

Niche construction across climate gradients: the case of *Empetrum nigrum* in tundra plant communities

Victoria González Tevendale

A dissertation for the degree of Philosophiae Doctor – June 2018



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The Arctic University of Norway
Faculty of Biosciences, Fisheries and Economics
Department of Arctic and Marine Biology
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Supervisor: Prof. Kari Anne Bråthen

Cover picture: *Empetrum nigrum* flowering shoot in early spring. Photograph by Victoria González

All photographs in this thesis are taken by Victoria Gonzalez except those explicitly stated.

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SUMMARY

The main purpose of this thesis was to evaluate the potential role of niche constructor species in mediating the effects of climate change. To achieve this, we studied at relevant spatial and temporal scales, how the evergreen dwarf shrub *Empetrum nigrum*, through its niche constructor ability, affects tundra plant communities along climatic gradients. *Empetrum* is a common dwarf shrub which is particularly abundant in many tundra ecosystems where it often creates vast areas of monospecific vegetation. As a niche constructor it has strong influence on many ecosystem processes and its direct effects can last well beyond its lifetime. Thus, it is important to understand how the abundance and distribution of *Empetrum* can affect tundra plant communities under climate change.

In this thesis, we first expanded the knowledge on the chemical interference by *Empetrum* leaves, humus and the leaf phenol batatasin-III, by performing a series of bioassays on a large array of tundra species (*Paper I*). All species were found sensitive to *Empetrum* and batatasin-III. Further, by using climate gradients, we studied the mediating role of *Empetrum* abundance on the effects of increasing summer temperatures on tundra plant community structure (*Paper II*). The results showed that when *Empetrum* was present with as low as 25% of total community biomass, the expected increase in biodiversity and herbaceous plant biomass were less positive under increasing temperatures, while shrub biomass was enhanced. Second, we investigated the vegetation recovery of tundra heathlands dominated by *Empetrum* after extreme events over nine years and along a climatic gradient (*Paper III*). We found an extremely low vegetation recovery along the entire climatic gradient, which confirms that when *Empetrum* is the dominant species in the plant community, it is the strong niche constructor legacy, and not climate, that determines the outcome of recovery after extreme events, and hence plant community structure. Finally, to get a deeper understanding of the future of the vast tundra heathlands dominated by *Empetrum*, we studied its resistance to fluctuating climatic conditions such as, varying growing seasons lengths and snow cover conditions along a climatic gradient (*Paper IV*). *Empetrum* appeared to be highly resistant to varying winter conditions and seemed to benefit from longer and warmer growing seasons, showing increases in vegetative and reproductive output.

The results of the research suggest that the outcome of climate change in tundra communities where *Empetrum* is present might differ sharply from the general predictions on climate change in northern ecosystems.

LIST OF PAPERS

Paper I

González VT, Junttila O, Lindgård B, Reiersen R, Trost K, Bråthen KA - Batatasin-III and the allelopathic capacity of *Empetrum nigrum*- Nordic Journal of Botany (2015) 33:225-231

Paper II

Bråthen KA, González VT, Yoccoz NG - Gatekeepers to the effects of climate warming? Niche construction restricts plant community changes along a temperature gradient- Perspectives in Ecology, Evolution and Systematics (2018) 30:71-81

Paper III

González VT, Lindgård B, Reiersen R, Hagen SB, Bråthen KA –Niche construction mediates climate effects on recovery of tundra heathlands after extreme event - Manuscript.

Paper IV

González VT, Moriana-Armendariz M, Hagen SB, Lindgård B, Reiersen R, Bråthen KA – High resistance to climatic variability in a dominant tundra species- Manuscript.

Papers I and II are included in this thesis with the kind permission of the publishers.

Author contributions

	Paper I	Paper II	Paper III	Paper IV
Concept and idea	VTG, KAB, OJ	KAB	VTG, KAB	VTG, KAB
Study design and methods	VTG, KAB, OJ	KAB, NGY	VTG, BL, RR, KAB	VTG, BL, RR, KAB
Data gathering and interpretation	VTG, OJ, BL, RR, KT, KAB	KAB, VTG, NGY	VTG, BL, RR, SBH, KAB	VTG, MM, BL, RR, SBH, KAB
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VTG: Victoria T. González; **KAB:** Kari Anne Bråthen; **BL:** Bente Lindgård; **RR:** Rigmor Reiersen; **OJ:** Olavi Junttila; **NGY:** Nigel G. Yoccoz; **SBH:** Snorre B. Hagen; **MM:** Mikel Moriana-Armendariz; **KT:** Kajetan Tröst.

INTRODUCTION

The tundra in a changing climate

Tundra ecosystems are often dominated by long lived, slow growing clonal plants which have adapted to the harsh winter conditions and short growing seasons. However, climate change is quickly modifying temperature and precipitation regimes at northern latitudes. There is already evidence of an increase in summer temperatures and growing season length (Epstein et al. 2017), varying snow cover conditions (Lawrence and Slater 2010) and a higher occurrence of climatic extreme events (Vikhmar-Schuler et al. 2016). Tundra temperatures are projected to rise between 2 and 9°C by 2100, and precipitation is also predicted to increase, and will be highly variable across seasons (IPCC 2013). The response of tundra plant communities to these changes is a critical and ongoing field of research.

In general, as temperatures increase, a northward migration of species is expected (Lenoir et al. 2008, Manuel J. Steinbauer et al. 2018) and tundra species are predicted to lose ground in favor of those with faster turn-over rates (Elmendorf et al. 2015). However, plant community responses to environmental perturbations caused by climate change may vary depending on a range of factors: the magnitude or duration of disturbances (Buma 2015), their ability to resist and recover from the disturbance (i.e. their resilience, Box 1) (Oliver et al. 2015) and their interaction with other abiotic or biotic ecosystem components such as herbivore grazing (Kaarlejarvi et al. 2017), or niche construction (Box 1) (Bråthen and Ravolainen 2015). Niche construction in particular, has been found to alter ecological processes along broad spatial and temporal scales (Hastings et al. 2007), in a range of ecosystems (e.g. Romero et al 2015). Hence, it is probable that niche constructing species might be able to, directly through their habitat modification capabilities, or indirectly through their legacy effects, mediate some of the effects of climate change in the tundra plant communities where they are present.

Box 1. Terminology

Resilience: The degree to which an ecosystem (or species) is able to resist or recover from environmental perturbation without losing functionality (Hodgson et al. 2015)

Recovery: capacity of an ecosystem to return to its former state or to a functionally similar state after environmental perturbation. (Oliver et al. 2015)

Resistance: the capacity of a species to remain stable in the face of environmental perturbations through persistence (Ingrisch and Bahn 2018)

Niche construction: the process by which organisms modify their own or other species habitats through their metabolism and legacy effects, resulting in changes in one or more natural selection pressures in the external environment of populations (Matthews et al. 2014). Key stone species and ecosystem engineers, in addition to dominant species are some examples of niche constructor species.

Allelopathy: an interference mechanism in which live or dead plant material, including plant litter, release chemicals which have an effect (usually negative) on other plants (Wardle et al. 1998).



Figure 1. Photograph of *Empetrum nigrum* taken in late August. Notice the abundant shoots, and the many black fruits it usually carries.

