



Høgskulen på Vestlandet

Master Thesis in Climate Change Management

GE4-304

Predefinert informasjon

Startdato:	10-05-2018 09:00	Termin:	2018 VÅR
Sluttdato:	28-05-2018 14:00	Vurderingsform:	Norsk 6-trinnsskala (A-F)
Eksamensform:	Master's thesis		
SIS-kode:	203 GE4-304 1 MA 2018 VÅR		
Intern sensor:	Inger Auestad		

Deltakar

Namn:	Sigbjørn Throndsen
Kandidatnr.:	604
HVL-id:	180607@hvl.no

Gruppe

Gruppenamn:	Enmannsgruppe
Gruppenummer:	10
Andre medlemmer i gruppa:	Deltakaren har levert inn i enkeltmannsgruppe

Sinking Islands in the Sky

Projecting the future distributions of *Ranunculus glacialis*, *Poa flexuosa* and *Trisetum spicatum* in Jotunheimen, Norway under climate change



Sigbjørn Throndsen

Department of Environmental Sciences, Faculty of Engineering and Science

WESTERN NORWAY UNIVERSITY OF APPLIED SCIENCES

Master Thesis in Climate Change Management

Sogndal
[May 2018]



Western Norway
University of
Applied Sciences

Sinking Islands in the Sky

Projecting the future distributions of *Ranunculus glacialis*, *Poa flexuosa* and
Trisetum spicatum in Jotunheimen, Norway under climate change

Master thesis in Climate Change Management

Author:
Sigbjørn Throndsen

Author sign.

Thesis submitted:

Spring 2018

Open thesis

Main Supervisor:
Julien Martin Marie Vollering
Co-supervisors:
Mark Gillespie and Knut Rydgren

Keywords:
Species distribution modelling, Maxent,
alpine ecology, alpine plants, climate change,
distributional shift.

Number of pages: 39
+
Appendix: 7

Sogndal, 28.05.2018

This thesis is a part of the master's program in Climate Change Management (Planlegging for klimaendringer) at the Department of Environmental Sciences, Faculty of Engineering and Science at the Western Norway University of Applied Sciences. The author(s) is responsible for the methods used, the results that are presented and the conclusions in the thesis.

Preface

This Master thesis is the final work in the master's program Climate Change Management at Western Norway University of Applied Sciences. This project was conducted over one semester and counts as 30 ECTS.

Julien Vollering presented the idea for this thesis back in January 2017. It caught my attention back then and I chose it as my thesis project in June 2017. I chose this topic because I was interested in doing a thesis in the field of ecology and because I was interested in learning more about species distribution modelling.

During my time working on this thesis, I have learned a lot about species distribution modelling and a lot about alpine ecology. However, I feel like I have merely scratched the surface on these large topics over the last five months.

I would like to thank my main supervisor Julien, for guiding me through the field of species distribution modelling, training and help with the Maxent software and for constructive comments on earlier versions of the manuscript. His door was always open if I ever needed help with Maxent, or if there was anything I didn't understand. I would also like to thank Mark Gillespie for help with setting the course for the study at an early stage. Finally, I would like to thank Knut Rydgren for his help and advice regarding alpine ecology.

Sogndal, May 28th 2018

Sigbjørn Throndsen

Abstract

Introduction

Changes in species distributional range as a response to climate change is well documented. The changes are substantial along elevational gradients, and the general trend is that the warming has caused an upward elevational shift for several alpine plants. The aim with this study is to project changes in (1) suitable habitat, (2) elevational range (3) and the level of habitat fragmentation for *Ranunculus glacialis*, *Poa flexuosa* and *Trisetum spicatum* under two different climate change scenarios in Jotunheimen.

Method

Species presence records and five pre-selected predictors, selected from a set of topographic and climatic variables, were used to model the species distributions. Projections for the year 2070 under climate change scenarios RCP4.5 and RCP8.5 were derived from the models of the current distributions using the Maxent software. Changes in suitable habitat were analyzed using ArcGIS.

Results

All species were projected to lose suitable habitat with an average reduction of 70 % under RCP8.5 and 48 % under RCP4.5. All species were projected to disappear from their lowest elevations, and the average elevational range contraction for the species was 524 m under RCP8.5 and 243 m under RCP4.5. The level of habitat fragmentation was projected to increase with an average increase in patch number of 72 % and 67 %, and an average reduction in patch size of 82 % and 65 %, under RCP8.5 and RCP4.5 respectively.

