ABSTRACT LIST

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 # 01

Long-term effects of seasonal warming scenarios on ecosystem functioning in a north Swedish blanket bog

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Since 2000 we use a combination of seasonal warming scenarios (year round, summer warming, spring warming, additional snow) in a blanket bog in Abisko, northern Sweden to simulate the effects of various climate scenarios on ecosystem functioning. The moss component of the bog is dominated by *Sphagnum fuscum.* The cover of vascular plants is about 25% and mainly consists of the evergreen dwarf shrubs *Empetrum hermaphroditum* and *Andromeda polifolia*, the deciduous dwarf shrubs *Betula nana* and *Vaccinium uliginosum*, the grass *Calamagrostis lapponica* and the forb *Rubus chamaemorus.* Our studies have included the effects of these scenarios on species composition, plant phenology, nutrient resorption, litter decomposition, soil nitrogen dynamics, greenhouse gas emissions, microbial communities, testate amoebae and soil mites.

The most important conclusions from these studies are: (1) plant related responses are much more driven by plant identity than by effects of the treatments. This implies that species dynamics determine plant-driven ecosystem responses to climate change: (2) Spring warming and (moderate) winter snow addition only have minor effects of the processes and functional groups under investigation, summer warming is the main driver; (3) Climatic extremes are far more important for ecosystem responses than gradually increasing average temperatures; (4) soil biogeochemical processes are extremely sensitive to moderate warming (1-1.5 ^{o}C). This underpins the importance of these ecosystems for climate change as they contribute disproportionally to greenhouse gas emissions, thereby causing a positive feedback loop to climate change.

02

Carbon fluxes and allocation above- and below-ground in high Arctic tundra

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In order to obtain more accurate future climate scenarios, it is relevant to estimate the contribution of terrestrial ecosystem components on carbon fluxes and the effects climate change has on them.

In Arctic regions, where the consequences of climate change are amplificated, it is of interest to study how climate change impacts the balance between sequestration and release of carbon. Global warming, on one side, stimulates permafrost thawing and, consequently, the availability of organic C for microbial decomposition. On the other side, air temperature increase, together with other climate drivers may affect plant photosynthesis in not univocal way. Moreover, foreseen future increase in the primary production at plant level may affect belowground carbon allocation which in turn may influence the rate of soil respiration, by priming the soil organic matter decomposition.

Aim of our study in high Arctic tundra is to disentangle the multiple uncertainties about the contribution of terrestrial ecosystem components to C fluxes and to evaluate how these components will be affected by future climate change. Last summer, we assessed the distribution of newly assimilated C between plant tissues and soil, including respiratory fluxes, as well as between different metabolic compounds. This, with the aim to define the allocation strategies of different Arctic plant species and quantify the residence time of newly assimilated C in the plant/soil continuum. For this purpose, we used a C isotope labelling/chasing approach. Preliminary results show differences in ^{13}C enrichment among plant species, possibly associated with differences in assimilation rates. As expected, the enrichment in leaves, roots and fluxes followed different patterns. Label was gradually transferred from leaves to belowground tissues and to respiratory fluxes. Belowground, the enrichment was not considerable in respect to other pools and fluxes which could be explained by root morphology and development of the root system.

 # 03

Variation in Tundra Plant Traits across a Latitudinal Gradient

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We document variation in plant traits of five tundra plant species across three research sites spanning a latitudinal gradient in northern Alaska (Utqiaġvik, Atqasuk, and Toolik Lake). We specifically looked at vegetative height, leaf fresh mass, leaf dry mass, leaf dry matter content (LDMC), leaf thickness, water band index (WBI), photochemical reflectance index (PRI), and normalized difference vegetation index (NDVI). One-way ANOVAs and Kruskal-Wallis tests were performed to test for variation in plant functional traits across research sites. Vegetative height, leaf fresh mass, leaf dry mass, and leaf dry matter content tended to increase in the southern sites. Leaf thickness tended to decrease in the southern sites. Leaf reflectance traits (WBI, PRI, NDVI), however, did not follow a consistent trend. Next steps include testing for variation in specific leaf area (SLA), photosynthetic capacity (A_{max}), dark respiration, and nitrogen content. Understanding how plant functional traits vary across a latitudianl gradient will help us explain why tundra plant species are responding to a warming climate the way they are, and make predictions about future changes in vegetation community structure.

 # 04

Impact of experimental warming on population and community plant functional traits

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Plant functional traits are closely related to multiple ecosystem functions, including primary productivity, water and nutrient cycling, and soil formation. As such, understanding the relationships between temperature and intra- and interspecific trait variation can help us better predict the consequences of climate warming for ecosystem functioning. We investigated the impact of experimental warming on population- and community-level functional traits at ten tundra locations, including both alpine and Arctic sites. We found that the impact of warming on traits varies by location and species, but typically impacts size-related traits more than traits related to plant economics. Interestingly, the direct impact of warming on the traits of individuals does not always mirror community-level trait shifts. Our results suggest that the consequences of warming will be varied, but that tundra ecosystem functions related to plant size are most likely to be affected by future climate change.

05

Increased methane consumption following 25 years of warming treatment

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Our current view on the terrestrial Arctic methane budget is strongly biased towards methane emission hotspots in carbon-rich wetlands, while less attention has been given to the carbon-poor mineral soils covering about 87% of the region. With increasing temperatures, this carbon can become available for microbial decomposition resulting in further carbon dioxide and methane release to the atmosphere and hence generating positive climate feedback. However, the actual release of methane to the atmosphere is dependent on two contrasting processes: methanogenesis (the production of methane) and methanotrophy (the consumption of methane). The former occurs during anoxic conditions in water-saturated soils, whereas the latter is pronounced in aerated and surface soils.

In recent years, several studies have confirmed that a warmer global climate leads to a changing vegetation pattern in the Arctic with an overall taller plant community, an increase in biomass, an expansion of shrubs as well as changes in the abundance of aerenchymous plants (facilitating soil-atmosphere gas exchange). This change in vegetation will influence several soil processes including soil moisture and in particular the oxygen availability regulating the methane consumption rates in surface soils.

Flux data from 5 plant communities at the Latnjajaure Field Station indicates a significant increase in methane consumption following 25 years of experimental warming. This is evident in both wet and dry communities (27% and 23% increase, respectively), increasing the sink strength at dry sites while reducing the emission or even turning the system from source to sink for wet sites. We hypothesize that the dominating process behind this is an increase in evapotranspiration (hence, higher biomass in warmed plots), reducing soil moisture and increasing oxygen availability in surface soils. Other contributing factors include a reduction in aerenchymous plants at the wet sites, while soil temperature differences are minimal at the investigated sites.

06

Monitoring long-term vegetation changes (1953-2018) in an alpine tundra ecosystem of the Italian Central Alps

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Alpine tundra ecosystems are particularly sensitive to climate change and are already affected at different levels of ecological organization (from species to landscape). In the European Alps, climate warming was more than twice the increase in global mean temperature over the last 60 years. Here we quantify the impacts of climate change on composition, structure and distribution of plant communities in an alpine tundra ecosystem of the Italian Central Alps (Stelvio pass), belonging to the ITEX network since 2014. The assessment of the vegetation changes were performed vegetation repeated survey, involving also an historical dataset. In particular, three different monitoring approaches were adopted: a) repeated vegetation mapping with comparison of phytosociological maps over a 65 year time period (1953-2003-2018); b) repeated phytosociological relevés and comparison over a 65 year time period (1953-2003-2018) within the area investigated for the phytosociological maps; c) resurvey of high elevation permanent plots (5x5 m) installed between 2700 and 3000 m a.s.l. since 20 years.