Empetrum nigrum, an allelopathic evergreen dwarf shrub

Empetrum nigrum (crowberry) is a member of the evergreen dwarf shrub family, common in the northern hemisphere (Büntgen et al. 2015, PanarcticFlora 2017). *Empetrum* can live over 140 years, is wind-pollinated, and one of the earliest tundra species to flower after snow-melt (Bell and Tallis 1973). *Empetrum* is shade intolerant, preferring open space, and is commonly found in treeless heathlands where it creates vast extensions of monospecific vegetation together with *Vaccinium* species, and *Betula nana*, bryophytes such as *Hylocomium splendens* and *Pleurozium schreberi* and lichens of the *Cladonia* family. *Empetrum* possesses a strong primary root and vertical shoot, which is eventually replaced by creeping lateral shoots with shallow lateral roots, resulting from the outspreading growth from a central point. Due to its shallow roots, *Empetrum* is intolerant to trampling and fire, as both disturbances quickly remove and kill the roots (Tybirk et al. 2000). *Empetrum* fruits are black fleshy drupes, with 6-9 one-seeded stones (Figure 1), which ripen in early August and might be eaten by a wide range of animals and birds, promoting *Empetrum* expansion through endozoochory (Bråthen et al. 2007a). The vegetative parts, however, are unpalatable, hence, *Empetrum* heathlands are mostly avoided by herbivores (Ims et al. 2007, Iversen et al. 2014).

From an ecosystem perspective, *Empetrum* is considered a niche constructor species (Bråthen and Ravolainen 2015) and its ecosystem modifying effects are well studied (e.g. Wardle et al. 1998, Tybirk et al. 2000). Niche construction by *Empetrum* is mainly attributable to the poor nutrient quality of its leaves and litter, with secondary metabolites playing a pivotal role.

Empetrum produces high quantities of the compound batatasin-III (3,3'-dihydroxy-5methoxy-dihydrostilbene) in addition to other secondary metabolites, which are released to the soil by leaves and litter through rain, dew and snowmelt (Odén et al. 1992, Gallet et al. 1999). In-soil batatasin-III and phenolic acids are very resilient and form recalcitrant complexes with soil organic matter reducing nitrogen availability to vascular plants (Wardle et al. 1998). Previous studies have found that batatasin-III and *Empetrum* leaves are able to reduce seed germination and seedling growth of several graminoid (Bråthen et al. 2010) and tree species (Nilsson et al. 1998), that they have negative effect on mycorrhizal symbiosis of coniferous trees (Nilsson et al. 1993) and that they inhibit growth of aquatic fauna (Brännas et al. 2004). Furthermore, the humus under *Empetrum* is highly unfavorable for microbial activity, drastically reducing decomposition rates and nutrient cycles (Wardle and Lavelle 1997, Nilsson and Wardle 2005). Thus, through its ability to modify the habitats where it is present, *Empetrum* has effects on multiple ecosystem components including other plant species, above-ground

primary consumers, decomposition processes, and soil biota. It can therefore be expected that changes in *Empetrum* abundance can have cascading effects on ecosystem functioning.

The future of *Empetrum* under climate change is currently unclear. There are studies showing an increase in its biomass, flowering and fruiting under high summer temperatures (Buizer et al. 2012, Kaarlejarvi et al. 2012), and repeated vegetation surveys suggest *Empetrum* has significantly expanded during recent decades (Vuorinen et al. 2017, Maliniemi et al. 2018). However, there are also indications that *Empetrum* heathlands might be sensitive to changes occurring during the winter season, such as attacks by the pathogenic fungus *Ardwidsonia empetrii* under increasing snow cover conditions (Olofsson et al. 2013) and to extreme winter warming events which may reduce biomass and flowering (Bokhorst et al. 2011, Bokhorst et al. 2015). Still, *Empetrum* was found resistant to ice encapsulation (Preece et al. 2012, Preece and Phoenix 2014) and *Empetrum* heathlands at continental sites have been found highly resistant to heavy disturbance (Nilsson et al. 2002, Aerts 2010). What is still unclear however, is whether or not niche construction by *Empetrum* is able to modify the predicted climate change effects on tundra plant communities across a range of climatic conditions.

AIMS

The main purpose of this thesis was to evaluate the mediating role of a common niche constructor species on some of the effects of climate change. To achieve this, we aimed to assess at relevant spatial and temporal scales, how the common dwarf shrub *Empetrum nigrum*, through its niche constructor ability, affects tundra plant communities along climatic gradients. The aims of each paper are briefly described below:

Paper I- In this paper, we performed a series of bioassays testing the effect of pure batatasin-III in addition to *Empetrum* leaves and humus on a large number of vascular plant species and several growing substrates. We were interested in expanding the knowledge on the chemical interference by *Empetrum*, and in particular, the allelopathic capacity of the most abundant leaf phenolic called batatasin-III.

Paper II- In this paper, we performed a large scale observational field survey in 1450 plots where we studied the effects of *Empetrum* presence and reindeer (*Rangifer tarandus*) density (i.e. low vs high) on tundra plant communities along a gradient of increasing summer

temperatures. In particular, we wanted to test if *Empetrum* and reindeer were candidates for mediating the effects of climate warming in tundra plant community structure due to their niche constructing abilities.

Paper III- In this paper, we performed a manipulation experiment where we simulated an extreme event (i.e. cut vegetation at surface level) in a total of 144 plots belonging to five *Empetrum* dominated heathlands along a 200 km climatic gradient. We then studied the vegetation recovery over nine years. We were interested in studying the capacity of tundra heathlands to recover from extreme events and to evaluate if niche construction by *Empetrum* was able to mediate the expected effects of climate on vegetation recovery.

Paper IV- In this final paper, to further deepen our understanding of the resilience of the common *Empetrum* heathlands, we investigated the resistance of *Empetrum* (i.e. its ability to keep a stable cover, shoot growth and berry production) to fluctuating climatic conditions along a climate gradient of oceanic to continental climate in *Empetrum* dominated heathlands over six years.

MATERIAL AND METHODS

Study area

All studies took place in northern Norway, between the latitudes 69.17-71.2°N and longitudes 18.75-31.3°E. *Empetrum* soil and plant material for *Paper I* were gathered from a site in Ifjorjfellet (Figure 2). Sites belonging to *Paper II* were characterized by climatically steep gradients from west to east as well as from coast to inland, covering a temperature gradient of 3.5 °C. Snow cover remains until late June and the main vegetation types are *Empetrum* and *Vaccinium*-dominated heathlands, grass and herbaceous dicotyledon meadows and *Eriophorum* and *Carex* marshes. *Empetrum* is often present in all vegetation types and is the most common shrub species of this region (Bråthen et al. 2007b). The sites used in *Paper III* and *Paper IV* were located in *Empetrum* dominated heathlands at the *Betula pubescens* tree line ecotone (Figure 3). Besides *Empetrum*, other common plant species found in the areas were other dwarf shrubs such as *Betula nana*, *Vaccinium uliginosum*, *Vaccinium myrtillus* and *Vaccinium vitis-idaea*. Sites were located along a gradient from oceanic to continental climate with contrasting temperature and precipitation regimes across all seasons (Figure 2). For a

quick overview of the temperature variation across the climatic gradient, see Figure 11 at end of the thesis introduction.

