

# Impact of climate warming on Arctic plant diversity: phylogenetic diversity unravels opposing shrub responses in a warming tundra

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## ABSTRACT

The Arctic biome is at significant risk, with recent observations suggesting that climate change is warming the Arctic nearly four times faster than the global average. Last decade, evidence from experimental warming studies and observations of ambient warming over time shows how increasing air temperature in the Arctic has led to changes to arctic vegetation, and encroachment of trees and shrubs into the tundra. Thus, this amplified Arctic warming is threatening biodiversity, changing vegetation patterns, and thawing permafrost with implications for carbon and nutrient dynamics. These are one of the main concerns of observed plant biodiversity changes (except the loss of biodiversity itself) as they feedback on the global climate through their effects on carbon cycling, albedo, and ecosystem energy balance. Studies of Arctic biodiversity have reported responses in either taxonomic, functional, or phylogenetic diversity, though phylogenetic has so far been understudied in the Arctic. These different measures of quantifying biodiversity will vary in their explanatory value and can have complementary value when looking at the implications of vegetation changes. The overall aim of this thesis is to deepen the knowledge of the effect of ambient and experimental climate warming on taxonomic, functional, and phylogenetic aspects of plant diversity within and between communities.

In Latnjajaure (northern Sweden) I used a long-term passive warming experiment using open-top chambers, which include five distinct plant communities. The communities had distinct soil moisture conditions, leading to community-specific responses of the plant growth forms (deciduous shrubs, evergreen shrubs, forbs, and graminoids) and phylogenetic dissimilarity. Moist communities tended to decrease in soil moisture, which drove similarity to dryer, more nutrient-poor communities. Warming significantly affected growth forms, but the direction of the response was not consistent across the communities. Evidence of shrub expansion was found in nearly all communities, with soil moisture determining whether it was driven by deciduous or evergreen shrubs. These changes are expected to affect climate feedback as the dry, evergreen-dominated heath community, has slower carbon cycling. This slowdown in carbon cycling is at least partially due to the evergreen shrubs whose material is harder to decompose than most other arctic vegetation. As the studied communities are common in the region, it is likely that future warming will drive community shifts in the tundra landscape.

On a Pan-arctic dataset of warming studies, I explored the effect of scaling abundance weighting as well as the importance of deeper against shallow nodes in the phylogeny on warming response and its interaction with soil

moisture and site temperature in the tundra biome. For all metrics, we looked at both plot level ( $\alpha$ -diversity), and the difference between plots ( $\beta$ -dissimilarity). We show that  $\beta$ -dissimilarity is more sensitive to warming than  $\alpha$ -diversity metrics. Furthermore, we show that sensitivity to abundance and phylogenetic weighting depends on local soil moisture conditions.

In conclusion, the combined use of taxonomic, phylogenetic, and functional diversity measures enhances the quality of our assessment of the implications of arctic vegetation response to warming.

## SAMMANFATTNING

Nya forskningsrön visar att det arktiska landskapet värms upp nästan fyra gånger snabbare än det globala genomsnittet till följd av klimatförändringar. Under det senaste decenniet har experiment med simulerad temperaturökning och dess påverkan på omgivande vegetation visat att den ökade lufttemperaturen i den arktiska regionen har lett till förändringar i vegetation, där träd och buskar gjort intåg på tundran. Den snabba uppvärmningen kring polerna hotar den biologiska mångfalden, ändrar vegetationsmönstret, tinar permafrosten samt har konsekvenser på kol och näringsomsättningen. Detta är några av de största utmaningarna med de observerade förändringarna (utöver förlusten av mångfald i sig självt) då det bidrar till den globala uppvärmningen genom sin påverkan på kolinlagring samt ekosystemens energi- och strålningsbalans. Idag visar flera studier på förändringar i den arktiska mångfalden avseende både taxonomiska, funktionella och evolutionära egenskaper, även om de evolutionära egenskaperna hitintills inte har studerats särskilt mycket i Arktis. Dessa olika metoder för att kvantifiera biologisk mångfald varierar i syfte och kan ha kompletterande värde när det kommer till att studera påverkan på vegetationen. Det övergripande syftet med den här avhandlingen är att fördjupa kunskapen kring effekten av naturlig och experimentell uppvärmning sett till taxonomiska, funktionella samt evolutionära aspekter av den biologiska mångfalden inom och mellan växtsamhällen.

I Latnajajaure (beläget i norra Sverige) använde jag miniväxthus, så kallade Open-Top Chambers, för att simulera långtidseffekter av uppvärmning. Experimentet inkluderade fem växtsamhällen med varierande markfuktighet, vilket ledde till samhällsspecifika responser inom växtfunktionella grupper (lövfällande buskar, vintergröna buskar, örter och graminider) och genetisk olikhet. Fuktiga vegetationstyper tenderade att få reducerad markfuktighet, vilket ledde till likheter med torrare, mer näringsfattiga vegetationstyper. Uppvärmningen påverkade i hög grad de olika växtformerna, även om responsgraden inte var stringent inom vegetationstyperna. Förbuskning observerades i nästan alla samhällen, där markfuktigheten avgjorde om den utgjordes av lövfällande eller vintergröna buskar. Dessa förändringar har konsekvenser för klimatförändringarna då de torra, vintergröna samhällena har en långsammare kolomsättning, vilket delvis beror på att förna från vintergröna växter är svårare att bryta ner jämfört med övrig arktisk vegetation. De studerade vegetationstyperna är vanligt förekommande i den arktiska regionen och det är troligt att framtida uppvärmning kommer att driva på förändringar av tundravegetationen.

Genom att använda Pan-arktiska data från tjugofem fältstationer över hela Arktis, där en måttlig temperaturökning simulerar den klimatuppvärmning som förutspås av FN:s klimatpanel till år 2050, studerade jag hur olika evolutionära processer påverkar den evolutionära mångfalden i Arktis. Över hela datasetet undersökte jag hur både mångfalden på försöksrutenivå ( $\alpha$ -diversitet) och skillnaden mellan försöksrutor ( $\beta$ -diversitet) påverkas av uppvärmning. Resultaten visar att  $\beta$ -diversitet är mer känslig för uppvärmning än  $\alpha$ -diversiteten. Vidare visar jag att känslighet för skalning och evolutionär viktning beror på lokala markfuktighetsförhållanden.

Genom att använda en kombination av taxonomiska, fylogenetiska och funktionella mångfaldsmått så förbättras vår förståelse om hur den arktiska vegetationen reagerar på klimatförändringarna.





## LIST OF PAPERS

This thesis is based on the following papers, referred to in the text by their Roman numerals. Note that co-author contributions are described in more detail within the respective papers.

**Paper I: Scharn, R.**, Little, C.J., Bacon, C.D., Alatalo, J.M., Antonelli, A., Björkman, M.P., Molau, U., Nilsson, R.H., and Björk, R.G. (2021). Decreased soil moisture due to warming drives phylogenetic diversity and community transitions in the tundra. *Environmental Research Letters*, 16, 064031.

**RS**, contributed to conceiving the idea for the paper and the collection of plant abundance data. He also led the data analysis and writing of the paper.

**Paper II: Scharn, R.**, Brachmann, C.G., Patchett, A., Reese, H., Bjorkman, A., Alatalo, J., Björk, R.G., Jägerbrand, A.K., Molau U., and Björkman M.P. (2021). Vegetation responses to 26 years of warming at Latnjajaure Field Station, northern Sweden. *Arctic Science*:1-20.

**RS**, contributed to conceiving the idea for the paper and the collection of plant abundance data. He also led the data analysis and equally contributed to the writing of the paper.