Discussion

All model results have a good or fair predictive performance measured by their AUC values. A sampling bias correction was done using locations of species from the same genus as the focal species (target group) as background points. There was large differences in the future projections between the models with no sampling bias correction and the models with correction. As the corrected models might “over” correct due to a narrow environmental range from which background was drawn, the truth would lie somewhere in between. The precipitation variable contributed the most to all models suggesting that precipitation is more influential than temperature on the species distributions within the study area.

Conclusion

These results was produced to gain knowledge on the expected vegetation changes in an alpine ecosystem of national interest. The projections show that all species will lose suitable habitat supporting previous findings that alpine habitats are particularly vulnerable to climate change.

Sammendrag på norsk

Introduksjon

Endringer i arters utbredelse som en respons på klimaendringer er vel dokumentert. Endringene er betydelige langs høydegradienter, og den observerte trenden er at oppvarmingen har forårsaket en forskyvning oppover i høyden for flere alpine planter. Målet med dette studiet er å finne endringene i (1) egnet habitat, (2) høydegradienten (3) og nivået av habitatfragmentering for *Ranunculus glacialis*, *Poa flexuosa* og *Trisetum spicatum* under to forskjellige utslippsscenarioer i Jotunheimen.

Metode

Artsobservasjonsdata og fem forhåndsvalgte prediktorer, valgt fra et sett med topografiske og klimatiske variabler, ble brukt til å predikere artenes utbredelse. Prosjeksjoner for år 2070 under utslippsscenarioene RCP4.5 og RCP8.5 ble utarbeidet med utgangspunkt i modellene av den nåværende utbredelsen ved hjelp av programvaren Maxent. Endringer i egnet habitat ble analysert ved hjelp av programvaren ArcGIS.

Resultat

Alle artene ble projisert til å miste egent habitat med en gjennomsnittlig reduksjon på 70 % under RCP8.5 og 48 % under RCP4.5. Alle artene ble projisert til å forsvinne fra deres lavest liggende områder, og den gjennomsnittlige sammentrekningen av høydegradienten for artene var på 524 under RCP8.5 og 243 under RCP4.5. Nivået av habitat fragmentering er projisert til å øke med en gjennomsnittlig økning i antal separate habitater på 72 % og 67 % og en gjennomsnittlig reduksjon i habitat størrelse på 82 % og 65 % henholdsvis under RCP8.5 og RCP4.5.

Diskusjon

Alle modell resultatene har god eller akseptabel prediksjonsverdi målt ut ifra deres AUC verdier. En korleksjon for eventuelt partisk artsdata påvirket av tilgjengelighet, ble gjennomført ved å bruke arter fra samme slekt som fokus artene som bakgrunn. Det var stor forskjell mellom modellene med denne korleksjonen og de uten korleksjon. Ettersom modellene med korleksjon sannsynligvis korrigerer for mye grunnet den smale rekkevidden på miljøvariablene bakgrunnen ble tatt fra, ligger sannheten et sted imellom de to modellsettene. Nedbørsvariabelen bidro mest til alle modellene noe som indikerer at nedbør har større påvirkning på artenes utbredelse enn temperatur innenfor området.

Konklusjon

Resultatene fra dette studiet bidrar til økt kunnskap rundt de forventede endringene i vegetasjonen i et alpint økosystem av nasjonal interesse. Prosjeksjonene viser at alle artene kommer til å miste egnet habitat, og støtter dermed tidligere studier som har vist at alpine habitat er sårbare for klimaendringer.

Table of contents

Preface.....	I
Abstract	III
Sammendrag på norsk.....	IV
Table of contents.....	V
1. Introduction.....	7
2. Methods	10
2.1. Study area.....	10
2.2. Species.....	11
2.3. Climate change scenarios.....	13
2.4. Data collection and preparation.....	13
2.4.1. Predictor data.....	13
2.4.2. Species occurrence data.....	15
2.4.3. Pre-selecting predictors.....	15
2.5. Species distribution modelling	16
2.5.1. Sampling bias.....	17
2.5.2. Threshold.....	18
2.6. Interpretation and analysis	18
2.6.1. GIS analysis.....	18
3. Results	19
3.1. Maxent models.....	19
3.1.1. Model performance.....	19
3.1.2. Variable importance	20
3.1.3. Species response	21
3.2. Distributional changes.....	23
3.2.1. Changes in habitat size.....	23
3.2.2. Changes in elevational range	26
3.2.3. Habitat fragmentation.....	27
3.2.4. Edge habitat.....	28
4. Discussion.....	29
4.1. Maxent models.....	29