Our results shown relevant changes of the vegetation spatial distribution, indicating that these dynamics involving areal changes of the different ecological series are still prosecuting also in the recent years (since 2003), involving also the establishment of tree seedlings and saplings. The phytosociological data allowed to assess that all communities suffered changes of floristic composition and dominance, and to compute their extinction and ingression debt. Climate change impacts were evident in the last 20 years from the high elevation vegetation (> 2700 m), with the ingression of several new species and relevant coverage changes. The prosecution of the long-term monitoring is essential to implement the knowledge of sensitive ecosystems to climate change, allowing to model their future responses, and plan management issues promoting climate change adaptation.

 # 07

Human trampling disturbance effects on *Silene acaulis* in the Colorado alpine

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Shifts in species geographic distributions in response to climate change have spurred numerous studies to determine which abiotic (e.g., climatic) and, less commonly, biotic (e.g., competitive), processes determine range limits. However, the role of disturbances on range limits and their interactions with climatic and biotic effects is not well understood, despite their potential to alter competitive relationships between species or override climatic effects. Disturbance might have differential effects at contrasting range limits, based on Darwin's theory that biotic interactions set abiotically benign range limits and abiotic factors set abiotically stressful range limits. We predicted that plants at lower elevation (abiotically benign) range limits experience a net positive effect of disturbance whereas those at higher elevation (abiotically stressful) range limits experience a net neutral effect. We examined plant populations along elevational gradients in the Colorado Rocky Mountains, in order to quantify the effects of human trampling disturbance at lower and upper elevational range limits of the common alpine cushion plants *Silene acaulis* and *Minuartia obtusiloba*. Our results are consistent with Darwin's theory. A disturbance-mediated reduction of competitive effects increases the performance of cushion plants at lower elevations, suggesting a range limit set by biotic factors. At higher elevations, where biotic interactions are minimal, disturbance has neutral or negative effects on cushion plants. We propose that disturbance can diminish competitive interactions at lower elevations, and thus, possibly stabilize alpine species populations susceptible to encroachment by lower elevation species. As the effects of disturbance and elevation interact to differentially impact species success at range limits, we highlight the importance of incorporating the effects of climate change into disturbance studies, and vise versa, for a comprehensive understanding of landscape-level impacts. Conservation and management approaches should therefore particularly account for the differential effects of disturbance across climatic gradients.

08

Thermal periodicity as a possible mechanism shortening local tundra plant species' active seasons under climate change

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Advancing plant green-up timing due to earlier snowmelt is reported as one of many effects of climate change. It is hypothesized that this phenomenon will lead to longer total growing seasons, based on the assumption that senescence timing will remain constant or even be delayed due to warming. While satellite-derived time series seem to confirm this hypothesis, senescence data from individual field studies, however, remain scarce.

Here, we present a 7-year senescence dataset of eight common circumarctic plant species from High Arctic Svalbard. We experienced many complications with snow removal at our site, so used snow fences instead to delay snowmelt in a controlled field experiment thus producing a clear signal for changing green-up timing. Based on the hypothesis above, we expected senescence timing to remain constant in spite of delayed green-up, as the conditions after snowmelt were unchanged in this study.

Instead, we found that senescence was delayed by the snow fences and reject external trigger events for phenology such as photoperiod or temperature thresholds, which were lacking during the time of senescence at the study site. Simultaneously, we found a shortening of the lead-time from snowmelt until senescence and that senescence occurrence seemed to be determined by accumulative temperature sums (thawing degree-days; TDD), i.e. senescence across all but one species occurred after the same amount of TDD irrespective of snowmelt timing.

Our findings propose thermal periodicity as the ecophysiologically underlying trait controlling senescence occurrence in High Arctic plant species. While understudied thus far, previously published studies show but hardly mention indicators of thermal periodicity, and we present a review of those. We suggest that remote sensing studies could confound changes in species composition and increased growth of native evergreens with constant or delayed senescence timing. We conclude that changes in snowmelt timing might not harm

plant performance of species native to our study region *per se*. However, invading aperiodic species might benefit and outcompete thermally periodic native species.

We suggest that the ITEX phenology database is analyzed for thermal periodicity and changing timing of senescence in response to snowmelt timing.

09

Dark diversity in the tundra: the source of future biodiversity change?

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Tundra plant communities are responding as the climate continues to warm, with shifts in community composition and traits observed across many tundra sites. However, where across the landscape new species come from and how the larger species pool influences local-scale biodiversity change remains unknown. Traditional plant surveys often capture scales of only several square meters, leaving many unmonitored species that by chance could be absent in small plots. This so-called “dark biodiversity” could be a hidden source of future biodiversity change. Here, we bring together decades of ITEX observations with the first findings from the ITEX Species Pool Protocol to reveal the magnitude of dark biodiversity in tundra ecosystems and the links between local compositional changes and the larger species pool.

Across 10 ITEX sites including 19 vegetation types, we found that on average there are 30 species present within 100 m radius of long-term monitoring plots, which have never been recorded inside the plots. The amount of dark diversity varied considerably among sites (sd = 21 species), as did the rate of species accumulation with distance across different landscapes (Figure 1). We are currently integrating the ground-based species pool and plot-scale community composition data with information on topography and microhabitats derived from aerial drone imagery. This combination will allow us to determine which parts of the tundra landscape this dark diversity occupies – environmentally similar or more variable habitats, or the warmest microclimates. Understanding the relationships between the species pool, dark diversity and plot-scale diversity can help us find the hotspots of plant biodiversity across tundra landscapes and will improve predictions of future changes in the richness and composition of tundra ecosystems with warming.

