OIKOS

Research article

Reindeer grazing reduces climate-driven vegetation changes and shifts trophic interactions in the Fennoscandian tundra

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Oikos
2024: e10595
doi: 10.1111/oik.10595

Subject Editor: Robin Pakeman
Editor-in-Chief: Dries Bonte
Accepted 31 May 2024

Herbivores drive shifts in plant species composition by interacting with vegetation through defoliation, trampling and nutrient addition: urine and faeces. As herbivore effects on vegetation accumulate over time, they might spillover to other trophic levels, but how and when this happens is poorly understood. Since it is methodologically demanding to measure biodiversity across spatial gradients, an alternative approach is to assess it through biodiversity indices of vascular plants. We employed the Index of biodiversity relevance developed for Swedish flora which provides an estimated number of organisms associated with a plant species, allowing the quantification of trophic community size. Values from this index were coupled with vegetation data from a network of 96 fenced and paired grazed plots across Fennoscandia. We analysed the role herbivory has on plant richness and diversity, and on the number of organisms that interact with the vegetation according to the index values. We also explored how herbivores influence the competitive effects of tall shrubs on other plants since the dominance of a vegetation type links directly to biodiversity. Plant diversity had no clear response to grazing. Overall vegetation and the vegetation subgroups herbs and non-fruit shrubs had higher biodiversity index values in fenced plots, indicating a higher number of plant–host interactions. Herb cover was negatively related to shrubs in both treatments but with a faster decline in the absence of herbivores. This study highlights the importance of maintaining herbivore populations in the Arctic to conserve the vegetation structure and biodiversity of the tundra. This method of coupling biodiversity indexes with vegetation data provides complementary information to the plant diversity, especially when methodological or time constraints prevent complete field inventories.

Keywords: Arctic, global change ecology, grazing, herbivory, index of biodiversity relevance, moose, reindeer, shrub, species coexistence

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Introduction

Large herbivores are key drivers of the structure and function of terrestrial plant communities by interacting with vegetation through several mechanisms (Côté et al. 2004, Ramirez et al. 2018). The size of herbivore populations mediates the strength at which they directly and indirectly interact with vegetation (Olff and Ritchie 1998). Defoliation caused by herbivores is not equal for all species whereby plants with low physical and chemical defences against herbivory (i.e. palatable) are consumed more than those with high defences (Ramirez et al. 2021a, b). By consuming more palatable and avoiding less palatable plants, herbivores indirectly alter competitive interactions by creating opportunities for other species when palatable plants are superior competitors (Augustine and McNaughton 1998). Trampling directly drives changes in vegetation composition by inflicting tissue damage, but also indirectly by compacting the soil and thereby limiting the ability of plant roots to secure below-ground resources (Ramirez et al. 2019, Tuomi et al. 2021). Herbivores redistribute seeds and nutrients across the landscape by moving and consuming plants at one location and depositing urine and faeces in another. By doing so, herbivores shape vegetation composition indirectly by enhancing soil nutrients and facilitating the establishment of plants with high nutrient requirements (Mosbacher et al. 2018). Shifts in vegetation structure and composition by indirect mechanisms usually take several years to build up and depend on the number of herbivores and the characteristics of the system (van der Wal and Brooker 2004, Olofsson and Post 2018). Ultimately, the strength of direct and indirect drivers is what determines overall plant structure and composition and the primary productivity of the system (Borer et al. 2014, Ramirez 2021, Ramirez et al. 2023). These herbivore effects nevertheless are scale-dependent (Sundqvist et al. 2019) given that resources are patchily distributed, and herbivore occurrence varies in time and space.

If herbivores alter plant community composition, diversity and productivity they may also influence other taxa that are dependent on specific primary producers (Hooper et al. 2000, Suominen and Olofsson 2000). For instance, two studies in the Arctic have determined that reindeer grazing decreased the density of leaf beetles and increased the diversity of ground beetles (Suominen et al. 2003, den Herder et al. 2004). With regards to arachnids, spider abundance and diversity may not be affected by reindeer grazing while individual spider species may be (Saikkonen et al. 2019). Simulated moose browsing has reduced leaf litter production in boreal forests, which in turn reduced the abundance of flying insects and the spiders that prey on them (Suominen et al. 2008). In temperate forests, deer browsing has reduced the depth of the litter layer, which subsequently decreased the diversity of ground invertebrates (Ramirez et al. 2021a). Deer have also reduced rodent activity by changing the structure of the forest understory (Ramirez et al. 2021a). Local environmental conditions and the intensity of herbivory overall determine if the effect from one trophic level spills to other levels (Augustine and McNaughton 1998, Pringle et al. 2007, Ramirez et al. 2021b). Although the effects of herbivores on trophic interactions have been studied, the number of interacting taxa studied is few and the spillover effects of herbivores on trophic communities are thus poorly known (Suominen et al. 2003, Filazzola et al. 2020, Huaranca et al. 2022).

