UiT The Arctic University of Norway

Faculty of Biosciences, Fisheries and Economics

Grazed vs the Ungrazed: Herbivory Effects on Leaf Nutrient Content and Chemical Defense

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Master’s thesis in Biology BIO-3950 May 2024

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Cover photograph: © Tabor Noteboom - Svalbard reindeer

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1 Abstract

Despite growing evidence of herbivory's influence on plant nutrient dynamics in the Arctic tundra, the short-term effects on leaf nutrient and phenolics contents across different tundra habitats and dominant plant species remain underexplored. This study enhances our understanding by analyzing the impacts of a 2-year herbivore exclusion (involving Svalbard reindeer and migratory geese) on leaf nutrient contents and phenolics, within three dominant tundra species—*Bistorta vivipara, Dryas octopetala*, and *Salix polaris*—and three habitat types: moss tundra, disturbed moss tundra, and dryas ridges. Our approach corrected for baseline nutrient levels for species-specific effects and accounted for differential Plant Functional Type (PFT) responses in the habitat-specific analysis.

The results indicate generally weak and non-significant changes in leaf nutrient and phenolics contents to short-term herbivory exclusion. However, significant increases were observed in phenolic content in *Bistorta vivipara* and phosphorus content in *Dryas octopetala*. The disturbed moss tundra also showed a significant reduction in phosphorus content. Thereby, only one out of 18 habitat-level models and two out of 18 species-specific models showed significant changes. These findings suggest that Arctic tundra habitats exhibit relative resilience to short-term herbivory in terms of leaf nutrient and phenolic contents responses.

Given the nuanced nature of these findings, further research is needed to fully elucidate the intricate interactions between herbivory, leaf nutrient and phenolic contents across the diverse Arctic tundra landscape.

2 Introduction

2.1 Climate change in the Arctic

As the Earth warms, the Arctic serves as a bellwether for climate change, undergoing transformations at an unprecedented pace (AMAP, 2021). With Svalbard in the middle of it, experiencing warming at nearly five times the global average (Isaksen et al., 2022). This is caused by a phenomenon, known as Arctic Amplification, and has triggered several ecological shifts, including changes in nutrient cycling, vegetation chemical composition and phenology (Bowen et al., 2020; Parmentier et al., 2013; Schuur et al., 2015). With spring-onset having advanced 12-days over the last 20 years in 2020 (Karlsen et al., 2022), affecting breeding timing for herbivores, and migratory geese arrival, thereby leading to trophic mismatches (Mallory et al., 2020; Post et al., 2019). In addition to changes in the weather conditions having variable impacts on the Svalbard herbivory presence. Such as so-called rain-on-snow events, leading to a decrease in Svalbard reindeer population growth (B. B. Hansen et al., 2013), range displacement (Stien et al., 2010) and increased mortality (Aanes et al., 2003). Whereas migratory geese populations are seen to increase in population size, attributed to reduced hunting and improved food quality (A. D. Fox & Madsen, 2017a; B. B. Hansen et al., 2013). These major ecosystem shifts place Svalbard in a vulnerable position to any additional disturbances that may affect the ecosystem. Further constrained by a short growing season and low temperatures (Hobbie et al., 2002). Svalbard inherently has low microbial activity, slowing down decomposition rates and nutrient turn-over rates (Cornelissen et al., 2007), thereby limiting the nutrient availability (Hobbie et al., 2002). But with the increased climate warming, nutrient turnover rates are expected to generally increase, enhancing nutrient availability for tundra plants (Rustad et al., 2001).

This may significantly impact broader ecosystem processes since nutrient availability often limits Arctic regions (Hobbie et al., 2002). More precisely the nutrient availability of nitrogen (N) and phosphorus (P), are pointed out to be crucial in regulating primary production. As these nutrients, along with temperature and moisture levels, regulate the rate of photosynthesis (Wright et al., 2004). Consequently, increased leaf nitrogen (N) and phosphorus (P) contents are positively associated with enhanced plant growth and photosynthetic activity (Güsewell, 2004). Increases in these same nutrient leaf concentrations are also known to increase litter decomposability, thereby further accelerating the nutrient-cycling (Zhang et al., 2008). Ultimately highlighting the complex interplay of changing nutrient dynamics in the Arctic and the cascading effect on the health of the overall ecosystems (De Deyn et al., 2008).

2.2 Feast or Famine: Nutrient Impact on Herbivory and Defense

Often being in greater demand than their availability, N and P leaf nutrient contents not only limit photosynthesis, but also affect the ecosystem’s herbivores (Aerts & Chapin, 1999). As nitrogen is crucial for protein synthesis and growth, while phosphorus plays a vital role in synthesizing ATP and forming bony structures (Sterner & Elser, 2002). This behavior drives herbivores to selectively feed on more nutritious plant parts, such as flowers and young leaves, which are high in nitrogen (N) and phosphorus (P) but low in structural and defensive compounds (White, 1983; Bråthen & Oksanen, 2001). This selective feeding behavior can cause a shift in vegetation composition and can trigger plant chemical defense responses. (Olofsson et al., 2009; Post & Pedersen, 2008; Soininen et al., 2013). This chemical response often precedes the changes in vegetational composition and can thereby serve as an effective indicator of plant-herbivore interactions (Hartley & DeGabriel, 2016, Moreira et al., 2018).

Herbivores need to balance maximizing their nutrient intake against the challenge of navigating plant chemical defenses like phenolics (Hartley & DeGabriel, 2016; Lambdon & Hassall, 2005). This makes the ratios of Carbon (C) to Nitrogen (N) and Phenolics to Nitrogen (Ph:N) a more comprehensive indicator of actual plant palatability rather than total nutrient content alone (Hartley & DeGabriel, 2016, Moreira et al., 2018). Generally speaking, fast-growing species are known to have low C:N and Ph:N ratios (Coley et al., 1985). As these species may respond with compensatory growth rather than increased defense to herbivory, as observed in *Salix polaris* (Skarpe & Van der Wal, 2002), this response enhances forage palatability and benefits herbivores (Brathen & Odasz-Albrigtsen, 2000). On the other hand, slow-growing species like the evergreen *Dryas octopetala* tend to prioritize protecting their long-lived perennial leaves, with higher innate phenolic contents (J. Tuomi et al., 1991).

These differing herbivory-responses among species can potentially be explained by the Resource Availability Hypothesis (RAH). This theory posits that nutrient availability dictates the vegetation responses, with nutrient-rich habitats favoring plant growth and nutrient-poor habitats pushing towards the prioritization of defense compounds, like phenolics (Endara & Coley, 2011). To study these vegetation responses studies often use a Plant Functional Type (PFT) framework, which groups species with similar environmental responses into the same functional trait group, simplifying the vegetation analysis (Chapin et al., 1996). Within this framework, forbs are expected to have the highest N and P content, followed by graminoids, deciduous shrubs, and evergreen shrubs (Chapin et al., 1996, Thomas et al., 2019).

2.3 Herbivory and Dual Vegetation Response

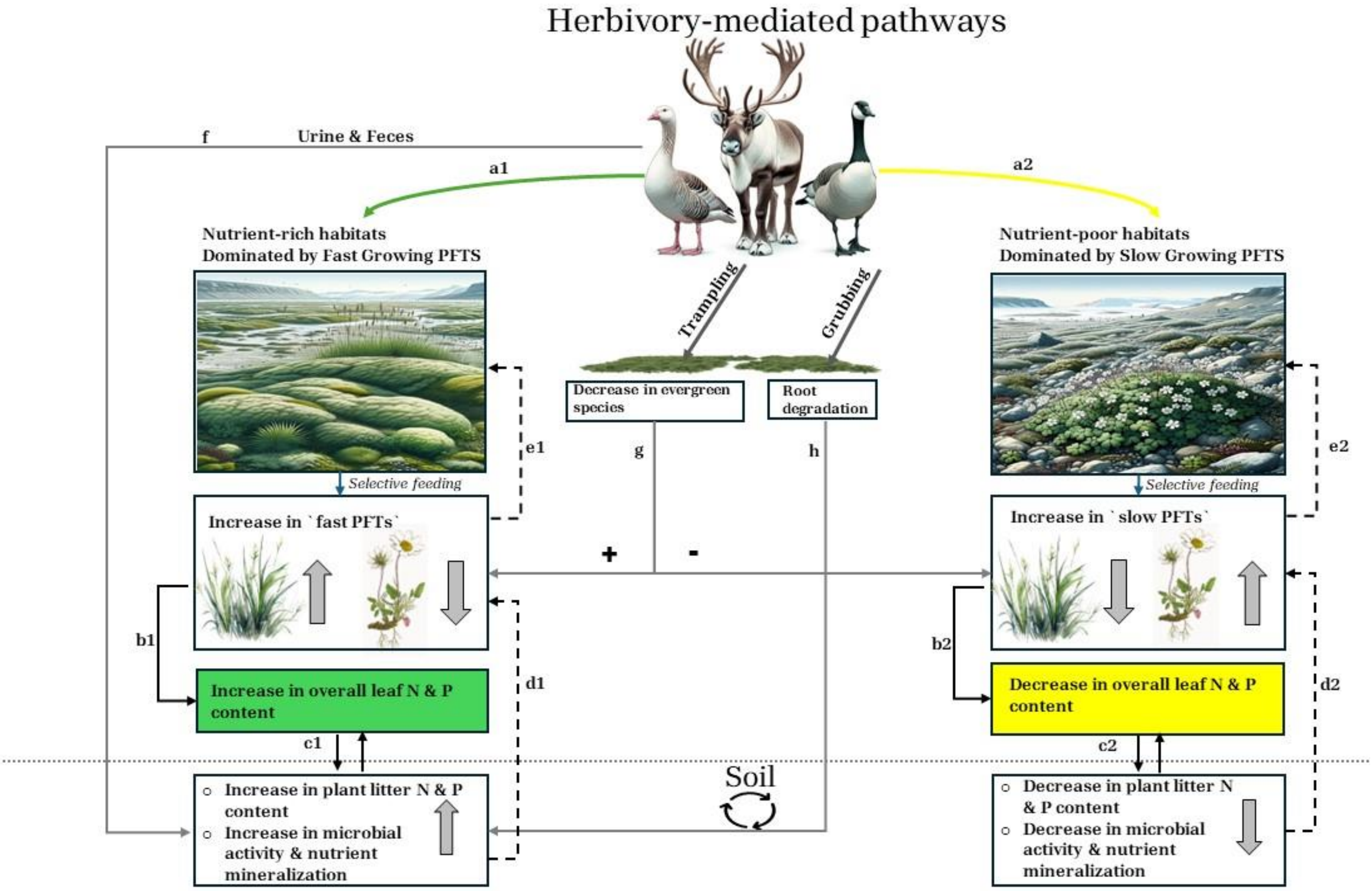


Figure 1. Conceptual illustration of herbivory-mediated impacts on vegetational composition, leaf nutrient content and the following soil-feedback mechanism. The figure depicts the expected shifts in nutrient dynamics through herbivory effects such as, selective feeding, grubbing and trampling, as is detailed in the text below. This study only focuses on the components highlighted in

green and yellow (leaf nutrient contents) across various habitats, which are anticipated to follow pathways a1 and/or a2, leading to changes in leaf nutrient contents. This illustration was inspired by the herbivore-pathway illustrations (M. Tuomi et al., 2019), and the habitat illustrations used where created with the help of OpenAI`s DALL·E

As depicted in Figure 1, pathway (a1) in nutrient-rich habitats, that are dominated by fast-growing Plant Functional Types (PFTs), herbivory likely accelerates nutrient cycling (Chapin III, 1991; Van Der Wal et al., 2004). Herbivores will most likely selectively feed on highly palatable species (low carbon (C) to nitrogen (N) ratios (Bardgett & Wardle, 2003), shortcutting the litter-decomposition pathway and depositing nitrogen-rich feces that fertilize the soil (Olofsson et al., 2004). This results in rapid nutrient enrichment, increasing nutrient availability and microbial activity, while grazing maintains plant material in an earlier more nutritious phenological stage (Petit Bon et al., 2020, Stark et al., 2002). This increase in nutrient availability can consequently on the long-term favor fast-growing plants (d1) (van der Wal, 2006), which in return increases the overall vegetation N and P leaf contents (b1) and thereby increases decomposition rates of the plant litter (c1). This will further enhance beneficial conditions for the fast-growing PFTS and keep the habitat in a nutrient-rich state (e1).

Conversely, pathway (a2) in nutrient-poor habitats, such as the so-called dryas ridges, dominated by evergreen dwarf shrubs (*Dryas octopetala)* (Donald et al., 2005), shows that selective grazing retards nutrient processes. While herbivores still shortcut the nutrient decomposition pathway, their selective grazing targets more palatable subdominant plant species, allowing less palatable, slow-growing species to avoid grazing (Augustine & McNaughton, 1998; Bardgett & Wardle, 2003). This selective pressure gives a competitive advantage to slow-growing species that are high in carbon and defense compounds and low in N and P (b2). Consequently, the plant litter from these slow-growers has a decelerating effect on litter decomposition and nutrient mineralization (c2) (Chapin & Shaver, 1996; Reich, 2014), leading to decreased N and P availability in the soil further enhancing the nutrient-poor state, favoring slow-growing, nutrient-poor PFTs (d2) (Ritchie et al., 1998).

Besides the most obvious consumptive effects of herbivores, they may also impact the vegetation in a less direct way, through means of trampling. In Arctic tundras, trampling typically reduces moss depth and leads to soil compaction, altering the physical environment of the vegetation (M. Tuomi et al., 2019; Van Der Wal & Brooker, 2004). Furthermore, it is shown to greatly affects evergreen species (see figure 1, g), which exhibit lower resilience to mechanical disturbances, thus highlighting its role in herbivory-mediated vegetation composition shifts (Egelkraut et al., 2020; Jonasson & Callaghan, 1992).

In addition to trampling, grubbing perturbations are also found to impact the tundra vegetation (Ravolainen et al., 2020; Speed et al., 2009). Grubbing is a destructive foraging technique used by geese, particularly prevalent in moss tundra`s. This technique involves the uprooting of roots, resulting in the degradation of this plant material and the nutrients leaching back into the soil (see figure 1, h) (Ravolainen et al., 2020; Speed et al., 2009). Due to the rapid increase of migratory geese populations in the Arctic (A. D. Fox & Madsen, 2017a), the short-term nutrient and phenolic responses of tundra ecosystems to grubbing disturbances caused by geese could be considerable.

Recent studies have shown that vascular plants are particularly sensitive to goose-grubbing, more so than other ecosystem components such as soil and mosses (Petit Bon, Bråthen, et al., 2023; Petit Bon, Hansen, et al., 2023). These studies highlight the significant impact of spatially aggregated migratory geese on tundra moss habitats, primarily through geese-grazing maintaining low levels of vascular plant biomass (Kuijper et al., 2009). This is evidenced by marked increases in vegetation biomass observed under both short-term and long-term geese exclosures (4 and 15 years) (Petit Bon, Hansen, et al., 2023). Similarly, a 21-year exclosure of the more widely distributed Svalbard reindeer also led to significant, albeit weaker, increases in biomass. Despite these biomass gains, weak alterations in leaf nutrient contents were found after goose exclusion and no significant alterations under reindeer exclusion (Petit Bon, Hansen, et al., 2023). These findings underscore that while herbivores markedly influence Arctic vegetation, the specific responses of vegetation nutrient content to herbivory across different tundra habitats remain inadequately understood and warrant further investigation.

2.4 Research Questions

Svalbard, with its nutrient-diverse landscapes ranging from nutrient-poor areas (Wookey et al., 1995) to strongly nutrient-enriched moss tundras near bird cliffs (Zwolicki et al., 2013), serves as an ideal location for exploring the heterogeneous impacts of herbivores. The region's long history of reindeer grazing and migratory geese populations, coupled with a relatively simple terrestrial food web and accelerated climate warming, provides a unique ecological backdrop (Descamps et al., 2017, Ims & Fuglei, 2005; Skarin et al., 2008; Soininen et al., 2013). Our research focuses on the herbivory-mediated alterations in leaf nutrient and phenolic contents through the exclusion of three key herbivores on Svalbard, specifically migratory barnacle geese (*Branta leucopsis*), pink-footed geese (*Anser brachyrhynchus*), and non-migratory Svalbard reindeer (*Rangifer tarandus platyrhynchus*). By excluding these functionally distinct herbivores, we hope to gain a comprehensive view of the total impact of herbivory on tundra vegetation (A. D. Fox & Madsen, 2017a; Le Moullec et al., 2019). Changes in vegetation responses to herbivory, especially following disturbances such as goose-grubbing, remain relatively underexplored (Madsen et al., 2014). Informed by prior studies that documented variable Arctic vegetational responses to herbivory, with vascular plants showing the highest sensitivity to this perturbation, our study has two main objectives (Olofsson et al., 2004, 2009; Petit Bon et al., 2021; Petit Bon, Hansen, et al., 2023). Firstly, we aim to asses herbivory effects on species-specific leaf nutrient contents of carbon, nitrogen, phosphorus, and phenolics as well as the ratios C:N, Ph:N. This leads us to our first research question:

1. **"How does the exclusion of herbivores influence the leaf nutrient contents, phenolics and ratios (C:N, Ph:N) in key Arctic species *Bistorta vivipara, Dryas octopetala,* and *Salix polaris*?"**

Secondly, we plan to assess habitat-specific vegetation nutrient and phenolic content responses, correcting for PFT response differences. Bringing us to the second research question:

2. **"Do tundra habitats in Svalbard, specifically moss tundra, disturbed moss tundra, and dryas ridges, exhibit distinct responses in leaf nutrient contents, phenolic contents, and ratios (C:N, Ph:N) following short-term exclusion of herbivores?"**

It is hypothesized that excluding herbivory will result in a reduction of nitrogen and phosphorus leaf nutrient content in the relatively fast-growing species *Salix polaris* and *Bistorta vivipara*. Without herbivory to shortcut nutrient cycling pathways or induce compensatory growth, nutrient availability may decrease (Herms & Mattson, 1992). Furthermore, without grazing maturing leaves may accumulate phenolic compounds, leading to an increase in C:N and Ph:N ratios. The slow-growing species, *Dryas octopetala*, is expected to react more slowly to herbivory exclusion treatments. We expect that although herbivory exclusion would on the long-term diminish the competitive advantage of *Dryas octopetala*, which often benefits from selective feeding by herbivores in grazed areas (Augustine & McNaughton, 1998; Bardgett & Wardle, 2003). On the short-term release from herbivory, this evergreen species might be able to accumulate carbon, nitrogen, and phosphorus in its leaves, thereby enhancing its inherent prioritization of phenolic compounds (Kielland & Chapin, 1992)**.**

In the context of tundra habitats, it is hypothesized that short-term herbivore exclusion will lead to distinct changes in leaf nutrient content in the different tundra habitats. In the nutrient-rich moss tundra and disturbed moss tundra, we expect a decrease in nitrogen (N) and phosphorus (P) contents under herbivore exclusion. This reduced leaf N and P contents is expected to decrease the vegetation photosynthetic rate, thus decreasing the vegetations carbon accumulation through primary production (Rustad et al., 2001). I anticipate this to go paired with a shift in the vegetations resource allocation towards increased defense, increasing leaf phenolic contents (Bryant et al., 1983; Herms & Mattson, 1992). This effect will most likely be more pronounced in the previously geese disturbed moss habitats. Conversely in the nutrient-poor dryas ridge habitat, we anticipate herbivory to have a retarding effect on nutrient turnover (Chapin III, 1991). Thus, herbivory exclusion would lead to a relative increase in N and P leaf contents compared to the open grazed sites. This would lead to a decreased prioritization in defense and reduce phenolic contents following the RAH theory (Endara & Coley, 2011). This would logically lead to a decrease in both C:N and Ph:N ratios leading to a relatively more palatable state.