The main herbivore at all sites studied in this thesis are the semi-domesticated reindeer (*Rangifer tarandus*). The entire region is divided in permanent reindeer herding districts where reindeer numbers are annually regulated by the Norwegian State (www.reindrift.no). Less common herbivores are Norwegian lemming (*Lemmus lemmus*) and gray sided voles (*Clethrionomys rufocanus*) which are found primarily during their outbreak years. One such peak year happened during the course of this thesis in 2011, however we did not register any damaging activity of rodents on the study sites.

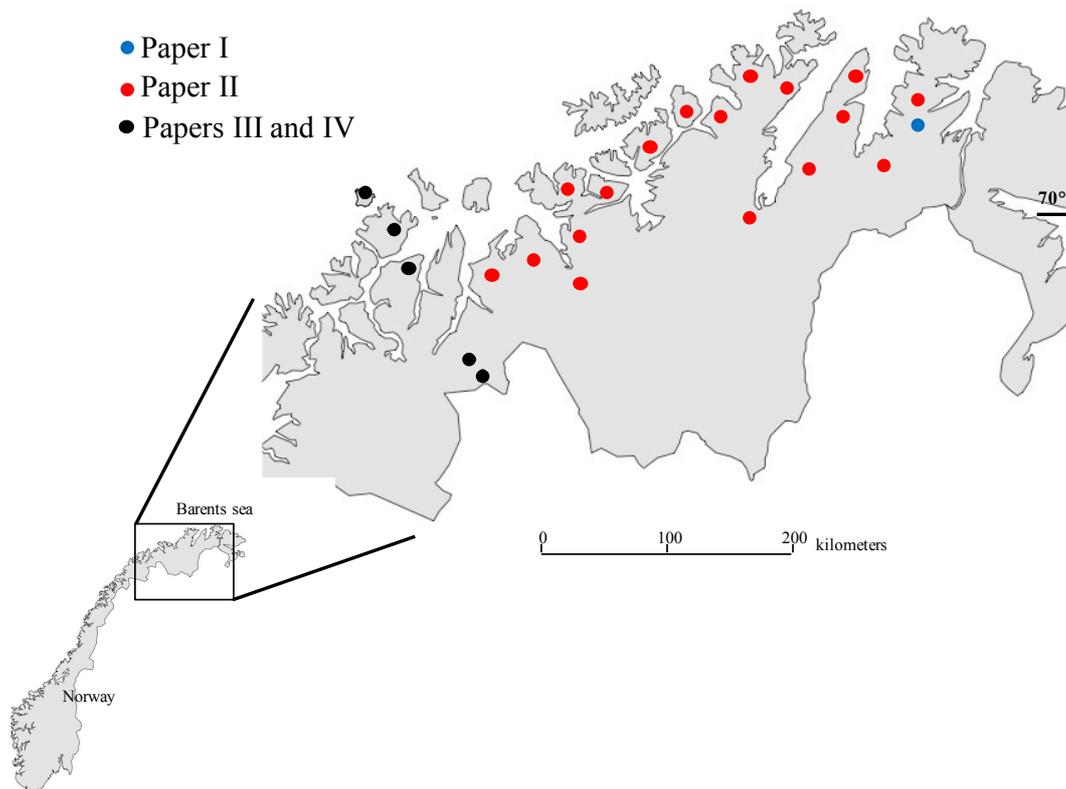


Figure 2. Approximate geographical locations where *Empetrum* plant and soil material was gathered for Paper I (blue circle), vegetation data was sampled for Paper II (red circles) and experiment was set up and data was gathered for Papers III and IV (black circles).



Figure 3. Examples of *Empetrum* tundra heathland used in *Paper III* and *Paper IV*. A-B) Landscape areas and C) close up of heathland vegetation.

Study designs

This thesis includes a variety of study designs which encompass a range of methodologies from both an experimental and observational standpoint. In the field studies, we make use of natural climatic gradients, which is a common approach to infer the effects of climate change on terrestrial ecosystems (e.g. De Frenne et al. 2013, Mayor et al. 2017) . The use of gradients has the strength of collecting data in natural settings and taking advantage of inter-annual variability, consequently having greater ecological validity. However, as conditions are not manipulated, and hence not controlled for, it might be challenging to establish cause and effect relationships (Dunne et al. 2004). Nevertheless, the large number of plots used in the gradient studies presented here, 1450 in *Paper II* and 144 in *Paper III* and *Paper IV*, increases the validity of the results and eases interpretation of possible trends.

Paper II, *Paper III* and *Paper IV* use a quasi-experimental study design approach (Shadish WR et al. 2002). Though mostly used in economics research (e.g. Greenstone and Gayer 2009), this type of approach can also successfully be applied in ecological studies (Butsic et al. 2017). Quasi-experimental designs allow for the inclusion of ecological processes that are non-random, such as reindeer density (i.e. high vs low) in *Paper I,I* or the continentality index along the climatic gradient (i.e. two oceanic sites, one mid-continental and two high continental sites) in *Paper III* and *Paper IV*. Further, *Paper III* has also a manipulation or experimental aspect to it. By simulating an extreme event at each site, we introduced a controlled experimental treatment to the study design and were able to isolate the single and interacting effects of this treatment (i.e. extreme event) with other variables along the climatic gradient. Thus, this paper combines a gradient and experimental approach, a method which has been called for in climate change research studies (e.g. Dunne et al. 2004, Sundqvist et al. 2013).

The temporal aspects of the study designs presented in this thesis also add to the strength of the results. In *Paper III* and *Paper IV* data were collected over a course of nine and six years respectively. A valuable aspect of long-term studies is that they provide the possibility of studying the role played by major disturbances, such as those projected by climate change, in maintaining and changing the character of ecosystems dominated by perennial species. Nevertheless, long term studies require often large economic and time investments. Thus, other approaches such as space-for-time techniques (Pickett 1989), are suitable substitutes for inferring, for example, the effects of increasing temperature over time as used in *Paper II* (Blois et al. 2013).

The bioassay-based study approach used in *Paper I* and in parts of *Paper III* is a common method used in allelopathy research (Inderjit and Dakshini 1995). Because the presence of inhibitory chemicals in plant tissues does not equal allelopathy, the biological effects of either the chemicals, or entire plant parts must be quantified through their biological activity on live tissue. Though controversial due to the often lack of simulated natural conditions as experienced by the plants themselves in nature, bioassays are still considered a valid research tool for pinpointing the source of allelopathy in many plant species (Inderjit and Callaway 2003). With this in mind, we carried out in *Paper I* three bioassays testing the allelopathic effect of purified batatasin-III (concentrations ranging between 0 and 4mM), and one bioassay testing the effect of leaves and humus of *E. nigrum* on seed germination and mean root elongation of 24 vascular plant species ranging from herbaceous to important tree species. In addition, we tested the effect of organic and mineral substrate on the growth inhibiting effect of purified batatasin-III. In *Paper III*, we tested the effect of soil from *Empetrum* heathlands collected along the climatic gradient on seedlings of four selected species.

The particular study designs of *Paper II*, *Paper III* and *Paper IV* are briefly described below.

In *Paper II*, data were gathered from 1450 plant communities located within ten pairs of neighbouring reindeer herding districts along the coast of Northern Norway (Figure 1 in *Paper II*). Each pair represents two decades of high versus low reindeer density (Bråthen et al. 2007b). Plant communities were selected using GIS and *a priori* rules set before sampling (*sensu* Mörsdorf et al. 2015).