**Paper III: Scharn, R.**, Negri, I.S., Sundqvist, M.K., Løkken, J.O., Bacon, C.D., Antonelli, A., Hofgaard A., Nilsson R.H., and Björk, R.G. (2022). Limited decadal growth of mountain birch saplings has minor impact on surrounding tundra vegetation. *Ecology and Evolution*, 12, e9028.

**RS**, contributed to conceiving the idea for the paper, co-supervised internship student, led the data analysis, and equally contributed to the writing of the paper.

**Paper IV: Scharn, R.**, Töpel, M., Bjorkman, A., Ou, T., and Björk R.G. (*with contribution of the ITEX consortium*). Plant abundance drives  $\beta$ -diversity changes in the Arctic. *Manuscript*

**RS**, led the conception of the paper. He also led the data analysis and writing of the paper of the first draft.

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# 1 INTRODUCTION

## 1.1 BIODIVERSITY

Biodiversity is nothing more than the variation we observe in the living natural world around us (Faith, 2008). On the surface it is a very intuitive concept, but biodiversity is hard to quantify practically.



*Figure 1. Arctic plot with warming (open top chamber)*

Let us, for the moment, assume that I am somewhere in the Arctic tundra, and you ask me to describe what I see. I report that I see five different species from my viewpoint (Fig.1). This information does not help much considering the goal is to enable you to picture what I am seeing. If I then expand on what species are present or describe that there are three different shrub species, one species of grass, and a herb, the picture becomes slightly clearer. Finally, when I give information on the cover of each species and maybe the average height or the fact that two individual shrubs are bearing a (white) flower, you have a pretty good idea of what I am looking at. All the steps I described above are components of biodiversity and together facilitate a good, albeit not perfect visual description. Thus, biodiversity is a multidimensional concept that cannot be reduced to a single number, and its value depends on the question or goal (Purvis and Hector, 2000). Commonly used metrics can be grouped into different aspects of biodiversity (Le Bagousse-Pinguet et al., 2019):

- **Taxonomic diversity**, such as species richness (number of species), and their abundance.

- **Functional diversity**, such as functional groupings (e.g., shrubs or grasses), which are assumed to affect and be affected by their environments in a similar way (Chapin et al., 1996). Or alternatively, functional traits; characteristics of organisms that explain their responses to the environment as well as their effect on their environment (e.g., Size and Leaf area; Díaz et al., 2013).
- **Phylogenetic diversity** incorporates the diversity of evolutionary lineages. Where shared heritage increases feature similarity among species and vice versa (e.g., we are most similar to chimpanzees because we have a recent common ancestor). Thus, a community with tigers and chimpanzees is more diverse than a community with chimpanzees and humans because chimpanzees and tigers have a less shared heritage and therefore share fewer (ecologically relevant) features (or traits). An expanded explanation of the use of phylogenetics in ecology can be found in box 1.

Any metric relating to any of these aspects of biodiversity is potentially useful. However, as their use depends on the value of interest, it is essential to understand not just how biodiversity is expected to change in the tundra but also what our values of interest are in the context of tundra climate change.

Another important concept related to biodiversity is scale, commonly grouped into  $\alpha$  (local or community level),  $\beta$  (between communities), and  $\gamma$  (the broader regional species pool) diversity (Whittaker, 1972). In the context of this thesis,  $\alpha$  diversity can be seen as plot-level diversity (e.g., the number of species within a given plot when using species richness). In the same context, the  $\beta$  diversity between two plots would be the number of species not shared. For example, let us say I have one plot containing a dog and a chicken and one containing a dog, a horse, and a cat. Plot I has an  $\alpha$  diversity of 2, and plot II has an  $\alpha$  diversity of 3. The difference in  $\alpha$  diversity is 1 (2 compared to 3), and the  $\beta$  diversity is 3 (chicken + horse + cat). It is important to note that the plot size heavily affects measurements of  $\alpha$  and  $\beta$  diversity. Using larger plots increases the chance of capturing more species, thereby increasing the measured  $\alpha$  diversity which also affects  $\beta$  diversity. However, the outcome depends on the similarity of communities (Magurran, 2004). Though I used species richness in the example above, plot size will affect  $\alpha$  and  $\beta$  diversity for most biodiversity metrics (Magurran, 2004).

**Box 1. Phylogenetics in ecology**

The use of phylogenetic information gives us a way to quantify differences between species. Basically, using Darwinian trees that denote species relationships, under the assumption that species are more ecologically different from one another the more time that has passed since two species shared a common ancestor (Webb et al., 2002, Cadotte et al., 2008). This gives us a tool to measure differences between assemblages even with limited species overlap. Measures of phylogenetic diversity (PD) have shown to be good predictors of ecological functioning in grasslands (Flynn et al., 2011, Cadotte, 2013) and forests (Steudel et al., 2016, Satdichanh et al., 2019), as well as a variety of functional plant traits (Devictor et al., 2010, Kembel and Cahill Jr, 2011). PD can also capture unknown traits important for ecological function and thus has the potential to provide a more holistic image than targeted functional traits (Devictor et al., 2010). However, on a global scale, the predictive value of PD on functional diversity (FD) shows a high variation (Mazel et al., 2018, Devictor et al., 2010). This is because PD can be decoupled from FD, through long stabilizing selection or the coexistence of closely related species, which can increase dispersion in traits (Losos et al., 2003, Prinzing et al., 2008). Thus, the strength of these relations depends on the focal area, the evolutionary history of its biota, and geographical scale (Cavender-Bares et al., 2009), and should be approached on a case-by-case basis.

## 1.2 THE TUNDRA BIOME

The tundra is found beyond the cold range limit of trees. Because of their height, trees do not experience the benefit of the heat accumulated through solar radiation close to the ground; this means that they experience harsher conditions than tundra vegetation which consists of low-stature shrubs, forbs (herbs), grasses, mosses, and lichens (Körner, 2020). On a global level, tree lines are heavily temperature-driven, generally coinciding with an average growing season temperature of 6 °C, and are thus heavily driven by temperature (Körner, 2021). Tundra vegetation experiences long winters, a short growing season, and thus limited time for reproduction and recovery of energy stores (Russell, 1940). As conditions get harsher with increasing latitude or altitude, tundra vegetation gets more sparse and lower in stature until only sparse patches of mosses or lichens eventually remain. The point where shrubs stop growing or “shrubline” is commonly used to delimit the boundary between low and high arctic as well as between the mid and high alpine zones (Bliss, 1962, Körner, 2020). Contrary to the treeline however, the shrubline is not defined purely by growing season temperature. For instance, snow can heavily affect local vegetation as it can protect plants from frost and provides soil moisture in spring (Happonen et al., 2022). On the contrary, too much snow can delay the growing season further as it takes too long to melt out. Snowfall is also one of the main differentiators between the Arctic and alpine tundra areas. The scarcity of snow cover in the Arctic tundra can lead to permanently frozen soil (permafrost) after snowmelt, leading to drier spring conditions (Kullman, 1989). Mountain areas at the fringes of the Arctic tundra naturally extend the vegetation beyond its southern limit at sea level. This vegetation is closely related to the Arctic tundra due to its proximity but is nonetheless affected by the same processes that structure the Alpine tundra (Virtanen et al., 2016). The resulting vegetation is distinctly different from both and is commonly referred to as oroarctic tundra (oro- mountain from Greek oros; Ahti et al., 1968).