3 Methods

3.1 Study Area

The study was conducted on Svalbard in the high-arctic, centered around two locations: Adventdalen (78°10′N, 16°05′E) and the Brøgger peninsula (Ny-Ålesund, 78° 54' 59.99" N, 11° 55' 59.99" E) as seen in figure 2 with nutrient differences detailed in Appendix Figure 5. To investigate vegetation responses to removal of herbivores, an exclosure experiment was established at Janssonhaugen in Adventdalen (set up February 2020) and on Brøggerhaløvya (summer 2021, 1 year later than Adventdalen due to covid-19). Adventdalen is one of the main valley systems near Longyearbyen, and displays well vegetated tundra areas, as well as dryas ridges. Where the vegetation is typically below 10 cm in height and characterized by a low biomass (Reidar Elven & Geir Arnesen, n.d.). A similar open tundra vegetation cover can be found in Brøggerhalvøya, being dominated by gravel ridges that are sparsely vegetated, with spontaneous long stretches off moss tundra and heath vegetation around the bird cliffs, such as Stuphallet and Simlestupet. Detailed vascular plant biomass data, temperature and precipitation specifics can be found in Table 1.

Study Location	**Year**	**Avg Temp (°C)**	**Precip (Annual) (mm)**	**Precip (Month) (mm)**	**Biomass moss tundra g/m²**	**Biomass disturbed moss tundra g/m²**	**Biomass dryas ridge g/m²**
Adventdalen	2020	9.1	232.9	10.5	33.63	35.62	51.66
Brøgger	2021	5.1	510.3	32.4	34.43	32.15	50.31
Adventdalen	2023	10.1	197.3	5.0	38.77	41.15	49.29
Brøgger	2023	6.4	503.4	59.7	44.08	42.96	46.83

Table 1. This table details the average temperature (°C), annual precipitation over the set-up and collection years, with specific monthly precipitation for the collection month, as well as vascular plant biomass densities (g/m²) for moss tundra, disturbed moss tundra, and dryas ridge habitats, based on most recent biomass data. The information in this table is sourced from Norwegian Meteorological Institute. (2023) and (Norwegian Polar Institute, n.d.).

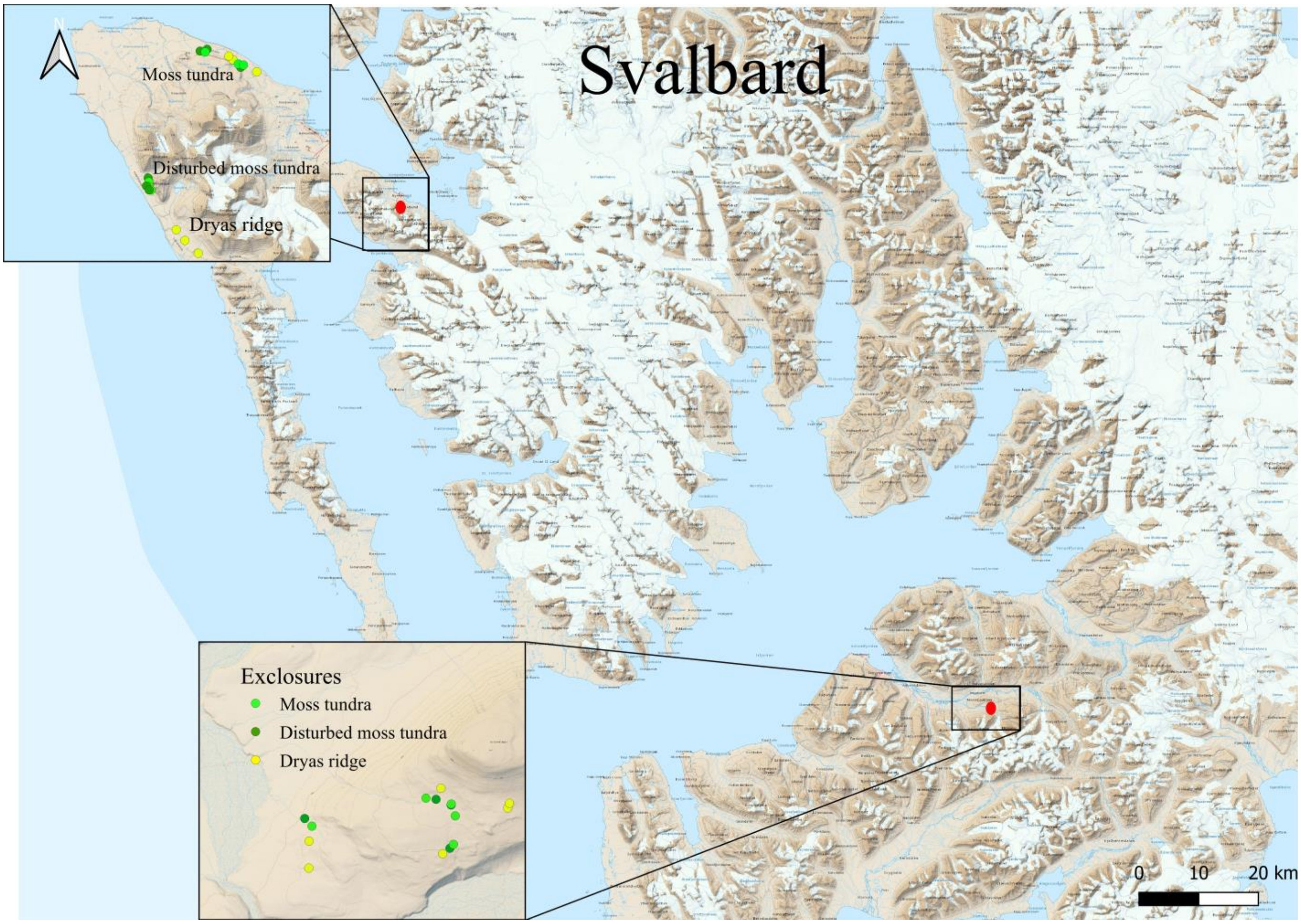
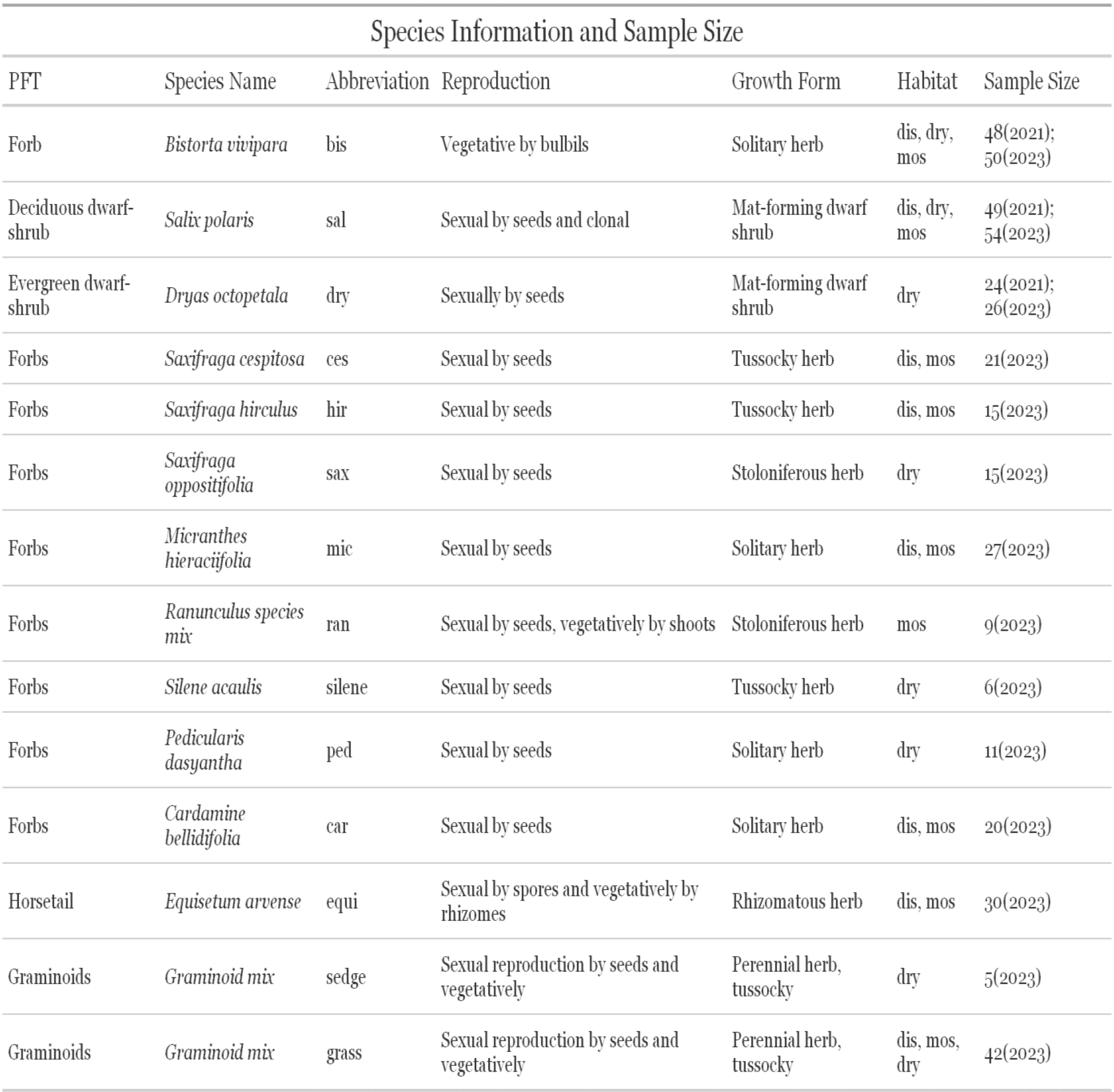


Figure 2 - Svalbard Site-Location Map

This figure displays the distribution of the three habitats used in this study, mapped over two primary locations marked with red dots: Brøgger Peninsula (on the left) and Adventdalen (on the right). The specific coordinates of the habitat exclosure sites are represented by color-coded dots. The base map is sourced from the Norwegian Polar Institute (Norwegian Polar Institute, n.d.).

The study sites are distributed over three different habitat types, dryas ridges, moss tundra and disturbed moss tundra as can be seen in Figure 2. Both moss tundra and disturbed moss tundra share similar topography and dominant plant species. Only differing in the fact that the disturbed moss tundra showed signs of previous vegetation disturbance by goose grubbing, see figure 3. The dominating vascular plant species found in the moss tundra, containing our moss and disturbed sites consist of a variety of species including: *Salix polaris*, *Bistorta vivipara*, *Equisetum arvense* ssp. *alpestre*, *Ranunculus* spp., *Saxifraga cespitosa*, *Saxifraga hirculus*, *Micranthes* spp., and *Cardamine bellidifolia*.

The dryas ridges are, however, dominated by *Dryas octopetala*, *Saxifraga oppositifolia*, *Pedicularis* spp., *Salix polaris*, as well as *Bistorta vivipara* and graminoids. These species along with additional sampled species, shown in table 2, were used as representatives of the general vegetation found across lower elevations in Svalbard, in the habitat-specific models (see Method section 3.5.2). While only the species *Salix polaris, Bistorta vivipara,* and *Dryas octopetala,* were used in the species-specific models. Due to their dominance in Svalbard tundra, these species allowed for consistent comparisons across multiple sites. Each of the species represents a distinct plant functional type (PFT) in the tundra ecosystem: *Bistorta vivipara* as an herbaceous forb, *Dryas octopetala* as an evergreen dwarf shrub, and *Salix polaris* as a deciduous dwarf shrub. Besides them being the only species collected in 2020 during the exclosure set-up, providing a nutrient baseline value which allows for a treatment specific analysis.



Species Information and Sample Size

PFT	Species Name	Abbreviation	Reproduction	Growth Form	Habitat	Sample Size
Forb	*Bistorta vivipara*	bis	Vegetative by bulbils	Solitary herb	dis, dry, mos	48(2021); 50(2023)
Deciduous dwarf-shrub	*Salix polaris*	sal	Sexual by seeds and clonal	Mat-forming dwarf shrub	dis, dry, mos	49(2021); 54(2023)
Evergreen dwarf-shrub	*Dryas octopetala*	dry	Sexually by seeds	Mat-forming dwarf shrub	dry	24(2021); 26(2023)
Forbs	*Saxifraga cespitosa*	ces	Sexual by seeds	Tussocky herb	dis, mos	21(2023)
Forbs	*Saxifraga hirculus*	hir	Sexual by seeds	Tussocky herb	dis, mos	15(2023)
Forbs	*Saxifraga oppositifolia*	sax	Sexual by seeds	Stoloniferous herb	dry	15(2023)
Forbs	*Micranthes hieraciifolia*	mic	Sexual by seeds	Solitary herb	dis, mos	27(2023)
Forbs	*Ranunculus species mix*	ran	Sexual by seeds, vegetatively by shoots	Stoloniferous herb	mos	9(2023)
Forbs	*Silene acaulis*	silene	Sexual by seeds	Tussocky herb	dry	6(2023)
Forbs	*Pedicularis dasyantha*	ped	Sexual by seeds	Solitary herb	dry	11(2023)
Forbs	*Cardamine bellidifolia*	car	Sexual by seeds	Solitary herb	dis, mos	20(2023)
Horsetail	*Equisetum arvense*	equi	Sexual by spores and vegetatively by rhizomes	Rhizomatous herb	dis, mos	30(2023)
Graminoids	*Graminoid mix*	sedge	Sexual reproduction by seeds and vegetatively	Perennial herb, tussocky	dry	5(2023)
Graminoids	*Graminoid mix*	grass	Sexual reproduction by seeds and vegetatively	Perennial herb, tussocky	dis, mos, dry	42(2023)

Table 2 - Species Information and Sample Size

This table presents the Latin names of the collected species alongside their corresponding abbreviations used in the database and R-script for this study. Each species is categorized by its Plant Functional Type (PFT) group. Additionally, the table includes details on the reproduction and growth forms as referenced from the (Elven, Arnesen, Alsos, & Sandbakk, 2020), as well as samples sizes for the years 2021 and 2023.

3.2 Herbivores

Three herbivores exert grazing pressure on our study sites: the native Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and migratory geese, specifically the barnacle goose (*Branta leucopsis*) and the pink-footed goose (*Anser brachyrhynchus*). Unlike their migratory counterparts, the Svalbard reindeer are sedentary, exerting consistent grazing pressure throughout the year at both study locations (Aanes et al., 2000; Fox & Madsen, 2017a). Despite varying life histories, herbivores in the Svalbard tundra often compete for the same plant resources (Bjørkvoll et al., 2009). Additionally, although the Svalbard rock ptarmigan (*Lagopus muta hyperborea*) is a year-round resident, its limited numbers render its impact on the vegetation negligible and in this study, it is therefore not given much attention.
In Adventdalen, the reindeer population has been fluctuating since the year 2000, with numbers ranging from 700 to 1,700 individuals. As of 2022, the population was estimated at 1,425 *(*Norwegian Polar Institute (2022). Meanwhile, the Brøgger Peninsula hosted a population of 186 reindeer in 2022, originating from an initial release of 15 animals in 1978 (Norwegian Polar Institute, 2022*)*. This population has reached a density of up to 0.89 individuals per km² (Aanes et al., 2000). Thus, both areas are subjected to substantial year-round grazing pressure from reindeer.

The populations of both the barnacle goose and pink-footed goose have notably increased over recent years, heavily utilizing wet mossy terrains across the Svalbard archipelago during the summer (A. D. Fox & Madsen, 2017b). Specifically, the barnacle goose population on the Brøgger Peninsula has been steadily rising over the past four decades (Layton-Matthews et al., 2019). These geese primarily inhabit wetlands during their peak summer season, a critical period of 3- to 5 weeks marked by flightlessness due to molting and the raising of their young.

Meanwhile the pink-footed geese population has been rising from 15000 individuals in 1965 to 90,000 individuals in 2017 (Fox & Madsen, 2017a). The geese were found to have a preference for wet habitats by (Speed et al., 2009), although during early spring pink-footed geese in particularly would resort to drier areas as frozen soils would limit their grubbing in wet habitats (A. Fox et al., 2006). Barnacle geese, however, tend to graze around the snow-patches (Fox & Bergersen, 2005), as their diet largely consists of mosses (Fox & Bergersen, 2005; Prop & de Vries, 1993)**.** Notably the total utilization of these drier habitats has been increasing because of the rise in population numbers (Pedersen et al., 2013), leading to a broader impact of the geese grubbing on the overall vegetation in Svalbard.

3.3 Experimental study design

In total, 14 exclosures were set up in Adventdalen, all located on Janssonhaugen, and 18 in Brøggerhalvøya, distributed as follows: 9 on Stuphallet, 6 on Simlestupet, and 3 at Leinstranda, as shown in Figure 3. The number of replicates for each exclosure was determined by the available area of the focus habitat types and logistical considerations.