For *Paper III* a factorial experiment was set up between 2009 and 2017 in five *Empetrum* dominated heathlands along a climatic gradient (Figure 1 in *Paper III*). At each of the five sites, ten blocks were established and within each block, three plots (50 x 50 cm) were permanently marked: control plot, where vegetation was undisturbed and two extreme event plots where the vegetation was cut at ground level and either removed (leaving a bare plot) or left as a litter layer. Vegetation was recorded once a year in all plots during nine years.

Data used in *Paper IV* was gathered between 2011 and 2016 from the same five *Empetrum* dominated sites along the climate gradient used in *Paper III*. At each site we established ten blocks, and within each block we permanently marked three plots of 50 x 50 cm with a minimum of 90% *Empetrum* cover where *Empetrum* measurements were taken (Figure 1 in *Paper IV*).

Vegetation sampling

Gathering of vegetation data in this thesis was done using several methods. Due to the large scale of the study designs, we choose techniques that provided a balance between efficient and reliable estimates of plant biomass and frequency/cover for single sampling in temporal plots, in addition to repetitive sampling in permanent plots. For biomass analyses we used a modified version of the pin point frequency method developed by Jonasson et al 1988 where recordings of each plant species are done through intercepts on pins attached to a sampling frame (three pins for *Paper II* and 20 pins in *Paper III* and *Paper IV*, Figure 3)(Bråthen and Hagberg 2004). The number of hits is then converted to biomass using established calibration functions (Ravolainen et al. 2010). For the frequency of vegetation presence and cover analyses used in *Paper III* and *Paper IV* we used 50 x 50 cm frames divided in 16 sub plots (0.0125 m² each, Figure 3), where presence/absence of each species (including berries/flowers) was recorded in each subplot (Austrheim et al. 2008). Vegetation frequency was recorded at the end of the growing season in late August. Further, annual shoot length used in *Paper III* was quantified by selecting five random annual shoots of *Empetrum* which were measured to the closest millimetre.

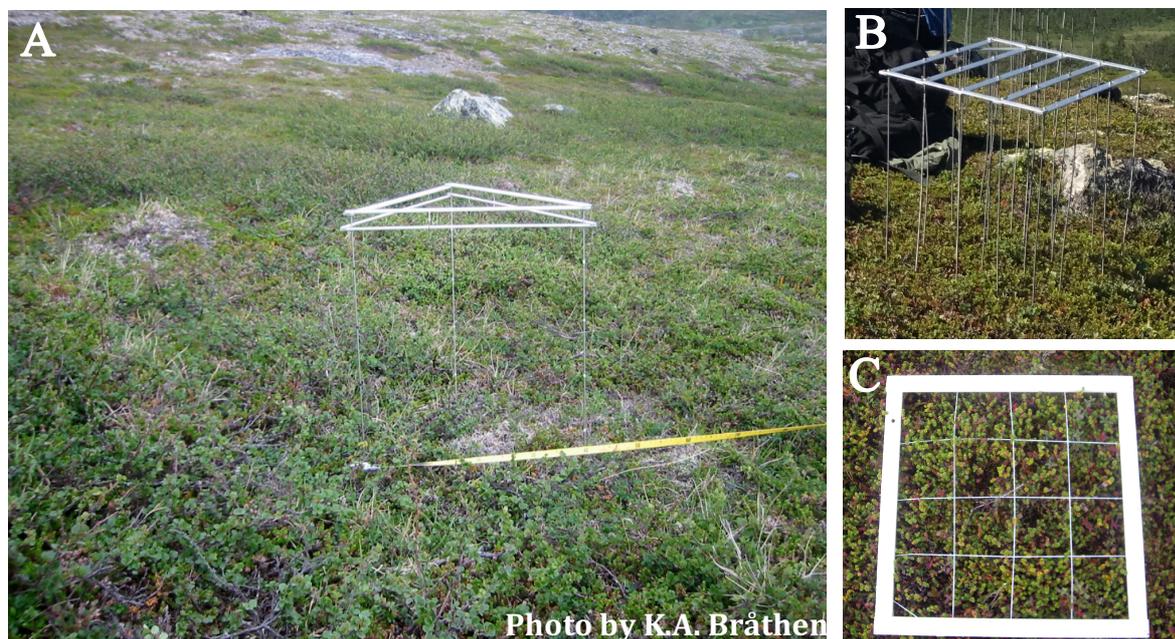


Figure 4. Methods used to gather plant data in this thesis, A-B) Pin-point intercept frame with pins, (A) with 3 pins as used in *Paper II*, and (B) 20 pins as used in *Paper III* and *IV*, and C) frequency frame divided in 16 sub squares (0.0125 m² each) used to measure frequency of plant and berry occurrence.

Environmental and climatic variables

Precipitation, snow depth and bedrock data were gathered from publicly available databases at the Norwegian water resources and energy directorate (NVE), the Norwegian meteorological institute, the Norwegian mapping authority, and the Geological Survey of Norway (i.e. www.senorge.no, www.eklima.no, www.ngu.no). Temperature data were gathered from the Norwegian meteorological institute (i.e. www.eklima.no) for *Paper II*, while temperature data used in *Paper III* and *Paper IV* were gathered with the use of temperature loggers (Thermochron iButtons®) which were placed at each study site at surface level. This allowed us to not only calculate temperature related variables, such as annual or summer temperature, but also growing season length and number of freezing days during winter (days with mean daily temperatures below -1 °C what suggests that there is an absence or low snow cover) (Table 2 in *Paper IV*). I found it was interesting to disentangle the relationship between data gathered at a broader scale (i.e. through online databases) and that gathered on-site (i.e. through the temperature loggers). For example, snow depth measurements gathered from online databases differed sharply with the actual snow cover on several of our sites which we inferred from our temperature loggers. That is, we often registered mean daily freezing temperatures, suggesting absence of snow cover, while online databases registered large amounts of snow (Figure 5). Though the resolution of most databases used in this thesis is 2 km x 2 km, hence it might not be unexpected that measurements differ from those at smaller scales, it is interesting to point out that, the overall conclusions, in *Paper IV* for example, might have been quite different if we would have only used online database data. This decoupling of micro and macroclimatic conditions along gradients is not uncommon (Graae et al. 2012) and our data supports the inclusion of data loggers in climate gradient studies.

Statistical methods

All data analyses in this thesis were done using the statistical environment R (R core team). According to the nature of the study designs and hypotheses we used linear models (*Paper I*), linear mixed effects models (*Paper II*, *Paper III* and *Paper IV*) and structural equation models (SEMs) (*Paper II*). Whenever necessary we transformed the data and applied model selection by using the Akaike Information Criterion (AIC).