Similar to biomes such as “temperate forests” or “grasslands “ globally, the tundra biome contains a lot more variation within the broad categories described here (see Walker et al., 2005). Consequently, any generalization of tundra response to perturbation will be similarly broad; accurate, but not precise. Moreover, due to the harsh climate conditions in the tundra, research tends to focus on a few accessible research sites (Metcalf et al., 2018). Even though patchy research is a natural consequence of the limitations of working in the tundra, we need to stay mindful that we are looking at the tundra through a biased lens.

## 1.3 ARCTIC CLIMATE CHANGE

The Arctic has warmed nearly four times faster than the global average (Rantanen et al., 2022) and is expected to warm further by between 2.4°C (SSP1-1.9) and 10°C (SSP5-8.5) by 2081-2100 (Lee et al., 2021). Arctic amplification is one of the main drivers behind this disproportionate increase in mean surface air temperature. It is related to various positive feedback loops often associated with the extent of Arctic sea ice. The complex nature of these interactions makes it hard to quantify their relative importance, but the main elements are commonly believed to be (Serreze and Barry, 2011, Goosse et al., 2018) :

- Sea ice extent. An increase in exposed ocean surface; decreasing sea ice cover removes the insulating ice cover from the relatively warm ocean, which increases heat transfer between ocean and surface air and thus surface air temperature (Serreze and Barry, 2011).
- Surface albedo. A decrease in surface albedo; the reduced sea ice cover exposes the underlying ocean. The lower albedo of the ocean surface reduces the reflection of short-wave radiation (sunlight), which in turn contributes to warming. The same feedback mechanism can be observed over land related to reduced snow cover and more vegetation.
- Water vapor content. An increase in air water vapor content; the increase in ice-free ocean also allows for more evaporation, combined with increased rates of water vapor transport from lower latitudes results in increased warming through the trapping of longwave radiation (this process outweighs the albedo decreasing effect of the increased cloud cover associated with higher water vapor content, in all seasons but summer; Park et al., 2015).
- Horizontal heat flux. An increase in the transport of warm and moist air from lower latitudes (Park et al., 2015, Graversen et al., 2008).

The relative importance of these processes varies by season. For instance, albedo is not as relevant during the polar winter because of the absence of sunlight. Whereas the effect of water vapor during this period is stronger as it is not offset by the albedo associated with increased cloud cover. Furthermore, the strength of Arctic amplification varies over the seasons but is greatest in winter (Bekryaev et al., 2010). Thus, arctic vegetation has to contend with the amplification of global warming and a large temporal variability as to its intensity.

## 1.4 VEGETATION RESPONSE TO CLIMATE CHANGE

This amplified global warming has many consequences for arctic vegetation (Post et al., 2009). Lower latitude vegetation adapted to slightly warmer conditions has been moving northward in the Arctic. This has been most visible in the movement of the treeline and the rapid advancement of various species of tall shrubs; also called shrubification (Tape et al., 2006). Synthesis studies of tundra plant warming response revealed biome-wide patterns such as increases in plant height and the abundance of taller growth forms, such as shrubs, at the cost of prostrate growth forms such as lichen and bryophytes (Walker et al., 2006, Elmendorf et al., 2012a, Elmendorf et al., 2012b). Furthermore, a study looking at seven functional traits found a shift toward taller plants with more resource acquisitive leaves in moist and wet communities (Bjorkman et al., 2018). These changes can heavily impact the feedback of tundra vegetation on climate. For instance, more resource acquisitive leaves tend to be easier to decompose by microbes, which leads to faster carbon cycling (Happonen et al., 2022). Similarly, higher vegetation captures more snow which warms the soil and can increase decomposition during winter (Cornelissen et al., 2007). On the other hand, the increase in woody vegetation might slow down decomposition due to the recalcitrant nature of wood. Similarly, an increase in evergreen rather than deciduous shrubs can lead to a slowdown in decomposition due to the lower decomposability of their leaves (Vowles and Björk, 2019). Thus, one of the main concerns of observed plant biodiversity changes (except the loss of biodiversity itself) in the Arctic is associated with potential feedback on the global climate through their effects on carbon cycling, albedo, and ecosystem energy balance.



## 2 AIM

Climate change in the tundra biome has a wide variety of effects on biodiversity. As biodiversity is multidimensional, it is essential to compare and contrast different aspects of biodiversity to identify how they relate to one another and our values of interest. The research presented here contributes to understanding the effect of ambient and experimental climate warming on taxonomic, functional, and phylogenetic aspects of plant diversity within and between communities. I address these questions in more detail in the following papers:

### *Paper I*

Paper one aimed to explore the use of phylogenetic diversity in identifying potential community shifts over a moisture gradient in the tundra biome. I also aimed to identify the possible consequences of these shifts by interpolating on known characteristics of these communities.

### *Paper II*

Paper two aimed to compare local patterns in the relative abundance of vascular plant functional groups with globally observed patterns within the tundra biome over a moisture gradient. Additionally, I aimed to contrast the patterns observed in long-term ambient plots with expectations from experimental warming and fertilization.

### *Paper III*

The aim of paper three was to assess whether encroachment of tree saplings in the tundra affected vascular plant community structure within taxonomic and phylogenetic diversity between and within communities.

### *Paper IV*

In paper four, I aimed to scale up and identify where taxonomic and phylogenetic diversity was most sensitive to experimental warming. I explored the effect of scaling abundance weighting and the importance of deep against shallow nodes in the phylogeny on warming response and its interaction with soil moisture and site temperature in the tundra biome.

### 3 METHODS

#### 3.1 STUDY AREA

**Paper IV** covers 71 plant communities located in 21 sites distributed throughout the circumpolar Arctic and northern temperate alpine regions (Fig. 2). Together, these sites cover a large range of growing season air temperatures (2 - 15°C) and precipitation (204 - 927 mm/year). Though these sites cover many plant communities and environmental conditions, there are also clear gaps in the distribution of included sites (most notably the Arctic coastline of Russia).

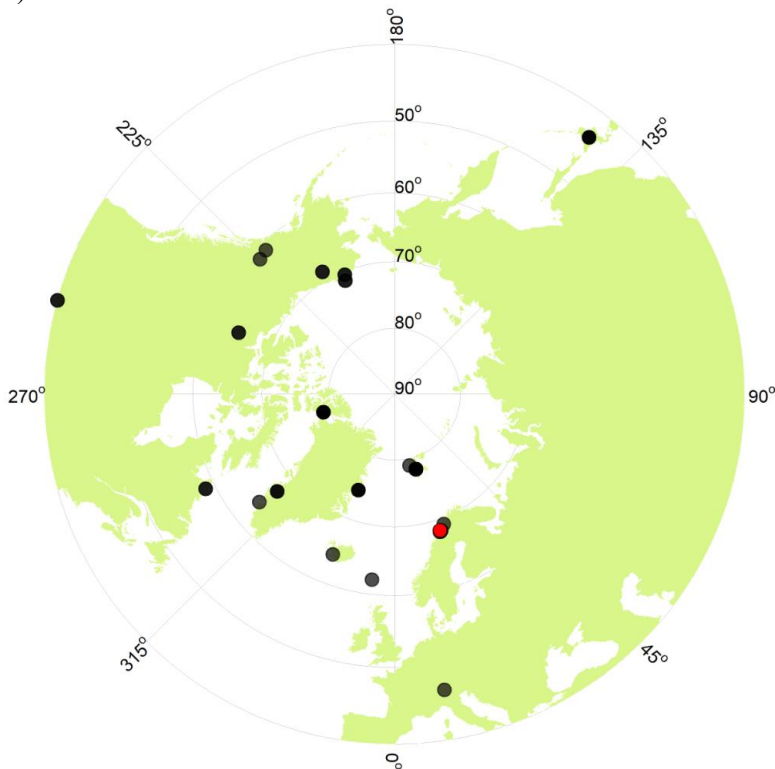


Figure 2. Locations of all 71 included in-situ warmed plant communities within 21 survey sites used in **paper IV** (Alexandra Fiord, Daring Lake, Kluane, Torngat Mountains, and Wolf Creek (Canada); Kilpisjärvi (Finland); Kangerlussuaq, and Zackenberg (Greenland); Adventdalen, Endalen and Ny-Ålesund (Norway); Sornfelli (Faroe Islands); Thingvellir (Iceland), Taisetsu Mountains (Japan); Abisko and Latnjajaure (Sweden); Val Bercla (Switzerland); Atkasuk, Barrow, Niwot Ridge, and Toolik Lake (U.S.)). Latnjajaure (paper **I-III**) is highlighted in red.