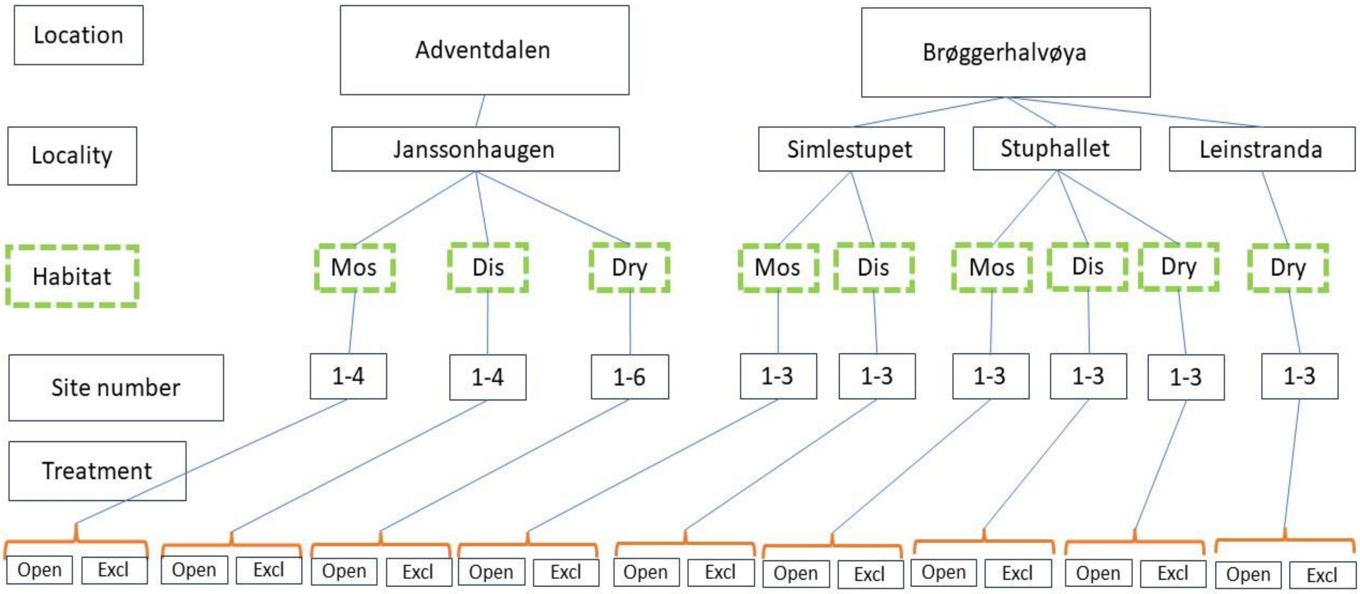


Figure 3 - Exclosure distribution

The figure illustrates the distribution of exclosures across various habitats and localities. Each site features the two treatments used in this study: the Open control site and the herbivory Exclosure (Excl).

The exclosures are factorial in nature and exist of 4 adjacent 5m x 5m treatment areas, of which two are utilized in this study, see figure 3. The exclosure quadrat is designed such that one part excludes reindeer, one part excludes geese, one excludes both herbivores and one is a control open to herbivore grazing as can be seen in figure 4 (b). The exclosures have horizontal bars at 20 cm and 60 cm above the ground level to exclude geese and at 60 cm and

130 cm for reindeer exclusion and three bars on all heights with an additional two top bars creating a cross over the exclosure to exclude both reindeer and geese. The setup was chosen because the reindeer frequently get entangled into materials including wires or net, hence the exclosures were constructed as fences.

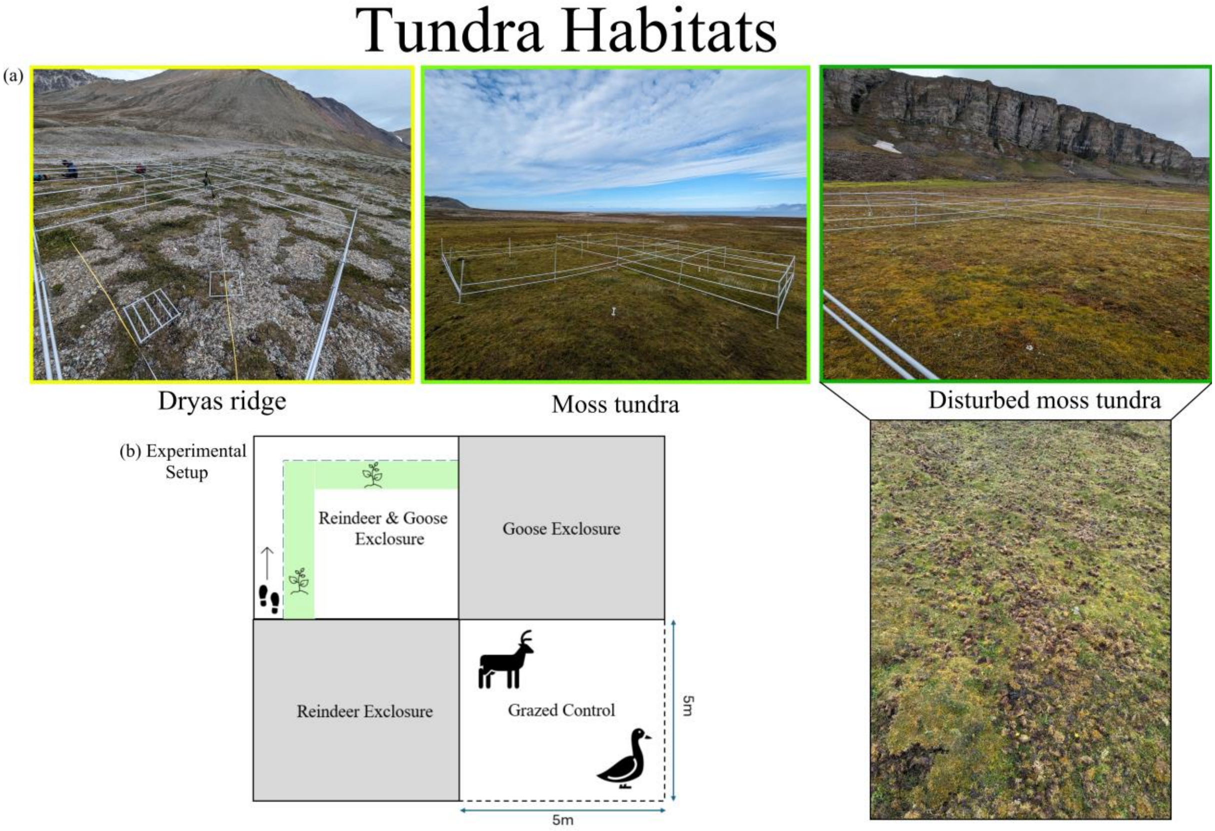


Figure 4 - Habitat Types and Experimental Setup

(a) This panel illustrates the three habitat types investigated in this study: dryas ridge, moss tundra, and disturbed moss tundra. The disturbed moss tundra habitat is depicted with a zoomed in picture of goose-grubbing effects below.

(b) This panel details the experimental setup of herbivory exclosures in Svalbard, featuring four different treatments. It shows in white the two treatments used in this study: the full herbivory exclosure (excluding both reindeer and geese) and the open Control and in grey the unused additional treatment Goose exclosure and Reindeer exclosure. The layout of walking paths and sampling areas within the exclosure site are indicated by the arrow and the green strips.

During the 2023 field season, we observed certain incidents where reindeer calves were able to enter reindeer exclosures. Additionally, the discovery of old reindeer winter droppings in some plots outside the exclosures suggests that the exclosure is not fully reindeer tight year-round, as accumulated high snow coverage may level with the fences, thereby making it easier for the reindeer to enter. Another possibility is that the poop would be wind blown into the exclosures. Nonetheless, no reindeer were observed in the Reindeer & Goose exclosure, in combination with the absence of over-winter cratering (as described by Beumer et al., 2017) indicating that the exclosures used in this study are largely effective in mitigating herbivory impacts.

3.4 Sampling Process

3.4.1 Sample collection

The leaf samples were selected within each exclosure walking along a predefined, L-shaped walking path of 50 cm width along the outer exclosure fences, as seen in figure 2b. Collecting the samples 20cm from this path into the exclosure to minimize edge effects. Per treatment 5 to 6 different species were collected to represent the 5 PFT groups following Chapin et all (Chapin & Shaver, 1996), forbs, graminoid, deciduous shrubs, evergreen shrubs, and horsetails. Certain plant functional groups are only represented by one plant species in this study (see table 2), such as deciduous shrubs by *Salix polaris*, evergreen shrubs by *Dryas octopetala*, as often is the case in Arctic ecosystems (Bliss & Svoboda, 1984; Cooper, 2011). Therefor for transparency's sake in the Result section we will name the individual species represented PFT groups by the species, whereas the forbs and graminoids PFT group included a variety of species due to the limited amount of vegetation at sites and no overarching species for all sites. The latter containing genera *Poaceae* and *Cyperaceae*, proved to difficult to identify to species level due to grazing damage, short leaves and inflorescence. During the sample collection, leaf samples were selected based on visual inspection to accurately represent the general condition and phenological stage of the vegetation at each site. The goal was to collect the same species across different sites per habitat (moss tundra, disturbed moss tundra and dryas ridge), although this was not always feasible due to the limited species biodiversity in the habitats (Bliss & Svoboda, 1984; Cooper, 2011). Consequently, a total of 454 samples were collected, representing 14 different vascular plant species. For a detailed breakdown of the samples, including their Plant Functional Type (PFT) group, refer to Table 2.

Upon collection, each leaf sample was immediately placed in a tea-filter bag. On Brøggerhalvøya the samples were oven-dried at a constant temperature of 60°C within 12 hours upon collection, for a period of 72 hours. In contrast, at Janssonhaugen, logistical constraints necessitated initial air-drying of samples in warm ambient conditions. These were then oven-dried for 72 hours upon returning to town, 5 days after the initial collection. After drying, leaves were sorted into envelopes by site number and packed in sealed plastic bags sorted per location, equipped with silica packets to prevent moisture absorption. These packets were then stored at room temperature in a dry location until laboratory analysis could be conducted.

3.4.2 Nutrient content analysis

A total of 454 leave samples, 121 in 2021 and 333 in 2023 (see figure 2) were collected. These leaves were used to analyze the dry weigh concentration (DW%) of Carbon (C), Nitrogen (N), Phosphorus (P), Silica (Si), and phenolic acids (Ph). The analysis was conducted using Near-infrared reflectance spectroscopy (NIRS) with a FieldSpec 3 instrument (ASD Inc.®, Boulder, Colorado, USA), covering a wavelength range of 350-2500 nm and employing a 4-mm light adapter for full-leaf scans, as described in by Petit Bon et al. (2020). To reduce the impact of water content on light absorption, samples were oven-dried for a second time preceding analysis, at 60°C for a minimum of 8, following the methodology of Smis et al. (2014). Post-drying, the samples were stored in sealed plastic bags with silica for storage during the analysis. For each leaf, 11 NIRS scans were performed to accurately represent the full leaf surface, where all scans were recorded in both an online and written scanning log of spectrum number to specific sample, represented by a specific sample ID, that included species, site, location, locality, and site number. In cases where the leaves were narrower than 4 mm, they were cut and merged to achieve the necessary surface area for analysis. This was necessary mainly for the species *Pedicularis dasyantha, Saxifrage oppositifolia* and graminoids. This process resulted in a total of 4982 individual spectra. Subsequently, the N, C, P, silica, and phenolic acid content were predicted using available prediction models (Murguzur et al., 2019, Petit Bon et al., 2020). To calculate the mean concentrations of the aforementioned nutrients for each individual sample, we determined the median values of the 11 replicate scans for data analysis, following a methodology comparable to that of Petit Bon, et al. (2020).

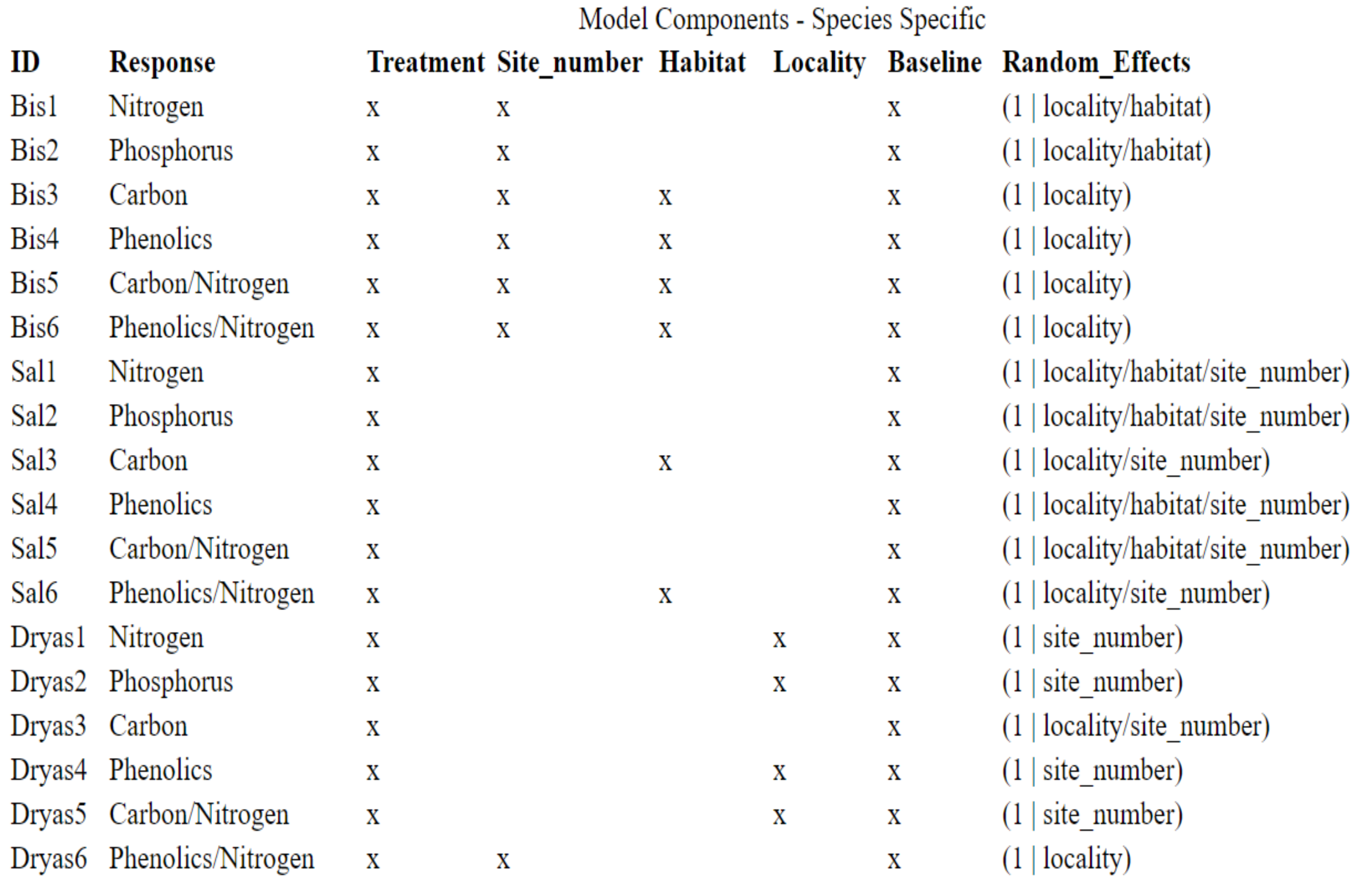
3.5 Statistical Analysis

I followed the protocol from (Zuur et al., 2010) in the exploratory data analyses. We retained outliers in our dataset to preserve the nutrient differences caused by the structural leaf variations. Baseline nutrient ratios for *Salix polaris, Bistorta vivipara*, and *Dryas octopetala*, taken from 2021 samples, were used as reference points in the models, as post-herbivore exclusion baseline nutrient content. Phenolics data was skewed by relatively very low concentrations in horsetails and graminoids. Attempts to normalize data using log transformations proved unfruitful; therefore we excluded horsetails and graminoids from the phenolics analysis, see table 1 in the Appendix. The data analyses were performed in R 4.3.2 (https://www.r-project.org) using the packages *ggplot2* (Wilkinson, 2011), *emmeans* ((Lenth, 2021) and *nlme* (Pinheiro et al., 2020).

3.5.1 Species-Specific Models

In analyzing *Salix polaris* (Sal), *Bistorta vivipara* (Bis), and *Dryas octopetala* (Dry), we fitted species-specific linear mixed-effects models to address how herbivory influences nutrient and phenolic, in dry weight percentage (DW%) for these species. I initially structured these models to mirror our experimental setup, incorporating nested random effects that reflected the hierarchical nature of our study design. Resulting in the nested random effects structure as follows: (1 | locality/habitat/site_number/PFT_group), in order to capture variability at each level.

I streamlined the models by shifting certain hierarchical levels from random effects to fixed effects as per (Bolker et al., 2009). This adjustment was made because these levels exhibited almost zero random variance (Appendix table 3), but treating them as fixed effects would allow the data`s variability to be estimated, thereby enhancing model performance. I used baseline nutrient values from 2021 as covariates to adjust for potential initial differences between species and treatments. Leading to the following model set up as shown in table 3.