The Arctic is experiencing stronger climatic changes than any other region (Zhu et al. 2016). Temperatures have risen nearly four times as fast as in the rest of the planet (Field and Barros 2014, Rantanen et al. 2022), and have resulted in the expansion of taller deciduous shrubs (Myers-Smith et al. 2020). The expansion is associated with a large-scale phenomenon known as the 'greening of the Arctic' (Zhu et al. 2016, Piao et al. 2019). Tall shrubs are expected to be strong competitors for nutrients and light and reduce the abundance of other plants (Pajunen et al. 2011, 2012). Herbivory by ungulates on the other hand favours small-stature plants by browsing on taller deciduous shrubs and increasing light availability to the lower vegetation (den Herder and Niemelä 2003, Kaarlejärvi et al. 2017, Vowles et al. 2017b, Eskelinen et al. 2022). In the case of graminoids, tissue consumption normally occurs above the basal meristem, allowing for rapid regeneration from below-ground tissues (van der Wal and Brooker 2004). Herbivory by reindeer reduces lichen abundance, particularly during summer when lichens are dry (Forbes and Kumpula 2009), while enhancing soil inorganic nitrogen (Sundqvist et al. 2019). Herbivore densities and soil nutrient availability are two additional factors that modulate plant community responses to herbivory. For example, higher reindeer densities have decreased plant species richness in low-productive sites and have increased species richness in high-productive sites (Sundqvist et al. 2019).

A remaining question is how reindeer influence trophic interactions and the diversity of taxa that form the bases of Arctic food webs. Directly sampling multiple taxa of herbivores, invertebrate shredders, pollinators, and mycorrhiza across numerous sites is logistically challenging, and sometimes not methodologically possible due to the small size of the experimental treatment. Relying on traditional diversity indexes and assuming that plant diversity is positively associated with the diversity of other taxa only provides a partial understanding since these indices do not account for trophic interactions and were not developed for local vegetation (Vowles et al. 2017a). In addition, multiple studies have shown that, depending on the study system, plant diversity may or may not be correlated with the diversity of other organismal groups (Huston 1979, Brunbjerg et al. 2018). An alternative indirect approach is via tailor-made indices on the biodiversity relevance (IBR) of plant species that occur in a particular region. Such indices describe the number of organisms that are associated (i.e. the total number of interactions) with a particular local plant species, which include insects, fungi and bacteria (Tyler et al. 2021). This index was developed in 2021 and requires extensive research on local flora and fauna before generating the index values associated with each plant.

In this study, we coupled the IBR values developed specifically for the Swedish flora with vegetation data from a network of 96 fenced plots and paired grazed plots across the Fennoscandian tundra to explore how reindeer can shape trophic communities associated with Arctic vegetation. As far as we know, this is the first time IBR has been employed for the quantification of overall trophic communities. We specifically evaluated the mediating effect herbivory has on A) plant richness and alpha diversity, and B) the number of organisms that interact with vegetation and the theoretical diversity of this community. We also explored C) how herbivores modulate the competitive effects of shrubs on other plants among vegetation types. We predicted that: 1) the net effect of reindeer on plant species richness and gamma diversity is neutral at a regional scale since we have low- and high-productive areas (Sundqvist et al. 2019). 2) A more structurally diverse vegetation provides more niches and thus, supports a higher number and diversity of interacting organisms. 3) Reindeer weaken the competitive response of climate-driven shrubs on graminoids and herbs.

Methods

Research area

The study was conducted in 14 locations across a latitudinal gradient in northern Fennoscandia (Fig. 1), during the vegetation seasons of 2014, 2017–2018. The study sites ranged in latitude (61°32′49″N to 70°25′30″N), elevation (400–800 m), mean annual temperatures (−3.0–6.5 °C) and mean annual precipitation (487–1031 mm) and thus, represent most of the environmental variation across the Fennoscandian tundra. The vegetation across sites mainly consists of mountain birch forest (*Betula pubescens* spp. *czerepanovii*), tundra heath with low-growing shrubs e.g. *Empetrum nigrum* and *Vaccinium myrtillus* and tundra meadows with small size herbs and grasses e.g. *Calamagrostis lapponica* and *Carex bigelowii*. The large herbivore guild mainly consists of reindeer *Rangifer tarandus* and moose *Alces alces* and to a lesser extent, domesticated sheep and cattle living on grazing land (Stoessel et al. 2022). Herbivore densities have fluctuated substantially during the last century but have been stable at a fairly high historical level during the last two decades (Uboni et al. 2016). The project has incomplete data on local herbivore densities across our entire study area and thus, they were not included in the analysis. See the Supporting information for a characterization of the areas.

Data source

This project sourced approximately half of the data (2014 fieldwork campaign) from Sundqvist et al. 2019 and the other half from the project's unpublished data (2017–2018 fieldwork campaigns; Supporting information). Data from both sources are compatible since standardized methods were used during fieldwork.