**Papers I-III** focus on Latnjajaure Field Station (LFS), located in the Latnjavagge basin (Fig. 2, highlighted in red). Latnjavagge is a periglacial drainage basin representative of mountainous tundra environments in northernmost Swedish Lapland (68.35°N, 18.49°E). The entire basin is approximately 9 km<sup>2</sup>, with the valley floor at approximately 950 m above sea level and peaks as high as 1440 m.

The long-term mean annual air temperature for LFS is  $-1.7\text{ }^{\circ}\text{C}$ , with February as the coldest month (average  $-9.7\text{ }^{\circ}\text{C}$ ) and July as the warmest month (average  $8.6\text{ }^{\circ}\text{C}$ ), with a low but significant increase of  $0.3\text{ }^{\circ}\text{C}$  per decade (Fig. 3). The LFS mean growing season (June–August) and non-growing season (September–May) temperatures also show increasing trends, both with a mean increase of  $0.2\text{ }^{\circ}\text{C}$  per decade, but these trends are not statistically significant. Annual precipitation ranges from 600 mm to 1100 mm with an average of 855 mm and no discernible trends over the investigated period, and thus, are higher than what is recorded in Abisko, which is situated in the rain shadow during westerly air flows (Callaghan et al., 2010).

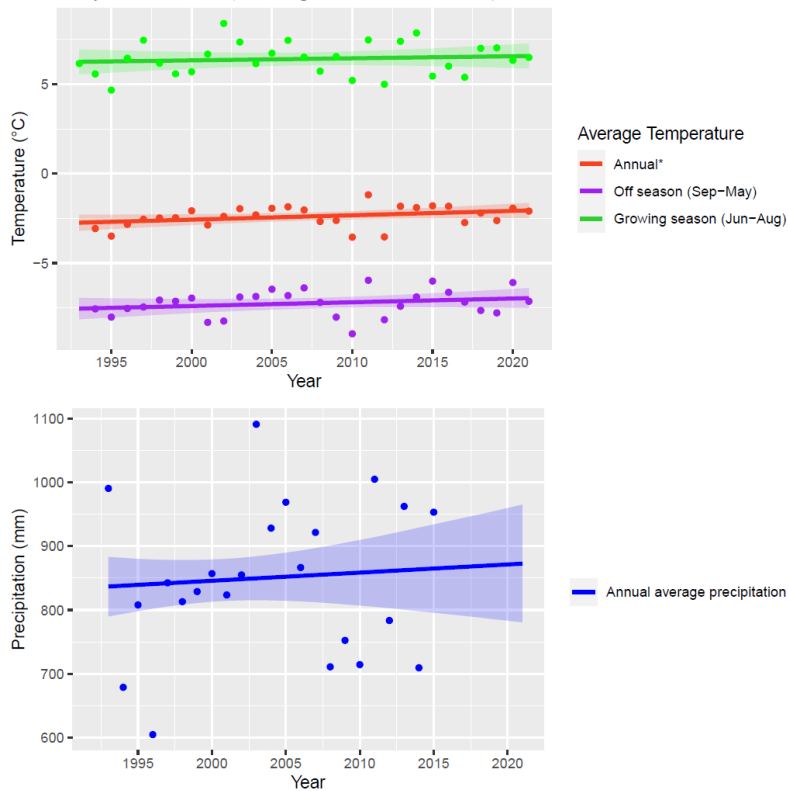


Figure 3. Linear temperature and precipitation trends over a 29-year study period (1992–2021) analyzed with a Bayesian framework. Significant trends are denoted by \*.

The dominant plant communities are differentiated based on soil characteristics, predominantly pH and moisture. Extensive chemical analyses, emphasizing nitrogen processes, have been conducted on organic and mineral soils in the dominant plant communities (Björk et al., 2007). Net N mineralization and C/N ratio distinguish the meadow and heath communities, where mineralization was higher in the meadow than in the heath. N mineralization rates were negatively correlated with organic soil C/N ratio, whereas they were positively correlated with organic soil pH.

### 3.1.1 PLANT COMMUNITIES

At LFS, five plant community types have been selected for ITEX monitoring: Dry Heath, Dry Meadow, Mesic Meadow, Wet Meadow, and Tussock Tundra (See Fig. 4 for a visual representation of all communities). These communities are differentiated mainly based on dominant plant species, soil pH, and moisture content. The three meadow communities, dry, mesic, and wet, are differentiated based on their growing season soil moisture content, resulting from variations in the thickness of winter snow cover and the influence of surface melt-water percolation. Note here that the dry meadow is relatively dry for a meadow community but is closer in soil moisture to the mesic meadow than to the dry heath (and is seen as “moist” in the arctic-wide dataset described above). All the meadow communities have relatively high pH and nutrient-rich soil, owing to the calcareous bedrock found below (Molau and Alatalo, 1998). In the wet meadow site, the vegetation has a high ground cover and increased dominance of forbs and grasses relative to the drier conditions of the dry meadow site. Across the three communities, graminoids (mainly sedges) become more dominant with increasing soil moisture. In contrast, evergreen prostrate dwarf shrubs such as *Dryas octopetala* L. and *Empetrum nigrum* L. are more prevalent in the lower moisture range. The dry heath site is found on acidic (siliceous) glacial moraine ridges and flats. The vegetation cover is sparse and characterized by species adapted to nutrient-poor dry soils such as *Empetrum nigrum*, *Diapensia lapponica* L., *Cassiope tetragona* (L.) D. Don, and *Kalmia procumbens* (L.) Gift, Kron & P.F. Stevens ex Galasso, Banfi & F. Conti. Like the dry heath site, the tussock tundra site has a more siliceous bedrock, making the soil slightly acidic. Stands of the tussock tundra community occur on water-soaked mineral soil (Molau, 2010). Tussock tundra communities are also usually associated with permafrost; however, the permafrost near Latnjajaure disappeared during the first decade of the study (Beylich et al., 2004, Molau, 2010).