Model Components - Species Specific

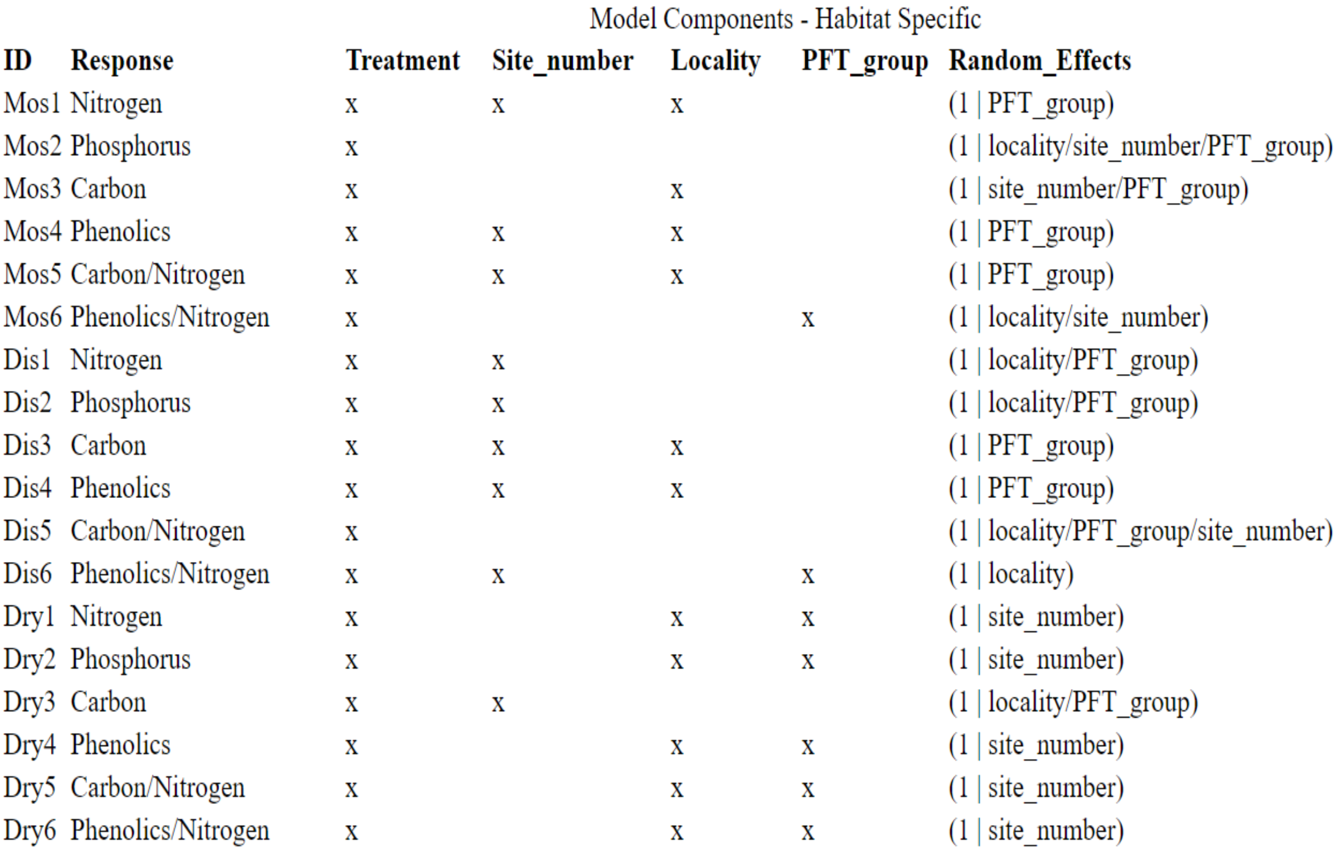
ID	Response	Treatment	Site_number	Habitat	Locality	Baseline	Random_Effects
Bis1	Nitrogen	x	x			x	(1 | locality/habitat)
Bis2	Phosphorus	x	x			x	(1 | locality/habitat)
Bis3	Carbon	x	x	x		x	(1 | locality)
Bis4	Phenolics	x	x	x		x	(1 | locality)
Bis5	Carbon/Nitrogen	x	x	x		x	(1 | locality)
Bis6	Phenolics/Nitrogen	x	x	x		x	(1 | locality)
Sal1	Nitrogen	x				x	(1 | locality/habitat/site_number)
Sal2	Phosphorus	x				x	(1 | locality/habitat/site_number)
Sal3	Carbon	x		x		x	(1 | locality/site_number)
Sal4	Phenolics	x				x	(1 | locality/habitat/site_number)
Sal5	Carbon/Nitrogen	x				x	(1 | locality/habitat/site_number)
Sal6	Phenolics/Nitrogen	x		x		x	(1 | locality/site_number)
Dryas1	Nitrogen	x			x	x	(1 | site_number)
Dryas2	Phosphorus	x			x	x	(1 | site_number)
Dryas3	Carbon	x				x	(1 | locality/site_number)
Dryas4	Phenolics	x			x	x	(1 | site_number)
Dryas5	Carbon/Nitrogen	x			x	x	(1 | site_number)
Dryas6	Phenolics/Nitrogen	x	x			x	(1 | locality)

Table 3. This table presents the model components used for each specifically tailored linear mixed model, corresponding to different nutrient and species combinations in the species-specific analysis. It covers *Bistorta vivipara* (Bis), *Salix polaris* (Sal), and *Dryas octopetala* (*Dryas*). Fixed variables in each model are marked with an "X," and the random effect structures are detailed within parentheses.

3.5.2 Habitat-Specific Models

In developing our habitat-specific linear mixed-effects models, we aimed to analyze the short-term impacts of herbivory on nutrient and phenolic contents and the ratio`s (DW%), while considering variations given by the Plant Functional Trait (PFT) groups.

The model structure was determined by the hierarchical experimental set-up and was simplified in some cases to address singularity challenges. The revised approach resulted in 18 models, as illustrated in table 3, aligning with our experimental design and accounting for the study design and replicates. This modification maintained our ability to detect treatment effect on each specific nutrient, across specific tundra habitats, while correcting for the PFT differences with our data's limitations.



Model Components - Habitat Specific

ID	Response	Treatment	Site_number	Locality	PFT_group	Random_Effects
Mos1	Nitrogen	x	x	x		(1 | PFT_group)
Mos2	Phosphorus	x				(1 | locality/site_number/PFT_group)
Mos3	Carbon	x		x		(1 | site_number/PFT_group)
Mos4	Phenolics	x	x	x		(1 | PFT_group)
Mos5	Carbon/Nitrogen	x	x	x		(1 | PFT_group)
Mos6	Phenolics/Nitrogen	x			x	(1 | locality/site_number)
Dis1	Nitrogen	x	x			(1 | locality/PFT_group)
Dis2	Phosphorus	x	x			(1 | locality/PFT_group)
Dis3	Carbon	x	x	x		(1 | PFT_group)
Dis4	Phenolics	x	x	x		(1 | PFT_group)
Dis5	Carbon/Nitrogen	x				(1 | locality/PFT_group/site_number)
Dis6	Phenolics/Nitrogen	x	x		x	(1 | locality)
Dry1	Nitrogen	x		x	x	(1 | site_number)
Dry2	Phosphorus	x		x	x	(1 | site_number)
Dry3	Carbon	x	x			(1 | locality/PFT_group)
Dry4	Phenolics	x		x	x	(1 | site_number)
Dry5	Carbon/Nitrogen	x		x	x	(1 | site_number)
Dry6	Phenolics/Nitrogen	x		x	x	(1 | site_number)

Table 4. This table presents the model components used for each specifically tailored linear mixed model, corresponding to different nutrient and habitat combinations in the habitat-specific analysis. It covers moss tundra (Mos), disturbed moss tundra (Dis), and dryas ridge (Dry). Fixed variables in each model are marked with an "X," and the random effect structures are detailed within parentheses.

We performed diagnostic checks for each model used in our habitat-specific and species-specific analyses to ensure robustness and validity. These checks included evaluating residuals for patterns or outliers, testing residual normality with Q-Q plots, confirming homoscedasticity using Scale-Location plots, and identifying influential observations with Cook's distance.

3.6 Plotting Results

For the results, we initiated our visual analysis with NMDS plots to assess habitat similarities, as well as the variations caused by PFT inherent differences. We then presented the nutrient and phenolic contents as dry weight percentage (DW%) for our species of interest using box plots, showing the mean as well as the 95%CI spread of the data. Having additional box plots detailing nutrient and phenolics contents (DW%) per separate habitats in the Appendix figures 2, 3 and 4.

Hereafter we plotted the prediction values (+ Standard Errors) from the models over the actual data spread in scatter plots, which allowed for a visual comparison of treatment effect and model functioning. Subsequently, the estimated treatment effects on nutrients and phenolics (DW%) were visualized using standardized effect sizes plots for both the habitat-specific and species-specific models separately. These standardized effect sizes were calculated to provide a measure of the magnitude of the treatment exclosure effect, independent of the units of the measured variables, as the scales of the nutrient variables naturally vary.

4 Results

4.1 Nutrient dry weight concentrations per species (DW%)

This section presents the leaf nitrogen, phosphorus, carbon, and phenolics content and their ratios (C:N and Ph:N) per species, separated by their plant functional types (PFTs). Detailed data on the minimum, mean, and maximum nutrient and phenolic contents (DW%), are provided in Appendix Table 2.

Figure 5 illustrates the diversity in nutrient DW% contents among PFTs. The forb group, exhibit the widest range in nutrient concentrations, with phenolic content varying significantly from 8 DW% to 99 DW%. In contrast, species within the *Dryas* group demonstrate a narrower phenolic range, from 49 DW% to 89 DW%, as detailed in Table 2 in the Appendix. Graminoids, along with horsetails and specific forbs such as *Cardamine bellidifolia, Silene acaulis,* and *Ranunculus spp*., show notably lower phenolic concentrations, as depicted in Figure 5.

The carbon concentration across PFTs shows minimal variability. For instance, the mean carbon concentration for forbs is approximately 44 DW%, and for *Dryas octopetala,* it is about 47 DW%. Horsetails and graminoids are shown as relatively rich in nitrogen and phosphorus, which contributes to their low nutrient ratios in C:N and Ph:N. Species including *Salix polaris, Dryas octopetala, Saxifraga oppositifolia*, and *Pedicularis dasyantha* exhibit relatively high concentrations of carbon and high phenolic to nitrogen ratios. For species-specific data within the forb PFT group, refer to Table 1 in the Appendix**.**

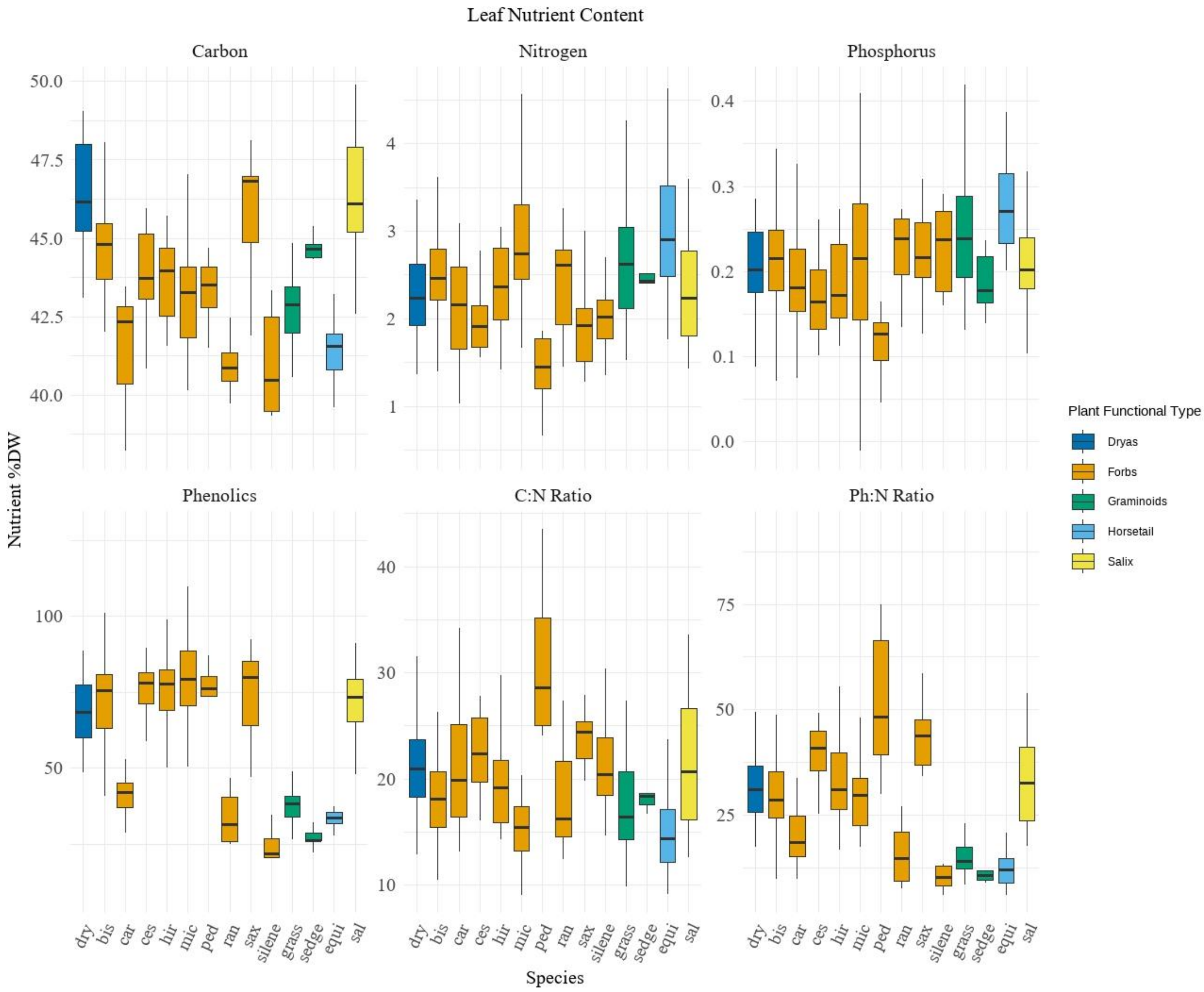


Figure 5 – Nutrient and Phenolic Profiles per Species

In this figure the boxplots represent the dry weight percentage (DW%) of key nutrients, phenolics as well as stoichiometric ratios, across all habitats combined. Each species abbreviation is listed below the x-axis and color-coded according to its plant functional type plant functional types (PFTs), forbs, graminoids, horsetail, and the species *Salix* and *Dryas*. The boxplots highlight the median nutrient value, the interquartile range, and the 95% confidence intervals (CIs) on a nutrient specific scale (y-axis).

Figure 6 presents an NMDS analysis that plots the relative similarities among the studied habitats, moss tundra, disturbed moss tundra, and dryas ridge, based on the leaf nutrient and phenolic contents of the sampled plant species. The plot shows considerable overlap among the habitats, suggesting strong similarities in their nutrient and phenolic profiles. The species are color-coded by Plant Functional Type (PFT) group, with the most significant overlap observed between moss tundra and disturbed moss tundra. For accessibility, a color-blind version of the figure is available as Figure 1 in the Appendix.

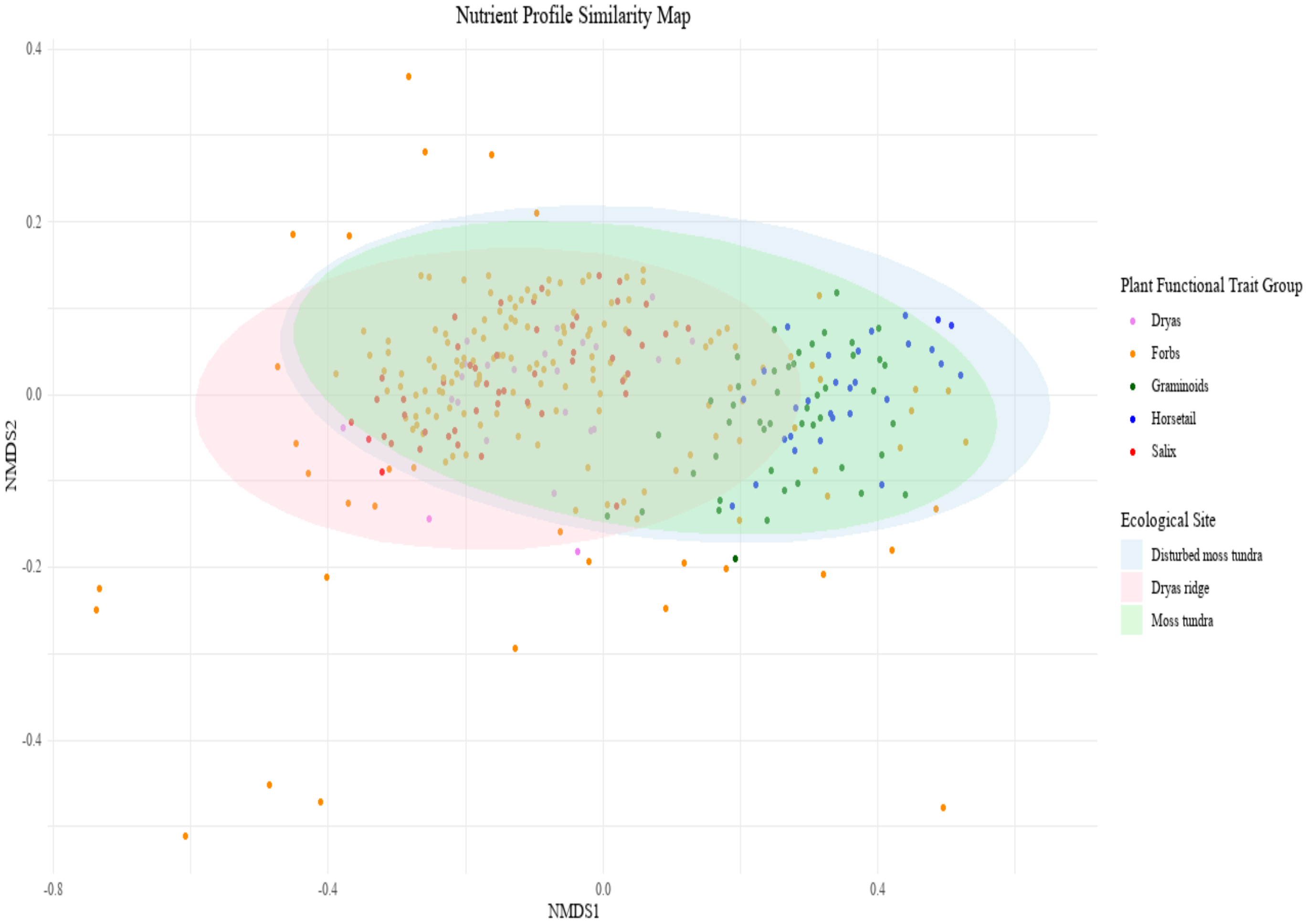


Figure 6 –Nutrient Profile Similarities by Habitats

This Non-metric Multidimensional Scaling (NMDS) plot illustrates nutrient profiles (%DW) over three habitats: moss tundra, disturbed moss tundra, and dryas ridge. It is organized along two dimensions that capture the most significant variation in nutrient content among species. Species are indicated by PFT color-coded dots, with proximity reflecting nutrient profile similarities

4.2 Species-Specific results

The herbivory exclusion treatment significantly influenced leaf nutrient contents in *Bistorta vivipara* and *Dryas octopetala*, while effects on *Salix polaris* were not significant. As illustrated in Figure 7, *Bistorta vivipara* exhibited a significant increase in phenolic content (DW%) under herbivory exclusion, with confidence intervals (CI) not overlapping zero (Model Bis4, 49.56 ± 1.92%, CI: 0.91 to 12.41; see Appendix Table 4 for details). Furthermore, *Dryas octopetala* demonstrated a significant increase in phosphorus content (DW%) under herbivory exclusion (Model *Dryas*2, Est: 0.12 ± 0.050%, CI: 0.02 to 0.08; see Appendix Table 4 for details).