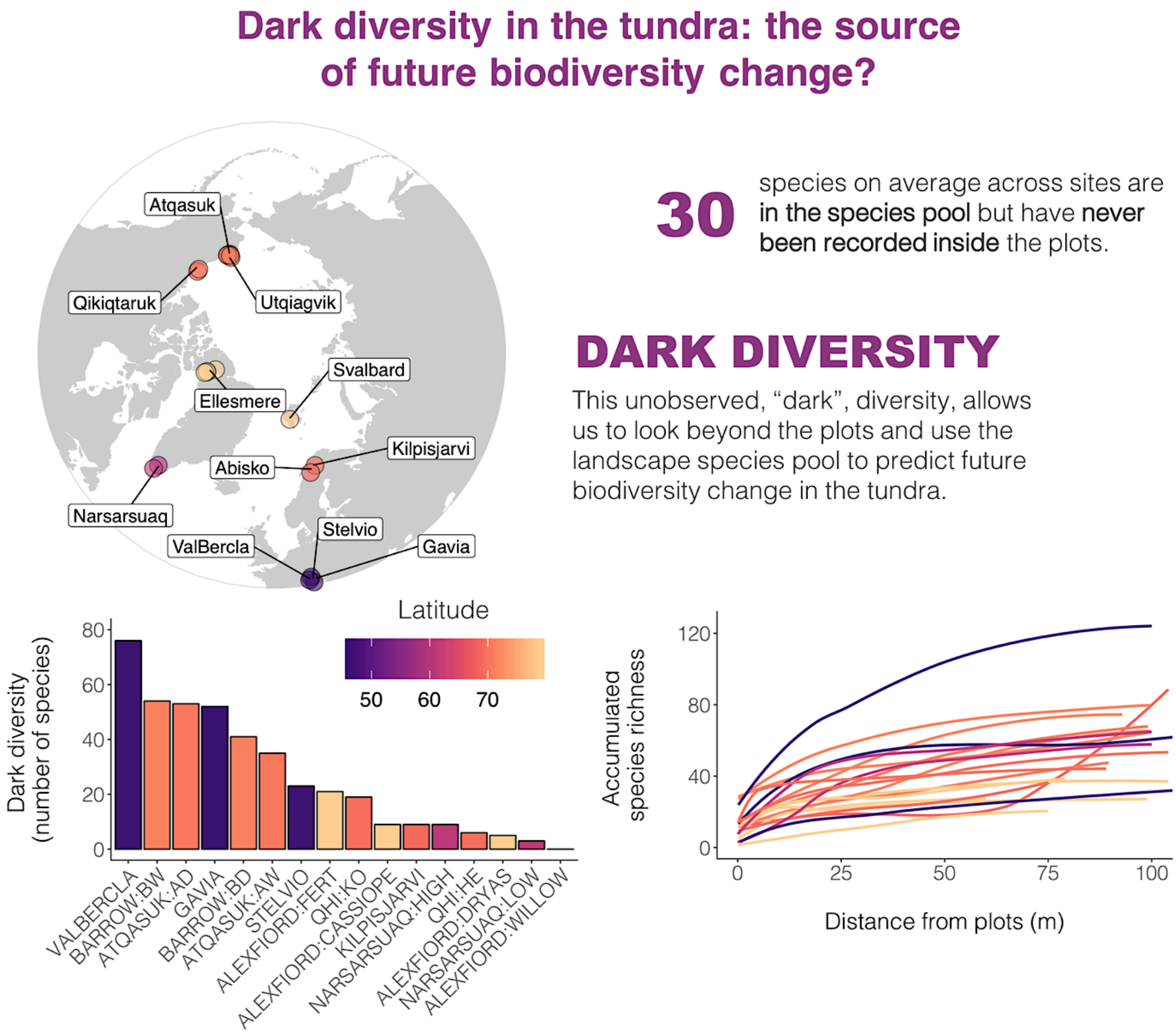

Figure 1. The tundra's dark diversity spans across all latitudes. Map shows sites which have completed the ITEX Species Pool Protocol and bars show the number of species which are part of the species pool but have never actually been recorded inside the plots. Lines show model estimates for the rate of species accumulation across tundra landscapes.

 # 10

Plant-soil-microbe responses to experimental climate change

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Tundra ecosystems store large amounts of organic carbon in plants and soil and therefore form an important potential feedback mechanism to ongoing climate change. Positive and negative feedback can occur through direct responses of vegetation (carbon uptake) and soil microbes (carbon loss) to changes in climate, or through indirect responses, via shifts in species composition or altered interactions between plants and soil processes. Over the past decades, much progress has been made in understanding how (experimental) climate change can alter the aboveground composition and characteristics of tundra plant communities (e.g. Elmendorf et al. 2012, Björkman et al. 2018), as well as how this may impact on carbon loss from fresh surface litter (e.g. Cornelissen et al. 2007). However, we still understand much less of how (experimental) changes in climate affect longer-term carbon losses from the soil, and how such changes are driven by belowground changes in plant and microbial communities and functioning across the arctic and alpine tundra.

We will present results from three experiments, manipulating summer and winter climate or plant species, to show that climate change can strongly alter belowground plant functioning (species-specific rooting patterns). Further, plant species can differentially affect the microbial community composition, and in turn, such shifts in microbial community composition can be important drivers of soil carbon decomposition. Experimental changes in climate can thus have strong effects on respiration losses of soil carbon through different mechanisms and are therefore likely dependent on local conditions and vary across the tundra. Finally, we will therefore present more details and invitation to contribute to a new ITEX synthesis, to unravel how experimental climate change affects respiration across the tundra, and how these responses depend on local changes in vegetation and microbial community.

 # 11

Biogeography of Arctic White Heather (*Cassiope tetragona*)

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The last major ice age ended approximately 11000 years ago. As the ice retreated species' range expansion is believed to have occurred rapidly. During this time, many tundra plant species may have dispersed out of Beringia and recolonized the Arctic. Understanding how organisms responded to climatic changes in the past could help us investigate how organisms will respond to the current rapidly changing climate. At sites on Ellesmere Island, entire communities of plants have been frozen under the glaciers for the last 400-2000 years. At Alexandra Fiord and Sverdrup Pass, *Cassiope tetragona* has been well preserved under the glacial ice and, in 2017, ancient *C. tetragona* DNA was extracted from samples found there. The genomics of these plants provide a window into the past and help us better understand how populations change and move across space. *Cassiope tetragona* samples were also collected across its range: the Canadian Arctic, British Columbia's Coastal Mountains, Greenland, Svalbard, Northern Europe and Russia. Researchers from 35 different sites (Figure 1) sent *C. tetragona* leaf samples back to UBC in the fall of 2017. We investigated the genomes of both the ancient and present day *C. tetragona* populations using genotyping by sequencing (GBS). This technique uses next generation technology to sequence thousands of matching DNA segments for many individuals. Comparing genetic diversity within and between populations, we can begin to investigate the rate of gene flow between today's populations. Using this high-resolution data, we tested the hypothesized recolonization patterns and glacial refugium using population structure analysis. As the climate continues to change, questions of species responses continue to arise. Estimating the amounts of gene flow between current populations could help us determine the dispersal limitations of some Arctic species. Understanding what limits species range expansions is essential to help predict where species can survive in the future.

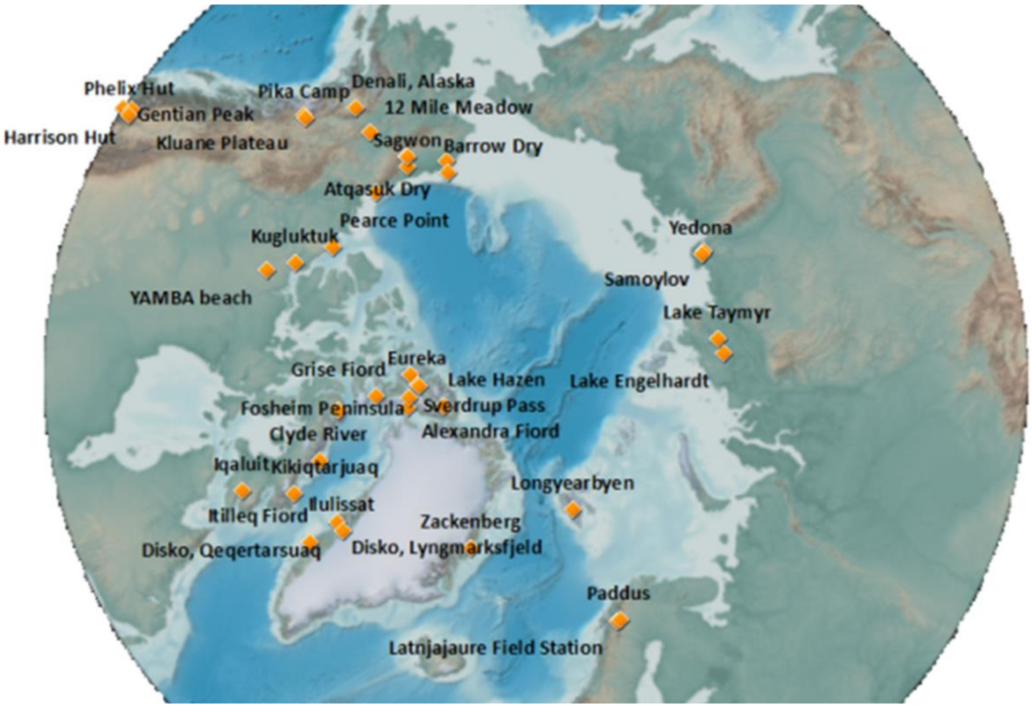

Figure 1: Locations where *Cassiope tetragona* samples were collected.