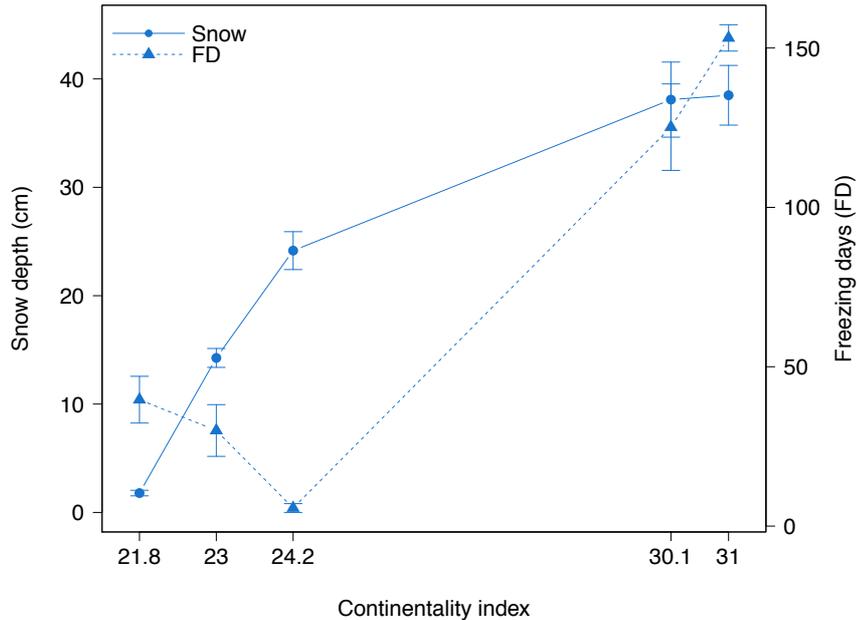


Figure 5. Mean snow depth (cm) (gathered from www.senorge.no) and mean number of freezing days (FD) (calculated from on-site temperature loggers), for each study sites across all six study years.

MAIN RESULTS AND DISCUSSION

In *Paper I*, we demonstrated how an abundant phenolic compound present in *Empetrum* leaves, namely batatasin-III, had inhibiting effects on seed germination and root elongation in all 24 vascular plant species tested. The majority of the species had never been tested before towards the allelopathic effects of batatasin III. Further, sensitivity to batatasin-III was dependent on the species and was modified by environmental conditions such as substrate type, finding a lower inhibitory effect of batatasin-III in soils with high organic matter content (i.e. humus) (Wallstedt et al. 2005). Finally, when testing for the direct allelopathic effects of *Empetrum* leaves and humus on seedling root elongation, we found a strong negative effect of *Empetrum* leaves and humus on mean root elongation but were unable to find a correlation between the amount of batatasin-III we measured in leaves or humus, and the root elongation. This suggests that though batatasin-III is an abundant phytotoxic compound produced in *Empetrum* leaves (Gallet et al. 1999), it may not be the only one responsible for the allelopathic capacity of *Empetrum* and that, most likely, it is a complex set of chemical compounds involved in the allelopathy of this species (Oden et al. 1992).

In *Paper II*, we aimed to evaluate the potential temperature mediating effect of *Empetrum* proportional abundance on tundra plant communities along a temperature gradient. The results from the large-scale survey across sites with contrasting reindeer numbers and summer

temperatures showed that *Empetrum* was present in 1230 out of the 1450 randomly chosen plant communities, and that it made up more than half the biomass across all plant communities. Further, with warmer summer temperatures, *Empetrum* had more berries and biomass, what suggests that under the predicted climate change scenarios of longer and warmer growing seasons, encroachment by *Empetrum* may be promoted by an increase in biomass and consequently, with establishment of new *Empetrum* individuals due to higher number of berries. As expected, warmer growing season conditions also increased the overall abundance of herbaceous growth forms and shrubs, thus, promoting ecosystem process rates (Elmendorf et al. 2012), however, the positive effect of temperature was reduced in the presence of *Empetrum*. That is, in communities where *Empetrum* was present with as low as 25% of total community biomass, total biodiversity and herbaceous plant biomass were less positive under increasing temperatures, while shrub biomass was enhanced (Figure 6). The effects of *Rangifer* were on average small in comparison to those of *Empetrum*, mainly finding that *Rangifer* had a negative effect on herbaceous biomass (Figure 6) and a slightly positive effect on *Empetrum* biomass. These results suggest that though herbaceous species can increase under warmer summer temperatures, they may do so at a slower rate when *Empetrum* is present, thus, *Empetrum* is able to mediate some of the effects of climate warming in tundra plant communities.

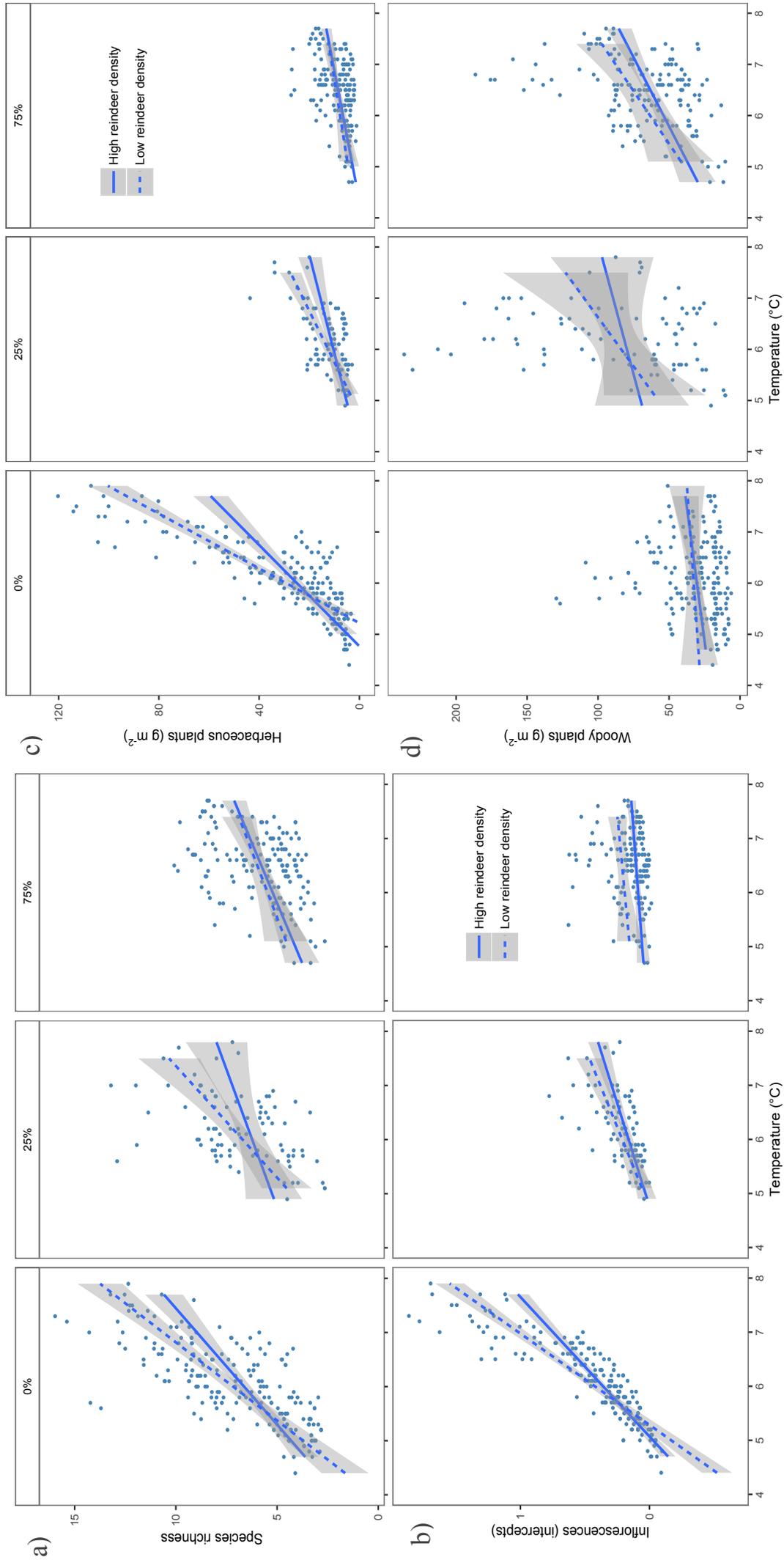


Figure 6. The effect of increasing summer temperature and reindeer density (high vs low) under increasing *Empetrum* biomass (0%, 25% and 75%) on a) Species richness, b) number of inflorescences, c) herbaceous biomass (herbs, grasses and sedges), and d) woody biomass (deciduous and evergreen shrubs)