Control

Warmed

Dry Heath

Dry Heath



Tussock Tundra

Tussock Tundra



Dry Meadow

Dry Meadow



Mesic Meadow



Mesic Meadow



Wet Meadow



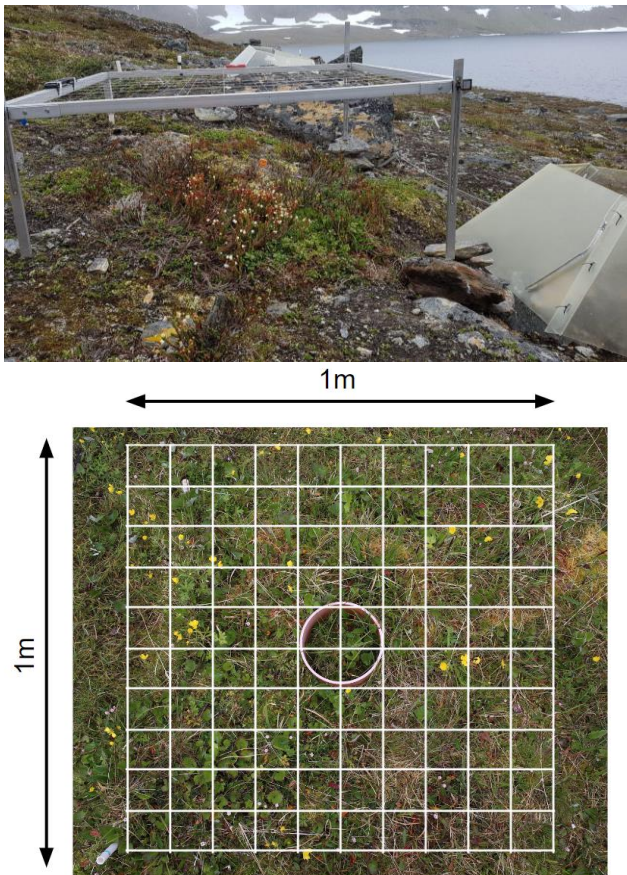
Wet Meadow



*Figure 4. Representative control and open-top chamber (OTC) plots of each plant community. Photos taken in July 2019, credit: Johan Martinelli.*

## 3.2 PLANT COVER

In all studies described in this thesis, I used species-level cover data. In **papers I, II, and IV**, I employed the 1 m<sup>2</sup> point-frame method according to Molau and Mølgaard (1996). I recorded the first species hit, in 100 evenly spaced points (10 rows with 10 points each; Fig. 5.). In paper IV, I synthesized data from a large number of sites, some of which used different plot sizes, and in some cases, multiple hits were recorded beyond the first (though only top hits were used in the manuscript). In paper III, I used the Braun–Blanquet method (Braun-Blanquet, 1932) for estimating plant abundance. The Braun–Blanquet method is a visual estimate that groups species into abundance categories. As an estimate of total vascular plant abundance (e.g. more than just the top layer is considered), cover can be higher than 100%.



*Figure 5. **top:** Point-frame set up in the dry heath at Latnjajaure Field Station, **bottom:** Point-frame set up as seen from above in the dry meadow at Latnjajaure Field Station.*

We chose the plant abundance measurements based on a continued sampling of established experiments, though point framing is commonly used in arctic environments because it allows for the exact resampling of the arctic vegetation. The use of top hits over multiple hits is a time-saving measure. As you might expect, abundance-sensitive metrics (e.g. Simpson diversity) are most sensitive to this simplification. However, there is limited loss in power when detecting community change, especially when relative numbers of diversity are used (May and Hollister, 2012).

### 3.3 WARMING TREATMENT

To study the effects of warming on plant diversity, we used open-top-chambers (OTC; Fig. 6; **papers I,II, and IV**). These little greenhouses allowed me to compare warmed vegetation diversity changes in warmed against ambient (non-warmed) conditions. OTCs are hexagonal chambers with walls at 90° made out of greenhouse fiberglass, plexiglass, or polycarbonate (Molau and Mølgaard, 1996). On average, OTCs warm the mean daily soil and air temperatures (up to 15 cm) by 1-3 °C (Marion et al., 1997). The main driver of the warming is the reduction in wind speed which reduces the loss of energy from air movement (Hollister et al., *in press*). The benefits of OTCs are mainly cost and ease of deployment and maintenance (Marion et al., 1997), which are crucial when working in remote Arctic areas. The precise effects of OTCs can vary between sites and years due to local conditions such as snow cover, wind, and soil moisture conditions, among others (Dorrepaal, 2007, Bjorkman et al., 2015, Delarue et al., 2015). Consequently, their secondary effect on environmental variables such as soil moisture and melt-out date varies too (**paper I**; Hollister et al., 2015, Jassey et al., 2011). On balance, however, warming studies using OTCs have shown to be similar to studies of ambient response to climate warming over time (Hollister and Webber, 2000, Elmendorf et al., 2015), suggesting that OTCs provide a decent prediction of plant response to climate warming (Hollister et al., *in press*).





*Figure 6. Open top chamber in the dry meadow at Latnjajaure.*

### **3.3.1 ITEX**

The studies in **papers I-II** and **IV** presented here are, to a large extent, enabled by the International Tundra Experiment (ITEX). One of the founding goals of ITEX as an organization was to investigate the effects of warming due to climate warming on tundra vegetation (Henry et al., *in press*). And although the organization has branched out since then, its easy-to-implement passive warming experiment (see warming treatment) and attitude towards sharing results have enabled the comparison and synthesis across sites for over 30 years.

### 3.4 PHYLOGENETICS

In the studies presented here, I used two different phylogenies (models of evolution). For **papers I and III**, I generated a phylogeny for all vascular plant species present within the ITEX site at Latnjajaure based on two chloroplast genes (*rbcL* and *matK*; Phylo I). For **paper IV**, I used a phylogeny for which we targeted all protein-coding sequences for the full chloroplast (up to 86 genes and 45,194 base pairs per species) for 360 species ITEX-wide (Phylo II). By increasing the alignment length, we aimed to increase the resolution of lower-level phylogenetic relationships (Parks et al., 2009) and, in doing so, alleviate the potential sampling bias when generating a phylogeny based on an area sample (Webb and Donoghue, 2005, Park et al., 2018). For Phylo I, we addressed issues with divergent sampling across the plant tree of life by adding our samples to an existing angiosperm-wide alignment (Magallón et al., 2015). This approach addresses uncertainties at order-level or above relationships but does not address uncertainties at family-level or below. In both phylogenies we constrained the ages of higher level nodes based on Magallón et al., (2015). In the case of phyllo II, however, most nodes in the phylogeny were constrained using secondary constraints, as many of the higher-level nodes dated using fossils by Magallón were absent. In the case of Phylo I, all nodes were present because of the extended dataset, and I could use the fossil constraints directly. Comparing the two phylogenies is difficult as Phylo I has more robust dating while Phylo II is based on a larger dataset, both in terms of alignment length and number of species included. To remedy this, I plan to expand Phylo II based on order-level chloroplast in public databases such as GenBank (Sayers et al., 2020). Then I would be able to assess if the increased sampling and sequencing effort affected any of the results presented in **papers I and III**.

### 3.5 DIVERSITY METRICS

In the papers in this thesis, I used a wide variety of diversity metrics. For ease of use, we grouped the metrics by the aspect of diversity (Taxonomic, Phylogenetic, and functional) and whether they pertain to  $\alpha$  (within community) or  $\beta$  (between communities) diversity.

#### *Taxonomic diversity*

##### $\alpha$ diversity:

- The Simpson index (**Paper III**) represents the probability that two randomly selected individuals (from an infinitely large community) belong to the same species (Simpson, 1949).

##### $\beta$ diversity:

- The Jaccard similarity index (used in **Paper III**; Jaccard., 1908) is the number of species shared between two communities (or plots) relative to the number of species not shared.
- Bray-Curtis dissimilarity (Bray and Curtis, 1957) is the number of individuals unique to each of two communities (or plots) relative to the summed total number of individuals in both communities. Note that this metric takes abundance into account, as it looks at individuals rather than species (e.g., if one plot has 12 roses and the other has 18, 12 individuals are shared and 6 are not).