Figure 8 illustrates the standardized effect size responses of *Salix polaris*, *Bistorta vivipara*, and *Dryas octopetala* to herbivory exclusion. Although not statistically significant, the effect sizes indicate a slight tendency for *Dryas octopetala* to increase its nitrogen content under herbivory exclusion. In contrast, *Salix polaris* shows a decreasing tendency in nitrogen, and both *Salix polaris* and *Bistorta vivipara* exhibit similar decreasing tendencies in phosphorus content. It is important to note that these changes are tendencies and not statistically significant findings.

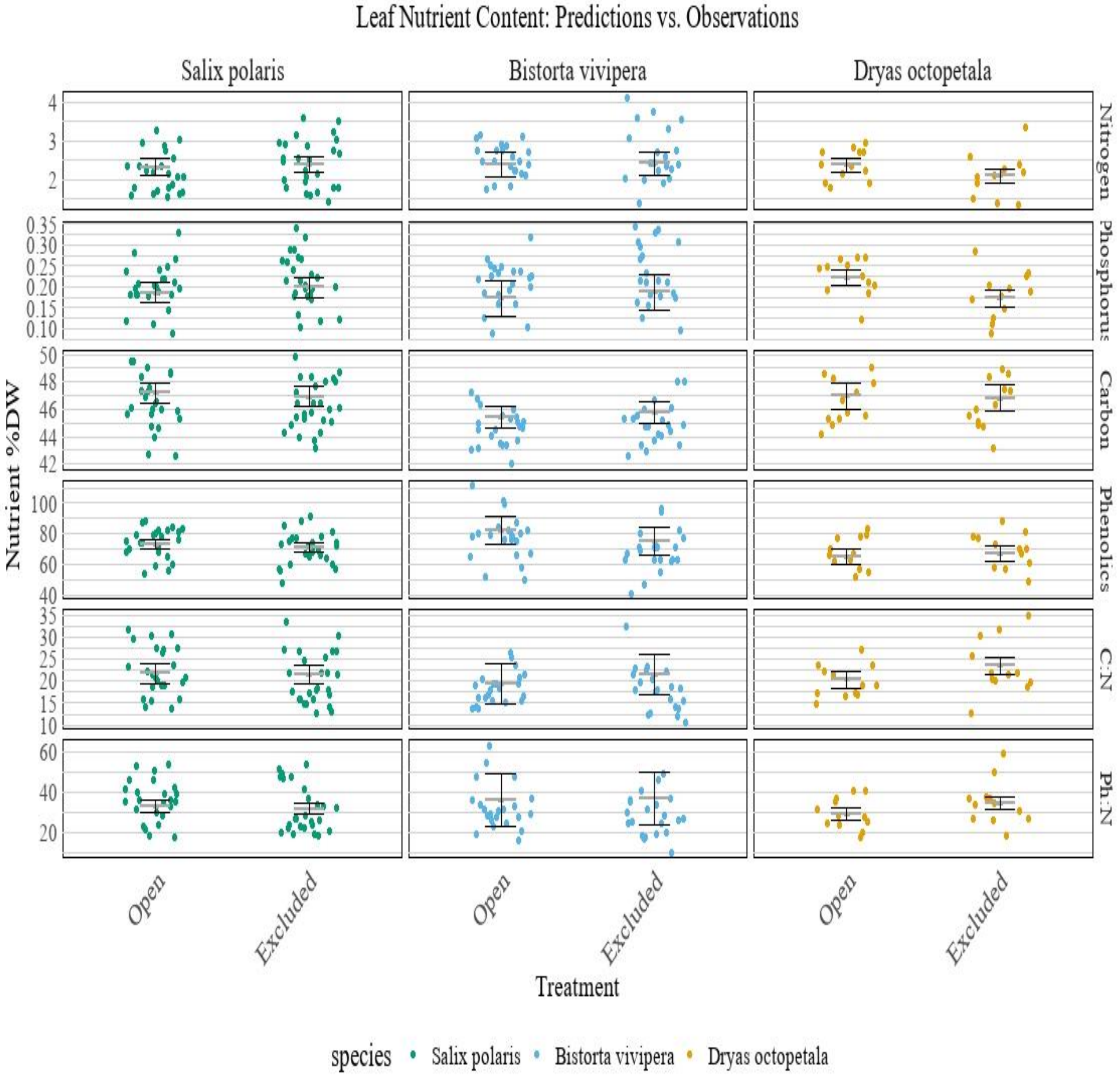


Figure 7 - Model Predictions and Raw Data for Species-specific

Grey dashes represent Model predictions ± SE (as black bars) for nutrient contents within each herbivory treatment (open vs excluded). Color-coded dots show raw data values for each species. Please note the varying scales on the y-axes to accommodate natural variations in nutrient contents (DW%).

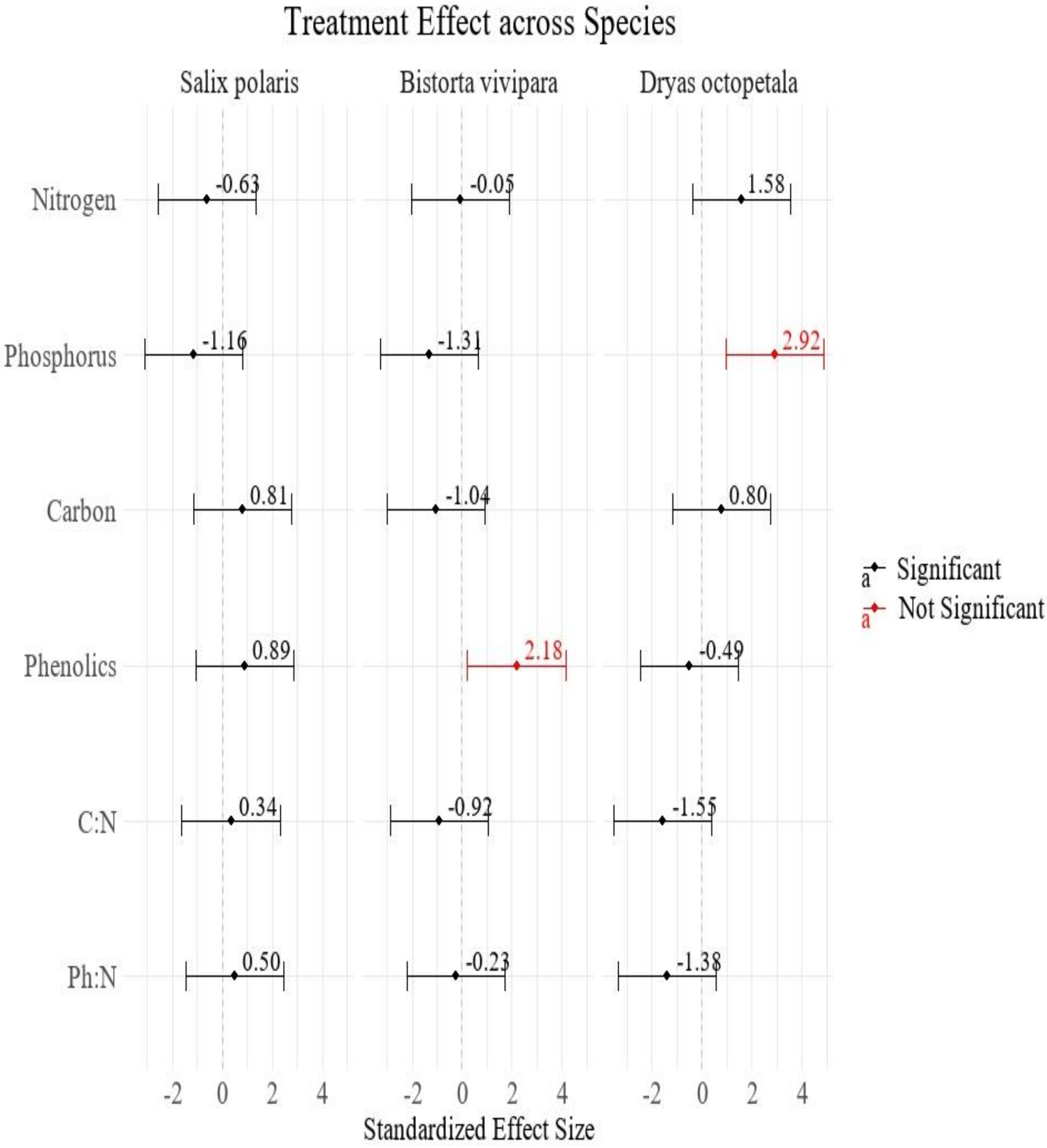


Figure 8 - Standardized Effect Sizes Species-specific

The plot shows the standardized effect sizes for the species-specific analysis across a consistent scale for the nutrient and phenolic contents, and the ratios of carbon:nitrogen and phenolics:nitrogen. Error bars represent 95% confidence intervals. The 0 line represents the intercept corresponding to the Open treatment (control open to herbivory-grazing), with other variables at their baseline levels. Error bars in red indicate significant differences in herbivory exclosure treatments.

4.3 Habitat-specific results

Herbivory exclusion treatment resulted in overall no nutrient content (%DW) responses in the different habitats, except for a significant decrease in phosphorus under herbivory exclusion in the disturbed moss habitat. This decrease is supported by confidence intervals not overlapping zero (Model Dis2, 0.28 ± -0.034%, CI: -0.06 to -0.01), see Appendix table 5 for all 18 model outputs. In all three habitats, other nutrient contents showed no significant alterations under herbivory exclusion, as visualized in Figure 9. The Estimated Marginal Mean (EMMean) prediction points between open grazed and herbivory excluded sites indicate only very slight differences.

Figure 10 illustrates the standardized effect sizes of herbivory exclusion. Both moss tundra and disturbed moss tundra exhibit minor tendencies towards reduced leaf nitrogen and phosphorus contents under herbivory exclusion. Additionally, the disturbed moss tundra shows a non-significant increasing tendency in the C:N and Ph:N ratios, at 1.60 and 1.75 respectively. It is crucial to emphasize that these are only subtle tendencies and do not represent statistically significant findings.

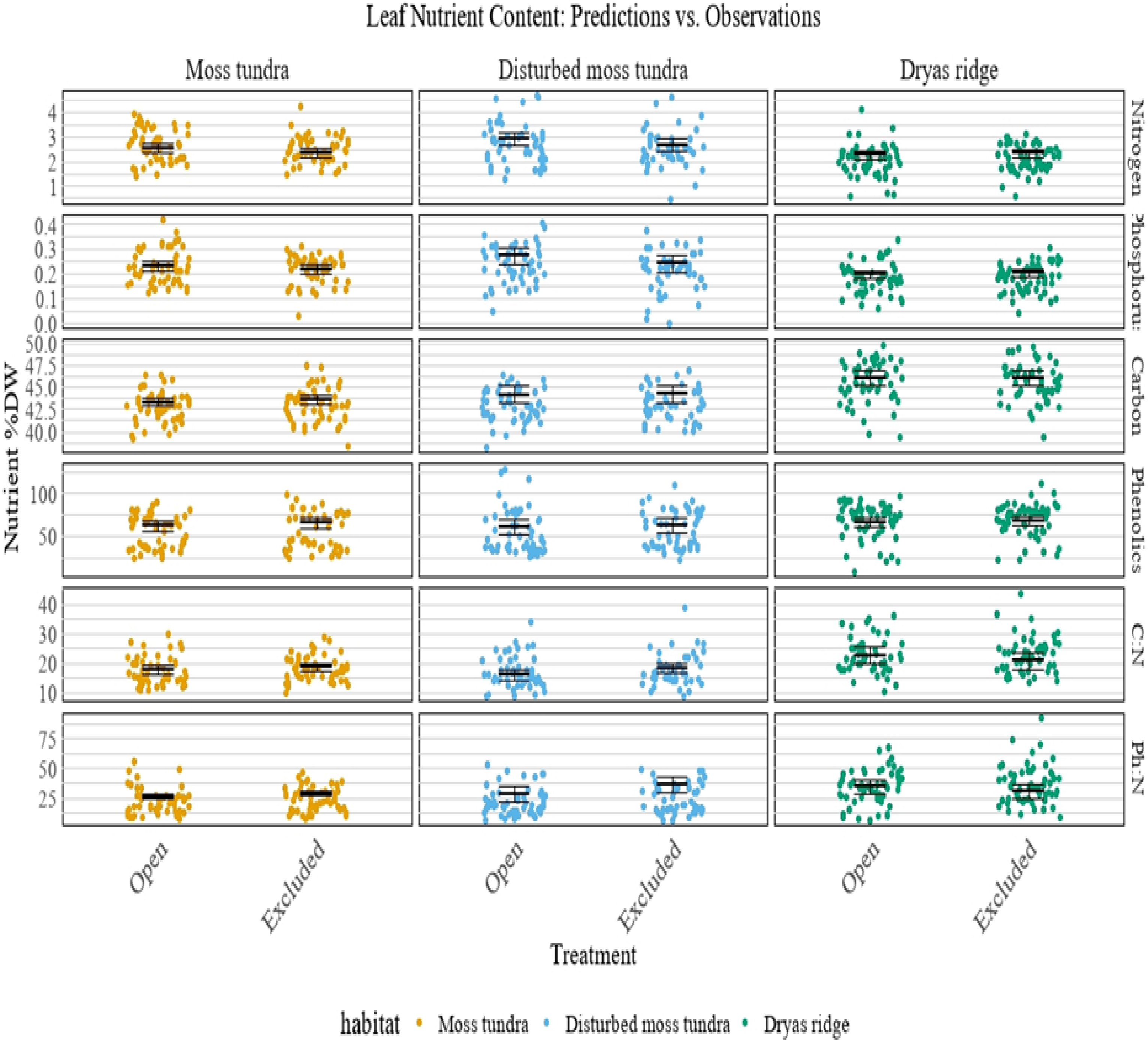


Figure 9 - Model Predictions and Raw Data for Habitat-specific

Grey dashed lines represent model predictions ± standard errors (SE) depicted by black bars, comparing nutrient contents between Open (grazed) and Exclosure treatments. Color-coded dots display raw data values for each habitat type. Please note the varying scales on the y-axes to accommodate natural variations in nutrient contents (DW%).

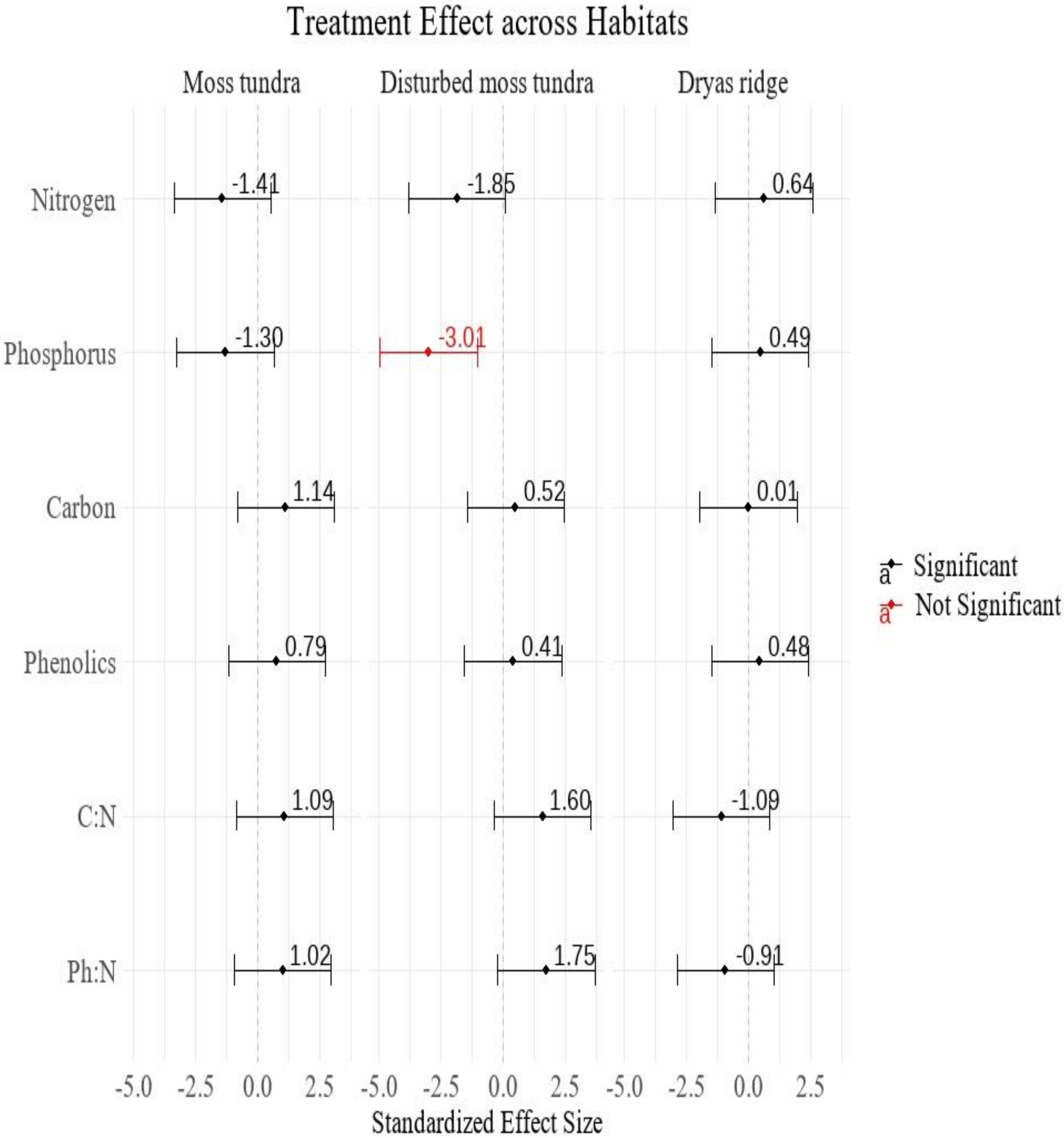


Figure 10 - Standardized Effect Sizes Habitat-specific

The plot displays standardized effect sizes for three habitats: moss tundra, disturbed moss tundra, and dryas ridge, across nutrients and phenolics, including C:N and Ph:N ratios. Error bars show 95% confidence intervals. The 0 line represents the intercept corresponding to the Open treatment (control open to herbivory-grazing), with other variables at their baseline levels. Error bars in red indicate significant differences in herbivory exclosure treatments.

