PRIMARY RESEARCH ARTICLE

Will borealization of Arctic tundra herbivore communities be driven by climate warming or vegetation change?

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Abstract

Poleward shifts in species distributions are expected and frequently observed with a warming climate. In Arctic ecosystems, the strong warming trends are associated with increasing greenness and shrubification. Vertebrate herbivores have the potential to limit greening and shrub advance and expansion on the tundra, posing the question of whether changes in herbivore communities could partly mediate the impacts of climate warming on Arctic tundra. Therefore, future changes in the herbivore community in the Arctic tundra will depend on whether the community tracks the changing climates directly (i.e. occurs in response to temperature) or indirectly, in response to vegetation changes (which can be modified by trophic interactions). In this study, we used biogeographic and remotely sensed data to quantify spatial variation in vertebrate herbivore communities across the boreal forest and Arctic tundra biomes. We then tested whether present-day herbivore community structure is determined primarily by temperature or vegetation. We demonstrate that vertebrate herbivore communities are significantly more diverse in the boreal forest than in the Arctic tundra in terms of species richness, phylogenetic diversity and functional diversity. A clear shift in community structure was observed at the biome boundary, with stronger northward declines in diversity in the Arctic tundra. Interestingly, important functional traits characterizing the role of herbivores in limiting tundra vegetation change, such as body mass and woody plant feeding, did not show threshold changes across the biome boundary. Temperature was a more important determinant of herbivore community structure across these biomes than vegetation productivity or woody plant cover. Thus, our study does not support the premise that herbivore-driven limitation of Arctic tundra shrubification or greening would limit herbivore community change in the tundra. Instead, borealization of tundra herbivore communities is likely to result from the direct effect of climate warming.

KEYWORDS
Arctic tundra, biome boundary, boreal forest, functional diversity, functional traits, herbivory, productivity, shrub, treeline

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1 | INTRODUCTION

Climate change is driving species distributions to cooler clines, with latitudinal and elevational shifts in plant and animal species (Chen et al., 2011; Lenoir et al., 2008; Parmesan & Yohe, 2003). Climatic warming is particularly pronounced in northern ecosystems, notably the Arctic tundra (Meredith et al., 2019; Serreze & Barry, 2011). Here, major vegetation shifts are underway, involving the establishment and spread of woody plants (both treeline advance and 'shrubification'; Hofgaard et al., 2013; Martin et al., 2017; Myers-Smith et al., 2011) and increases in primary productivity ('greening'; Beck & Goetz, 2011; Ju & Masek, 2016; Myers-Smith et al., 2020). Borealization, defined as northward shifts of species and communities in the Arctic (Fossheim et al., 2015), has also become increasingly evident. In the Arctic tundra, vertebrate communities have started to become more boreal in nature. For example, the distributions of boreal species including moose (*Alces alces* Tape et al., 2016), beaver (*Castor canadensis* Tape et al., 2018), red fox (*Vulpes vulpes* Elmhagen et al., 2017) and multiple boreal bird species (Sokolov et al., 2012) have all been observed to be expanding into the Arctic tundra. Such northward advances are often linked to climate. However, it remains unclear whether herbivore species directly track climate change, or rather if the changing Arctic tundra vegetation is the proximal driver of these range shifts (Zhou et al., 2017).

The main direct driver of poleward shifts in species distributions and community structure is believed to be climate (Walther, 2010). Yet, indirect effects of climate, mediated through biotic drivers, can also play a role in determining community structure at macroecological scales. For example, vegetation productivity has been linked to the species composition (Barrio et al., 2016) and functional structure (Speed et al., 2019) of Arctic herbivore communities. Shrub cover has a positive influence on many Arctic herbivore species (Wheeler et al., 2018), and has been proposed as a driver of expansion of moose populations in the Arctic (Zhou et al., 2017). In addition, increases in vegetation productivity can increase forage availability for Arctic herbivores such as the Arctic ground squirrel (*Urocitellus parryii*; Wheeler et al., 2015). Conversely, tundra greening has been associated with decreases in *Rangifer* populations (reindeer/caribou), likely also due to the higher incidence of shrub species, providing a lower quality of forage (Fauchald et al., 2017). Thus, vegetation productivity and woody plant cover are clearly possible determinants of the extent of borealization of herbivore communities.