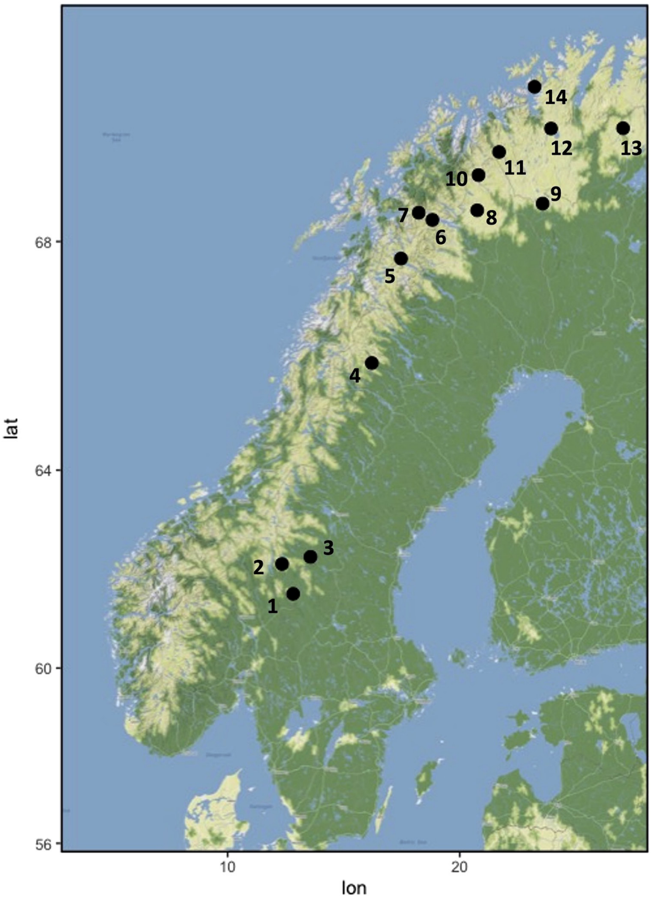

Figure 1. Map of the Fennoscandia including the 14 research sites. Locations are marked with black circles and labelled as follows: (1) Fulufjället, (2) Långfjallet, (3) Sonfjället, (4) Ammarnäs, (5) Ritsem, (6) Abisko, (7) Vassijaure, (8)-Pulsuvuoma, (9) Näkkälä, (10) Kilpisjärvi, (11) Reisa, (12) Joatka, (13) Kevo and (14) Seiland. The vegetation cover is depicted with green colour for forest and light yellow for grasslands and shrubs. See the Supporting information for a characterization of the research sites.

Experimental setup

A network of 96 paired fenced and grazed plots that varied in age (15–68 years since establishment) and size (64–10 000 m^2) distributed across 14 locations were used for this research (Supporting information). Within each plot, a series of 1–20 quadrats with a size of 0.21–1.0 m^2 were randomly distributed to quantify vegetation. Variation in the number and size of quadrats was to capture vegetation heterogeneity at different locations.

Vegetation

In each quadrat, vegetation composition and species cover were determined with the point intercept method (Jonasson 1988) by lowering pins every 10 cm in rows with a width of 50 cm. Depending on the size of the quadrat, a total of 50 to 100 pins were used. For vascular plants, all intercepts were for each separate species, but for the ground layer (including liverworts, hornworts, mosses, lichens and algae) only one intercept per pin (the uppermost) was recorded. The total number of hits was normalized to hits per 100 pins in each quadrat (Väisänen et al. 2014, Sundqvist et al. 2019). Data was then grouped in the following vascular vegetation groups: herb (all herbs), graminoid (rush, sedge and grass), fern (fern and club moss), fruit shrub (shrub with fleshy fruits) and shrub (shrub with non-fleshy fruit). Species richness and diversity were calculated for vascular plants per plot (Shannon 1948, Simpson 1949). The index of biodiversity relevance (IBR) is defined as the number of organisms that depend on or interact with a particular plant species, which was sourced from Tyler et al. (2021). IBR is given on a logarithmic eight-degree scale (1 =< 6 associated species, 2 = 6–12, 3 = 13–24, 4 = 25–50, 5 = 51–100, 6 = 101–200, 7 = 201–400, 8 => 400) and does not account for biodiversity redundancy between plant species. To determine the overall IBR of each plot or in other words the size of the trophic community, we multiplied the abundance of each species with its respective biodiversity relevance value and values across all species, were summed. The sum was used instead of a community weighting because we are interested in the total number of interactions and much of the contribution of herbivores to plant composition and plant–host interactions is by reducing plant cover and not by extirpating plant species (Crête et al. 2001). We also calculated for each of the vegetation groups a lower-end (i.e. the plant species with the highest IBR) and an upper-end (i.e. the addition of IBR values of all present plant species) biodiversity value to qualitatively understand how this biodiversity range compares to IBR (i.e. the size of the trophic community) values and between treatments. The lower-end biodiversity value assumes maximum redundancy between plant species and their associated biodiversity and thus, the IBR value of one plant envelops the IBR values of all other plants. The upper-end biodiversity value assumes no redundancy between plant species and thus, the IBR of each plant is unique.