In *Paper III*, we simulated an extreme event (i.e. cut all aboveground vegetation) in *Empetrum* tundra heathlands along a climatic gradient and studied the vegetation recovery over nine years. In theory, coastal sites with milder winters, cool summers and longer growing seasons might be expected to recover faster from disturbances. However, based on previous vegetation removal studies on continental *Empetrum* heathlands (e.g. Aerts 2010, Nilsson et al 2002), and on the temperature mediating effect of *Empetrum* presented in *Paper II*, where high abundance of *Empetrum* was found to limit the capacity of faster growing species in tundra communities to respond positively to climate warming, we hypothesized that climatic conditions would have no effect on the recovery of the disturbed heathlands. Our results showed, nine years after we simulated the extreme event, lower species richness, lower total plant biomass and *Empetrum* biomass in extreme event plots as compared to control plots across the entire climatic gradient (Figure 7). The lack of vegetation recovery along the entire climatic gradient was dramatic, finding nearly total absence of plant biomass in disturbed plots at the end of the study in 2017 (Figure 8). No new species were registered in the disturbed plots and subordinate species managed barely to gain their pre-disturbance species richness and occurrence rate. In order to get a better understanding of the mechanisms behind the slow recovery of the *Empetrum* heathlands along the climate gradient, we performed a series of studies focused on the regenerative capacity of the ecosystem. First a seed bank and seed rain study showed there was very low availability of germinable seeds in the soil, and low seed input from seed rain. Second, because the system was seed poor, we added seeds of eight different faster growing species including herbs, forbs and one tree and followed their establishment through-out the study years (2011-2016). We found that some seeds germinated in the plots but failed to establish into adult individuals most likely due to the allelopathic compounds released by *Empetrum* and present in the soil (Nilsson et al. 1993, Wallstedt et al. 2001 and *Paper I* in this thesis) . Nevertheless, because we only visited the site once a year, we wanted to make sure that sub-optimal growing conditions in the field were not affecting the establishment of seedlings, so, we collected soil from the *Empetrum* heathlands and conducted a bioassay experiment under controlled conditions in a green house. We planted seedlings of five of the species sowed in the field in soil from both the disturbed and controlled plots and compared their growth with seedlings sowed in commercially available peat.

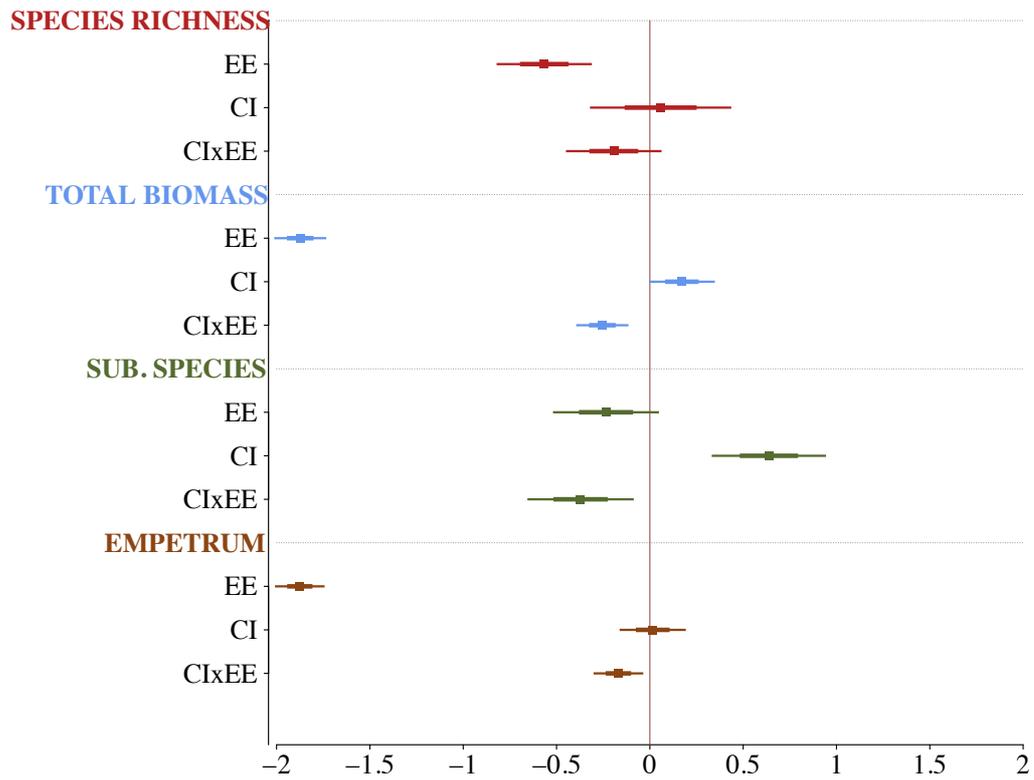


Figure 7. Standard coefficients from the linear mixed models showing the effects of extreme event treatment (EE), continentality index (CI) and their interaction (EExCI) on mean species richness and biomass (total, subordinate species and *Empetrum* alone).

a) Control vegetation



b) Vegetation nine years after extreme event



Figure 8. Photographs taken during summer 2017 showing a) Control plot, and b) Extreme event plot where the vegetation was removed 9 year ago. Take note of the low plant biomass and bare soil in the extreme event plot

After three weeks, and though all seedlings were given the same optimal conditions of air humidity, light and water, those growing in *Empetrum* soil showed arrested growth when compared to seedlings grown in peat (Figure 9). Our results support previous studies showing the strong legacy effect *Empetrum* has on plant community structure when it is removed (Shevtsova et al. 1997, Nilsson et al. 2002, Aerts 2010) and confirms our hypothesis that this effect is consistent in *Empetrum* heathlands along a range of climatic conditions. In all, the positive effect of a milder climate on vegetation recovery did not take place due to the niche constructing effect by *Empetrum*.