Species' interactions with their environment are captured by functional traits (Suding et al., 2008). In herbivores, population and community response to increasing productivity and woody plant expansion, as well as their ability to prevent shrub expansion are likely to be related to traits such as body size and diet (Olofsson & Post, 2018). The impact of herbivores on vegetation varies depending on the structure of the herbivore community (Deraison et al., 2015). While species richness is a key part of community structure, it does not give insight into the evolutionary history or the role of the different species in communities. The inclusion of different metrics such as phylogenetic diversity and functional diversity can provide an improved

overview of the community assembly and function (Cadotte et al., 2013; Safi et al., 2011). To achieve a comprehensive understanding of herbivore community assembly across the boreal forest and Arctic tundra biomes, adjoining biomes with fundamentally different vegetation structure, we here integrate all these measures.

In this study, we test whether climate or vegetation are the primary drivers behind differences between herbivore communities of the boreal forest and the Arctic tundra. To achieve this, we characterize herbivore communities of boreal and tundra biomes at a macroecological scale and test the following hypotheses: **H1**: That threshold changes in the structure of herbivore communities occur across the boreal forest—tundra biome boundary. **H2**: That vegetation productivity and woody plant cover have a greater impact on the structure of herbivore communities than temperature. To test these hypotheses, we focus on species richness, phylogenetic diversity and functional diversity of herbivore communities, as well as two herbivore functional traits expected to be critical in changing northern ecosystems—body mass (Olofsson & Post, 2018) and the contribution of woody plants to herbivore diets (Ravolainen et al., 2014).

2 | METHODS

2.1 | Study region and species

The study region was defined as the Arctic tundra and boreal forest biomes (using the WWF Terrestrial Ecoregions of the World shapefiles; Olson et al., 2001). All mammalian and avian herbivores, defined as species with greater than or equal to 30% diet contribution of plant leaf and stem tissue ('Plant Other' in Elton traits database; Wilman et al., 2014), with distributions overlapping with the Arctic tundra and boreal forest biomes were selected. Range maps for each of these species were downloaded from IUCN (2019) and Birdlife International (BirdLife International & Handbook of the Birds of the World, 2016), these represent species ranges as assessed between 2008 and 2015 for mammals and between 1999 and 2015 for birds. Species with a predominant aquatic feeding habitat including diving ducks (*Aythya* spp, *Oxyura leucocephala* and *Netta rufina*) and seaducks (*Melanitta* spp) were excluded as their diets were assumed to be largely independent of terrestrial vegetation dynamics. Similarly, obligatory granivores such as *Allocricetulus eversmanni* were excluded as we retained focus on folivorous herbivores that are likely more directly associated with woody plant cover and productivity. The final species list comprised 184 species including 57 avian herbivores (37 Anseriformes and 20 Galliformes) and 127 mammalian herbivores (93 Rodentia, 17 Artiodactyla, 16 Lagomorpha and 1 Carnivora [*Ursus arctos*, the brown bear]; Table S1). Range data were rasterized with a 100 × 100 km cell size.

2.2 | Functional traits and diversity

A suite of functional traits was characterized across the study species. This was developed from the functional traits used to

characterize Arctic vertebrate herbivore functional diversity (Speed et al., 2019), including body mass, litter/clutch size, foraging traits, mobility traits, wintering strategy and diet composition at a level of plant functional groups. The list of traits used was expanded to reflect boreal and tundra herbivores by including canopy strata of foraging (Table S2). Traits for the additional species were quantified or qualified on the basis of the Handbook of the Birds of the World (Hoyo et al., 2019) for avian herbivores and the Mammals of the World (Wilson et al., 2019) for mammalian herbivores. The databases PanTHERIA (Jones et al., 2009) and the IUCN (2019) were used for data that were either missing or ambiguous in the sources above. There was a considerable lack of ecological and behavioural information for six species and this missing information was inferred from 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 (Table S3). The full list of traits for each species is shown in Table S1.