4.2. Distributional changes.....	31
5. Conclusion	34
6. References.....	35
7. Appendix.....	1
7.1. Coefficient values	1
7.2. Threshold values.....	4
7.3. Correlation matrix	5
7.4. Edge habitat.....	6

1. Introduction

Climate change is a major threat to biodiversity (Settele et al., 2014; Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005). The different components of climate change (e.g. changes in temperature, rainfall, extreme events, CO₂ concentrations) are expected to affect different levels of biodiversity, from individual organisms, up through populations, species, communities, ecosystems and up to biomes, which are all different levels of biodiversity (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012). Threats to the higher levels of biodiversity are often the result of changes at the lower levels. For example, climate change could decrease genetic diversity of populations due to migration and directional selection of individuals, which again is likely to affect ecosystem functioning, production and resilience (Bellard et al., 2012; Botkin et al., 2007). Climate change effects are commonly studied at intermediate and higher levels of biodiversity (Bellard et al., 2012). Specifically, impacts on species are commonly explored since they often are used as discrete entities in ecosystems, and since a lot of ecological theory applies at the species level.

At the species level, the three different changes as a response to climate change are changes in physiology, changes in phenology and changes in range (Bellard et al., 2012; Root et al., 2003). Physiological changes as evolutionary responses – as opposed to plastic responses at the individual level – are likely to occur when species adapt to changing climatic conditions within their local range rather than tracking their current optimal environmental conditions (Bellard et al., 2012). Examples of this can be when species develop a higher tolerance to warmer and drier conditions, or behavioral modifications of their diet, activity and energy budget (Bellard et al., 2012). Changes in phenology – or the timing of life cycle events, such as flowering, fruiting and seasonal migration – as a response to climate change is already well documented (Bellard et al., 2012; Parmesan, 2006). A wide range of plants and animals has experienced a significant shift in key phenological events the last 50 years (Root et al., 2003). Finally, species can also shift their range as a response to climate change. In this case range shifts or distributional shifts are related to a species' climatic tolerance, and species track their optimal environmental conditions to a greater or lesser extent (Bellard et al., 2012).

Some species will show larger changes in distributions than others in the face of climate change (Chapin & Shaver, 1985; Lenoir, Gégout, Marquet, Ruffray, & Brisse, 2008; Parmesan, 2006). The different responses can be related to the different species' traits such as reproductive and dispersal ability, ecological tolerance and life-form (Klanderud & Birks, 2003; Lenoir et al., 2008). For example, species that have a restricted range due to a lower temperature boundary might shift their range as new areas become suitable with increasing temperatures, and species characterized by faster population turnover is likely to have a larger shift than others (Lenoir et al., 2008). Plant distributions are affected by climate and biotic interactions (Cornelissen et al., 2001; Thuiller et al., 2008; Woodward, 1987), which means that changes to these variables can lead to changes in species distributions.

Several studies have shown changes in species distributions as a response to climate change (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Parmesan, 2006; Parmesan & Yohe, 2003; Rosenzweig et al., 2008; Walther, 2010). The changes are substantial along elevational and latitudinal gradients, which is expected since surface air temperatures decrease with increasing elevations and latitudes. A recent study has estimated that species distributions have shifted to higher elevations at a median rate of 11 meters per decade, and a shift towards higher latitudes at a median rate of 16.9 km (Chen et al., 2011).

Alpine species are especially likely to be negatively affected by climate change. Specifically, distributional changes are likely to be larger in areas where temperature changes are predicted to be more pronounced, like in alpine areas (Chen et al., 2011). Moreover, the upper elevational boundary of alpine plants is strongly determined by temperature (Körner, 2003), so the expected warming will likely have a strong effect on this distributional limit of alpine plants. Changes in alpine areas are already observed, and on a global scale the upper treeline has had an upward elevational shift as a response to warmer temperatures (Harsch, Hulme, McGlone, & Duncan, 2009). The same trend is also observed over the last century in several alpine plants and increased precipitation is identified as a contributing factor (Felde, Kapfer, & Grytnes, 2012; Klanderud & Birks, 2003; Lenoir et al., 2008; Odland, Høitomt, & Olsen, 2010). This upward shift is followed by an increased abundance of vascular plants in European alpine areas (Gottfried et al., 2012; Odland et al., 2010; Pauli et al., 2012). These observed changes over the last century are likely to continue under a future warming of the earth. As species temperature niche expand upwards due to a warmer climate, the lower elevation areas of alpine habitats are predicted to be colonized by new competitors from lower areas (Choler, Michalet, & Callaway, 2001; Körner, 2003; Thuiller et al., 2008). The lower elevational boundary for alpine plants is often determined by competition from other species (Choler et al., 2001; Kulonen et al., 2017). This in combination with the expected upward shift will likely reduce suitable habitat for alpine plants due to mountains roughly conical shaped topography.