#### *Phylogenetic diversity*

##### $\alpha$ diversity:

- intraMPD (**Paper III**). MPD refers to the **mean** of all **pairwise distances** within a phylogenetic tree (phylogeny). Where “pairwise distance” refers to the summed length of all branches between two given species. When used with a phylogeny dated to absolute time, the mean pairwise distance is the mean amount of time since two different species within a given plot diverged from each other (Webb et al., 2002). “intra” refers to intraspecific, in other words, the distance of a species to itself (which is 0) is also taken into account (Miller et al., 2017). Weighting by species abundance then reflects the average time between two randomly selected vascular plants (or points within the point frame) within a plot.

$\beta$  diversity:


- The netMPD (Described in **Paper I**, used in **papers I and III**) is the in-between plot difference in intraMPD. In essence, I calculate the contribution of each branch in the phylogeny to plot level intraMPD and then subtract the value of the first plot to the value of the second plot for each branch, then take the sum of absolute values of all branches in the phylogeny.

*Taxonomic and phylogenetic hill diversity*


In **paper IV**, we used Hill diversity, sensitivity towards abundant and rare species. Hill diversity is a framework in which the sensitivity to abundance is controlled by a single parameter (Alberdi and Gilbert, 2019a). Adjusting this parameter, called the abundance factor ( $q$ ), allows the emulation of close relatives of existing metrics. For instance,  $q=0$  represents species richness,  $q=1$  represents raw abundance (the exponential of the Shannon index), and  $q>1$  overweighting abundant taxa ( $q = 2$  equalling the multiplicative inverse of the Simpson; Jost, 2006). For all these metrics, a given hill number can be interpreted as the number of equally abundant species required to reach the same level of diversity (Alberdi and Gilbert, 2019b). In **paper IV**, we used extensions of the hill diversity framework for taxonomic and phylogenetic  $\alpha$  and  $\beta$  diversity metrics (Chao et al., 2014, Chao et al., 2010). We also tested the sensitivity of the phylogenetic hill diversity metrics to contrast against deep evolutionary time by transforming the phylogenetic tree, adding more “time” (length), either recent or old branches in the tree prior to the analyses.

*Functional diversity*

To compare global with local patterns, in **paper II** I looked at four functional growth forms commonly used to categorize vascular tundra vegetation (Evergreen shrubs, Deciduous shrubs, Graminoids, and Forbs; Fig. 7). These groupings are based on a cluster analysis of 21 plant traits and are generally assumed to predict both responses to and effects on the environment due to their similarity in traits (Chapin et al., 1996, Thomas et al., 2019).

Graminoids 




Evergreen shrubs 



Forbs 



Deciduous shrubs 



*Figure 7. Vascular plant growth forms used in **paper II**.*

## 4 PAPER SUMMARIES

**Paper I:** Decreased soil moisture due to warming drives phylogenetic diversity and community transitions in the tundra

Climate warming in the tundra biome has drastically affected tundra ecosystems and their biodiversity. Taxonomic and functional diversity has been shown to respond to warming, although observed patterns show high levels of uncertainty. Phylogenetic diversity has been understudied in the tundra and has been shown to have complementary value to taxonomic and functional diversity as it captures interspecific variation in traits that are not typically measured. We investigated whether phylogenetic  $\beta$  diversity responds to warming over a moisture gradient in a 25-year warming experiment using relative similarity between communities and community characteristics to assess potential consequences of warming.

We show that changes in the source, amount, and/or timing of soil moisture input modulate community-level responses in phylogenetic  $\beta$  diversity, and the use of  $\beta$  diversity enabled the detection of patterns within commonly used plant functional types.

More specifically, we concluded that:

- In a warmer Arctic, decreased soil moisture can lead to community turnover from meadow to heath communities.
- A more consistent water supply would promote the development of *Salix* (willow)-dominated meadows.
- The disappearance of permafrost can lead to a drop in soil moisture and a rapid initial community response, but a long-term change was inhibited by the longevity of the local community.
- Shrubification is driven by different plant lineages in the different communities indicating variability within the shrubification response masked by the commonly used plant functional types.

**Paper II:** Vegetation responses to 26 years of warming at Latnjajaure Field Station, northern Sweden

Studies of biome-wide responses in tundra vegetation elucidated patterns such as increases in plant height and the abundance of taller growth forms, such as shrubs, at the cost of prostrate growth forms such as lichen and bryophytes. However, the results of previous Pan-Arctic syntheses have also demonstrated large variations in the responses of individual study sites to the passive warming treatment. Thus, individual site responses should be analyzed to provide a more detailed understanding of how warming affects vegetation. We measured responses to warming of plant growth forms (deciduous shrubs, evergreen shrubs, forbs, and graminoids) over 26 years in five communities with distinct soil moisture conditions (Dry Heath; Tussock Tundra; and Dry, Mesic, and Wet Meadow). In addition, we compared and contrasted these growth form responses to fertilization and warming treatments analyzed based on a seven-year community-level interaction experiment.

We show that growth form responses to warming at Latnjajaure are mediated by edaphic characteristics (most notably soil moisture), of the communities and their interactions with climate.

More specifically, we concluded that:

- Community-specific soil moisture conditions lead to community-specific responses of the plant growth forms (deciduous shrubs, evergreen shrubs, forbs, and graminoids).
- Soil moisture determines whether shrub expansion is driven by deciduous or evergreen shrubs.
- Ambient changes over time significantly impact many of the growth forms across communities, regardless of warming.
- In some cases, we see responses only in ambient communities indicating that open-top chamber treatment can buffer temporal responses observed in ambient plots
- A warming response was only visible in long-term (7+ years) experiments.
- Long-term ambient responses are more in line with warming rather than fertilization responses. Though fertilization has only been tested at “unrealistically” high levels compared to ambient conditions.

**Paper III:** Limited decadal growth of mountain birch saplings has minor impact on surrounding tundra vegetation

Due to climate warming, Arctic vegetation is changing, and trees are encroaching into the tundra. In this study, we examine the establishment and growth of mountain birch (*Betula pubescens* ssp. *tortuosa*), which forms the treeline in subarctic Europe, and its impact on community composition across the treeline ecotone nearby Abisko, Sweden.

We show that birch occurrence above the treeline does not affect plant community composition. Regardless, over a decade, the overall tundra community structure shifted toward a novel community dissimilar from the forest plant community found below the treeline.

More specifically, we concluded that:

- Future treeline advancements are more restricted than commonly expected, implying that the vegetation change may be slower than hitherto assumed.
- Mountain birches above the treeline are growth limited and do not ameliorate their habitat enough to buffer surrounding neighbor plants from the stress that would lead to a vegetation shift.



**Paper IV: Plant abundance drives  $\beta$ -diversity changes in the Arctic**

There are metrics of biodiversity that could be employed that do not necessarily lead to the same results even within aspects of biodiversity (e.g., functional traits vs. functional types, or Shannon vs. Simpson diversity). Therefore, it is essential to explore if different biodiversity metrics respond similarly to climate warming and what drives the plant diversity patterns in the Arctic. We explored the effect of scaling abundance weighting as well as the importance of deeper against shallow nodes in the phylogeny on warming response and its interaction with soil moisture and site temperature in the tundra biome. For all metrics, we looked at both plot level ( $\alpha$ -diversity), and the difference between plots ( $\beta$ -dissimilarity).

We show that  $\beta$ -dissimilarity is more sensitive to warming than  $\alpha$ -diversity metrics. Furthermore, we show that sensitivity to abundance and phylogenetic weighting depends on local soil moisture conditions.