Herbivore community structure was characterized in terms of species richness, phylogenetic diversity and functional composition. Species richness was calculated as the number of species present in each raster cell. To quantify phylogenetic diversity, we developed a molecular phylogeny of all study species (full details in Supplementary Text T1). Phylogenetic diversity was then calculated as the proportion of the total species pool phylogenetic branch lengths represented by all the species within each cell. The functional composition of herbivore communities was quantified in three ways for each raster cell. First, *community mean functional traits* were calculated for body mass and for woody plant diets as these traits are important in determining herbivore responses to environmental change. Since the species range data were of presence–absence form, the estimates are not weighted. Second, we estimated a functional diversity index *functional richness* (FRic) to capture the total multidimensional functional space occupied by the herbivore community. This is represented by a convex hull volume around all species' traits in multivariate space (Villéger et al., 2008). Third, since we expect species richness to vary across our study region, and functional richness will increase with species richness in a null model, we also selected a measure of multivariate deviance in functional trait space; here we used the index *functional dispersion* (FDis; Laliberté & Legendre, 2010). The functional diversity indices were calculated on the species presence–absence data, using the R package FD (Laliberté et al., 2014). All traits were standardized first, to avoid large-magnitude traits dominating the indices (Villéger et al., 2008).

2.3 | Environmental variables

We estimated the *distance to the biome boundary* as the distance to the nearest raster cell through which the biome boundary passed. Positive distances were given to cells north of the boundary, and negative distance to cells south of the boundary (Figure S1). To assess the impact of climate on herbivore community, we used the mean temperature of the warmest quarter of the year (*mean summer temperature* herein), and acquired this from WorldClim 2 bioclimate variables at 2.5° resolution (averages 1970–2000; Fick & Hijmans, 2017). To assess the impacts of vegetation on herbivore communities, we used w*oody plant cover* and *net primary productivity (NPP).* Woody plant cover was estimated as the sum of fractional tree cover and shrub cover from Copernicus Global Land Service land cover data set (2015, 100 m resolution; Buchhorn et al., 2019), and estimates from MODIS were used for NPP (means from 2000 to 2015, 30-arc second resolution; Zhao et al., 2005). All environmental variables were resampled using bilinear interpolation to the grid of 100 × 100 km raster cells used by the species distribution data (Figure S1).

2.4 | Data analyses

In all our analyses, the variables describing herbivore community structure were species richness, phylogenetic diversity, functional richness, functional dispersion, and community mean body mass and contribution of woody plants to herbivore diets. That is, all models were run for all of these six response variables.

To test our first hypothesis (i.e. that boreal and tundra herbivore communities are functionally different, and that changes in herbivore community structure occur across the forest–tundra ecotone), we used segmented regression. We first investigated if there was a significant difference between tundra and boreal forest cells using mixed effects models. Since we assume spatial autocorrelation across our study region, we fitted the environmental variables as fixed effects and ecoregion (with 57 ecoregions within the boreal forest and Arctic tundra biomes, sourced from Terrestrial Ecoregions of the World; Olson et al., 2001) as a random effect. Environmental variables were examined for potential collinearity (Figure S2). We then tested for the presence of a break point in the relationship between herbivore community structure and distance from the treeline. We used the Davis test (Davies, 2002) within the R package *segmented* for this (Muggeo, 2008).