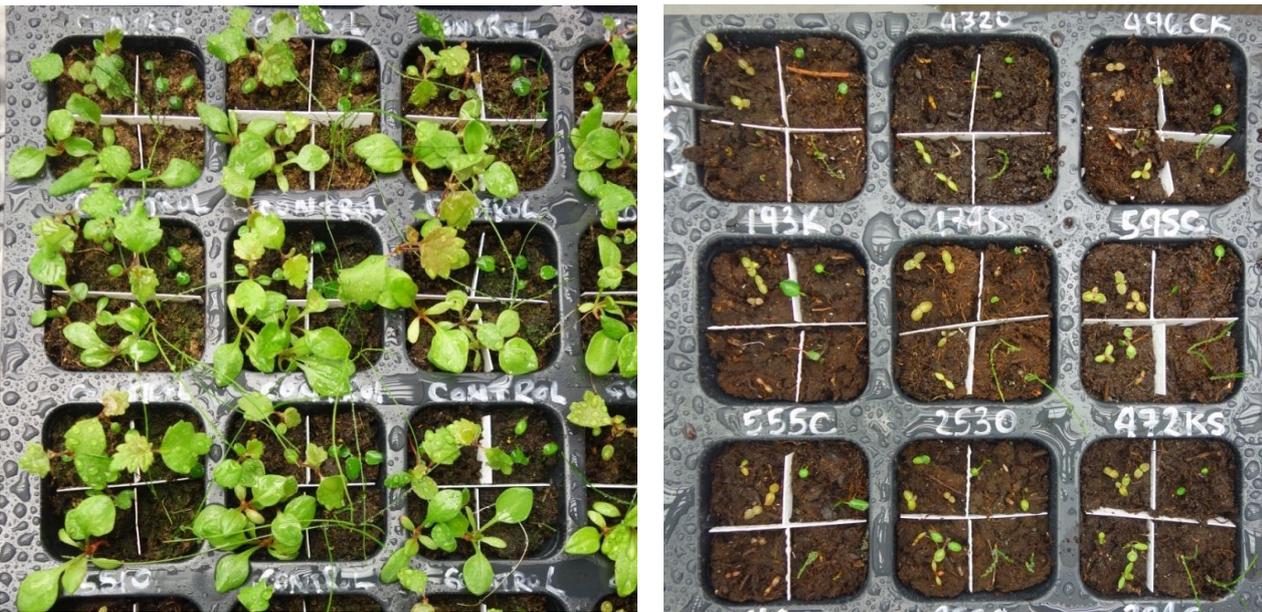


Figure 9. Three week old seedlings planted in commercially available peat (left), and in soil from extreme event and control plots in *Empetrum* dominated heathlands (right). All seedlings were kept under equal optimal growing conditions in the greenhouse.

In *Paper IV*, we evaluated the resistance of *Empetrum* (i.e. its ability to keep a stable cover, shoot growth and berry production) to fluctuations in climatic conditions over six years in five *Empetrum* dominated heathlands with contrasting climatic conditions. When looking at the climatic data, we found large climatic fluctuations among sites, especially during the winter months when the most continental sites experienced a low snow cover and, consequently, the vegetation was exposed to freezing temperatures for long periods of time each winter (Figure 11). Our results show *Empetrum* was able to grow and produce berries at all sites and during all years, though *Empetrum* shoot length was shorter and *Empetrum* produced less berries in sites where vegetation was exposed to freezing temperatures. These negative effects however, could be compensated if the following growing season was warm and long (Figure 10). Though we did not account for the presence of dead or damaged shoots, we did not observe any indications of browning, which is a phenomenon predicted to happen when plants are exposed to freezing temperatures during winter due to absence

of snow cover, and vegetative and flowering buds are damaged. In all, *Empetrum* appears to be frost hardy and resistant to a range of climatic conditions, especially during the winter months, showing increased reproductive and vegetative output under warmer growing season conditions. Thus, it can be expected that *Empetrum* might be able to cope with, or even benefit from, some of the environmental modifications brought by climate change, such as varying snow cover conditions and an increase in growing season length (Bienau et al. 2014, Krab et al. 2018) .

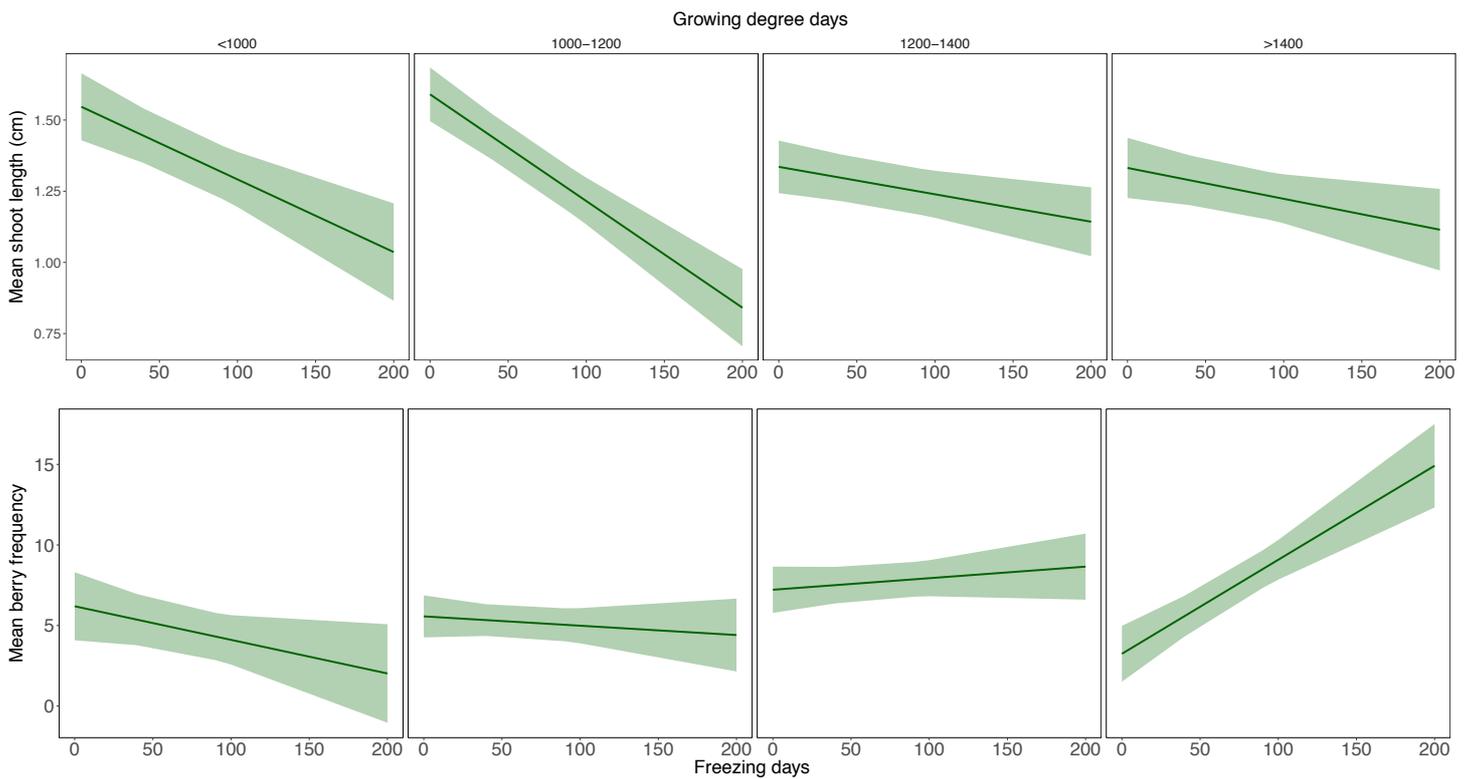


Figure 10. Interactive effect of number of freezing days and growing degree days on mean shoot length (cm) and mean berry production. The mean is presented with 95% confidence intervals.