Reduction in habitat size is likely to be accompanied by changes in the composition of the habitat matrix – that is, in the level of habitat fragmentation. As suitable habitat disappears a fragmentation process, defined as a process of breaking up habitat into smaller patches (Forman, 1995), will occur as the distance between patches of suitable habitat increases and patches become more isolated (Andrén, 1994). The main causes of habitat fragmentation has usually been related to human activities, specifically through land use changes (Bogaert, Farina, & Ceulemans, 2005), but a changed composition of the habitat due to an upward elevational shift – as a response to climate change – could also break up habitats. Negative effects of habitat fragmentation impact particularly genetic biodiversity through a reduction in gene flow among populations leading to an increase in genetic drift, and potentially inbreeding (Young, Boyle, & Brown, 1996). It has been suggested – in combination with altered mating systems and changes in pollinator behavior – that this could lead to a reduced individual fitness and in the worst case increase the extinction risk of populations (Young et al., 1996). In addition, dispersal generally and habitat tracking specifically is compromised in a fragmented landscape, due to increasing areas of unfavorable conditions between suitable areas (Honnay et al., 2002; Thuiller et al., 2008).

Effects of fragmentation may be more pronounced for alpine species, for which lowland areas may act as barriers to dispersal. The increased isolation can cause problems for alpine species within isolated populations, as they might be unable to migrate to new suitable locations as their current locations become unsuitable (Jump & Peñuelas, 2005). As the dispersal abilities in alpine ecosystems are limited (Körner, 2003; Ryvarde, 1971; Scherrer & Körner, 2011), and the migration between populations is very restricted (Körner, 2003), it is likely that increased isolation will have negative effects on migration. In addition to increased distance between populations due to topography, lowland species that have moved upwards could compromise the dispersal abilities of alpine plants. Species from lower elevations have different growth strategies than alpine plants such as they grow larger in size and have a higher specific leaf area (Steinbauer et al., 2018), which could act as barriers for dispersal of seeds and propagules from alpine plants.

Reduction in total suitable habitat or in amount of contiguous habitat may affect the abundance of the species negatively. This is because habitat size and abundance is often highly correlated (Roque, Koptur, & Sah, 2017). Isolated populations are also more likely to experience a reduction in genetic diversity than others, which can decrease individual fitness (Jump & Peñuelas, 2005). Small and isolated populations will be prevented from being rescued by migration from other populations, and have a higher probability of extinction, because of their lower number of individuals (Leimu, Vergeer, Angeloni, & Ouborg, 2010). The combination of reduced fitness due to changing climatic conditions, and a potential reduction in diversity may compromise species abundance in alpine habitats, and in the worst case lead to local and widespread extinctions (Jump & Peñuelas, 2005). In addition, increased competition from lowland species such as shrubs is documented to decrease the species richness of alpine vascular plants (Klanderud & Birks, 2003; Wilson & Nilsson, 2009).

Predicting future distributional changes can help management decisions surrounding alpine vegetation. Any decisions around the management of a species arises from the identification of a problem (Guisan et al., 2013). Future predictions of distributional changes allows for an early detection of potential future problems that is likely to be caused by climate change (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011). Identifying problems at an early stage or even before they occur can allow conservation managers to define objectives, look at possible actions and explore the consequences of these actions before implementing them (Guisan et al., 2013). Predictions of the future spatial distribution of a species occurrence allows for a better understanding of a species response to certain environmental variables such as temperature and precipitation.