To investigate our second hypothesis, that is vegetation structure is a more important determinant than temperature of herbivore community structure, we used structural equation modelling (SEM). We choose a SEM approach since tundra vegetation productivity and woody plant cover are also expected to be affected by climate (Forbes et al., 2010; Myers-Smith et al., 2015). SEM allows us to explore the different pathways of determination of the structure of herbivore communities as laid out in Figure 1a. We used mixed models, fitting the environmental variables as fixed effects and ecoregion (Terrestrial Ecoregions of the World; Olson et al., 2001) as a random effect. SEM were fitted using the *piecewiseSEM* package (Lefcheck, 2016). All variables were standardized allowing direct comparison of coefficients. We fitted a correlated error between NPP and woody plant cover. This is because while woody plant cover is likely to increase with potential ecosystem productivity (Forbes et al., 2010), realized NPP is likely also a response of woody plant cover (Mekonnen et al., 2021). There were
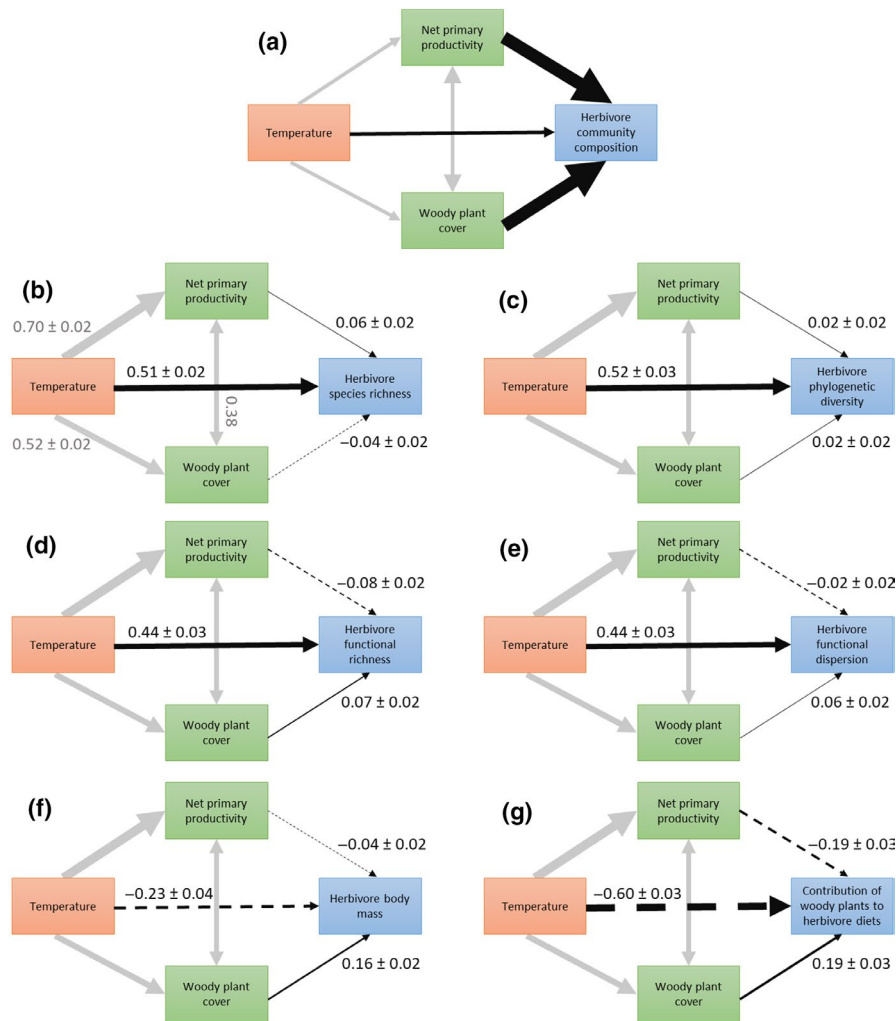
FIGURE 1 SEM pathway diagrams. In all parts, black arrows relate to the hypothesis 3, while grey arrows are not part of the study hypotheses. Arrow widths are proportional to regression coefficients. Solid arrows show positive coefficients and dashed arrows represent negative coefficients. (a) shows the hypothesized relative coefficients (hypothesis 3). Coefficients from parameterized models are shown in panels (b–g): Species richness (b), phylogenetic diversity (c), functional richness (d), dissimilarity (e) and community mean body mass (f) and woody plant contribution to diet (g) are all hypothesized to be affected by temperature and the two vegetation structure variables—net primary productivity and woody plant cover. The vegetation structure variables are expected to be related to temperature. Mean summer temperature is an exogenous variable, unaffected by others in the model framework. A correlated error (shown by a double-headed arrow) was fitted between productivity and woody plant cover (see Section 2). Coefficients for these are constant between response variables and are only shown in panel (b). In other panels, regression coefficients and standard errors are shown

no independence claims left in the resulting structural equation model (Figure 1a).

3 | RESULTS

Herbivore communities were more diverse in the boreal forest than those in the Arctic tundra (Figures 2 and 3; Table 1) in terms of species richness, phylogenetic diversity, functional richness and functional dispersion. On average, the boreal forest had 28 (±standard error of 1.8) species of vertebrate herbivores per 100 × 100 km cell, while there were 19 (±1.6) species of vertebrate herbivores per Arctic tundra cell. All four diversity variables were strongly correlated with one

another (.57 ≤ r ≤ .97; Figure S2), so the proportional differences in phylogenetic diversity and functional richness and dissimilarity were similar (Table 1). The two community mean traits (body mass and contribution of woody plants to diet) were uncorrelated with each other and with the diversity indices (|r| ≤ .4; Figure S2). Community mean body mass was slightly lower for the boreal forest (15 kg ± 1.9) than that for the Arctic tundra (19 kg ± 1.8), but the difference was not statistically significant (Figure 2; Table 1). The average contribution of woody plants to herbivore diets was greater in Arctic tundra communities (index of 2.8 ± 0.03) than that in boreal forest communities (mean index of 2.6 ± 0.03).