5 Discussion

Our study indicates that short-term exclusion of herbivores, specifically reindeer and geese, elicited weak nutrient and phenolic content responses within different species and habitats. While most nutrient contents showed no significant changes, species-specific analysis revealed significant increases in phenolic levels in *Bistorta vivipara* and phosphorus content in *Dryas octopetala*. Additionally, consistent with our hypothesis, we observed a significant decrease in phosphorus content in the disturbed moss tundra habitat under herbivory exclusion. These findings suggest that Arctic tundra vegetation demonstrates considerable resilience in its nutrient and phenolic content responses to short-term changes in herbivory.

5.1 Species specific response to herbivore exclusion

In line with our hypothesis, herbivory exclusion lead to an increase in leaf phenolics content (DW%) in *Bistorta vivipara*. We anticipated that species with annual leaves would exhibit a quicker response in leaf phenolics compared to those with perennial evergreen leaves, which typically have higher constitutive phenolic defenses (Tuomi et al, 1991). This response in *Bistorta vivipara* is likely due to the herbivory exclusion allowing leaves to progress further phenologically and accumulate phenolics, a process that is enhanced by leaf maturation and the short Arctic summers (Bliss, 1971; A. H. Hansen et al., 2006; Reich, 2014; Sitters et al., 2019).

In line with our expectations, the herbivory exclusion led to increases in leaf phosphorus contents in *Dryas octopetala*, contrasting the non-significant responses in the fast-growing species. This was somewhat unexpected, as previous studies have indicated that fast-growing plant functional types (PFTs) typically respond more rapidly to changes in nitrogen (N) and phosphorus (P) than slow-growing PFTs (Reich, 2014; Sitters et al., 2017). This might be attributed to *Dryas octopetala*'s ability to compensate for inherently low nutrient availability in dryas ridges through its high 'absorption potential' when nutrients become available (Kielland & Chapin, 1992). This capability enables *Dryas octopetala* to rapidly respond to any increase in soil nutrient levels following short-term herbivory exclusion. The brief duration of the exclosure (two years) likely did not permit significant changes in nutrient cycling and plant litter decomposition, which might have allowed faster-growing plant functional types (PFTs) to outcompete *Dryas octopetala* following the release from herbivory

(Stark et al., 2002; van der Wal, 2006). Additionally, the immediate relief from direct mechanical stressors, such as trampling, which significantly impacts evergreen species like *Dryas octopetala*, likely facilitated an increased resource allocation of phosphorus content in its perennial leaves.

The insignificant responses in leaf nutrient and phenolic contents over short-term herbivory exclusion, coupled with no alterations in species palatability based on Ph:N and C:N ratios (Hartley & DeGabriel, 2016, Moreira et al., 2018), support the notion that Arctic ecosystems may exhibit resilience against short-term environmental perturbations (Lamb et al., 2011). Contrasting with previous studies that have reported rapid nutrient content responses in vascular plants to herbivory, particularly by geese (Bazely & Jefferies, 1985; Beard et al., 2019).

5.2 Habitat-specific response to herbivore exclusion

In line with earlier studies (Petit Bon et al., 2023), our study showed that herbivory exclusion in the Arctic typically resulted in minimal changes in leaf nutrient and phenolic contents in the three habitats in question. This finding supports previous observations that the overall impact of herbivory on vegetation in circumpolar regions is typically weak (Bernes et al., 2015) and that the idea of a highly sensitive Arctic-ecosystems may only become evident when relatively high disturbance thresholds are exceeded (Lamb et al., 2011).

This could be attributed to the fact that despite the abundant presence of ungulate herbivores such as reindeer in Svalbard (Van Der Wal et al., 2004), their actual biomass consumption rates remain low. Similar patterns have been observed in muskox populations in Greenland (Mosbacher et al., 2016). However, this contrasts sharply with the more pronounced vegetation responses to herbivory observed in lower Arctic regions, where semi-domesticated reindeer exert significant effects on vegetation nutrient contents and composition (Olofsson et al., 2001).

However, the 2-year herbivory exclusion did lead to significant decreases in phosphorus content in moss tundra habitats previously disturbed by geese, while similar moss tundra habitats without prior geese disturbance did not show change in phosphorus levels (see Figure

10). This pattern aligns with the expectation that previous pulse perturbations (Olofsson et al., 2012), such as geese grubbing, can elevate plant nutrient contents of nitrogen and phosphorus in subsequent summers (Petit Bon et al., 2020, 2022; Ravolainen et al., 2020). The observed decrease in phosphorus, without a corresponding response in nitrogen, challenges the conventional understanding of reindeer herbivory, typically having larger effects on N and driving nutrient-rich habitats, in a more P limited state (Mekuria et al., 2007; Sitters et al., 2017)

5.3 Study limitations

The study's findings are constrained by the brief duration of the herbivory exclusion (two years), which primarily captures short-term herbivory-mediated changes, such as nutrient enrichment through feces. However, this duration may not adequately reflect long-term effects, such as changes in vegetational composition that influence decomposition rates (Chapin & Shaver, 1996; Reich, 2014). These long-term changes are critical for understanding the heterogeneous effects of herbivory, as depicted in Figure 1 (Chapin III, 1991; Stark et al., 2002).

Additionally, the short-term nature of the exclosure increases sensitivity to annual climatic variations (Førland et al., 2011), which can significantly affect biomass production and biogeochemical processes in the Arctic tundra (Van Der Wal & Stien, 2014). Variability within habitats in microbial activity (Lamb et al., 2011), soil nutrient levels as well as interspecific differences between plant species (Albert et al., 2010), are other processes whose influence were not quantified in this study.

Our experimental setup neither accounted for potential herbivore patch choices (Iversen et al., 2014), assuming uniform herbivory effects across the tundra. Additionally, our species-specific analysis overlooked the dietary proportions of dominant species in herbivore diets. Although, *Salix polaris* is found to be a major component in the reindeer diet throughout, particularly in the winter. *Bistorta vivipara* constitutes a smaller portion, making up less than 5% during winter and approximately 11.8% in summer, while *Dryas octopetala* comprises less than 5% year-round (Bjørkvoll et al., 2009). Whilst geese are found to feed on the below-ground storage organs of *Bistorta vivipara* (A. Fox et al., 2006), it might be beneficial a more comprehensive species-specific analysis to include species that are more heavily utilized by both herbivores, such as graminoids—which account between 30% and 60% ± 13.8% of the reindeer diet and are also significant in the diet of migratory geese (Bjørkvoll et al., 2009; A. Fox et al., 2006).

5.4 Future research

With the rising herbivory presence on Svalbard (A. D. Fox & Madsen, 2017a; B. B. Hansen et al., 2013) and rising temperatures altering nutrient cycling rates in the Arctic (Rustad et al., 2001). There is a need for future studies to clarify the inconsistent responses of Arctic vegetation to herbivory reported in various studies (Barthelemy et al., 2015; Van Der Wal et al., 2004).

Extended exclusion studies over longer periods are essential to fully understand the long-term vegetational responses mediated by herbivory and to clarify the observed decreasing tendencies in nitrogen (N) and phosphorus (P) in both moss tundra and disturbed moss tundra, as well as in *Salix polaris* and *Bistorta vivipara* under herbivory exclusion (see Result section). In contrast, *Dryas octopetala* exhibited an increasing tendency in N and a significant increase in P. These divergent responses among habitats and species suggest a potentially heterogeneous effect of herbivores, possibly enhancing vegetation nutrient content levels in moss habitats while retarding them in nutrient-poor dryas ridge habitats, dominated by *Dryas octopetala* (Chapin III, 1991; Stark et al., 2002). However, these findings are currently not statistically significant and may become more pronounced with time.

To improve the accuracy of leaf nutrient response studies across different habitats, I recommend that future studies correct for species-specific responses rather than relying solely on the Plant Functional Type (PFT) framework, which has been found less accurate in Arctic tundra vegetation (Speed et al., 2010). Additionally, incorporating species-specific biomass data could provide a more comprehensive understanding of total plant nutrient contents. It is suggested that Svalbard reindeer initially select for high leaf nitrogen (N) and phosphorus (P) content in early summer but later prioritize biomass over nutrient content as leaves mature through phenological stages (Johnson et al., 2021; Staaland et al., 1983). This perspective is supported by findings from Bon Petit (2023), which observed no changes in leaf nutrient content after reindeer exclusion but significant changes in biomass and, consequently, nutrient pools of the vegetation.

Implementing these methodological adjustments could significantly enhance future research, enabling a more effective exploration of the heterogeneity in Arctic vegetation responses (Myers-Smith et al., 2015). To better our understanding of how herbivory impacts leaf nutrient and phenolic contents, with potential implications for broader ecosystem processes (Olofsson et al., 2004).

6 Conclusion

In conclusion, our study reveals that short-term (two-year) herbivory exclusion in the Arctic results in few significant changes in leaf nutrient contents. Notably, we observed significant increases in phenolic content in *Bistorta vivipara* and phosphorus content in *Dryas octopetala*, as well as a significant decrease in phosphorus in the disturbed moss tundra. These findings highlight the resilience of Arctic tundra vegetation to short-term herbivory impacts. Given the Arctic's sensitivity to environmental changes, a deeper understanding of leaf nutrient dynamics is crucial.

7 References

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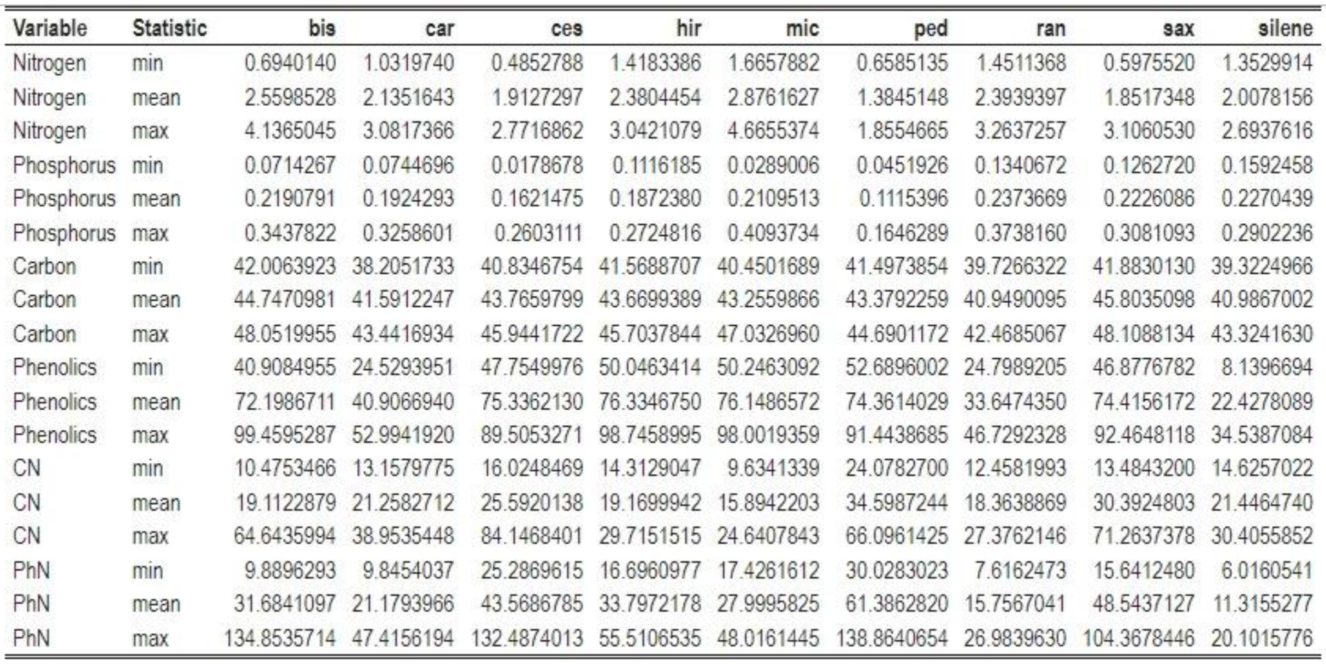
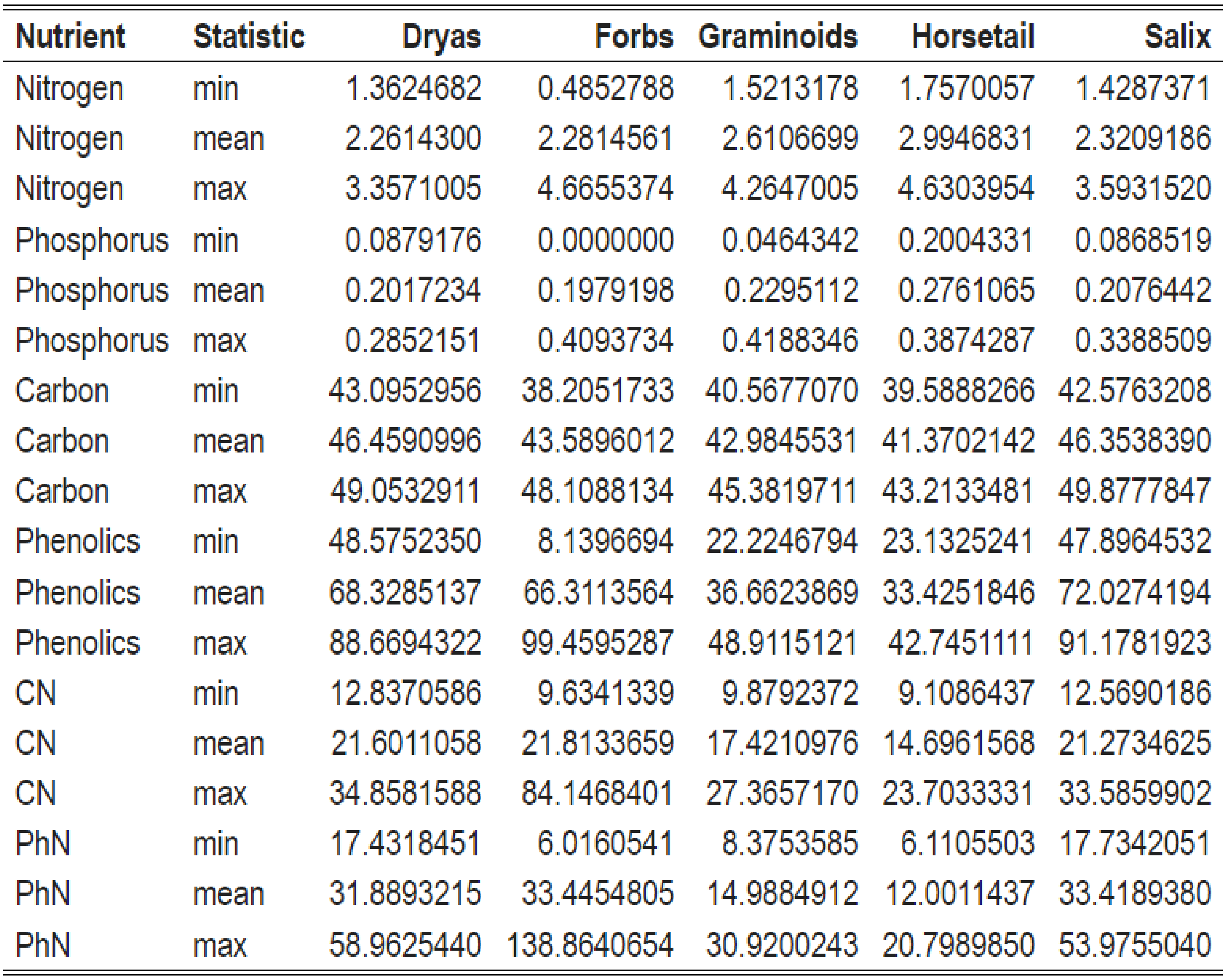
8 Appendix



Variable	Statistic	bis	car	ces	hir	mic	ped	ran	sax	silene
Nitrogen	min	0.6940140	1.0319740	0.4852788	1.4183386	1.6657882	0.6585135	1.4511368	0.5975520	1.3529914
Nitrogen	mean	2.5598528	2.1351643	1.9127297	2.3804454	2.8761627	1.3845148	2.3939397	1.8517348	2.0078156
Nitrogen	max	4.1365045	3.0817366	2.7716862	3.0421079	4.6655374	1.8554665	3.2637257	3.1060530	2.6937616
Phosphorus	min	0.0714267	0.0744696	0.0178678	0.1116185	0.0289006	0.0451926	0.1340672	0.1262720	0.1592458
Phosphorus	mean	0.2190791	0.1924293	0.1621475	0.1872380	0.2109513	0.1115396	0.2373669	0.2226086	0.2270439
Phosphorus	max	0.3437822	0.3258601	0.2603111	0.2724816	0.4093734	0.1646289	0.3738160	0.3081093	0.2902236
Carbon	min	42.0063923	38.2051733	40.8346754	41.5688707	40.4501689	41.4973854	39.7266322	41.8830130	39.3224966
Carbon	mean	44.7470981	41.5912247	43.7659799	43.6699389	43.2559866	43.3792259	40.9490095	45.8035098	40.9867002
Carbon	max	48.0519955	43.4416934	45.9441722	45.7037844	47.0326960	44.6901172	42.4685067	48.1088134	43.3241630
Phenolics	min	40.9084955	24.5293951	47.7549976	50.0463414	50.2463092	52.6896002	24.7989205	46.8776782	8.1396694
Phenolics	mean	72.1986711	40.9066940	75.3362130	76.3346750	76.1486572	74.3614029	33.6474350	74.4156172	22.4278089
Phenolics	max	99.4595287	52.9941920	89.5053271	98.7458995	98.0019359	91.4438685	46.7292328	92.4648118	34.5387084
CN	min	10.4753466	13.1579775	16.0248469	14.3129047	9.6341339	24.0782700	12.4581993	13.4843200	14.6257022
CN	mean	19.1122879	21.2582712	25.5920138	19.1699942	15.8942203	34.5987244	18.3638869	30.3924803	21.4464740
CN	max	64.6435994	38.9535448	84.1468401	29.7151515	24.6407843	66.0961425	27.3762146	71.2637378	30.4055852
PhN	min	9.8896293	9.8454037	25.2869615	16.6960977	17.4261612	30.0283023	7.6162473	15.6412480	6.0160541
PhN	mean	31.6841097	21.1793966	43.5686785	33.7972178	27.9995825	61.3862820	15.7567041	48.5437127	11.3155277
PhN	max	134.8535714	47.4156194	132.4874013	55.5106535	48.0161445	138.8640654	26.9839630	104.3678446	20.1015776

Appendix table 1 - Leaf Nutrient and Phenolic Contents Across Species in Forbs PFT-Group

This figure presents the minimum, mean, and maximum leaf nutrient contents, expressed as a percentage of dry weight (% DW), for each species within the Forbs Plant Functional Type (PFT) group. Detailed species names corresponding to the abbreviations used in the figure are provided in Table 2 of the Methods section.



