

High resistance towards herbivore-induced habitat change in a high arctic arthropod community

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Abstract

Mammal herbivores may exert strong impacts on plant communities, and are often key drivers of vegetation composition and diversity. We tested whether such mammal-induced changes to a high Arctic plant community are reflected in the structure of other trophic levels. Specifically, we tested whether substantial vegetation changes following the experimental exclusion of muskoxen (*Ovibos moschatus*) altered the composition of the arthropod community and the predator-prey interactions therein. Overall, we found no impact of muskox-exclusion on the arthropod community: the diversity and abundance of both arthropod predators (spiders) and of their prey were unaffected by muskox presence, and so was the qualitative and quantitative structure of predator-prey interactions. Hence, high Arctic arthropod communities seem highly resistant towards even large biotic changes in their habitat, which we attribute to the high connectance in the food web.

Key words: Araneae, Molecular diet analysis, Metabarcoding, Predator-prey

1. Background

Communities consist of species and their interactions. They are thus conveniently described as networks, with species as nodes and interactions as links. Of topical interest is how disturbances reverberate between trophic levels within such networks, and how link structure dampens or amplifies such transmission. Importantly, it has been suggested that interaction structure may respond more sensitively to habitat modification than will species richness, as being the mere count of nodes [1].

That mammal herbivores may influence plant communities is well-documented, with impacts including changes in species composition and vegetation structure [2], trampling [3] and translocation of nutrients [4]. However, there is less information about the extent to which such herbivore-induced changes to plant communities may cascade through the food web [2] (but see e.g. [5,6] for examples).

Only few mammal herbivore species are found in the Arctic, but these may exert a strong impact on the plant communities there. We have previously documented that excluding muskoxen (*Ovibos moschatus*) from parts of their preferred summer foraging habitat [7], results in a rapid and marked shift and homogenization in an arctic fen community towards lower graminoid

biomass and increased moss biomass [8]. Since arthropods constitute the vast majority of arctic biodiversity and dominate the food webs [9], we here specifically ask whether the mammal-induced changes to the fen habitat alter how the arthropod community is structured and how the arthropod predator and their prey interact.

Spiders (Arachnida: Araneae) are central in the arctic predator-prey interactions [9]. As generalist predators [10], we expect the diet of spiders to reflect the overall availability of prey taxa. Just as leeches [11] and carrion flies [12], spiders may thus act as sentinels of local invertebrate communities, revealing subtle changes in the composition and structure of the arthropod community.

We first quantify spiders in plots from which muskoxen were experimentally excluded versus controls, then resolve their diet. Through this approach, we quantify muskox impacts on three hierarchical levels: on the predator community, on their prey community, and on the interaction structure between the two. Specifically, we hypothesize that 1) the increased plant biomass in the exclosures [8] has initiated a cascade within the arthropod community, resulting in more arthropod prey and ultimately in more predators (spiders), 2) the increasing homogenization of the plant community observed in the exclosures [8] has resulted in lower diversity within the arthropod community (spiders as well as their prey base), and 3) these changes have affected the structure of the arthropod interaction web inside the exclosures.

2. Methods

(a) Study area and sample collection

Samples were collected at Zackenberg in high arctic Greenland (74°28'N, 20°34'W). Muskoxen are found there in high densities [13], and stay in the area year-round [14]. During summer, they forage intensively in the wet graminoid-dominated areas [7] where we in 2010 established permanent muskox exclosures with five replicate blocks, each including an un-manipulated control and a fenced exclosure plot. Plots measure 10x10m. For more details, see [8].

In August 2015, we placed 30 yellow sticky traps (5x20cm; Barretine Environmental Health, UK) for passive trapping of ground-dwelling spiders in each plot. Traps were spaced out within plots, with approximate 1.5 meters between traps. Traps were placed horizontally in the vegetation and fastened with small sticks. We deployed traps within the 3 driest blocks, with running water preventing trapping in the last two blocks. Traps were left in place for 4-7 days, yielding a total of 2700 trap days equally split between blocks and treatments. All spiders were then removed from the sticky traps using citric oil (Barretine Environmental Health, UK), and stored individually in 96% ethanol at -18°C until further processing.