 # 12

Multiple sources of variation in leaf toughness of plants in northern Alaska

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We measured leaf toughness as force to punch for 11 species of Arctic plants in tussock tundra and dry heath tundra in northern Alaska. *Rubus chamaemorus* and the graminoids occupied opposite ends of the leaf toughness spectrum, with *R. chamaemorus* requiring the least force to punch, while one of the graminoids, *Eriophorum vaginatum,* required the most. The other graminoid, *Carex bigelowii* ranked below the evergreen shrub, *Vaccinium vitis-idaea,* and similar to another evergreen shrub, *Rhododendron tomentosum*. Leaf toughness increased with decreasing mean summer temperature for *E. vaginatum* and *Betula nana*, while it declined for the other species. On the other hand, there was little variation in *E. vaginatum* due to population origin when sampled in a common garden. On the other hand, application of N and P fertilizer decreased leaf toughness in three species while it had no effect on four others. There was no difference in community-weighted mean leaf toughness between tussock tundra and dry heath, but variance was much higher in tussock tundra. We used variance components to estimate inter- and Intraspecific variation in leaf toughness and found that the amount of variation due to different populations within a species was similar to variation due to species.

 # 13

Could climate extreme events elicit unexpected vegetation dynamics in mid-latitude alpine snowbeds?

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In recent decades, climate change has been identified as one of the main drivers of recorded changes in composition and structure of tundra communities. In snow- and temperature-limited systems, such as snowbeds, the effects of longer and warmer growing seasons are believed to enhance growth and induce shifts in richness and diversity. However, the more frequent occurrence of climatically anomalous seasons may affect expected vegetation dynamics by acting on available water resources, hampering the positive effects of warming on plant performance in the short-term and constituting an advantage for those plant functional types (PFTs) that are more tolerant to drier conditions.

A manipulation experiment simulating early snowmelt alone and in association with warming was performed in two snowbed communities situated in the Italian Alps. The aim of the study was to assess the short-term effects of simulated climate scenarios on richness, diversity and cover of the main PFTs – i.e. mosses, shrubs, forbs and graminoids. The strong inter-annual climate variability which occurred was used to identify climatic drivers influencing PFTs cover.

Unexpectedly, no significant effect of treatments emerged on the studied parameters, except for diversity, with the two target communities exhibiting different responses across treatments, mainly due to shifts in abundance of the dominant species. Inter-annual cover variations appeared inconsistent across PFTs, highlighting a constant decline in the trend for forbs, and major oscillations for shrubs and mosses corresponding to the two hottest and driest years of the study period. Solar radiation appeared to be the main climate variable influencing cover, with diverse responses of PFTs to current and previous year irradiance values, highlighting possible legacy effects of climatically anomalous seasons on forbs.

In view of the increasing frequency of climate extremes, these results suggest that other environmental factors related to water availability could divert warming-induced vegetation dynamics in mid-latitude alpine snowbeds.

 # 14

Cassiope tetragona as a dendroecological proxy: A retrospective analysis of experimental warming in the Arctic Tundra

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Annual stem growth and flowering of *Cassiope tetragona* exhibit a strong positive relationship to summer temperature and can be used in dendroclimatology analyses to reconstruct climate variability in tundra communities. We conducted a full retrospective reconstruction of the impacts of long-term experimental warming in tundra communities at Alexandra Fiord (Ellesmere Island) and other experimental sites across the Arctic using a before-after-control-intervention design, from before the installation of open-top-chambers (OTCs) in 1992 to 2018. It was found that the growth indices immediately capture the amplified warming effect of treatment, and that in each year since OTC installation flowering and seed ripening have taken place earlier in the growing season. Furthermore, reconstructions of climate based using growth and reproductive chronologies at Alexandra Fiord can explain up to 74% of the annual summer temperature variability. This talk will also present a comparison of the proxy's relationship with summer temperature at a range of ITEX sites, and present a model methodology for future studies using multiple *C. tetragona* growth and reproductive chronologies as proxies of environmental change.

15

Effect of increased snow depth on plant autumn phenology and physiology in a subarctic mire

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During autumn senescence, physiological processes take place in plants such as the resorption of nutrients and the development of frost hardiness. The timing of these processes is crucial so that plants can benefit from a long growing season while avoiding the loss of nutrients due to early frosts. In subarctic peatlands, increases in snow cover can influence the timing of autumn senescence directly, by causing shifts in phenology, and indirectly, by influencing the supply of soil moisture and nutrients to the plants. Furthermore, the insulating snow cover increases the thaw depth of permafrost in summer and autumn. In this study, we investigated the effect of snow fences, which increase winter snow cover, on plant autumn senescence and physiology from August to October 2018 in a subarctic mire near Abisko, Sweden. Increased snow cover increased permafrost thaw depth and accelerated the thawing from September onwards compared to control plots where it leveled off in September. The NDVI was slightly higher in snow fence plots compared to controls. Chlorophyll and anthocyanin indices did not seem to be affected by snow depth. We also present results about the effect of the snow fence on the timing of senescence in *Andromeda polifolia*, *Betula nana*, *Eriophorum* vaginatum and *Vaccinium uliginosum*.

20th INTERNATIONAL TUNDRA EXPERIMENT MEETING

16

Using a common protocol to measure invertebrate herbivory: responses to warming across tundra sites

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Warming can influence the responses of tundra plants indirectly through its effects on herbivores and herbivory rates. Leaf damage by invertebrate herbivores is widespread across the tundra biome, although it generally occurs at low rates. Invertebrate herbivores are likely to respond strongly to warming, as their physiology depends directly on temperature. The rates of invertebrate herbivory are predicted to increase in a warmer Arctic, so integrating these altered herbivory patterns is essential to understand the responses of tundra plants to warming. We used a common protocol designed in collaboration with the Herbivory Network, to compare the frequency of leaf damage by invertebrates in plots subjected or not to long-term passive warming at 5 sites participating in the International Tundra Experiment (ITEX) and an additional site with only control plots. As expected, the frequency of invertebrate herbivory was low across the range of studied tundra plant communities (<7%). Invertebrate herbivory increased in warmer plots at most sites, except at one High Arctic site. Differences in the plant and invertebrate communities might drive local deviations from the general pattern. Importantly, the standardized protocol provided a comparable and easy-to-implement way of assessing invertebrate herbivory at ITEX plots. Monitoring invertebrate herbivory could be used as an indicator of ecological responses to ongoing environmental changes.

 # 17

Does intraspecific trait variability contribute to plant community resistance to warming in high Arctic island ecosystems?

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Plant communities may respond to environmental change in both taxonomic and functional space. In contrast with the low Arctic, high Arctic plant communities generally show small responses to experimental warming in species composition. This resistance to change in taxonomic space can be related to smaller species pools and migration barriers, two features that are accentuated in island ecosystems. Warming responses in functional space are, however, not as well established for high Arctic plant communities.

Functional trait variation has two components, interspecific and intraspecific, reflecting species turnover and phenotypic plasticity or genetic differentiation, respectively. Globally, high intraspecific variability is negatively related to species richness and positively related to climatic variability. It is therefore possible that slow plant community responses to warming in the high Arctic in terms of composition and species turnover, might be compensated by relatively high intraspecific trait variability.

To address this question we studied plant community responses to warming in Svalbard, an archipelago in the high Arctic, characterized by a small species pool and large climatic variability. We assessed plant community responses to 15 years of experimental warming, both in taxonomic and functional space, in three habitats of contrasting snow and moisture regimes.

Plant communities responded slowly to experimental warming in taxonomic space and unexpectedly significant responses were only detected in the driest habitat, a *Dryas octopetala* heath. Most plant traits differed strongly among habitats, while only two traits related to leaf size (leaf area and mass) responded positively to warming and only in the *Dryas* heath. Consequently, relatively large functional variation was attributed to habitat differences and only a small variation to treatment demonstrating high community

resistance to warming in both taxonomic and functional space. However, the small trait variation explained by warming tended to be intraspecific rather than interspecific, which partly supports our hypothesis.