Data analysis

Linear mixed models (LMM) were used for all analyses. In the first set of models, vegetation cover (measured as an average of 100 pin hits per plot), richness and diversity (i.e. Shannon and Simpson) were set as responses, treatment (i.e. fence versus grazed plots) as fixed factor, study location and treatment pair as random factors. In a second set, the same model was tested but this time we added herbaceous cover (including herbs, grasses, sedges and rushes) and treatment as fixed factors and non-linearity was tested by including a quadratic term. We used a principal component analysis (PCA) to test the associations between the most common plant species (> 300 hits across all plots) and treatment because some species are expected to be favoured by grazing. To test the response of IBR to grazing, we set IBR overall values grouped by different plant functional groups (i.e. grouped by all vegetation, herbs, graminoids, ferns, fruited shrubs and non-fruited shrubs) as a response, treatment as a fixed factor, study location and treatment pair as random factors. To understand what drives IBR, we tested the response of IBR to different plant composition metrics. Specifically, we set IBR as a response, plant metrics (i.e. cover, richness and diversity independently) and treatment as fixed factors, study location and treatment pair as random factors. A descriptive analysis was performed to understand the effect of grazing on overall biodiversity (i.e. lower- and upper-end of the biodiversity range) and IBR. We tested the effect of grazing on the co-existence between herbaceous and woody plants. Herbaceous cover was set as a response, woody cover and treatment were set as fixed factors, study location and treatment pair as random factors. Overall, we also tested non-linearity with a square term and the effect of age and plot size; no significance was found and thus they were omitted from the final analysis. Akaike's information criterion was used for model selection and diagnostics of the residuals were used for assessing model fit. All statistical analysis was done in 'R studio' ver. 1.3.1056 (www.r-project.org), in combination with the 'stats' ver. 4.0.2' package for data transformation (www.r-project.org), the 'lme4' ver. 1.1-23 package for LMM (Bates et al. 2015) and the 'vegan' package for the PCA (Oksanen et al. 2013).

Results

Vegetation richness and diversity

Grazing reduced vegetation cover ($\bar{x}_{\text{fence}} = 190.88$ and $\bar{x}_{\text{grazed}} = 177.14$; $\beta = -13.74$ and $p = 0.039$, Fig. 2) when comparing openly grazed to fenced plots but did not affect vascular plant richness or alpha diversity (i.e. Shannon and Simpson indices, Supporting information). However, plant

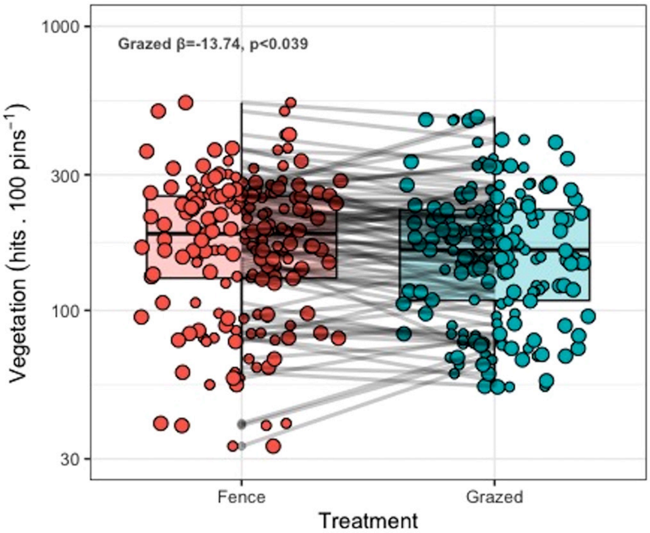

Figure 2. Boxplot contrasting the extent of vegetation cover (plotted on a $\log_{10}$ scale) between fence (in red colour) and grazed (in cyan colour) plots across the Fennoscandian tundra. Grey lines depict the relationships between paired control–treatment values at different locations.

richness was positively associated with herbaceous cover in both fenced and grazed plots (Fig. 3A, Supporting information), and plant diversity (i.e. Shannon and Simpson) was also positively associated with herbaceous cover (Fig. 3B–C, Supporting information), but only in grazed plots. In fenced plots, plant diversity peaked at medium herb cover. At the species level, *Deschampia cespitosa* (R = 0.63, Supporting information), *Calamagrostis lapponica* (R = 0.55), *Carex vaginata* (R = 0.31), *Salix phylicifolia* (R = 0.18) and *Betula nana* (R = 0.17) occurred more in fenced plots whereas *Vaccinium myrtillus* (R = −0.17) and *Carex magellanica* (R = −0.18) occurred more in grazed plots.

Biodiversity relevance

There was a higher IBR (i.e. the size of the trophic community) of the total vegetation in fenced than in grazed plots ($\bar{x}_{\text{fence}} = 826$ and $\bar{x}_{\text{grazed}} = 759$; $\beta = -67.41$ and $p = 0.05$; Fig. 4A, Supporting information). When analysing plant functional groups separately, we found that herbs ($\bar{x}_{\text{fence}} = 37$ and $\bar{x}_{\text{grazed}} = 26$; $\beta = -10.90$ and $p = 0.004$; Fig. 4B) and non-fruit shrubs ($\bar{x}_{\text{fence}} = 190$ and $\bar{x}_{\text{grazed}} = 121$; $\beta = -68.79$ and $p < 0.001$; Fig. 4C) both had higher IBR in fenced plots. There were no differences between treatments for graminoids, ferns or fruit shrubs. In terms of the theoretical minimum and maximum biodiversity, there were only small qualitative differences between treatments grouped by functional vegetation groups (Fig 5, Supporting information). Despite the wide age gradient of the exclosures (1950–2002), there was no age effect on vegetation composition, diversity, and IBR (Supporting information).

Drivers of IBR

IBR in fenced and grazed plots significantly increased with total vegetation cover ($\beta_{\text{fence}} = 4.57$; $\beta_{\text{grazed}} = 4.87$; Fig. 6A) and species richness ($\beta_{\text{fence}} = 29.01$; $\beta_{\text{grazed}} = 19.60$ Fig. 6B). No relationship was found with plant diversity (Supporting information).