(b) Sample processing

Spiders liquefy their prey prior to ingestion, thus impeding morphological identification of prey, and we therefore used molecular detection of prey [15]. Hence, we subjected all spider specimens to DNA metabarcoding, which simultaneously sequences short fragments for multiple taxa in a mixed sample. Resultant sequences were translated to the lowest possible taxonomic units by comparing them to reference libraries of 'DNA barcodes' [16]. We used whole body DNA extractions to get both prey and predator DNA. The DNA procedures are described in detail in Supplementary material.

(c) Statistical analyses

For the predator communities, we compared counts per spider species using a general linear model (assuming a log link and Poisson-distributed errors) with treatment and spider taxa as fixed factors and block as random factor. For the prey communities, we first compared family-level incidence per

taxa by comparing the number of prey families detected per spider specimen using a glmm (gaussian) with treatment and family as fixed factors and block as random factor. Then, we visualized the prey composition of the spider specimens using principal component analysis (PCA). As the prey community data were zero-inflated, we applied the Hellinger transformation to the data prior to the PCA [17].

To evaluate whether predator-prey associations differed between treatments, we calculated structural metrics for each block-by-treatment combination: connectance, link density, vulnerability, and generality using the R package bipartite [18]. We used glmm's to test for an effect of treatment with block as a random factor.

3. Results

Of 297 spiders collected (Table 1), 270 individuals were molecularly identified as line weaving spiders (Linyphiidae), of which 232 were assigned to *Erigone psychrophila*, 36 to *Hilaira vexatrix*, and two to *Erigone arctica*. One spider was identified as wolf spider *Pardosa glacialis* (Lycosidae). The species-identity of the remaining 26 specimens could not be univocally determined (Table 1). The number of spiders caught was similar among treatments ($P=0.68$ and $P=0.57$ for all spiders and spiders containing prey, respectively).

We were able to extract prey remains from 198 spiders (Table 1), resulting in 925 prey taxa identified to family level or lower. All analyses were therefore conducted at the family level. Prey taxa represented 28 different families of which 27 were found in control plots and 25 in enclosure plots. In both treatments, spider diets were dominated by Chironomidae and Muscidae (Figure 1A), with no detectable difference in spider prey composition between treatments ($P=0.57$). When comparing the treatment-specific prey compositions of the individual spiders in the PCA, we found highly overlapping spider diet compositions in the two treatments (Figure 1B).

We found no effect of excluding muskoxen on the spider-prey food webs (Figure 2), and none of the network-level descriptors of interaction structure varied significantly with treatment ($P>0.13$) (Supplementary material).

4. Discussion

We found no significant changes in the arthropod community, despite the marked changes observed in the plant community following the exclusion of muskoxen [8]. Quite the contrary, the community composition of both predators and their prey appeared similar in plots with and without muskoxen, and both groups consisted of taxa common in the Zackenberg valley [19,20]. This lack of effect extended to all levels examined: The predator community, the prey community, and the interaction structure between them.

Importantly, the predator communities of the focal habitats were strongly dominated by small-bodied, web-building spiders in family Linyphiidae. These species build minute sheet webs in the low, arctic vegetation, and the spider hangs inverted below the sheet [21]. The more mobile wolf spiders in family Lycosidae [21] constituted a negligible minority. Thus, the predator community is characterized by sedentary species confined to the local prey pool, and their gut contents will reflect prey available at the relevant scale of the treatments (10x10m).

The composition of the arthropod prey community, as revealed by the spider diets, was unaffected by the exclusion muskoxen. Hence, in both treatments spider diets consisted of a broad spectrum of taxa common to the area [20], and were dominated by Chironomidae and Muscidae. These are also the most abundant arthropod families at Zackenberg [22]. High arctic spiders are generalists feeding on almost every taxa available [23], and the similarity in diet composition, combined with the similar frequency of occurrence of the various prey taxa in the two

treatments, therefore suggest that the availability of prey taxa (both in terms of diversity and abundance) was not affected by the exclusion of muskoxen.