More specifically, we concluded that:

- Changes in  $\beta$ -dissimilarity in moist sites are sensitive to abundance though neither rare nor abundant species disproportionately drive them.
- We find no indication that phylogenetic diversity adds information in moist sites, but does indicate shifts in divergent rare species at dry sites.
- Changes in phylogenetic  $\beta$ -dissimilarity of dry communities suggest turnover in distantly related rare species.
- Sensitivity in colder sites is higher in all observed responses
  - Potentially because our use of relative abundance inflates the value of the few vascular plants in high arctic plots.

## 5 DISCUSSION & SYNTHESIS

### 5.1 LOCALE SCALE PATTERNS IN FUNCTIONAL AND PHYLOGENETIC DIVERSITY

**Paper I** and **II** focus on the same plant communities at Latnjajaure using different metrics of diversity. Though we did not make a statistical comparison between the two approaches, several insights can be gained from comparing their results. Moist communities that became drier, either through warming or the loss of permafrost, increased in similarity to dry, nutrient-poor (heath). This community shift generally went hand in hand with an increase in the cover of evergreen ericaceous shrubs. Interestingly the mesic meadow community, which responded strongest in phylogenetic dissimilarity measurements, showed no response to warming in our analysis of functional types. Both mesic meadow control and warmed plots did, however, change over time. They increased in evergreen and deciduous shrubs, where the warmed plots mainly increased in Betulaceae (Deciduous) and Ericaceae (Evergreen/Deciduous), but the control plots also increased in Rosaceae (foremost the evergreen *Dryas octopetala*) and Salicaceae (Deciduous). In other words, the warming response in the mesic meadow was obscured because of the opposing responses of species within the same functional groups (Fig. 8). This has implications for how we interpret the potential consequences of warming. For instance, Ericaceous shrubs form an association with a specific type of mycorrhiza (the fungal partners of plants). These ericoid mycorrhizae have melanized cell walls that are harder to decompose, which leads to increased C storage in the soil (Clemmensen et al., 2015, Fernandez and Kennedy, 2018).

We also found responses in plant functional types that we did not observe when measuring phylogenetic dissimilarity. Within the control plots of our dry, nutrient-poor heath we found an increase in deciduous shrubs and a decrease in evergreens. This has implications for the interpretation of the warming response. The leaf litter of deciduous shrubs is easier to break down, thus the increase of deciduous relative to evergreen shrubs speeds up carbon cycling. Deciduous shrubs also tend to be taller than their evergreen counterparts therefore, they capture more snow in winter, which increases winter snow depth, leading to higher soil temperatures through the protection snow offers from the cold winter air (Vowles and Björk, 2019). Moreover, the presence of tall shrubs, if they are taller than the snow cover, can reduce surface reflectance (albedo), which enhances warming.

In conclusion, the use of both phylogenetic and functional diversity measures enhances the quality of our assessment of the implications of arctic vegetation response to warming.

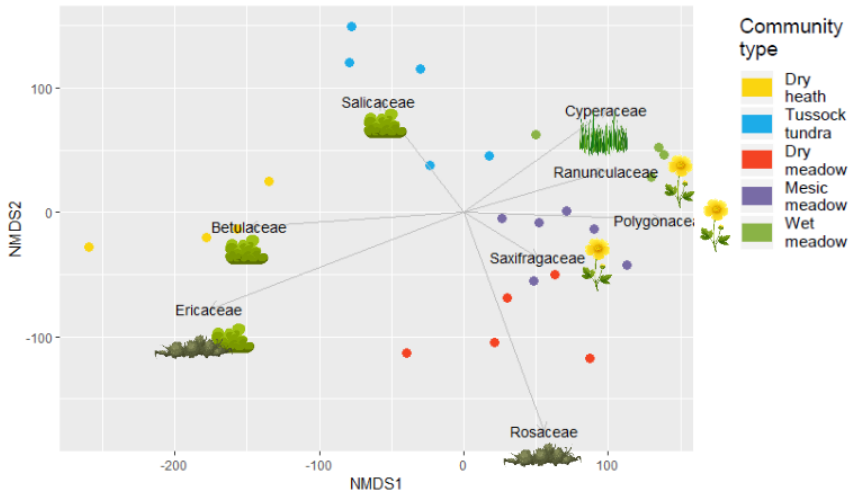


Figure 8. The first-year measurements of control plots at Latnjajaure (colored points) fitted with vectors representing plant family contributions to the patterns in phylogenetic dissimilarity (intra MPD). Functional groups of local species within each family are indicated by images under the family names. The length of the arrows is proportional to the correlation between variables and the ordination of the plots. Only families with a vector fit of  $R^2 > 0.2$  and  $P > 0.05$  were plotted to preserve figure legibility. Functional groups of local species within each family are indicated by images under the family names.

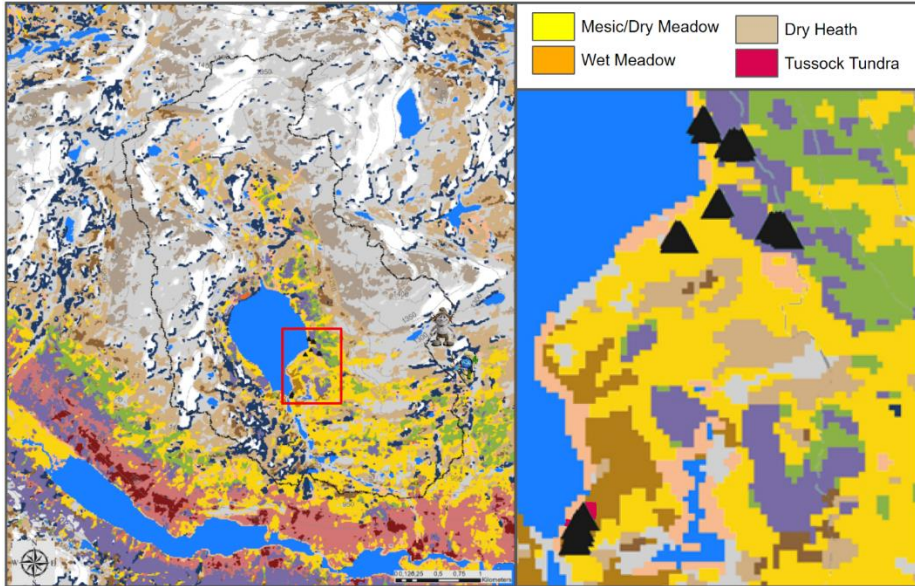
## 5.2 LOCAL PATTERNS IN AMBIENT CLIMATE CHANGE COMPARED TO EXPERIMENTAL WARMING

When we observed community shifts through phylogenetic dissimilarity over time in control plots, we generally observed the same pattern under experimentally warmed conditions, albeit larger in magnitude (**Paper I**). This suggests that warming is an important factor in driving ambient changes in plant community structure at Latnjajaure and that OTCs do a good job of simulating climate change. For functional types, we generally see the same pattern where responses in the controls over time tend to follow the responses observed in warmed communities. Alternatively, if only one treatment condition shows a response it is found in the warmed plots. One exception however is the dry, nutrient-poor heath where the observed differences between warmed and control plots were driven by changes in the control plots themselves. One explanation could be that the OTC provided a mitigating effect from changing ambient conditions. The dry heath is located on an exposed ridge and is more exposed to harsh conditions, and similar communities have exhibited dieback in the vascular plant community in other locations in the valley (A Patchett, personal communication, September 29th, 2022; Bokhorst et al., 2009). If this is the case, the main treatment effect of the OTC is not the warming, which in turn means that the OTC did not have a comparable between communities effect even within Latnjajaure (although this line of reasoning is mainly speculation at this point, it does highlight the need for more detailed measurements of OTC effects). Indeed, a recent review (Hollister et al., *in press*) of OTC effects has highlighted the importance of documenting the impacts of the OTC on the physical environment at the community level as precise effects of OTCs can vary between sites and years due to local conditions such as snow cover, wind, and soil moisture conditions among others (e.g., snow cover, wind, soil moisture conditions, etc.; Dorrepaal et al., 2007, Bjorkman et al., 2015, Delareu et al., 2015). However, when the same patterns are observed in artificial warming as occur in ambient plots over time, the difference between the warmed and control plots is most likely primarily due to temperature (Hollister et al., *in press*). This is supported by a biome-wide analysis which showed that the magnitude of artificial warming is roughly the same as ambient change over time, at least regarding the thermal niche of species responding (Elmendorf et al., 2015). In other words, besides the dry, nutrient-poor community itself, responses at Latnjajaure were generally driven by temperature.