Future distributions can be predicted by characterizing the present distribution in terms of environmental predictors. In species distribution modelling – also known as habitat suitability modelling or ecological niche modelling (hereafter only referred to as SDM) – field observations of a species are linked with environmental variables to spatially predict a species distribution within an area (Guisan et al., 2013). The models builds on statistically and theoretically derived response curves that best reflects the ensemble of ecological requirements of the species (Guisan, Thuiller, & Zimmermann, 2017), and predicts the area of suitable habitat under a given set of environmental conditions. Future predictions are made by projecting the model on to a set of future environmental conditions while assuming no change in the relationship between species performance and the environmental variables (Pearman, Guisan, Broennimann, & Randin, 2008). The use of SDM has increased over the last few decades (Guisan et al., 2013), and this has led to an improvement of the computing tools used (Guisan et al., 2017). Today, SDM is the most popular method to derive spatial explicit predictions of environmental suitability for species (Guisan et al., 2013).

SDMs describe a species distribution in terms of the environmental variables that structure it. The environmental variables that affect growth, development, survival and distribution of plants can be divided into three groups; resource, direct and indirect variables (Guisan & Zimmermann, 2000). Resource variables are the matter and energy consumed by plants (e.g. nutrients, water, light). Direct variables, like climate or soils, are also of physiological importance but are not used up or consumed. Indirect variables such as topography have no direct physiological relevance for species performance but may affect the species indirectly through the action of a related resource or direct variable. These variables in combination determine species distributions. For modelling however, the scale determines which variables are relevant to use as predictors (Guisan & Zimmermann, 2000). At relatively coarse scales, climatic and topographical variables are the main structuring factors. Data sets offering these variables on a global scale are widely available and easy to obtain. This makes modelling at coarse scale popular. For

example, recent SDMs using these kinds of variables have predicted that between one third and half of alpine species across all major European mountain ranges will lose more than 80 % of their suitable habitat by the end of the century (Engler et al., 2011).

Thus, this study aims to predict how much range shift will occur in three alpine plant species in a nationally important alpine region in Norway. I use occurrence data and environmental variables in SDM to predict the future distributions of *Ranunculus glacialis*, *Poa flexuosa* and *Trisetum spicatum* under two different climate change scenarios in Jotunheimen. Specifically, I have looked in to the expected changes in (1) suitable habitat, (2) elevational range (3) and the level of habitat fragmentation for the three species.

2. Methods

2.1. Study area

The study area selected for this study is Jotunheimen, a Caledonian mountain chain that is located in central Norway (Figure 1). The area is situated within 61° 05' – 61° 55' N and 7° 24' – 9° 38' E. The elevational range of the study area is from 0 to 2469 m a.s.l. The bedrock in the area consists of Pyroxene Granulite, with compositions of Gabbro, Quarts and Mangerite. Amphibolite which is transformed from Pyroxene Granulite, is also found (Geological Survey of Norway, 2018b). The soil found in the area is mainly moraine cover, with a thin moraine cover dominating in the western parts, and a thicker moraine cover dominating in the east, and consists of bare rock at higher elevations (Geological Survey of Norway, 2018a). The vegetation in the area consists mostly of broadleaved forests, mainly birch in the lower lying areas in combination with bilberry heaths, and some snowbed areas at higher elevations (NIBIO, 2018). The topography in the area varies from high mountains with steep slopes in the western parts, to lower and more rounded mountains in the east. The area is the highest lying area in the Scandes, and the watershed between western and eastern Norway runs through the study area (Odland et al., 2010). The area has the highest climatic treeline (1200 m a.s.l. on south facing slopes) and altitudinal vegetation belt in Scandinavia (Klanderud & Birks, 2003). The upper limit of the low alpine zone has been recorded to be at 1400 m a.s.l. (Odland et al., 2010). Jotunheimen National park is located within the study area, mainly above the treeline. The national park was established in 1980, and makes up 1151 km² (Snøtun, 2011).

An important climatic gradient in the study area runs from west to east. The western parts have a more coastal climate with milder winter temperatures and cooler summer temperatures compared to the eastern parts. Data from a weather station at Fanaråkki in the western part, based on monthly normals from 1961-1990, shows that the mean temperature in January is -9.5 °C and the mean July temperature is 2.7 °C, with a mean annual temperature of -4.4 °C (Norwegian Meteorological Institute, 2018a). A station located in Sikkilsdal in the eastern part of the study area shows a mean temperature in January of -10.2 °C and a mean July temperature of 10.4 °C, with a mean annual temperature of -0.2 °C (Norwegian Meteorological Institute, 2018b). Precipitation data for the same weather stations shows a mean annual precipitation of 100 mm at Fanaråkki, and 79.1 mm at Sikkilsdal. The last century there has been a temperature increase in the region, with a mean annual temperature increase of 0.4-1.2 °C. (Hanssen-Bauer & Nordli, 1998). The mean annual precipitation increased in the same period by 5-18 %, mainly caused by an increase in autumn precipitation (Hanssen-Bauer & Førland, 1998).