18

Warming effects on community-level functional traits of vascular plants, lichens and bryophytes in an alpine ecosystem

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Functional traits can be used in climate change effect studies to predict how communities respond to a warming climate. So far, most trait-based studies have focused on vascular plants, while there is limited knowledge on non-vascular primary producer groups such as lichens and bryophytes. Knowledge on trait responses of lichens and bryophytes is needed, especially in ecosystems where they contribute substantially to aboveground biomass, such as alpine and arctic ecosystems. We measured community-level functional traits of vascular plants, lichens and bryophytes in *Dryas octopetala*-dominated heath in Finse, alpine Norway, after 18-19 years of experimental warming by open top chambers (OTCs). In addition, we quantified how much of the variation was driven by changes in species composition, and how much was driven by intraspecific variation. We found that for vascular plants, community-level specific leaf area (SLA) and nitrogen (N) decreased while carbon to nitrogen ratio (C:N) increased under experimental warming. All of these trait responses were driven by intraspecific variation. In contrast, community-level traits of lichens did not respond to the warming treatment. For the bryophytes, community-level carbon (C) and biomass decreased while shoot length to biomass ratio increased under experimental warming. The variation in biomass and length:biomass were mainly driven by changes in species composition, while C was driven by intraspecific variation. We show that different primary producer groups within the same community may respond differently to warming. Further, our findings indicate a shift from a resource acquisitive community under ambient temperature, to a more resource conservative community under warming, contrary to our expectations. Finally, our findings highlight the importance of including intraspecific variation in trait-based studies.

 # 19

Moss-associated bacterial communities in a warming Arctic

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Mosses contribute substantially to biomass and vegetation cover in northern ecosystems. They play an important role in terrestrial carbon storage, directly due to their recalcitrant tissues and indirectly via interactions with microorganisms. These moss-associated microorganisms also contribute to nitrogen fixation, providing major nitrogen input in high-latitude ecosystems.

Mosses can be studied at the scale of the bryosphere, defined as the combined complex of living and dead moss tissue and associated organisms. Current knowledge of the moss microbiome and its role in biogeochemical cycles is sparse. Addressing this knowledge gap is especially important in the light of climate change.

We investigated effect of warming on nitrogen fixation and the composition bacterial communities associated with the moss *Racomitrium lanuginosum* in a dwarf-shrub heath in Iceland, by acetylene reduction assays, 16S rRNA gene amplicon sequencing and quantitative PCR of *nifH* and 16S rRNA genes.

The majority of the bacterial communities was similar between the warmed and the control treatment, but 297 OTUs were more abundant under warming and 135 OTUs more abundant in the controls. Warming also led to a richer moss-associated bacterial community, primarily due to an increase in the number of Proteobacteria. Nitrogen fixation rates did not change, but a trend towards lower *nifH* gene copies was found in the warmed samples. Nitrogen fixating taxa were less dominated by Cyanobacteria and more dominated by Alphaproteobacteria in the warmed samples.

The effect of warming on the moss-associated bacterial taxonomic composition is found at lower taxonomic levels. Even with a lower potential for nitrogen fixation, nitrogen fixation rates do not change, potentially because the responsible bacterial community shifts towards a better adapted community to the warmer conditions. Warming might thus change the underlying mechanisms for nitrogen fixation in the bryosphere, with consequences for carbon and nitrogen cycling in tundra ecosystems.

 # 20

Warming and precipitation effects on species-specific N_2 fixation in mosses in subarctic tundra

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Nitrogen fixation by cyanobacteria associated with mosses is a major input of new nitrogen (N) into pristine ecosystems in the boreal, subarctic and arctic regions, where N limits plant production. N_2 fixation is a temperature-sensitive process expected to increase with projected climate warming. At the same time, warming can decrease moisture levels in mosses and water is a major control of N_2 fixation activity. Further, the amount of precipitation is predicted to increase at high latitudes. The net effect of these changes on N_2 fixation is therefore uncertain. The aim of this study was to understand how these two forms of climate change impact on N-input into N-limited tundra ecosystems through N_2 fixation in different moss species. Specifically, we wanted to understand how warming responses in N_2 fixation depend on moisture conditions, i.e. precipitation and moss species with different moisture holding capacity. To answer this, we measured in situ N_2 fixation throughout the growing season in three dominant moss species projected to increase with climate warming (*H. splendens*, *P. schreberi* and *Sphagnum* spp.). Alpine tundra patches dominated by each of the moss species were subjected to eight summers of warming by open top chambers at each of eight sites distributed along a precipitation gradient in northern Sweden. The preliminary results suggest that inherent moisture status of the moss species helps predict N_2 fixation response to climatic changes. These results will have implications for upscaling N input into heterogenous tundra ecosystems in a future climate.

 # 21

Alpine grassland and snowbed species after five years of manipulation experiments: phenology and growth

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Alpine and polar tundra are the most sensitive ecosystems to climate change. In situ manipulation experiments are useful to predict vegetation response to future climate change and their potential feedbacks. Here we report the results of 5-years (2014-2018) in situ manipulation experiments at the Stelvio Pass ITEX site, located at a high elevation area (2700 masl) of the Italian Central Alps, where climate change already affected vegetation composition, distribution and dynamics.

Manipulation experiments aimed to investigate the impacts of warming (through open top chambers, OTC), changes of water availability and soil moisture (through precipitation shields, PS) and changes of snow accumulation and snow melting (snow fence, SF) on plant species composition, structure and phenology, plus relative control plots. For this aim, we selected two different vegetation communities, alpine grasslands and snowbeds, representative of the high elevation alpine environment and with highest sensitivity to climate change. Environmental data were recorded by dataloggers and snowcameras, whereas biological monitoring was performed through field observations. During the five years we quantified the changes of vegetation floristic composition and dominance for all plots (2014 – 2018). The phenological monitoring involved 14 target species surveyed since 2014 every 3-4 days during the growing season (i.e., from the snowmelt to the beginning of the permanent snow cover), according to the ITEX protocol.

Temperature resulted the most important driver for the coverage of the main vegetation layers and growth forms, with opposite responses to warming: negative for the crytogamic and positive for the vascular layer. Many reproductive and vegetative phenological stages were found to be extremely sensitive both to the environmental driver manipulations and to the extreme climatic years, but with species-specific differences due to community types and ecological niches, stressing the importance of the ITEX network as unique tool to understand the future changes in tundra ecosystems.

 # 22

Role of tundra community cover in seasonal albedo values at four sites in northern Alaska

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Climate change is warming the temperatures and lengthening the Arctic growing season with potentially important effects on vegetation community structure and phenology. Landscape scale spectral properties change seasonally and as a result of these community structure alterations. Here we show the results of a 5 year study investigating seasonal changes in community level albedo. While the effect of changes in temperature on phenology and species composition have been observed at the plot and at the regional scale, a systematic assessment of albedo at medium spatial scales using recent non-invasive sensor techniques has not been performed yet. At four sites across the North Slope of Alaska changes in albedo were observed by Mobile Instrumented Sensor Platforms (MISP) that are suspended over 50 m transects spanning local moisture gradients. Measurements were collected on a near-daily basis providing fine temporal scale resolution of albedo changes. Seasonal albedo changes vary in rate and magnitude year to year across the latitudinal gradient with more variability in the northernmost sites. Community structure differences have a large impact on albedo values with decreases in values associated with increases in vegetation cover and canopy complexity. Short-term (< 1 week) heating and drying events also cause albedo value anomalies of similar lengths. Changes in tundra vegetation community albedo values can alter landscape scale transpiration rates and serve as a positive feedback mechanism to vegetation community change.