All diversity variables had a clear break point around the biome boundary (all within 170 km of the biome boundary; Figure 3;
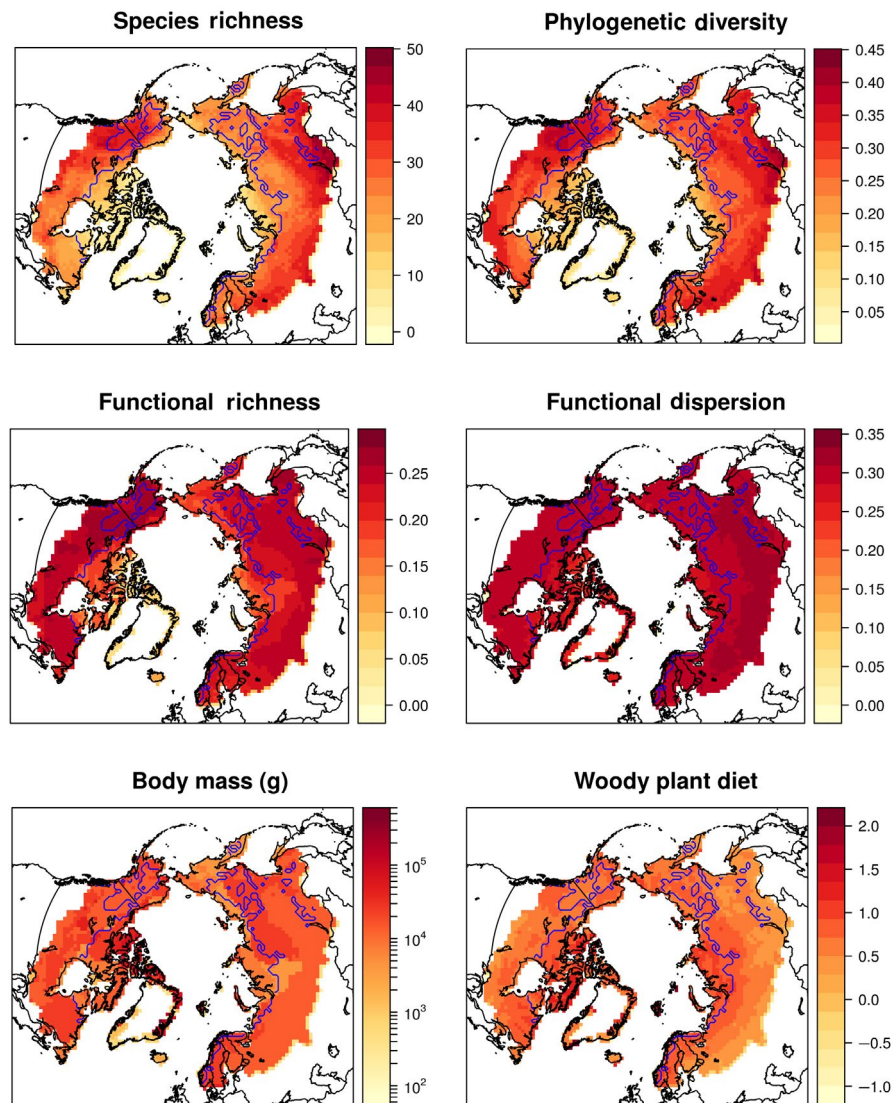
Species richness

Phylogenetic diversity

Functional richness

Functional dispersion

Body mass (g)

Woody plant diet

FIGURE 2 Vertebrate herbivore community diversity and selected community mean traits across the Arctic tundra and boreal forest biomes. The biome boundary is shown by a blue line. Darker red shades indicate higher diversity or community average traits. Note that the body mass colour scale is log-transformed

Table 1). They all decreased faster with latitude when north of the biome boundary, that is within the tundra biome. Community mean body mass showed a consistent and slightly negative relationship with latitude with no significant break point (Davies test, $p = .74$), although there was a high degree of variation in community mean body mass in the Arctic tundra (Figure 3). The community mean contribution of woody plants to diets increased with latitude within the boreal forest and low and mid-Arctic, but decreased with latitude above a break point which was estimated at 1270 km north of the biome boundary (Figure 3; Table 1).