Jotunheimen is a well studied area by botanists, and plant occurrence data for the region dates back to the early 20th century (Jørgensen, 1933; Nordhagen, 1943). Since the area is well studied, there is a high abundance of occurrence data available in the Norwegian Species Map Service (Artskart). These historical records have also provided the basis for previous studies of Jotunheimen in regards to changing distributions of alpine plants the last century (Felde et al., 2012; Klanderud & Birks, 2003).

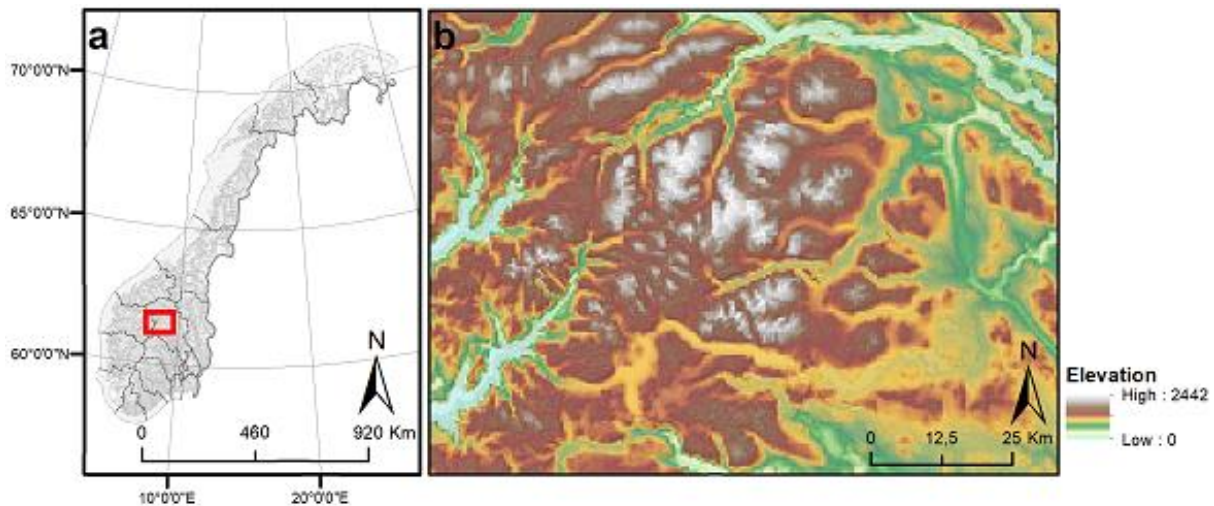


Figure 1: (a) Location of study area within Norway (red outline), and (b) elevation within the study area.

2.2. Species

The focal species in this study are *Ranunculus glacialis*, *Poa flexuosa* and *Trisetum spicatum*. These species were selected based on three requirements. The first selection criterion was that the species should be restricted to alpine habitats. Secondly, the species needed to be abundant in the study area, or at least have widely available occurrence data in Artskart. The final criterion stipulated that the species should be previously studied in relation to changing distributions or habitat fragmentation. The species needed to be alpine or subalpine since I aimed to investigate changes to alpine habitats. A sufficiently high abundance of occurrence data is needed for the models to make accurate predictions of the suitable habitat. Previously studied species gives the opportunity to compare the modeled predictions to empirical historical trends. In addition to the set requirements, the species were selected to compare species with different life history traits (e.g. stress tolerance, adaptable or competitive species versus species at the other end of the scale) in order to compare responses of more generalist species to more specialist species. The focal species are all sub-alpine vascular plants, and they are all previously studied in regards to changing distributions the last century and they are all found to disappear from their lower elevations (Klanderud & Birks, 2003).