23

Climate influence on plant-pollinator interactions in the keystone species *Vaccinium myrtillus*

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Climate change is altering the world's ecosystems through direct effects of climate warming and precipitation changes, but also indirectly through changes in biotic interactions. For instance, climate-driven changes in plant and/or insect communities may alter plant-pollinator interactions, thereby influencing seed production and ultimately population dynamics of insect-pollinated plants. To increase our understanding of how the importance of pollinating insects for fruit set in plants varies with climate, we conducted a pollinator exclusion experiment along temperature and precipitation gradients in the forest-tundra ecotone in Central Norway using cages of varying mesh size. Our target species was the partially insect-pollinated dwarf shrub *Vaccinium myrtillus*, which is a keystone species in forest and low-alpine ecosystems and an important spring pollen source for bumblebees. Preliminary results show that reducing pollinator access did not influence fruit set in *Vaccinium myrtillus*, whereas completely excluding pollinators significantly decreased both the number of berries produced and berry weight. Contrary to our expectations, the negative effect of pollinator exclusion was less pronounced in forest compared to alpine sites, suggesting that insect pollination is more important for fruit set at low temperatures. Moreover, recordings of pollinator visits, as well as genetic analyses of corbicular pollen collected from bumblebees, shows that *Vaccinium myrtillus* is frequently visited by both alpine and lowland bumblebee species. Together, our findings indicate that the keystone species *Vaccinium myrtillus* is relatively robust to changes in plant-pollinator interactions in a warmer climate.

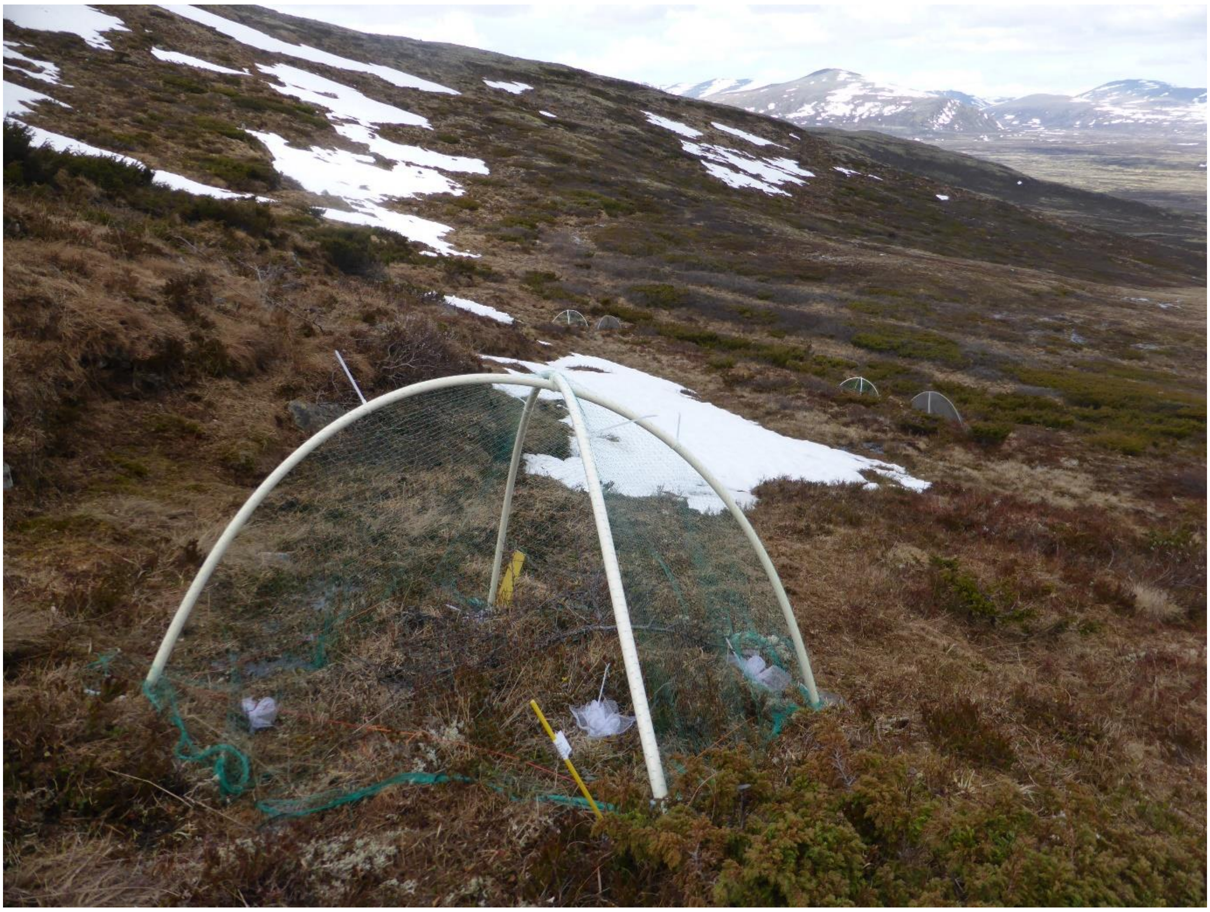

Figure 1: Pollinator access to *Vaccinium myrtillus* was experimentally manipulated using cages of varying mesh size, here exemplified by a pollinator reduction cage with relatively large mesh size.

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High-Arctic phenology shifts under a changing climate: consequences for reproductive success and plant community composition

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The warming Arctic climate is resulting in earlier snow melt and higher temperatures, which, in turn, is causing earlier flowering and green-up of most Arctic tundra plant species. The very few studies of reproductive effort and success in tundra species have shown that warming also increases the production of viable seed from historically very low viability levels. However, flowering time, green-up time and seed viability responses to climate change differ markedly among Arctic plant species. We may, therefore, expect a shift in species composition towards a greater proportion of species that benefit most from climate change. The objectives of our research are to determine 1) the relationship between changes in phenology and reproductive success of tundra plant species, and 2) how phenology-reproductive success relationships relate to changes in species composition and abundance. We are assessing these relationships at the ITEX long-term experimental warming plots at Alexandra Fiord, Ellesmere Island, Nunavut. We are recording the flowering and green-up times of tagged plants in experimentally warmed and control plots. To measure reproductive success, we are (i) counting and weighing seeds produced by each tagged plant and (ii) germinating and growing-on collected seeds to determine seed viability and seedling vigour for each species-plot combination. Species composition and abundance in the plots have been measured approximately every 5 years since 1995 using the point-frame method. Our results indicate that, in general, plants from warmed plots produced heavier seeds with higher germinations rates. Plants that flower earlier tended to produce heavier seed. Species that had higher germination rates in warmed plots are becoming more dominant in the landscape. While species that had higher germination rates in control plots are declining in abundance in the warmed plots. Our results suggest a link between phenology, reproductive success and plant community composition/species abundance.

 # 25

Plant competition for nutrients in a phosphorus-limited tundra ecosystem

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In nutrient-poor arctic ecosystems, competition for nutrients is an important driver of plant species composition and growth. As arctic temperatures increase, enhanced decomposition of soil organic matter may lead to increased soil nutrient availability. The ability to acquire newly available nutrients, especially organic nitrogen, provides an important competitive advantage, both in terms of plant-plant and plant-microbe interactions. In turn, this may result in the proliferation of certain plant species, potentially leading to changes in species composition and ecosystem productivity.