In agreement with these findings, we found no significant changes in the simple spider-prey food webs reconstructed. While interaction structure has been proposed to offer alternative, more sensitive measures complementing mere species counts [1], all metrics examined here were remarkably similar among treatments – despite the clear-cut impacts on primary producers [8]. This lack of structural differences in the predator-prey food webs further attests to a lack of change in the arthropod community following even long-term muskox exclusion.

The high arctic arthropod community thus exhibited a high degree of resistance towards significant changes in its habitat, with no indications of cascading effects. However, we do acknowledge that these findings are based on a relatively limited sample size, which cautions extrapolation of our findings. Still, in the same ecosystem, we have previously manipulated predator densities, and found no cascading effects of the manipulation [24], suggesting a high degree of community resistance towards disturbances. Hence, the current results add to the notion that high arctic arthropod communities are highly resistant to trophic cascades reverberating through multiple trophic levels. This resistance is likely attributable to the high connectivity of high arctic arthropod food webs [9]. Importantly, interaction structure remained essentially unchanged across treatments, thereby attesting to network-level resilience to habitat change.

Data accessibility. Supporting data can be accessed via the Dryad data repository (<http://datadryad.org/review?doi=doi:10.5061/dryad.3d154>).

Authors' contributions. N.M.S. and T.R. conceived the idea and drafted the manuscript. J.B.M. conducted fieldwork, J.B.M. and B.E. prepared the samples and E.J.V. conducted lab analyses and bioinformatics. All authors contributed to manuscript revisions and approved its final version.

Competing interests. We have no competing interests.

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Table 1. Number of spider specimens caught in the individual blocks in the two treatments. Numbers in brackets are number of spiders with prey remains.

Treatment	<i>Erigone arctica</i>	<i>Erigone psychrophila</i>	<i>Hilaira vexatrix</i>	<i>Pardosa glacialis</i>	<i>Erigone/Hilaira</i>	<i>Erigone/Hilaira/Pardosa</i>	Unknown species	Total
Control	2 (2)	119 (83)	19 (13)	0 (0)	8 (4)	0 (0)	4 (1)	152 (103)
Block 1	0 (0)	40 (31)	15 (9)	0 (0)	2 (0)	0 (0)	2 (0)	(40)
Block 2	0 (0)	35 (26)	1 (1)	0 (0)	4 (2)	0 (0)	0 (0)	(29)
Block 3	2 (2)	44 (26)	3 (3)	0 (0)	2 (2)	0 (0)	2 (1)	(34)
Exclosure	0 (0)	113 (81)	17 (10)	1 (0)	10 (3)	1 (0)	3 (1)	145 (95)
Block 1	0 (0)	40 (32)	5 (4)	0 (0)	2 (1)	1 (0)	1 (1)	(38)
Block 2	0 (0)	31 (19)	7 (5)	1 (0)	4 (0)	0 (0)	2 (0)	(24)
Block 3	0 (0)	42 (30)	5 (1)	0 (0)	4 (2)	0 (0)	0 (0)	(33)