In the SEM, both vegetation structure variables (productivity and woody plant cover) were strongly determined by temperature (standardized coefficients between temperature and NPP 0.70 ± 0.02 and between temperature and woody plant cover 0.51 ± 0.02). The direct effect of temperature was the dominant factor shaping community structure in species, phylogenetic and functional space (Figure 1b–e; Figure S3). Temperature had a positive effect on species richness, phylogenetic diversity, functional richness and functional dissimilarity (Figure 1), but had a negative effect on body mass (-0.23 ± 0.04, Figure 1b) and woody plant diet (-0.60 ± 0.02, Figure 1g). The main

effects of vegetation were on the community mean functional traits: NPP had a negative effect on the use of woody plants by herbivores (-0.19 ± 0.02), while woody plant cover had a positive effect on both community mean body mass (0.16 ± 0.04) and woody plants in the diet (0.19 ± 0.02, Figure 1; Figure S2). In contrast, the impacts of vegetation on diversity measures were minor, with all of the absolute standardized coefficients being <0.07 (Figure 1). For all the herbivore community structural equation models, the marginal R^2 (.02 to .37) was low in relation to the conditional R^2 (accounting for the effect of ecoregion; ≥.63, Figure S5). This indicates that herbivore community structure varied considerably between ecoregions, and that fitting ecoregion as a random effect effectively handled spatial autocorrelation (Figure S4).

4 | DISCUSSION

Plant and consumer communities in the Arctic show evidence of recent borealization trends (Hofgaard et al., 2013; Tape et al., 2016). In this study, we show that Arctic tundra herbivore communities are

FIGURE 3 Diversity indices and selected functional traits plotted along the distance to the biome boundary distance (south of biome boundary as negative values, with green background). For indices and traits for which a significant break point was identified, vertical lines show the position of the break point. Standard errors of regression lines and break points are shown by shaded regions and dashed lines respectively
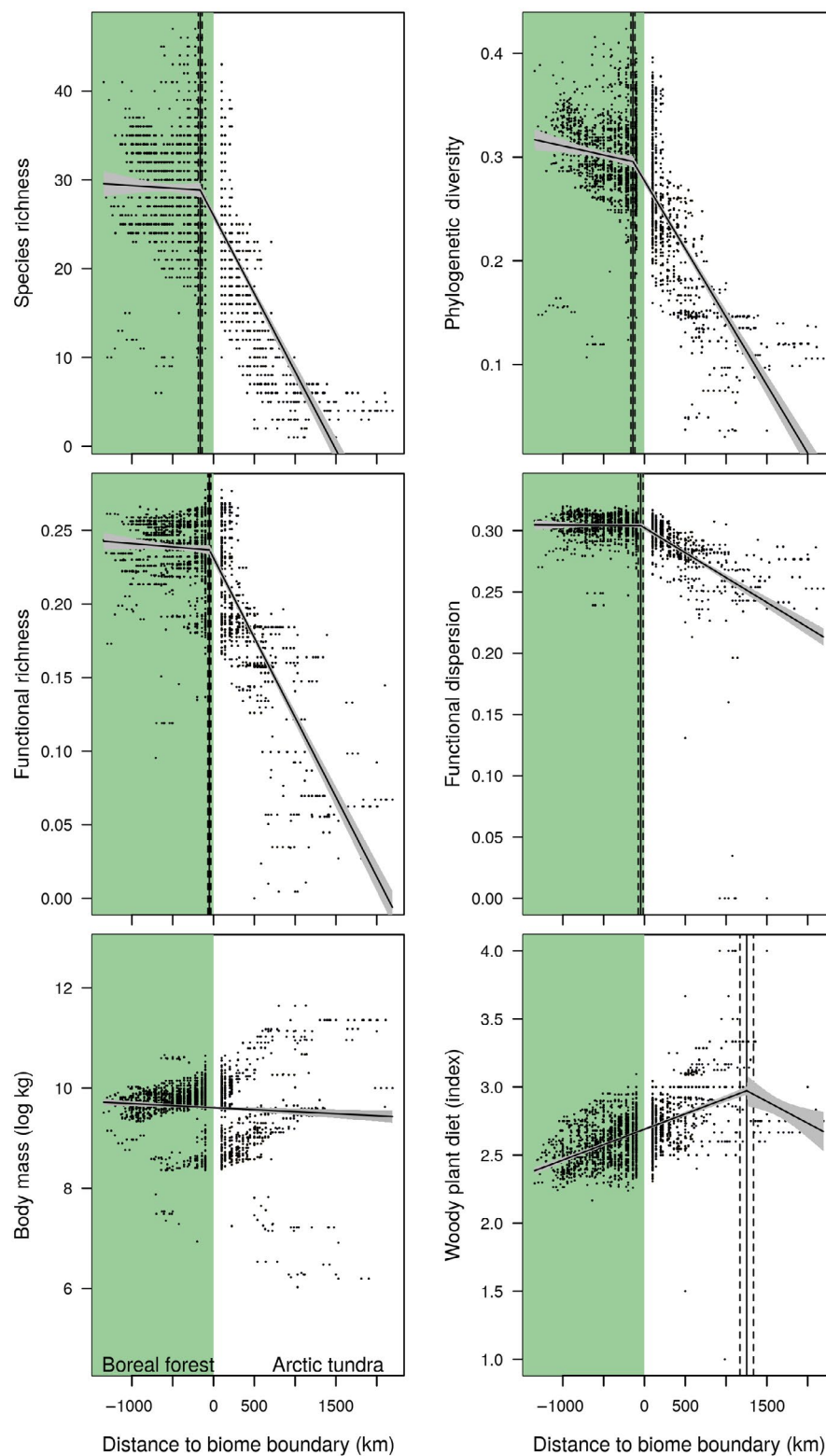
less diverse than their boreal counterparts, with threshold changes in herbivore community structure occurring across the forest–tundra ecotone. This suggests that further borealization will lead to fundamental changes in the structure of herbivore communities. In contrast, the key functional traits which link herbivores to vegetation change (body mass, proportion of woody plants in diet) did not differ greatly between Arctic tundra and boreal forest communities.