While plant growth in most arctic ecosystems is considered nitrogen-limited, plants growing in soils underlain by basaltic bedrock are likely phosphorus-limited. Consequently, strong phosphorus limitation may prevent plants from taking advantage of newly available nitrogen. At the same time, phosphorus availability is in part restricted by water availability, which is predicted to change with climate-induced precipitation changes. Plant responses to altered water balance and nutrient availability may therefore be linked and could have important implications for other ecosystem processes.

In this study, we investigate plant uptake of organic (amino acid) nitrogen and carbon turnover in response to increased phosphorus and water availability. The study was conducted in a low arctic heath tundra ecosystem on Disko Island, western Greenland, using full factorial water and phosphorus addition combined with in situ isotopic labeling with double-labeled (15N13C) amino acid. Plant and microbial nutrient uptake, and plant and ecosystem carbon turnover were monitored throughout the entire growing season. Preliminary results reveal clear species-specific differences in nutrient uptake, suggesting different competitive strategies. Plant and soil analyses point towards phosphorus limitation, however, responses to increased phosphorus availability are not unidirectional. Further exploration of these results will provide insights into the patterns of plant-plant and plant-microbe competition and the potential for consequent changes in plant species composition related to climate-induced changes in arctic nutrient availability.

 # 26

The biogeochemistry of high-Arctic ecosystems: heterogeneity in response capacity to perturbations and the role of natural inter-annual variability

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Most studies in Arctic ecosystems have assessed whether carbon (C) and nitrogen (N) biogeochemistry of either soil or vegetation responded positively or negatively to simulated environmental change scenarios. However, few studies have integrated biogeochemical processes in both soil and vegetation compartments and focus on their response capacity to environmental changes. Different response rate and strength of these compartments may ultimately indicate whether the tight link between C and N cycling within Arctic ecosystems is prone to destabilization following perturbations.

We investigated the response capacity of the three major ecosystem compartments (i.e. soil, mosses, and vascular plants) to herbivore disturbance and summer warming in terms of their peak-season C- and N-content and C:N ratio. A field experiment was undertaken in the high-Arctic archipelago of Svalbard, in which spring goose disturbance and summer warming were simulated for two consecutive growing seasons in three habitat-types distributed along a gradient of soil moisture (mesic < moist < wet habitats).

Overall, response capacity to treatments differed between and within ecosystem compartments (vascular plants > soil > mosses) and proxies of biogeochemical processes (N > C > C:N). Among ecosystem compartments, we found vascular plants to have the greatest responses (i.e. effect sizes) to treatments in terms of biogeochemical change and with N-content as the most responsive biogeochemical proxy. Furthermore, biogeochemical response capacity of ecosystem compartments to treatments varied spatially between habitat-types (mesic > moist > wet) and temporally between years (second experimental season > first experimental season). Strong natural between-season variability in ecosystem compartment biogeochemistry was also detected.

Our findings highlight the importance of integrating response capacity of different ecosystem compartments to fully understand the sensitivity of tundra ecosystem biogeochemistry to a variety of predicted climate-change scenarios. Moreover, the strong natural between-season variability in ecosystem biogeochemistry points to that future studies should include this latter in order to better understand how the biogeochemistry of tundra ecosystems may respond to future environmental changes.

Pink-footed geese foraging on below-ground plant parts (*grubbing*) in spring

(Adventdalen, Svalbard archipelago, 78° 10′ N, 16° 05′ E)

 # 27

Plant species removal decreases magnitude and variation in nitrogen mineralization in mountains

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Climate change will result in the loss of plant species from many ecosystems around the world, essentially reshaping both the structure and function of aboveground communities. The consequences of these species losses will likely depend on the identity of the species lost, the climatic context of each ecosystem, and the nature of plant species interactions within each community. To understand the biotic and abiotic variables that shape the impact of plant species loss on belowground ecosystem processes, we used a series of four unique plant removal experiments across an elevational gradient and conducted a lab incubation of soil samples from each experiment to measure the mineralization of carbon (C) and nitrogen (N). We found that regardless of the identity of the removed species or the environmental conditions at each site, plant removal decreased both the magnitude and variation in N-mineralization rates and marginally decreased C-mineralization rates. Our results present a surprisingly simple pattern of belowground response to plant species loss and a foundation for more mechanistic experiments in the future.

28

Effects of warming on herbivore-induced plant volatiles in the tundra

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Warming by open-top chambers (OTCs) causes large increases in the release of volatile organic compounds (VOCs) from tundra vegetation to the atmosphere. The high temperature sensitivity can be explained both by stimulated VOC biosynthesis, increased evaporation of the compounds from storage reserves in plant tissue and increased biomass of emitting plant species. As insect herbivores can also induce production and release of VOCs, we aimed to assess the importance of herbivore-induced plant volatiles and interactions with warming in the Sub-Arctic tundra. We conducted an experiment *in situ* with dwarf birch (*Betula nana*) in which we used application of methyl jasmonate (MeJA), a plant hormone which is naturally released upon herbivory, and combined this treatment with warming by OTCs. *Betula nana* was selected as the target species as it is a circumpolar, common dwarf shrub increasing in abundance with climate change, and a known emitter of terpenoids. We compared MeJA-application to herbivory by autumnal moth (*Epirrita autumnata*) larvae and observed similar responses in the release of terpenoids from *B. nana*. The OTC warming doubled the emission of monoterpenes and homoterpenes, and the MeJA-application caused a fourfold and 13-fold increase in the emissions of these compounds, respectively. When warming and MeJA-application were combined, monoterpene emission was 11-fold and homoterpene emission 46-fold higher than in the ambient control. The observed drastic herbivore-induced increases in plant volatile emissions from *B. nana* suggest potential implications on the chemical communication steering the biotic interactions in the warming Arctic. In the atmosphere, VOCs participate in oxidation reactions with potential impacts on the lifetime of methane, and they also contribute to the formation of secondary organic aerosol, with local/regional cooling impacts on climate.

 # 29

Intra-specific trait variation along elevation gradients

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Climate warming is shifting the distributions of species to higher elevations and polewards. Cold-tolerant plant species are receiving increasing pressure from novel and often more competitive neighbors shifting upwards from lower elevations/latitudes. The ability to respond to such pressure can be expressed in the plasticity of traits within a species. Therefore, knowing intraspecific trait variability along climatic and biotic gradients can be a measure of a plant's adaptability and persistence under climate change. Although some examples suggest their potential as a promising indicator for species' vulnerability to environmental change, intraspecific trait distributions along gradients such as elevational or latitudinal temperature gradients are unknown for most species. To explore the general relationship between species' resistance to climate change and trait variation, we are currently building a world-wide network of intraspecific trait variation along elevation gradients as a basis for a large-scale collaborative study. Embedded therein, we have just completed an extensive dataset in the Swiss the Australian and the NZ Alps. In this talk I will present first results of trait variability along elevations spanning multiple taxa and mountain ranges.

 # 30

Long term experimental warming mediated drought facilitates shrubification responses: a phylogenetic perspective

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At Latnjajaure Field Station we used evolutionary diversity in the form of the net mean pairwise distance as an alternative to PFT's to measure plant response to long term experimental warming. We found that warming mediated drought in the mesic meadow community increased their phylogenetic similarity to dry heath plots. The wet meadow on the other hand became more distinct from the other communities. This pattern was found even though particularly shrub species were responding. Thus, our results suggests that measurement of evolutionary diversity can be a useful tool for measuring tundra plant response to warming.

 # 31

Species composition has no effect on overall C-N-P stoichiometry or total biomass in Moist Acidic Tundra

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In Alaskan moist acidic tundra, thirty-five years of monitoring species composition, biomass allocation, total biomass, and plant element content (C, N, and P) allows detailed examination of the effects of species composition on biomass accumulation under nutrient limitation. This report focuses on two harvests, completed after 20 and 35 years of observation, of both unmanipulated plots and plots that were fertilized annually.