R. glacialis is a long lived perennial herb adapted to low temperatures and the unpredictable seasonal conditions of high mountains (Körner, 2003) (Figure 2). It is considered an arctic-alpine pioneer species, and is found in sparsely vegetated snowbeds and in high alpine areas in Scandinavia and the European Alps (Totland & Alatalo, 2002; Wagner, Steinacher, & Ladinig, 2010). The plants can grow 10 – 15 cm and the color of the flower is white, and gradually changes to pink and finally to a deep purple color (Gjærevoll,

1989). *R. glacialis* is mainly pollinated by small flies which are weak pollinators (Wagner et al., 2010). A long flower lifetime, however, increases the frequency of pollinator visits and increases the probability of reproductive success (Wagner et al., 2010). *R. glacialis* flower early in the growing season, because of floral preformation – by which two future cohorts of flowers are initiated as the plant enter winter (Körner, 2003). The early development of seeds is advantageous for colonizing cool and wet sites where the growing season is short (Wagner et al., 2010). Flowering usually occurs 2 – 3 weeks after snowmelt (Totland & Alatalo, 2002). A study examining the effects of experimental climate change on *R. glacialis*, using open-top chambers for three seasons at Finse, an alpine site in Southern Norway (60° 36' N, 7° 30' E), found that the reproductive abilities, growth and phenology was not affected by climatic warming (Totland & Alatalo, 2002). The study also found that the reproductive output and ramet size differed little from year to year, despite large differences in average date of snowmelt. Felde et al. (2012) found a range contraction for *R. glacialis*, with a 111 m upward shift in the lower elevation limit and a 36 m downward shift in the upper elevation limit in Sikkilsdalen located in Jotunheimen. The observed elevational range for *R. glacialis* in this study was between 1336 and 1514 m a.s.l., while a study by Holten et al. (2011) conducted in a transect covering a large part of central Scandinavia, found an elevational range between 305 and 1910 m a.s.l. The highest elevation recorded for *R. glacialis* in Norway is 2370 m a.s.l. (Holten et al., 2011).

P. flexuosa is a member of the *Poaceae* family and is considered rare (Figure 2). It prefers moist, exposed, rocky and gravel dominated soils in the mountains, but is also found in snowbeds, scree slopes and on ledges (Mossberg & Stenberg, 2012). It grows in tight tussocks, and the top is 2 -5 cm long with a grey-violet color that develops between 2 – 4 flowers (Mossberg & Stenberg, 2012). The species is not nutrient demanding (Lid, Lid, & Elven, 2005), and the distributional range in Scandinavia is between 750 and 1910 m a.s.l., and the highest elevation recorded in Norway is 2350 m a.s.l. (Holten et al., 2011).



Figure 2: The focal species in this study. (a) *Ranunculus glacialis* (Glacier buttercup) (photo by Rigmor Wang), (b) *Poa flexuosa* (Wavy Meadow-grass) (photo by Rolv Hjelmstad) and (c) *Trisetum spicatum* (Spike false oat) (photo by Rolv Hjelmstad).

T. spicatum is a member of the *Poaceae* family and is considered a pioneer species (Figure 2). It is often prominent in the early successional stages on glacier forelands (Matthews & Whittaker, 1987). It can grow to heights between 10 – 25 cm and is often found on meadows, heaths and ledges, and prefers alkaline soils (Gjærevoll, 1989). The top is short and small, tight and plump and has a brown-black color, and develops 3 flowers (Lid et al., 2005). Felde et al. (2012) reports a small elevational range contraction for *T.*

spicatum, with a 45 m upward shift in the lower elevation limit and 28 m downward shift in the upper elevation limit. This study reports that the observed elevational range is between 1270 and 1512 m a.s.l. in Sikkilsdalen, Jotunheimen, while the study by Holten et al. (2011) found the elevational range to be between 730 and 1810 m a.s.l. The highest elevation recorded for *T. spicatum* in Norway is 2220 m a.s.l. (Holten et al., 2011).

2.3. Climate change scenarios

This study uses representative concentration pathway (RCP) scenarios to model the future distribution of the focal species. The RCP scenarios are designed to explore a wide range of future climates characterized by future concentration of different greenhouse gases and other anthropogenic forcing agents including consistent short-lived gases and land use changes (Collins et al., 2013; Cubasch et al., 2013). The scenarios are identified by their 21st century peak or stabilization value of radiative forcing (RF) derived by a reference model and given in $W\ m^{-2}$ (Collins et al., 2013). The scenarios used in this study are RCP4.5 and RCP8.5. RCP4.5 – which is considered a medium low emission scenario – aims at stabilizing the RF at 4.5 $W\ m^{-2}$ around 2100, while RCP8.5 – which is the highest emission scenario – implies an RF of 8.5 $W\ m^{-2}$ by 2100 but a rise in RF beyond that date (Cubasch et al., 2013). These scenarios were chosen to reflect a broad spectrum of the future emission scenarios.