Figures legends

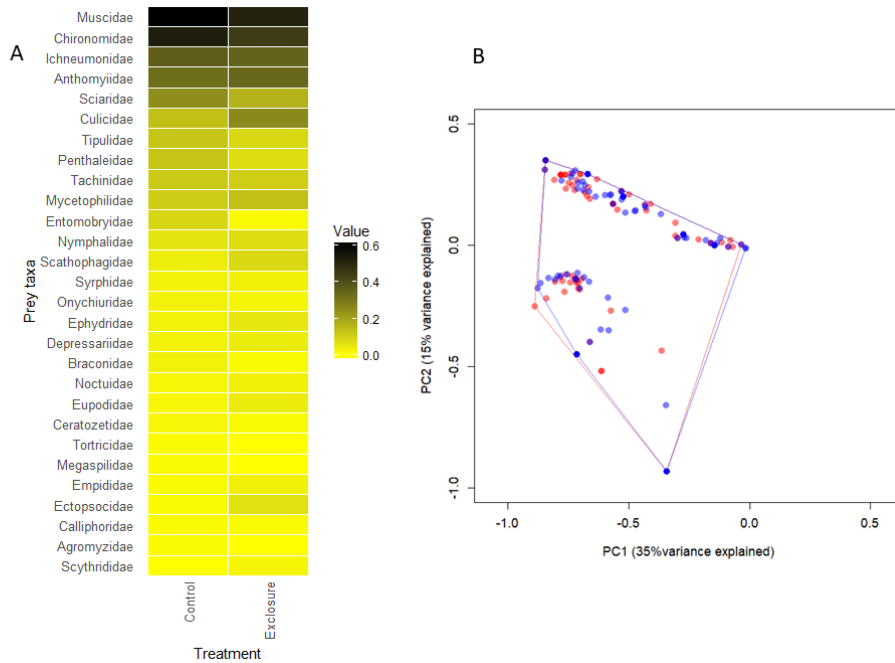


Figure 1. Prey communities in control and enclosure plots as revealed by predator gut contents. A) Heat map showing the frequency of occurrence of prey taxa in spider diets. B) PCA plot visualizing the Hellinger transformed prey composition of individual spiders in the two treatments. Control plots are shown in red, enclosure plots in blue. Darker colors indicate overlapping data points.

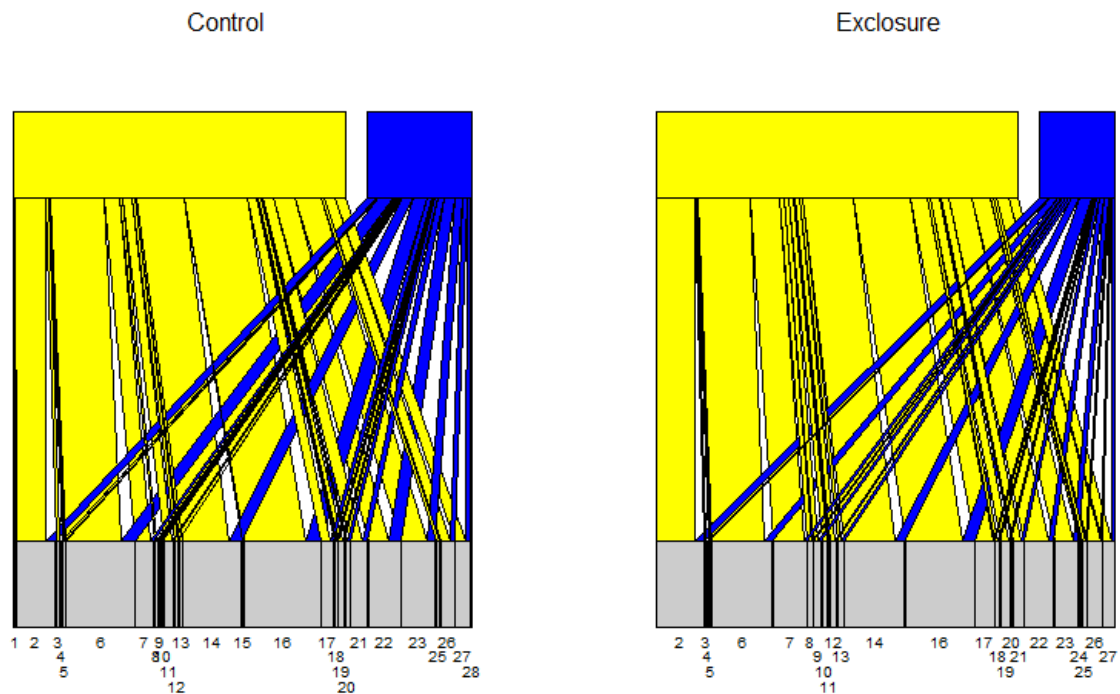


Figure 2. The general food web of the two most abundant spiders *Erigone psychrophila* (green) and *Hilaira vexatrix* (blue) in control and enclosure plots. Numbers below refer to prey families (Supplementary material Table S1).