The analysis consists of comparisons of biomass, C, N, and P relationships when the same total vegetation biomass and C, N, and P mass are subdivided (1) by species of different functional types (evergreen, deciduous, graminoid, forb, moss, lichen) or (2) by tissue types of different functions (leaves, stems, roots, inflorescences, moss, lichens). The principal conclusions are:

1.) Aboveground net primary production roughly doubled under annual fertilization, but total biomass and C mass were unchanged because aboveground biomass increased while root biomass decreased. Species composition also changed dramatically with fertilization, with loss of several forb and evergreen species and increases in the deciduous shrub *Betula nana*.
2.) N+P fertilizers increased total N and P mass, reflected as increased N and P concentration in all species and tissues.
3.) Tissues varied in C/N/P stoichiometry, reflecting their different functions.
4.) For whole plants of different species, C/N/P mass relationships were essentially constant over 4-6 orders of magnitude in biomass in control or fertilized treatments. Stoichiometric convergence at whole-species level reflects similar functional requirements for whole plants of all functional types. Slightly positive slopes indicate higher C: N and C:P ratios in larger plants, with greater allocation to woody support tissues (stems).
5.) Overall, variation in biomass of whole vegetation is due more to variation in total N and/or P acquisition than to variation in C/N/P stoichiometry or N or P concentration among species.

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Spatiotemporal Variability of Plant Community Phenology Across Northern Alaska: An Inter-comparison of Remote Sensing Approaches

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Rates of climate change have been documented to be highest in the Arctic when compared to other ecosystems across the globe; however, the positive temperature trend is accompanied by substantial variability. Plant phenology can shift rapidly in response to interannual change in temperature, with important consequences for ecosystem properties and processes. Traditionally, ecosystem phenology has been quantified using both satellite and ground-based observations but each approach has limitations especially in high latitude ecosystems. Mid-scale remote sensing platforms that measure plot to landscape scale optical properties (e.g. robotic tram systems, unmanned aerial systems (UAS), and pheno-cams) have shown to provide alternative, and in most cases, low-cost solutions with comparable results to those acquired traditionally. This study contributes to the US Arctic Observing Network (AON) and assesses the effectiveness of using RGB images from pheno-cams, and kite aerial photography (KAP) for deriving key phenometrics (e.g. start of season (SOS), peak greening and end of season (EOS)) for dominant tundra vegetation plant communities near Utqiaġvik (formerly Barrow) and Atqasuk, Alaska. Using eight growing seasons of digital imagery acquired from these platforms, the Green Chromatic Coordinate (GCC) was derived from RGB raw digital numbers (DN) and interannual variability in phenology was compared to phenometrics derived from seasonal patterns in NDVI as measured both with ground-based spectral reflectance measurements and MODIS. This cross-scale analysis highlights the capacity of mid-scale remote sensing platforms for detecting landscape level phenological variability and offer an insight into how these data compare across spatial scales and over time to traditional ecological approaches.

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Changes in winter climates of tussock tundra in Arctic Alaska: Long-term ecosystem consequences

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Winter climate changes have been predicted since the 1990's and have now manifested themselves in many regions of the Arctic. We have used the longest snow fence experiment in the Arctic to address these changes (more or less snow) at Toolik Lake, AK, going back to the beginning of ITEX in 1994. Our studies have focused on community and ecosystem processes including: trace gas feedbacks, permafrost C emissions, plant and soil mineral nutrition and the role of snow melt water in the ecohydrology of these landscapes. This presentation will highlight these changes and share our future endeavours and anticipated discoveries in a winter driven Arctic system.

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Development of vegetation and soil in the glacier forelands in Svalbard

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The rapid deglaciation of Arctic glaciers over more than one century, gives a unique opportunity to investigate process of primary succession and soil development. Both these processes are inseparably linked and influence each other. Tundra plant communities are dominated by cryptogams that are perfectly adapted to harsh environment. However, still little is known about colonisation of the barren substrate of glacier forelands by cryptogamic species such as lichens, mosses and liverworts as well as about their impact on initial soil formation. Due to that our research aimed to investigate the diversity of cryptogams in the forelands, determine environmental variables affecting species succession, and study the changes of selected soil parameters along forelands. Research was carried out in the forelands of nine glaciers in Svalbard. In eight forelands sampling plots were designated in 200x200 m grid, while in Irenebreen foreland plots were located along transects designated from the glacier forehead till the end of foreland. In each plot, the cover of particular species of vascular plants and cryptogams as well as overall vegetation cover were investigated in 1 m^2 plots. Moreover, for each plot, soil sample and environmental data were collected. Altogether, 41 species of vascular plants, 133 species of lichens, 85 species of mosses, 20 species of liverworts were identified. The studied forelands differed in terms of species number and composition of the initial communities. Within 30 studied variables, only several significantly affected species distribution, including both chemical and physical habitat features. Analyses showed that total soil properties were correlated with the time after the glacier retreat and the distance from the glacier forehead as well as interrelated with vegetation cover.

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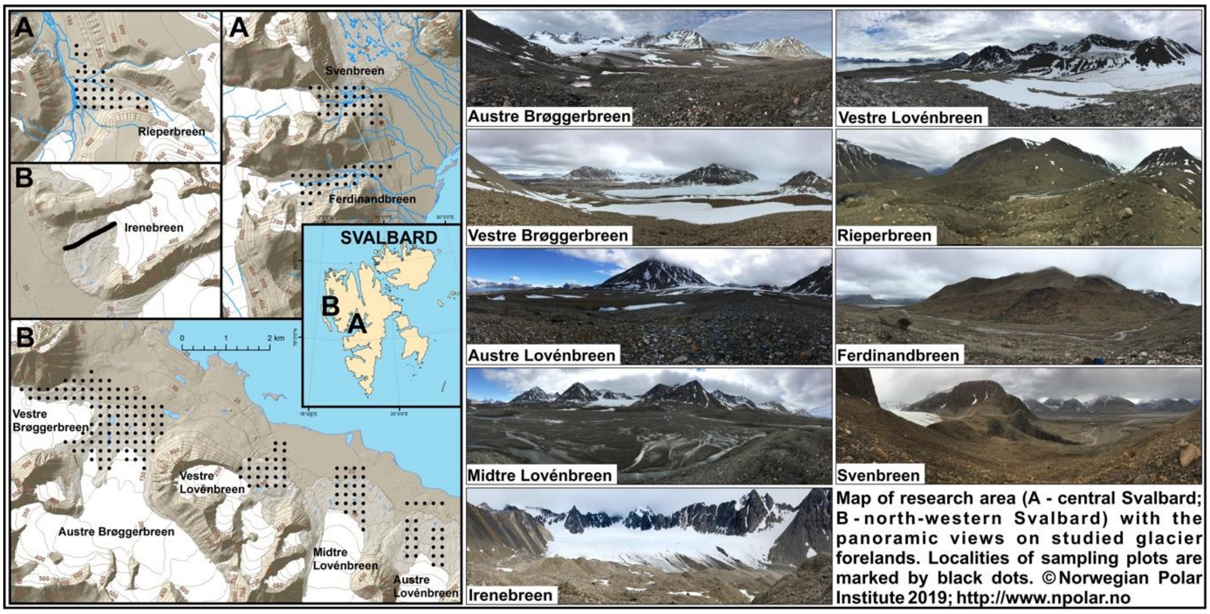

Map of research area (A - central Svalbard; B - north-western Svalbard) with the panoramic views on studied glacier forelands. Localities of sampling plots are marked by black dots. ©Norwegian Polar Institute 2019; http://www.npolar.no