Co-existence of herbaceous and woody vegetation

The cover of herbaceous plants was negatively related to the cover of woody plants (Fig. 7), but the relationship was steeper in fenced plots (AIC = 2130, $r^2_{\text{marginal}} = 0.05$; $r^2_{\text{conditional}} = 0.86$; $\beta = -0.37$; p-value < 0.001) compared to grazed plots ($\beta = -0.13$; p-value = 0.002).

Discussion

Tyler et al. (2021) developed an IBR that expresses the number of non-plant species that interact with a plant species as a source of food and energy for all Swedish vascular plant species. By combining these so-called biodiversity relevance values with vegetation data from a network of fenced and grazed plots scattered across sites with low and high primary productivity in the Fennoscandian tundra, we revealed that reindeer grazing decreased IBR for total vegetation and a subset of taxonomic groups, despite having an increasing effect on plant diversity when controlling for to the extent of herbaceous cover. The lack of an age effect indicates that the vegetation changes in the fenced plots have already approached an asymptote after two decades and further changes will depend on grazing-intolerant species colonizing the exclosures (Olofsson et al. 2013).

Biodiversity relevance

As we predicted, vegetation changes in response to grazing led to shifts in the number of organisms interacting with the vegetation. When considering all vegetation, the IBR which was computed on a log scale was 67.4 points – or somewhere in the millions of plant–host interactions – higher in the fenced compared to the grazed plots. When considering

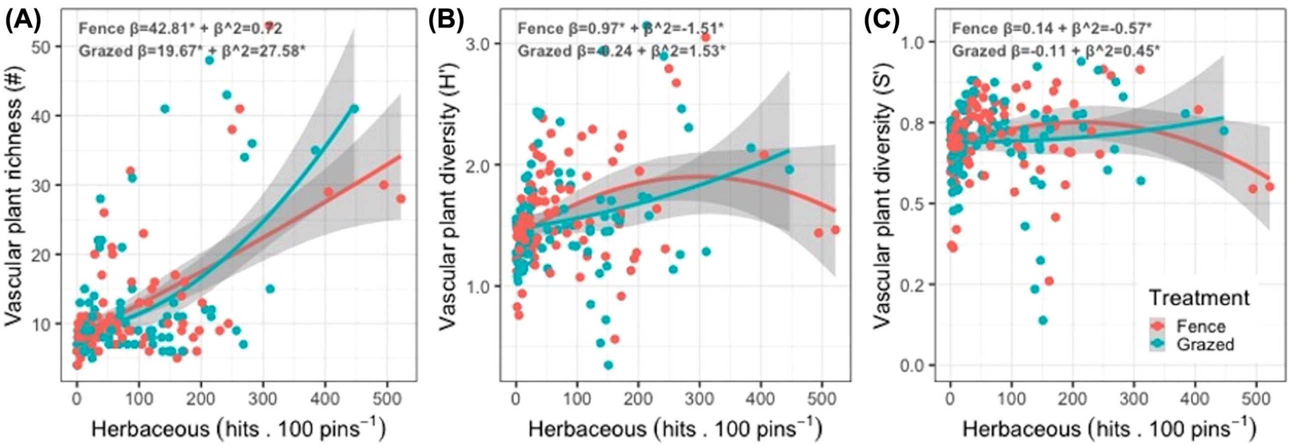

Figure 3. Linear mixed model fits for the relations between plant species richness (A) and diversity (B = Shannon and C = Simpson) with herbaceous cover and treatment (fence versus grazed). Fenced plots are shown in red colour and grazed in cyan. The grey shading on the scatterplots shows the standard confidence interval. The asterisk indicates significant coefficients (i.e. * < 0.05 p value).