Nutrient	Statistic	Dryas	Forbs	Graminoids	Horsetail	Salix
Nitrogen	min	1.3624682	0.4852788	1.5213178	1.7570057	1.4287371
Nitrogen	mean	2.2614300	2.2814561	2.6106699	2.9946831	2.3209186
Nitrogen	max	3.3571005	4.6655374	4.2647005	4.6303954	3.5931520
Phosphorus	min	0.0879176	0.0000000	0.0464342	0.2004331	0.0868519
Phosphorus	mean	0.2017234	0.1979198	0.2295112	0.2761065	0.2076442
Phosphorus	max	0.2852151	0.4093734	0.4188346	0.3874287	0.3388509
Carbon	min	43.0952956	38.2051733	40.5677070	39.5888266	42.5763208
Carbon	mean	46.4590996	43.5896012	42.9845531	41.3702142	46.3538390
Carbon	max	49.0532911	48.1088134	45.3819711	43.2133481	49.8777847
Phenolics	min	48.5752350	8.1396694	22.2246794	23.1325241	47.8964532
Phenolics	mean	68.3285137	66.3113564	36.6623869	33.4251846	72.0274194
Phenolics	max	88.6694322	99.4595287	48.9115121	42.7451111	91.1781923
CN	min	12.8370586	9.6341339	9.8792372	9.1086437	12.5690186
CN	mean	21.6011058	21.8133659	17.4210976	14.6961568	21.2734625
CN	max	34.8581588	84.1468401	27.3657170	23.7033331	33.5859902
PhN	min	17.4318451	6.0160541	8.3753585	6.1105503	17.7342051
PhN	mean	31.8893215	33.4454805	14.9884912	12.0011437	33.4189380
PhN	max	58.9625440	138.8640654	30.9200243	20.7989850	53.9755040

Appendix Table 2 - Leaf Nutrient and Phenolic Contents Across PFT Groups

Descriptive statistics of nutrient contents (%) by plant functional trait group. The table presents the minimum, mean, and maximum values of nitrogen, phosphorus, carbon, and phenolic compounds, along with carbon-to-nitrogen (C:N) and phenolic-to-nitrogen (Ph:N) ratios for each specified plant group.

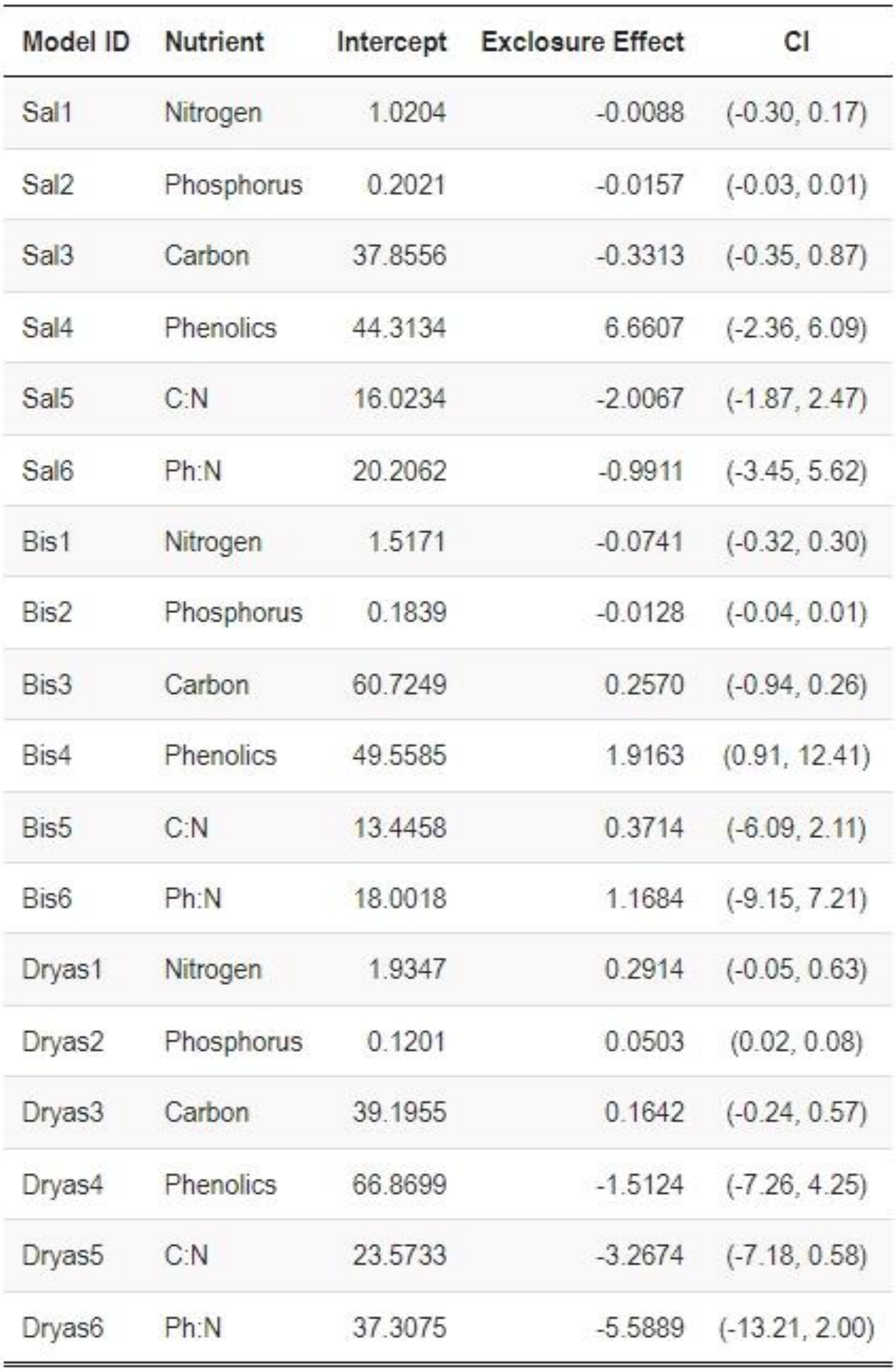
Appendix table 3 – Species Distribution in Nested Site Setup

This figure shows the species *Salix polaris*, *Bistorta vivipara* and *Dryas octopetala* found in each site for both collection years 2021 and 2023 to enable the use of a baseline value. This illustrates the hierarchical nested site setup structure used in the species-specific models, as detailed in the Methods section. The structure involves grouping site numbers within sections, sections within habitats, and so forth.

The nested design led to zero variance issues in some cases, primarily due to the unequal number of levels within our sampling framework. For instance, the figure shows variability in the number of sites and species across different habitats nested within localities. This disparity resulted in insufficient variation in certain nutrients to accurately calculate variance at every hierarchical level, thereby leading to zero variance estimates in some of the models.

Salix, Bistorta & Dryas Distribution

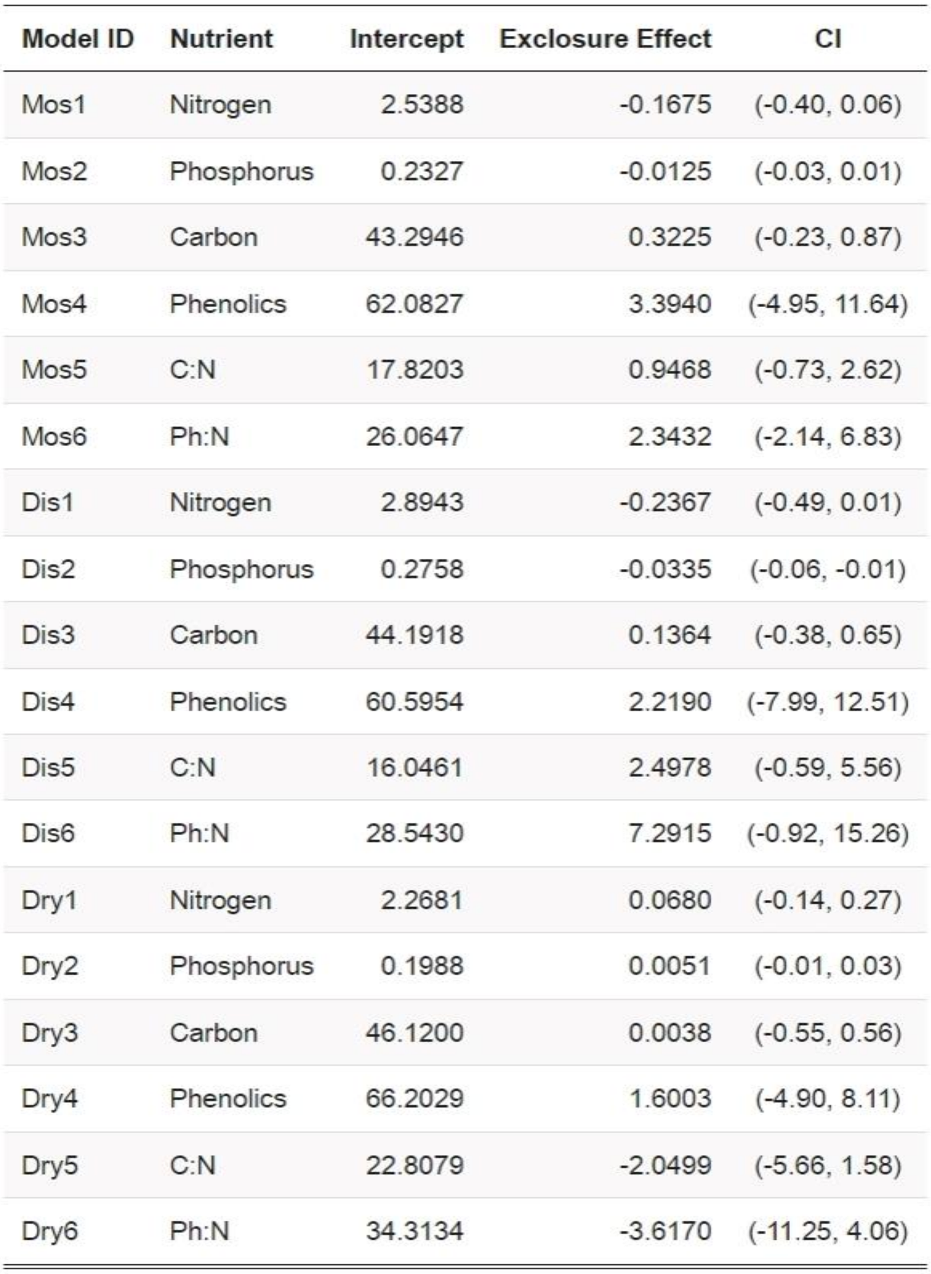
Locality	Habitat	Site	Species
jan	dis	1	Bistorta, Salix
jan	dis	2	Bistorta, Salix
jan	dis	3	Bistorta, Salix
jan	dis	4	Bistorta, Salix
jan	dry	1	Dryas, Bistorta, Salix
jan	dry	2	Dryas, Bistorta, Salix
jan	dry	3	Dryas, Bistorta, Salix
jan	dry	4	Dryas, Bistorta, Salix
jan	dry	5	Dryas, Bistorta, Salix
jan	dry	6	Dryas, Bistorta, Salix
jan	mos	1	Bistorta, Salix
jan	mos	2	Bistorta, Salix
jan	mos	3	Bistorta, Salix
jan	mos	4	Bistorta, Salix
lei	dry	1	Dryas, Bistorta, Salix
lei	dry	2	Dryas, Bistorta, Salix
lei	dry	3	Dryas, Bistorta, Salix
sim	dis	3	Salix
sim	mos	1	Salix
sim	mos	2	Salix
sim	mos	3	Salix
stu	dry	1	Dryas, Bistorta, Salix
stu	dry	2	Dryas, Bistorta, Salix
stu	dry	3	Dryas, Bistorta, Salix



Model ID	Nutrient	Intercept	Exclosure Effect	CI
Sal1	Nitrogen	1.0204	-0.0088	(-0.30, 0.17)
Sal2	Phosphorus	0.2021	-0.0157	(-0.03, 0.01)
Sal3	Carbon	37.8556	-0.3313	(-0.35, 0.87)
Sal4	Phenolics	44.3134	6.6607	(-2.36, 6.09)
Sal5	C:N	16.0234	-2.0067	(-1.87, 2.47)
Sal6	Ph:N	20.2062	-0.9911	(-3.45, 5.62)
Bis1	Nitrogen	1.5171	-0.0741	(-0.32, 0.30)
Bis2	Phosphorus	0.1839	-0.0128	(-0.04, 0.01)
Bis3	Carbon	60.7249	0.2570	(-0.94, 0.26)
Bis4	Phenolics	49.5585	1.9163	(0.91, 12.41)
Bis5	C:N	13.4458	0.3714	(-6.09, 2.11)
Bis6	Ph:N	18.0018	1.1684	(-9.15, 7.21)
Dryas1	Nitrogen	1.9347	0.2914	(-0.05, 0.63)
Dryas2	Phosphorus	0.1201	0.0503	(0.02, 0.08)
Dryas3	Carbon	39.1955	0.1642	(-0.24, 0.57)
Dryas4	Phenolics	66.8699	-1.5124	(-7.26, 4.25)
Dryas5	C:N	23.5733	-3.2674	(-7.18, 0.58)
Dryas6	Ph:N	37.3075	-5.5889	(-13.21, 2.00)

Appendix Table 4 - Species-Specific Model Outputs

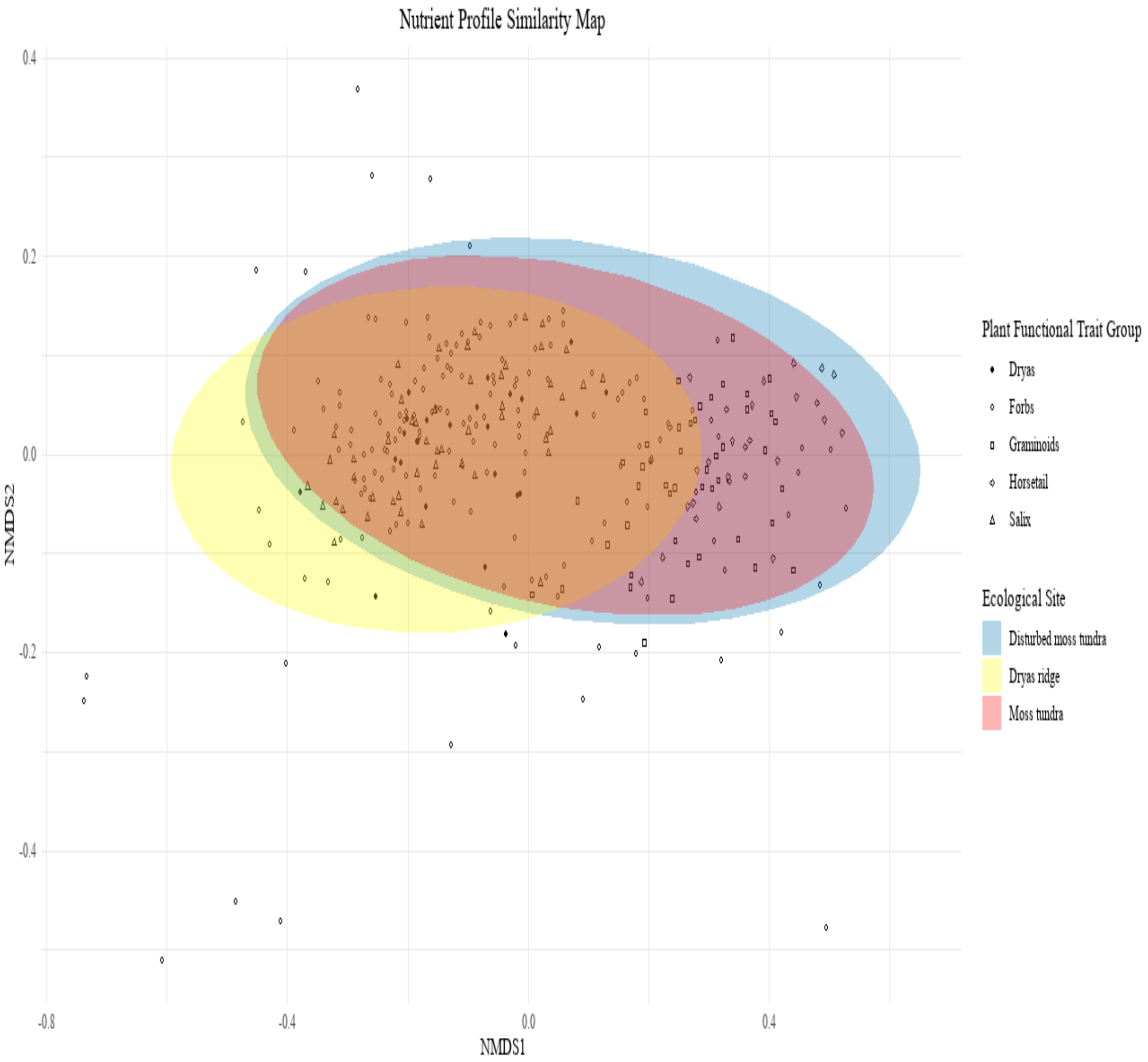
This table displays the outputs from tailored models for each of the three species: *Salix polaris*, *Bistorta vivipara*, and *Dryas octopetala*. Specifically, it presents the intercepts for the treatment level 'grazed' and the estimates of the effect of herbivory exclosure on nitrogen, phosphorous, carbon, phenolics and the ratios C:N and Ph:N. Each entry includes a model ID for reference, and the estimates for herbivory exclosure effects are accompanied by their respective confidence intervals (CI).