### 5.3 LOCAL-SCALE DIVERSITY IN A REGIONAL CONTEXT

In **paper II** I show a satellite-based vegetation map of Latnjajaure and the surrounding area (Latnjavagge; Fig. 9). The map not only illustrates the importance of our focal plant communities within the region but can also be used to extrapolate the results of the plot scale ITEX warming experiment to the catchment level. Dry heaths are among the most dominant plant communities and are expected to increase as soil moisture in mesic communities decreases under a pure climate warming scenario. We might also expect increases in comparable communities (Extreme Dry Heaths, Grass Heaths, and Mesic Heaths). The increase in *Salix* (willow) shrubs in the warmed wet meadow at Latnjajaure further suggests that the willow community type will start moving further upslope. These results are in line with my findings in **paper III**, where I found community shifts in the overall tundra community structure which shifted toward a novel community dissimilar from the forest plant community found below the treeline. Nonetheless, the results from the ITEX warming experiment (**papers I and II**) suggest that this novel community will be taller, dominated by both evergreen and deciduous shrubs, where ericoid and betula shrubs respond stronger in mesic and dry communities and willows dominate the response in wet communities.

Overall, however, experimentally warmed communities varied in the strength of their response in both phylogenetic dissimilarity and within functional types. This suggests that some communities are more sensitive to climate warming than others. Variability in environmental conditions, including soil moisture and nutrients, will likely result in a mosaic pattern of responses based on each community's sensitivity to climate changes at a regional scale. Bearing in mind that the Arctic ITEX sites experimentally increase annual mean air temperature by 1–3 °C (Marion et al., 1997), these future predictions are in the lower end of future scenarios, RCP 2.6 (Meredith et al. 2019). Thus, future vegetation shifts are potentially larger than those observed in **papers I-II**.



*Figure 9. Vegetation classification derived from five dates of Sentinel-2 satellite images (Copernicus Sentinel data 2018, 2019, 2020), a color-infrared orthophoto (Lantmäteriet 2018), a ground elevation model at 2 m grid cell size (Lantmäteriet 2015), and field data. Black triangles show studied communities. The legend only shows communities represented by these studies. The same map with a more detailed legend can be found in **paper II**.*

## 5.4 GLOBAL PATTERNS OF LOCAL PHYLOGENETIC AND TAXONOMIC DIVERSITY

In **paper IV**, we found that changes in both taxonomic and phylogenetic  $\beta$ -dissimilarity were strongest at colder sites. This was unexpected as increased shrub abundance and vegetation height are usually associated with Low Arctic, warmer, sites (Elmendorf et al., 2012a), and our results from **Paper I** and **II** suggested that phylogenetic diversity can measure variation in shrubification response. High Arctic sites tend to be comparatively more resistant to change than Low Arctic sites (Prach et al., 2010), possibly due to their lower soil nutrient status (Epstein et al., 2004). Moreover, ambient warming in High Arctic sites is generally higher, which could mean that artificial warming is less impactful (Rantanen et al., 2022). One potential reason for the lack of observed response at warmer sites is that  $\beta$ -dissimilarity is calculated on a within-community basis. Thus, it is not unreasonable to expect community-level responses to be different if the interaction between community-level soil moisture and warming is influenced by other site-level variables (e.g., topography, wind, precipitation, or nutrient status). For instance, artificial warming using OTCs has been shown to cause both decreases (**Paper I**; Rasmussen et al., 2020), and increases in soil moisture (Bernareggi et al., 2015, D'Imperio et al., 2017). In **Paper I**, the responses in the meadow communities were driven by different clades in the phylogeny. In contrast, using the method I employed in paper IV they would all be measured as an increase in  $\beta$ -dissimilarity as the only response parameter. It is therefore likely that a multivariate approach or more detailed community-level edaphic and environmental characteristics, as well as OTC effects measurements, would improve the quality of our results.

## 6 FUTURE PERSPECTIVES

In this thesis, the discussion around climate feedback driven by vegetation change has been informed by either preexisting knowledge on either functional groups (**Paper II**) or community types (**Papers I, III**) but has not been directly compared to measurements of ecosystem functions directly driving these feedbacks (e.g., net ecosystem exchange, productivity, or nutrient cycling, etc.). Especially the explanatory taxonomic and phylogenetic aspects of diversity (see, Sørensen et al., 2019 and Happonen et al., 2022 regarding functional trait diversity) in measuring ecosystem functioning or multifunctionality has been underexplored in the Arctic tundra (But see; Liu et al., 2022 regarding alpine grasslands). The ever-increasing availability of arctic-wide datasets (such as the upcoming synthesis of ITEX of ecosystem CO<sub>2</sub> fluxes) provides a unique opportunity to explore the effects of different aspects of biodiversity on ecosystem functioning. Moreover, the generation of the ITEX-wide phylogenetic tree (**Paper IV**) enables us to explore the fit of different evolutionary models such as gradual unconstrained change (Brownian motion) and niche conservatism (Ornstein-Uhlenbeck model) to specific ecosystem functions or multifunctionality (Cadotte et al., 2017).

In **papers II, III**, and the discussion section above, we extrapolated plot level results to discuss potential regional impacts. Validating these predictions with future remote sensing observations, thus upscaling plot level trends to regional patterns, will be crucial in improving the reliability of our estimates of arctic vegetation change and its consequences (Myers-Smith et al., 2020), especially considering the limited number of arctic research sites available.

Lastly, **Papers I and II** showed a large amount of variability in response between communities within a single site. This suggests that the availability of community-level measurements of environmental and soil characteristics, as well as OTC effects, would improve the quality of the results of arctic syntheses (**Paper IV**, Elmendorf et al., 2012a, Walker et al., 2006). It is therefore likely that a multivariate approach or more detailed community-level edaphic and environmental characteristics, as well as OTC effects measurements, would improve the quality of our results.



# ACKNOWLEDGEMENT

Saving the best for last they say, but here I am thinking this would have gone a lot smoother if I wrote it a few hours ago. It might sound cliché, but I do not think these words can properly convey the gratitude I feel to everyone though I will try to scribble something down nonetheless.

Family first, because any former Ph.D. student knows, that is not where they have been that last couple of days. Thank you Elina for picking up my slack and still helping to have the energy and will to help out; you are amazing. Thank you Lifv, and Esmee; I promise I will make up for the bedtime stories/movie nights missed. Thank you Albus for being unreasonably happy even when I come home late at night. Of course, I cannot forget my Mother, brothers, and friends. Thank you for always supporting me.

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