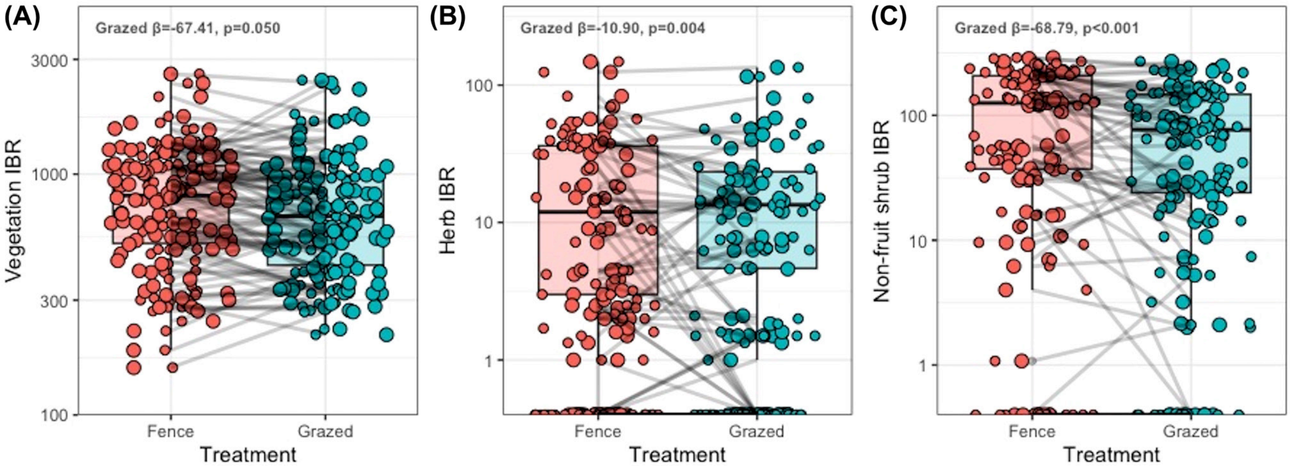

Figure 4. Boxplots contrasting the differences in the indices of biodiversity relevance (i.e. IBR, plotted on a $\log_{10}$ scale) between fence (in red colour) and grazed (in cyan colour) plots across the Fennoscandian tundra. IBR is defined as the number of organisms that depend on the vegetation of the plot. (A) illustrates IBR when considering all vascular vegetation, (B) herbs and (C) non-fruit shrubs. Grey lines depict the relationships between paired control–treatment values at different locations.

narrower vegetation groups, we also found that IBR was higher both for herbs (10.9 points or in the thousands of plant–host interactions) and non-fruit-bearing shrubs (68.8 points or in the millions of plant–host interactions) in the fenced compared to the grazed plots. The differences among treatments are substantial and denote that grazing decreases the size and possibly the composition of trophic communities that host insects, fungi and bacteria responsible for ecosystem processes (Tilman et al. 1997). Thus, the trophic community in a situation without herbivory is not only larger but may also perform a distinct spectrum of ecosystem functions (Naeem et al. 1994, Naeem and Wright 2003), which in the long-term can threaten the conservation of the tundra by leading to fundamental changes in how this ecosystem is structured and functions. The trophic community size however is partially the result of taller vegetation

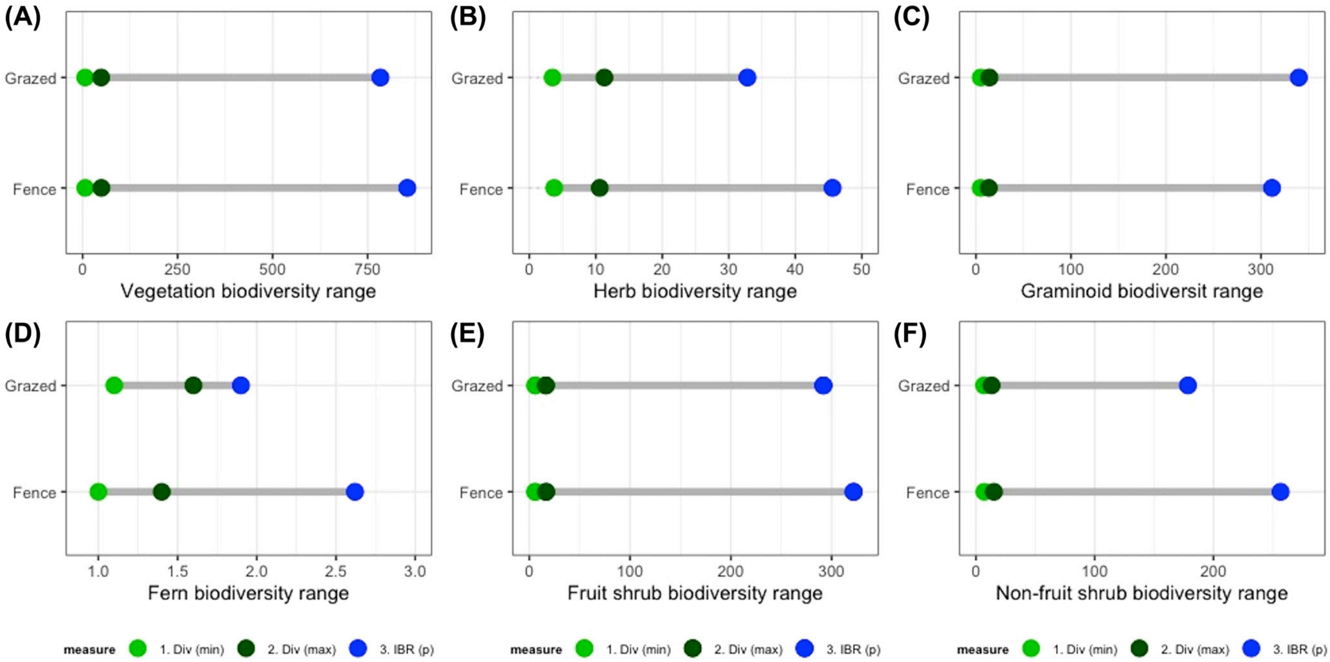

Figure 5. Biodiversity ranges for vegetation between grazed and fence plots grouped by plant functional groups (A–F). Three biodiversity metrics are used: the light green circles indicate the lower-end of biodiversity when maximum redundancy is assumed between associated species for the different plant species (i.e. the species with the highest IBR hosts all the organisms which all other plants host), whereas the dark green circles indicate the upper-end of biodiversity when no redundancy is assumed (i.e. no plant species host the same organisms). The blue circles depict the maximum potential of interactions (i.e. IBR), regardless of species redundancy.