Oceanic to Continental climate

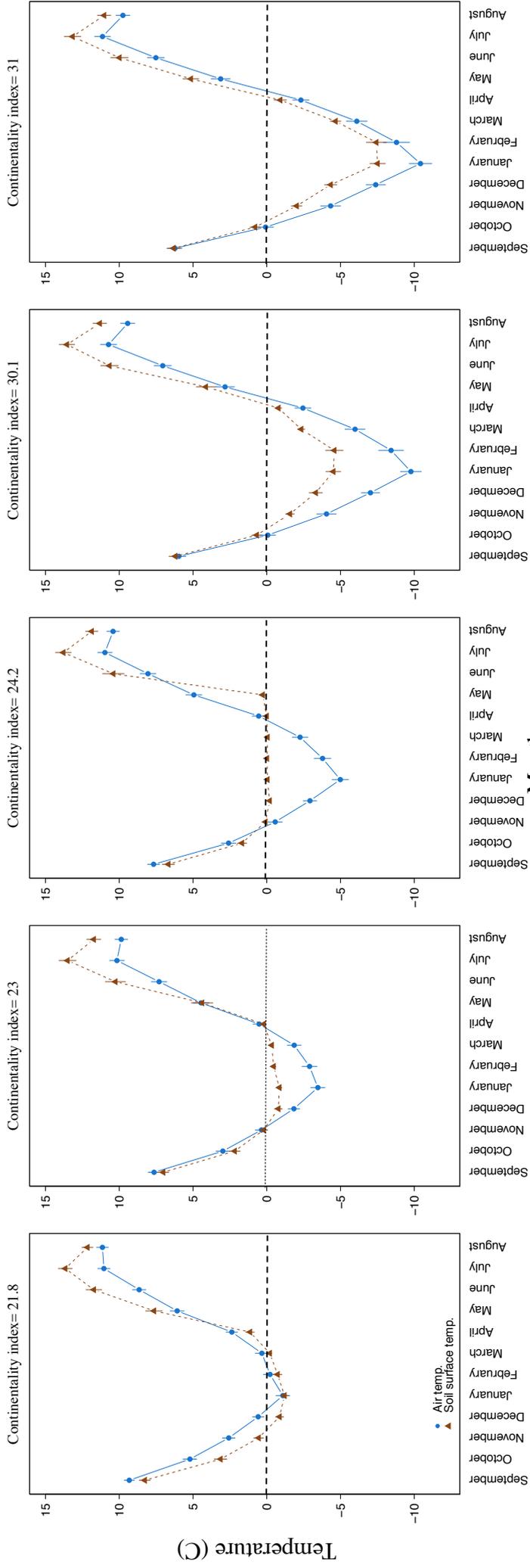


Figure 11. Mean air temperature extracted from publicly available online sources (blue) and soil surface temperature measured on site with temperature loggers (brown) through-out the course of the study years (2010-2016) for all five sites along the climatic gradient (continental index= 21.8-31). The mean is presented with 95% confidence interval

CONCLUDING REMARKS

The results presented in this thesis, suggest that the common niche constructor species *Empetrum nigrum* is capable of modifying some of the predicted effects of climate change in tundra plant communities and that its presence will be promoted by climate warming. First, it was particularly interesting how increasing *Empetrum* abundance appeared to mediate the effects of increasing temperatures on plant community structure, hence restricting the expected increase in biodiversity and abundance of faster growing species connected with warmer temperatures in tundra plant communities. Second, we found that when *Empetrum* was the most abundant species in the plant community, climate was no longer a reliable predictor for plant community structure due to the strong niche construction by *Empetrum*, as suggested by the overall lack of recovery of the tundra heathlands after the extreme event. And third, we expanded the knowledge on the allelopathic capacity of *Empetrum* and found *Empetrum* to be a resistant species, capable of growing and producing berries under a range of contrasting climatic conditions indicating it could cope with some of the climatic instability brought by climate change.

Though there already exists a large body of literature on the ecosystem modifying effects of *Empetrum* in tundra ecosystems (e.g. Tybirk et al 2000, Aerts 2010, Bokhorst et al. 2015) , this thesis has contributed to advancing the knowledge on the niche construction effects of *Empetrum* on tundra plant communities under to a range of climatic conditions. Thus, we might be a step closer to understanding the encroachment of *Empetrum* that is already apparent today and which is predicted to happen under climate change (Vuorinen et al. 2017, Maliniemi et al. 2018). It is likely that the resistance of *Empetrum* to varying climatic conditions, together with its niche constructing ability, are facilitating its encroachment in tundra plant communities. The results presented here also encourage for the inclusion of niche constructor species, and their effects, in climate change model predictions.

Though *Empetrum* was found resistant to a range of climatic conditions, repetitive or severe extreme events might damage the heathland vegetation (Bokhorst et al. 2009, Bokhorst et al. 2015). The results presented here, suggest that *Empetrum* dominated heathlands have a low recovery capacity to heavy disturbance, indicating low resilience to extreme events, we did not find any indications of the change in plant community composition predicted to happen in these heathlands after extreme events at any of the sites along the climatic gradient (Bokhorst et al. 2015). On the contrary, over time, the disturbed *Empetrum* heathlands will likely return to their previous

Empetrum dominated state. However, this might only be the case when extreme events cause severe disturbance, as the one we simulated. It is possible that if not all vegetation is damaged, subordinate dwarf shrubs will manage to take over instead of *Empetrum*. Nevertheless, the plant community will still most likely be dominated by dwarf shrubs and only an alleviation of others stressors, such as increases in nitrogen could bring any community changes to the tundra heathlands (Aerts 2010, Nilsson et al 2002).

The results of the research suggest that the outcome of climate change in tundra communities where *Empetrum* is present might differ sharply from the general predictions on climate change in northern ecosystems.

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The idea to develop this PhD came from my supervisor, Kari Anne Bråthen, after discovering the vast amounts of *Empetrum nigrum* present across Northern Norway. How and why does this slow growing tundra species manage to dominate these vast areas? Once we started doing a little digging, we found out much had been done on *Empetrum* in Sweden. *Empetrum* is an important part of the forest understorey vegetation in Swedish forests, and studies on its capacity to inhibit growth of several important tree species had taken place since the late 90's. However, little had been done in tundra ecosystems and nothing as far north as northern Norway. Thus, out we went in summer 2009 looking for the perfect *Empetrum* dominated heathlands where we could get some answers to our many questions. The project evolved and expanded as the years went by (and my family size increased), data was gathered and lots of experiments and studies took place over a total of nine years. I am forever grateful to Bente and Rigmor for coordinating and gathering data when I was unable to be part of the field work. Thank you for challenging me when details were a little loose and for engaging in this project of mine as if it were your very own. There have been several field assistants through-out these nine years, thank you Xavi, Metha, Anna Katarina, Mikel, Mildrid and a special thank you to Sissel for your enthusiasm even when we had rain and 2 degrees for days on end, or 20 degrees and loads of mosquitoes.

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Paper I



Paper II



Paper III



Paper IV