The structure of herbivore communities across the biomes was best explained by temperature, rather than vegetation structure, suggesting that herbivore borealization will track direct climate effects rather than changing vegetation.

Borealization of the Arctic tundra is an example of a climate-induced ecological shift (Fossheim et al., 2015), with parallels in the tropicalization of temperate biomes (Osland et al., 2021).

TABLE 1 Community structure within boreal forest and Arctic tundra biomes

	Difference between biomes				Latitudinal variation	
	Boreal forest	Arctic tundra	T	p	Break point (km north of biome boundary)	p
Species richness	27.73 ± 1.75	19.10 ± 1.65	−3.58	<.001	−163 ± 23.3	<.001
Phylogenetic diversity	0.294 ± 0.014	0.227 ± 0.013	−3.58	<.001	−141 ± 24.6	<.001
Functional richness	0.233 ± 0.01	0.189 ± 0.01	−3.17	.003	−50.8 ± 17.9	<.001
Functional dispersion	0.3 ± 0.004	0.286 ± 0.004	−2.33	.023	−45.6 ± 29.9	<.001
Community mean body mass (g)	15,701 ± 1871	19,082 ± 1759	1.32	.194	—	.74
Community mean diet contribution of woody plants	2.59 ± 0.03	2.77 ± 0.03	4.39	<.001	1273 ± 78	<.001

Note: Mean ± standard errors within each biome are shown. Statistical output (*t* and *p*) from mixed linear models with ecoregion as a random factor. Break points in the latitudinal (with respect to the biome boundary) gradient of the community structure are shown on the right where statistically significant (Davies test, probability of non-zero difference-in-slope across the latitudinal gradient). Marginal and conditional R^2 for each model are shown in Figure S5.

Borealization and tropicalization are linked to warming climate. Warmer temperatures are also expected to lead to greening and shrubification of the Arctic tundra (Forbes et al., 2010; Myers-Smith et al., 2015). Our results suggest that vertebrate herbivore community structure will respond to direct temperature changes, rather than the associated vegetation changes. Similar direct impacts of climate have been observed for other Arctic consumer taxa, although primarily for ectothermic species. For example, invertebrate herbivores also appear to track direct climate effects, with population eruptions extending to tundra habitats (Finger-Higgens et al., 2021; Jepsen, 2008). On the other hand, shrubification is associated with expansion of specialist bird species that utilize canopy-forming shrubs as habitats (Sokolov et al., 2012).