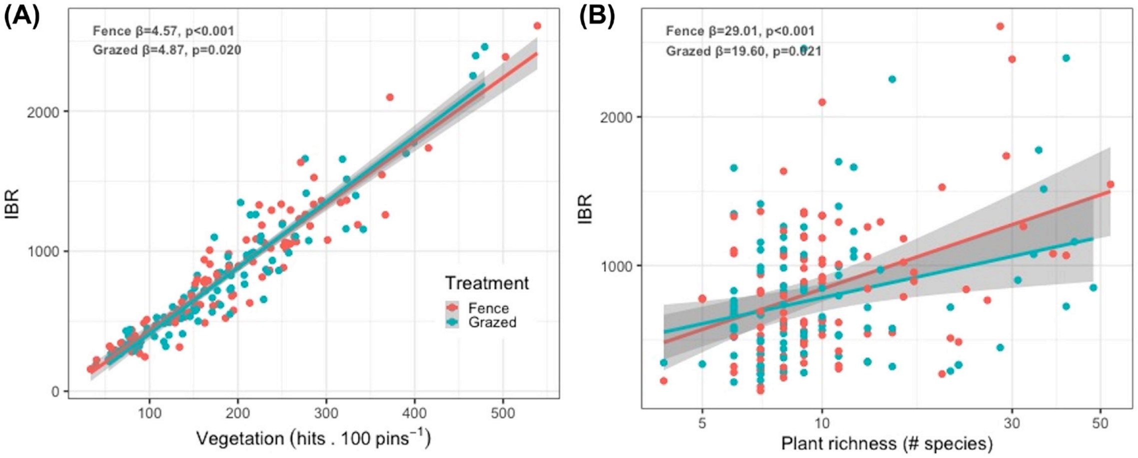

Figure 6. Linear mixed model fits for the relations between the indices of biodiversity relevance (IBR) and vegetation cover (A) and plant species richness (B) grouped by treatment (fence versus grazed). Fenced plots are shown in red colour and grazed in cyan. Confidence intervals are given in grey shade.

delivering more surveying hits during fieldwork and how these hits were computed for obtaining the IBR. Both graminoids and shrubs with high IBR values were associated with fenced plots and they occurred at higher abundance compared to the grazed plots, corroborating this methodological and mathematical effect (Supporting information). It remains unclear whether the higher IBR values in the fenced plots are a result of taller and more complex vegetation that facilitates a greater variety of niches for different organisms to occupy (Kaarlejärvi et al. 2017).

A series of empirical studies that targeted the effect of herbivory on different taxa in the Fennoscandian Arctic corroborate our finding that herbivory may shape the size and composition of trophic communities. Lightly grazed areas for example were associated with denser shrub vegetation and larger microbial communities compared to heavily grazed areas (Stark et al. 2015). Whereas, the abundance of soil fungi, lichens and mosses was higher in fenced plots compared to grazed plots, plausibly because herbivory reduced woody vegetation (Olofsson et al. 2010, Santalahti et al. 2018). Regarding invertebrate herbivores, previous findings are inconsistent. One study conducted reported higher densities of common insects (leaf beetles and gall-inducing sawflies) inside fenced plots compared to grazed plots (den Herder et al. 2004), while a second study stated higher abundance of Curculionid beetles and lower abundance of Carabid beetles inside fenced plots compared to grazed plots (Suominen et al. 2003), suggesting that herbivory effects are species-specific and plausibly mediated by external factors like primary productivity and temperature. Thus, our IBR values serve as tools to identify the size of ecological communities and overall biodiversity patterns.

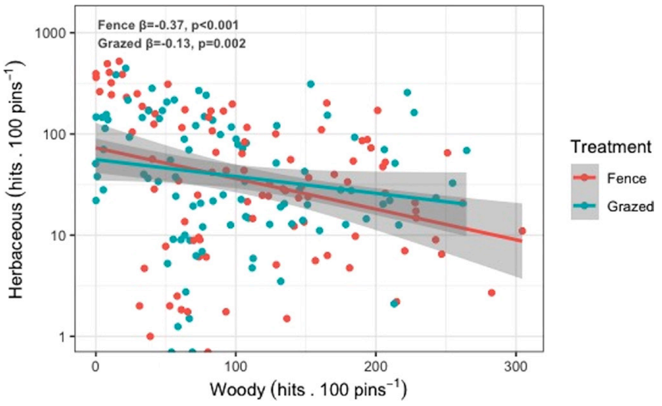

Figure 7. Linear mixed model fits for the relations between herbaceous and woody cover in fence (red colour) and grazed (cyan) plots across the Fennoscandian tundra. Confidence intervals are given in grey.

Herbivory had little or no visible effect on the lower-end of biodiversity when maximum species redundancy is assumed and also at the upper-end of biodiversity when no species redundancy is assumed. The true biodiversity value for each of the treatments grouped by vegetation type probably falls somewhere along this range; yet, it is impossible to predict where and it would be unreasonable to assume that the mean would be a good representation since this is a logarithmic scale and we have no insight into the true degree of species redundancy. We hypothesise when combining this result with the evidence that herbivory reduces IBR, that reindeer shape vegetation composition by reducing the abundance of palatable species and not by extirpating plant species (Crête et al. 2001).

