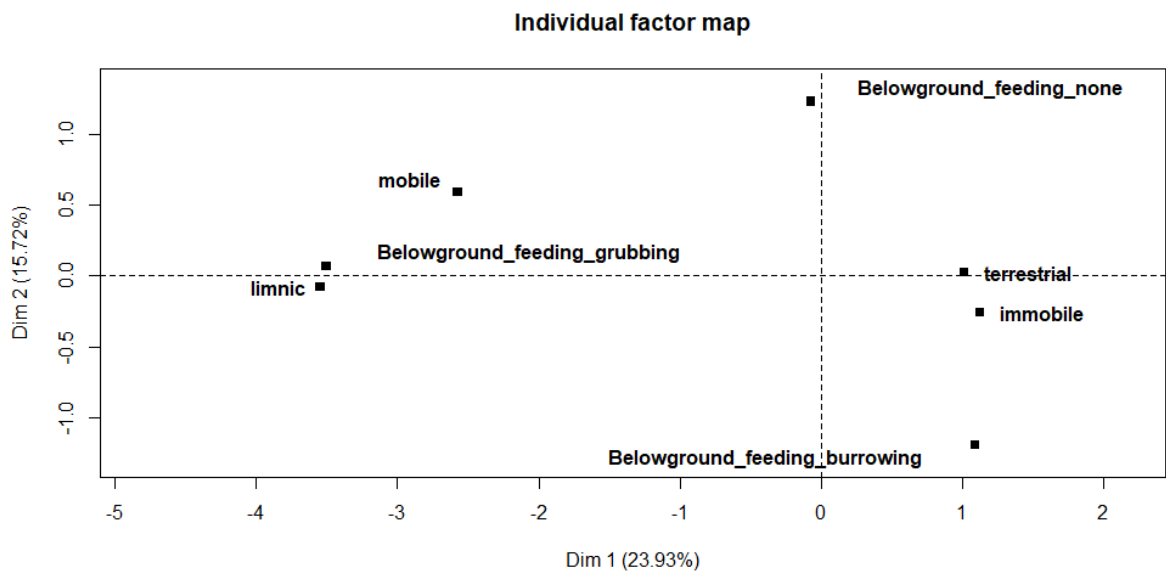
Figure S3. A) Quantitative variables presented as vectors along the two axes form the FAMD. B) Qualitative (Rename) variables levels plotted along the first two axis. The percentage of the variation captured by the first two axis is shown.
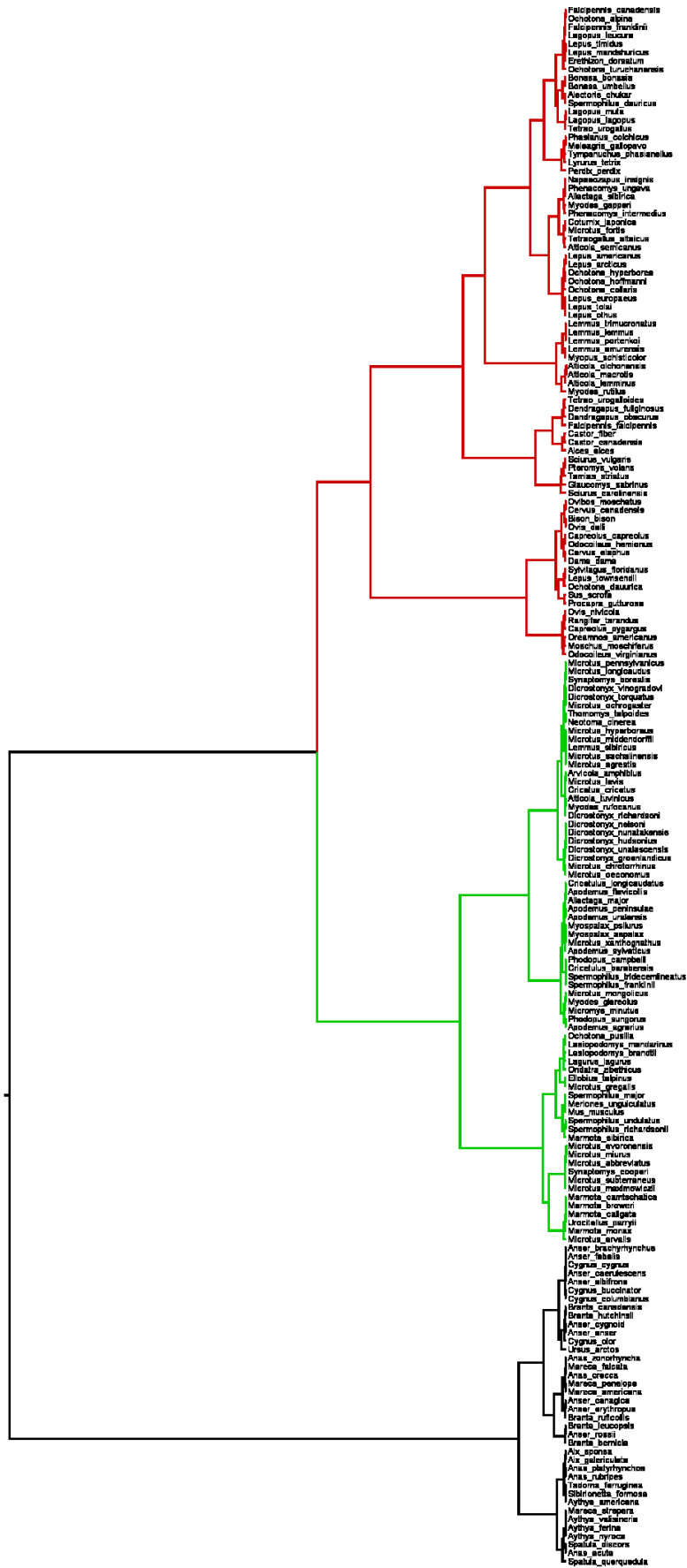
Hierarchical clustering