One explanation to our finding that the vegetation variables had minor impacts on herbivore community structure is that greening and shrub expansion may have opposing impacts on herbivore populations. For grazer species, greening is likely to be beneficial if the functional group composition of the vegetation remains unchanged. However, shrub expansion will likely be to the detriment of grazers (Fauchald et al., 2017) but have positive influences on browser species (Zhou et al., 2017). A meta-analytical study summarized that consumer species had more positive responses to shrub cover in unproductive (less green) regions (Wheeler et al., 2018). Additionally, Wheeler et al. (2018) reported that under 40% of studies documented a positive effect of shrub cover on the expansion of boreal species. This is thus consistent with our finding that shrub cover was of minor importance in determining the functional structure of herbivore communities across the boreal and Arctic tundra biomes. An additional potential explanation is that the vegetation variables are derived from remote sensing data and may therefore be inherently noisy (Beamish et al., 2020), or at a different scale at which vertebrate herbivores respond to vegetation. Field-based studies of borealization trends in relation to vegetation change and temperature are required to understand the mechanisms at finer spatial scales.

Herbivore community structure showed threshold changes around the biome boundary in terms of species richness, phylogenetic

diversity and functional diversity. This was as hypothesized, given the differences in ecosystem structure between the biomes. There were stronger trends in community composition with distance from the biome boundary in the tundra than in the boreal forest, indicating that temperature may be a stronger determinant of community composition in the tundra biome than in the boreal forest biome. In contrast, the functional traits that were analysed did not show threshold changes across the biome boundary. Community mean body mass was on average greater in the forest than that in tundra ecosystems, and related to both temperature and woody plant cover. This is in contrast with the study by Floejgaard et al. (2020), who found that large herbivore biomass had a negative relationship with primary productivity at a global scale. We did find a threshold change in the contribution of woody plants to herbivore diets (browsing). Interestingly, this threshold was far above the biome boundary, and was loosely associated with the boundary between Arctic subzones B and C (i.e. where erect shrubs disappear from the tundra vegetation; CAVM Team, 2003). Thus, the environmental variables describing vegetation appear to be more informative in explaining spatial variation in community mean traits than latitude and the coarse biome categories.

There are multiple examples of vertebrate herbivores impeding climate-induced changes in tundra vegetation and ecosystems (Olofsson et al., 2009; Post & Pedersen, 2008; Speed et al., 2011, 2013). In particular, vertebrate herbivores have been shown to reduce shrub establishment, growth and spread in tundra ecosystems (Christie et al., 2015; Verma et al., 2020) This effect has mostly been documented with ungulate herbivores, but there is also evidence of ptarmigan (Tape et al., 2010), lagomorphs (Vowles et al., 2016) and rodents (Ravolainen et al., 2014) influencing tundra shrub dynamics. Consequently, herbivores may also modify the spread of boreal, shrub-dependent species, to the tundra. Our findings suggest, however, that herbivore modification of shrubification does not have a major importance for the borealization of the herbivore community.

In our study, we used summer temperatures as proxy linked to predicted climatic change. However, many other factors are likely to

determine future trophic dynamics in the Arctic. In particular, snow cover and icing events have strong impacts on Arctic herbivore populations (e.g. Anderson et al., 2016; Hansen et al., 2011). Wintertime climate change, including season length and extreme events, should therefore also be accounted for when considering borealization. In addition, factors other than climate and vegetation have been linked to boreal species expanding distributions into the tundra; for example, the northward spread of red foxes into the Canadian Arctic has been shown to be more closely associated with human presence than a warming climate (Gallant et al., 2020). However, such direct positive associations with anthropogenic activity are more likely in scavenger guilds or other synanthropic species, than in herbivores.

The implication of our findings is that borealization of herbivore communities in the Arctic is likely to follow climatic warming. Even if herbivores can dampen shrubification of the tundra (Olofsson & Post, 2018), borealization of herbivore communities may still occur. Thus, the ecology of individual species, in terms of responses to changing climate and vegetation, and impacts on vegetation dynamics, could be more important in determining future ecosystem state. Species that are characterized as ecosystem engineers or keystone species are most relevant here. A noteworthy example may be the moose *Alces alces*, a large browser often classed as an ecosystem engineer or keystone species in boreal forests due to its ability to shape forest successional dynamics (Kolstad et al., 2017; Olmsted et al., 2021), which is expanding in distribution into the Arctic tundra (Tape et al., 2016).

DATA AVAILABILITY STATEMENT

The functional trait and phylogeny data that support the findings of this study are available in the supplementary material of this article. The species range data were derived from the following resources available in the public domain: BirdLife International and Handbook of the Birds of the World (2016) and IUCN (2019).

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