Model ID	Nutrient	Intercept	Exclosure Effect	CI
Mos1	Nitrogen	2.5388	-0.1675	(-0.40, 0.06)
Mos2	Phosphorus	0.2327	-0.0125	(-0.03, 0.01)
Mos3	Carbon	43.2946	0.3225	(-0.23, 0.87)
Mos4	Phenolics	62.0827	3.3940	(-4.95, 11.64)
Mos5	C:N	17.8203	0.9468	(-0.73, 2.62)
Mos6	Ph:N	26.0647	2.3432	(-2.14, 6.83)
Dis1	Nitrogen	2.8943	-0.2367	(-0.49, 0.01)
Dis2	Phosphorus	0.2758	-0.0335	(-0.06, -0.01)
Dis3	Carbon	44.1918	0.1364	(-0.38, 0.65)
Dis4	Phenolics	60.5954	2.2190	(-7.99, 12.51)
Dis5	C:N	16.0461	2.4978	(-0.59, 5.56)
Dis6	Ph:N	28.5430	7.2915	(-0.92, 15.26)
Dry1	Nitrogen	2.2681	0.0680	(-0.14, 0.27)
Dry2	Phosphorus	0.1988	0.0051	(-0.01, 0.03)
Dry3	Carbon	46.1200	0.0038	(-0.55, 0.56)
Dry4	Phenolics	66.2029	1.6003	(-4.90, 8.11)
Dry5	C:N	22.8079	-2.0499	(-5.66, 1.58)
Dry6	Ph:N	34.3134	-3.6170	(-11.25, 4.06)

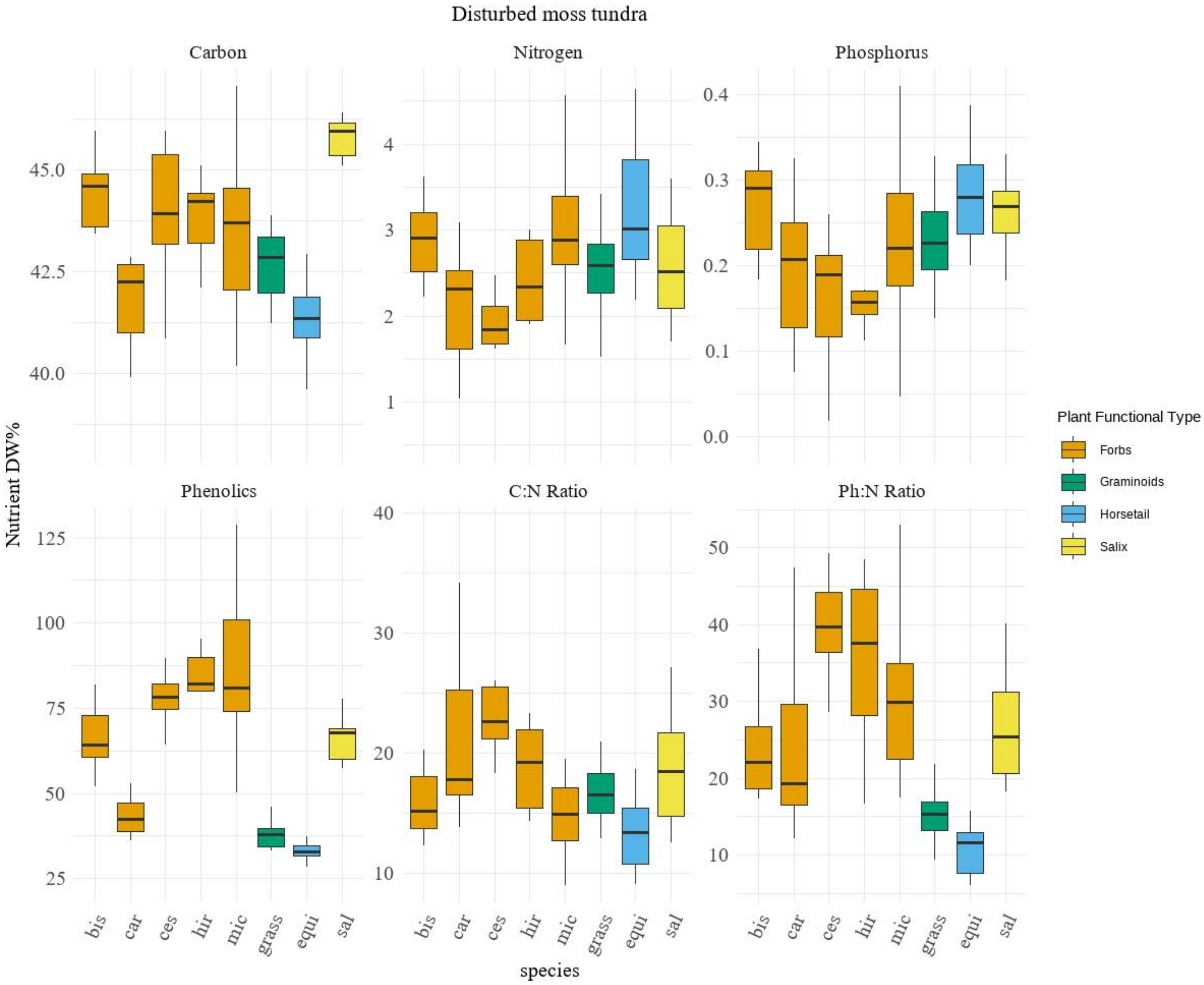
Appendix Table 5 - Habitat-Specific Model Outputs

This table displays the outputs from tailored models for each of the three habitats: moss tundra, disturbed moss tundra and dryas ridge. Specifically, it presents the intercepts for the treatment level 'grazed' and the estimates of the effect of herbivory exclosure on various nutrients. Each entry includes a model ID for reference, and the estimates for herbivory exclosure effects are accompanied by their respective confidence intervals (CI).



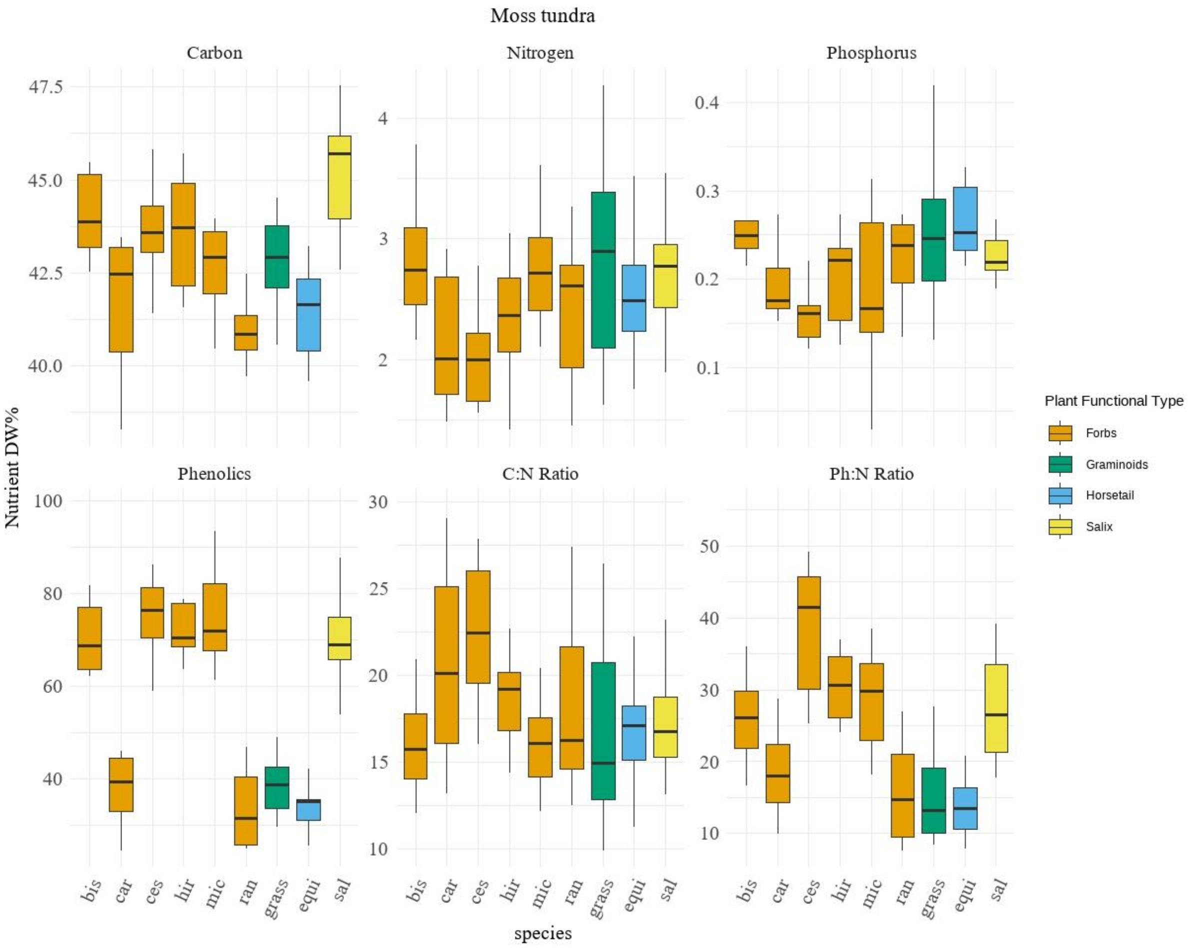
Appendix Figure 1 – NMDS Plot Colorblind Version

This is the colorblind corrected NMDS plot, using different shapes to indicate the different Plant Functional Trait groups. Further on illustrating nutrient profiles (%DW) across three habitats: moss tundra, disturbed moss tundra, and dryas ridge. The plot is organized along two dimensions that capture the greatest variation in nutrient content (%DW) among the sampled species. The species are represented by PFT based color-coded dots, with proximity indicating similarity in nutrient profiles. Both axis are abstract dimensions that reflect relative similarities and differences in nutrient profiles.



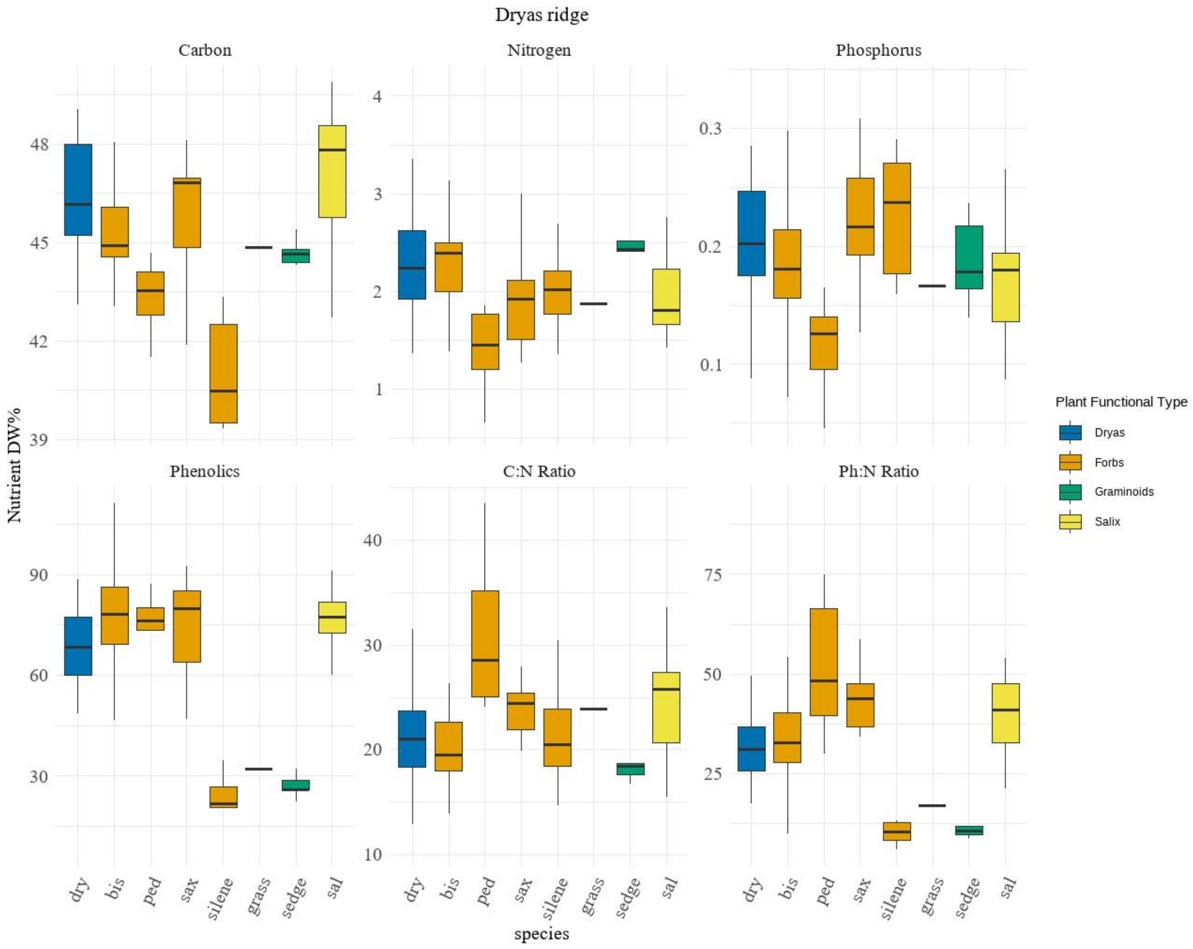
Appendix Figure 2 - Leaf Nutrient and Phenolic Contents DW% in Disturbed Moss Tundra

This figure presents boxplots of leaf nutrient contents for each species located within the disturbed moss tundra habitat. The nutrients in question are displayed on varying y-axis scales to accommodate differences in their ranges. Each boxplot includes error bars representing the 95% confidence intervals and a horizontal line indicating the mean nutrient content.



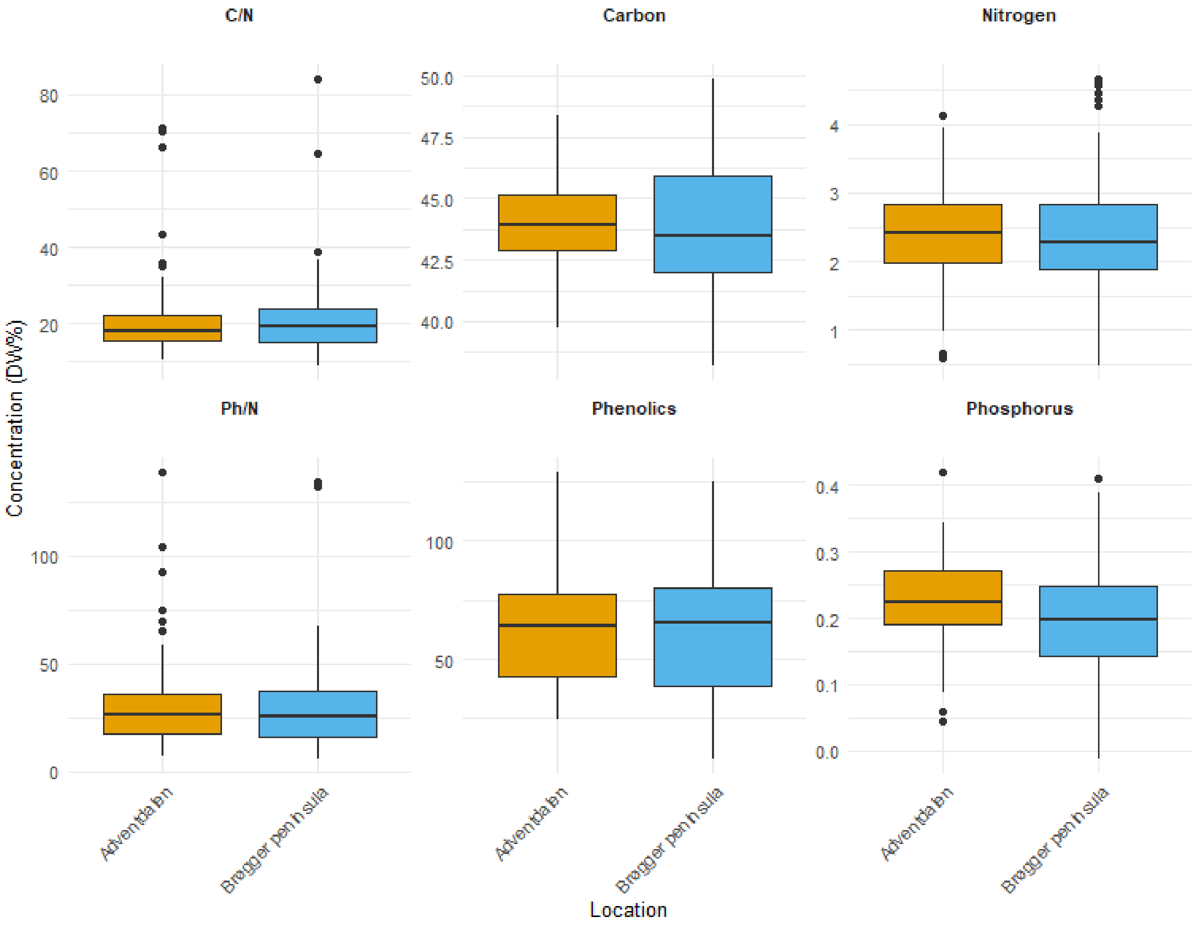
Appendix Figure 4 - Leaf Nutrient and Phenolic Contents DW% in Moss Tundra

This figure displays boxplots of leaf nutrient contents for each species situated within the moss tundra habitat. To accommodate the diverse ranges of the nutrients, different y-axis scales are used. Each boxplot is equipped with error bars illustrating the 95% confidence intervals and includes a horizontal line that represents the mean nutrient content.



Appendix Figure 4 - Leaf Nutrient and Phenolic Contents DW% in Dryas Ridge Tundra

This figure showcases boxplots of leaf nutrient contents for each species found within the dryas ridge habitat. The nutrients are depicted on distinct y-axis scales to reflect variations in their concentration ranges. Each boxplot features error bars that denote the 95% confidence intervals, with a horizontal line marking the mean nutrient content.



Appendix Figure 5 - Leaf Nutrient and Phenolic Contents by Location

This figure illustrates the leaf nutrient contents, expressed as a percentage of dry weight (% DW), for the specified nutrients across two distinct locations: Adventdalen and Brøgger Peninsula. Note the varying scales on the y-axes to accommodate the substantial differences in nutrient values between locations.

The analysis reveals no significant or notable differences in nutrient contents between the two locations. This consistency supports the validity of comparing different habitat types across Adventdalen and Brøgger Peninsula without location-based bias.