Figure S4. This figure demonstrates the hierarchical clustering of the functional dendrogram. The colour squares represent the three identified clusters in which the taxa were separated. The three functional groups are shown as limnic (black), burrowers (green) and grazers/browsers (red).

Functional dendrogram

Figure S5. The functional dendrogram generated by the FAMD and HCPC. Includes all 184 species included in the analysis. The three functional groups are shown as limnic (black), burrowers (green) and grazers/browsers (red).

Absolute Values of the three biodiversity measures
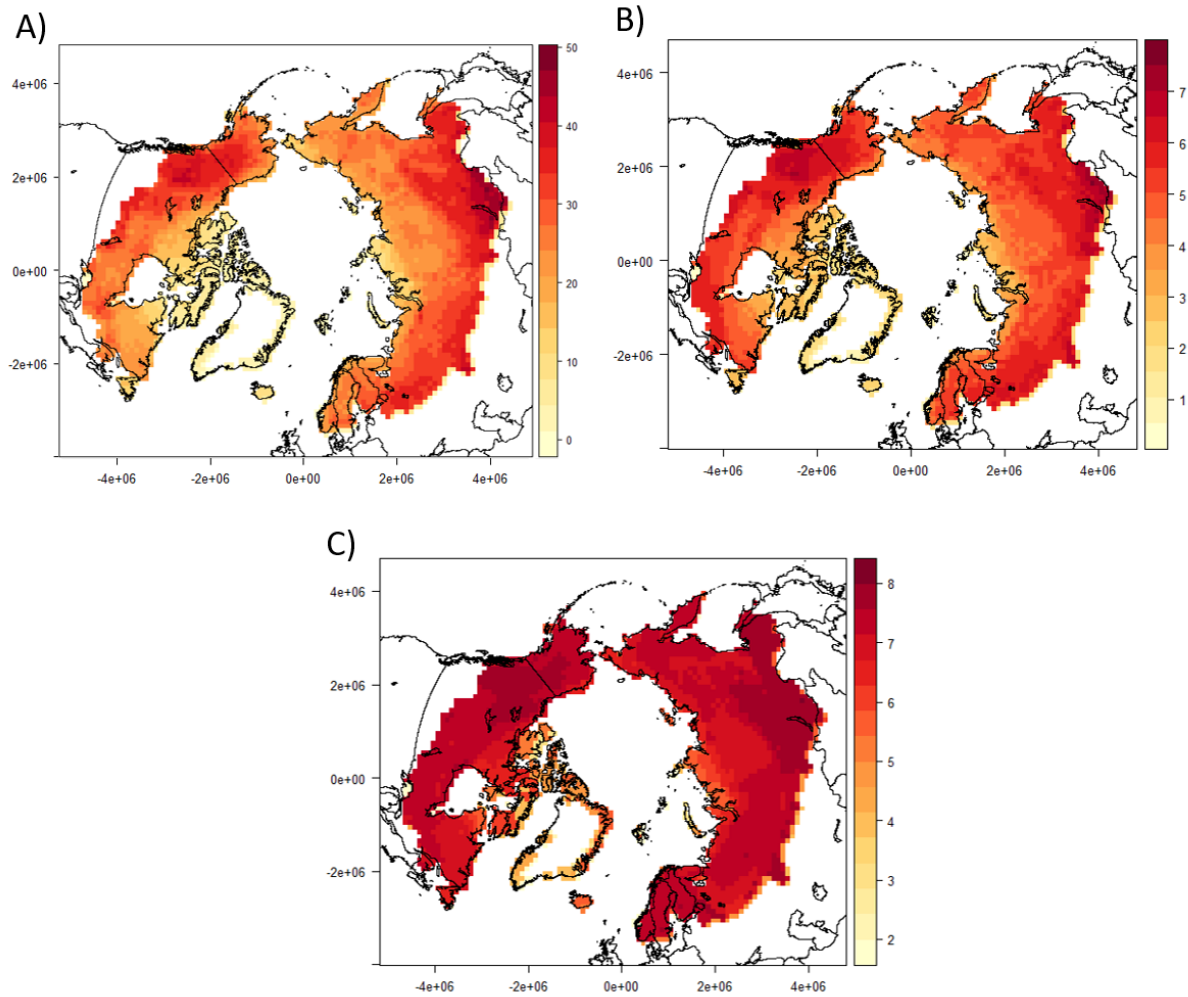
Figure S6. Maps presenting the absolute values of species richness (A), phylogenetic diversity (B) and functional