Vegetation composition, richness and diversity

We predicted and found that across the latitudinal gradient (61°32′49″N–70°25′30″N), excluding reindeer did not affect overall plant species richness and diversity. The absence of a herbivore effect in overall plant diversity patterns is explained by variations in primary productivity and ecosystem heterogeneity across our sites (Sundqvist et al. 2019). Albeit the lack of overall differences in plant diversity, there were clear differences in the composition of the plant community with more shrubs and graminoids in the fenced plots. *Salix phylicifolia* and *Betula nana* are two species presenting high trait plasticity which allows them to occur in small sizes in the tundra without shading the graminoids whereas in forests, these species can achieve greater height (Bret-Harte et al. 2001, Aradóttir et al. 2007). This shift in plant composition became evident in this study when assessing the associations of richness and diversity to herbaceous cover between fenced and grazed plots. Plant species richness and diversity were positively associated with herbaceous cover in grazed plots; whereas in fenced plots, plant species richness presented a less steep increase and plant diversity peaked at intermediate herbaceous cover.

The shift in plant composition was also manifested when we tested the response of herbaceous cover to woody cover. As predicted, we found that herbaceous cover was negatively associated with woody cover, particularly inside the fenced plots. Woody plants overall limit the establishment, development and reproduction of herbaceous plants by shading them (Eskelinen 2008). In contrast, herbivory modulates the strength of the competition between these two groups by directly limiting the expansion of shrubs by consuming their leaves and trampling and indirectly, by alleviating light limitation for ground herbaceous cover (Olofsson et al. 2001, Lindén et al. 2021).

These results highlight the key function large herbivores play in maintaining the open structure and the vegetation composition of the Arctic tundra in the face of climate change. Grazing holds back climate-driven shrub dominance (Olofsson et al. 2001, 2009) while it promotes a wider plant diversity by favouring the establishment of other plant species that are commonly associated with grazed steppes like herbs and graminoids. Alternatively, it can also be explained by the composition of the herbaceous group. For example, if the herbaceous group compared to other vegetation groups has more species that share a set of grazing tolerant traits (Barton and Koricheva 2010), this would ultimately facilitate a higher richness and diversity in the grazed plots. From a conservation perspective, it remains unclear what densities are required for large herbivores to increase plant beta and gamma diversity and whether these responses will remain constant with warmer temperatures.

Outlook

Ecological indicators are convenient tools that can rapidly assess the overall biological state of less complex ecosystems like the tundra. Indicators overall provide insights that empirical data cannot provide since collecting data across large spatial and temporal dimensions is logistically challenging and requires the participation of staff with extensive taxonomic knowledge to conduct field inventories. Therefore, indicators save the investment of resources that would be required for carrying out traditional field monitoring efforts.

The development of IBRs entails extensive ecological research of the region before generating the index value for a specific plant species. Consequently, limiting the application of this method to other less studied biomes. This approach remains to be tested broadly, including intricate ecosystems like in the tropics that host a vast number of interacting species, to grasp the ecological potential of quantifying the size of trophic communities.

The downside of using IBRs is that the resolution of the results is lost because a single index value does not transmit the species identification or the exact number of organisms. More importantly, it assumes that the biodiversity values are constant within species and not context-dependent (Tyler et al. 2021). IBR estimates are likely to correlate with overall biodiversity by summing the number of unique plant species interacting with other non-plant species, but IBR estimates inherently hold a high degree of species redundancy since different plant species, in particular, if closely related, may be interacting with the same non-plant species (and vice versa). Even if not directly translatable to species richness, the number of unique species-to-species interactions may be highly relevant as a measure of the complexity of the food web or ecosystem which, in turn, may indicate its stability and ability to cope with climate change or other environmental stressors.

Conclusion

We found evidence that reindeer herbivory in the Fennoscandia promotes the conservation of the tundra's biodiversity and ecosystem functions by favouring small-size (i.e. herbaceous) over the climate-driven tall-size (i.e. woody) plants and by doing so, herbivory decreases the overall number of taxa interacting with vegetation based on an IBR analysis. Interacting diversity was quantified by binding the presence of plants in our network of plots (i.e. fence and grazed) with a biodiversity index developed for Swedish vascular plants. This approach allowed us to promptly quantify the magnitude of plant–host interactions in the presence and absence of herbivores. We reckon that most advancement in this line of research, including complex ecosystems, will be done by combining biodiversity indices with surveys performed in a range of habitats that include species belonging to different trophic levels, enabling a holistic understanding of the important role that herbivores play in the structure, composition and functioning of ecosystems.

Acknowledgements – We thank our funding agencies (Belmont Forum-BiodivERsA, the Swedish Research Council and Formas) for financing this project.

Funding – This project was financially supported by the FATE: Future ArcTic Ecosystems project under the Belmont Forum-BiodivERsA 2017-2018 joint call, Formas (2019-00890 & 2018-02439) and the Swedish Research Council (2017-04515).

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Data availability statement

Data used in this study are available in Tyler et al. (2021) https://doi.org/10.1016/j.ecolind.2020.106923 and Sundqvist et al. (2019) https://doi.org/10.1111/1365-2745.13201).

Supporting information

The Supporting information associated with this article is available with the online version.

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