diversity (C). The resolution employed in these maps is 100x100 km cells. The darker colours represent higher values of the diversity measure.

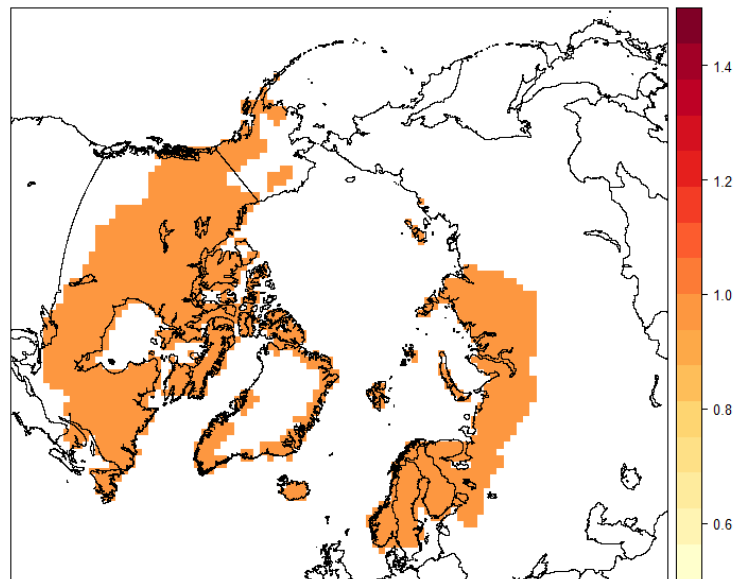**Ice distribution in the last glacial maximum**

Figure S7. A visualization of the last glacial maximum (circa 21,000 years ago). This map corresponds to the data obtained from Peltier (1994). We changed the resolution (100 x 100km cells) for a better comparison with the results in this study. The values are all equal to "1" which indicates the presence of ice during the last glacial maximum.

Appendix C

References employed for the gathering of the information in the trait table (See Appendix A table S2).

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