2.4. Data collection and preparation

2.4.1. Predictor data

The predictor data to be used in the distribution models consisted of climatic and topographic variables. Specifically, the climate data consisted of 19 bioclimatic variables in 30 arc second resolution, obtained from Worldclim.org (version 1.4) (Table 1). The bioclimatic variables are derived from the monthly temperature and rainfall values in order to generate more biologically meaningful variables. The variables represent annual trends (e.g. mean annual temperature and annual precipitation), seasonality (e.g. annual range in temperature and precipitation), and extreme or limiting climatic factors (e.g. temperature of coldest month and warmest month, and precipitation of the wettest and driest quarters) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). 30 arc second resolution is equivalent to a raster cell size of approximately 500 x 500 meters at the latitude of the study area and represents the finest resolution climate data available for the study area. Values for the bioclimatic variables were obtained for current climatic conditions (WorldClim, 2005c) and for projected conditions in the year 2070 under the RCP4.5 scenario (WorldClim, 2005a) and the RCP8.5 scenario (WorldClim, 2005b). The values for current conditions are interpolated from weather station data (Hijmans et al., 2005), while the values for the projected future conditions are derived as downscaled results from a general circulation model called CCSM4 developed by the National Center for Atmospheric Research in the U.S.. This particular circulation model has high horizontal (surface) resolution over land and ocean (Flato et al., 2013).

To obtain square cells of equal size, the climatic raster data was projected to the WGS 1984 UTM zone 33N coordinate system in ArcGIS. In the reprojection, cell size was set to 500 x 500 m, and values were resampled from the original raster by bilinear interpolation. The extents of all rasters were set to line up exactly. All GIS work was done using the Esri software ArcGIS version 10.5.1.

<i>Environmental index</i>	<i>Code</i>	<i>Description</i>	<i>Unit</i>	<i>Source</i>
Climatic variables	Bio1	Annual mean temperature	Degrees Celsius*10	http://www.worldclim.org
	Bio2	Mean diurnal range (mean of monthly (max temp – min temp))	Degrees Celsius*10	http://www.worldclim.org
	Bio3	Isothermality (Bio2/Bio7)*100	Dimensionless	http://www.worldclim.org
	Bio4	Temperature seasonality (standard deviation * 100)	Degrees Celsius*10	http://www.worldclim.org
	Bio5	Max temperature of warmest month	Degrees Celsius*10	http://www.worldclim.org
	Bio6	Min temperature of coldest month	Degrees Celsius*10	http://www.worldclim.org
	Bio7	Temperature annual range (Bio5-Bio6)	Degrees Celsius*10	http://www.worldclim.org
	Bio8	Mean temperature of wettest quarter	Degrees Celsius*10	http://www.worldclim.org
	Bio9	Mean temperature of driest quarter	Degrees Celsius*10	http://www.worldclim.org
	Bio10	Mean temperature of warmest quarter	Degrees Celsius*10	http://www.worldclim.org
	Bio11	Mean temperature of coldest quarter	Degrees Celsius*10	http://www.worldclim.org
	Bio12	Annual precipitation	Millimeters	http://www.worldclim.org
	Bio13	Precipitation of wettest month	Millimeters	http://www.worldclim.org
	Bio14	Precipitation driest month	Millimeters	http://www.worldclim.org
	Bio15	Precipitation seasonality (coefficient of variation)	Fraction	http://www.worldclim.org
	Bio16	Precipitation of wettest quarter	Millimeters	http://www.worldclim.org
	Bio17	Precipitation of driest quarter	Millimeters	http://www.worldclim.org
	Bio18	Precipitation of warmest quarter	Millimeters	http://www.worldclim.org
	Bio19	Precipitation of coldest quarter	Millimeters	http://www.worldclim.org
Topographic variables	DTM 50	Elevation	Meters	http://www.kartverket.no
	Slope	Slope	Degrees	Derived from DTM
	Aspect	Aspect	Cos (degrees)	Derived from DTM

Table 1: The 19 bioclimatic variables and the topographic variables derived from the DEM that was downloaded and prepared for modelling.

The topographic data consisted of three variables obtained from a digital elevation model (DEM) for the study area: elevation, slope and aspect. The DEM was obtained from the Norwegian Mapping Authority (Kartverket) with a cell size of 50 x 50 m. To get a DEM that covered the study area, the DEM tiles 6701, 6702, 6801 and 6802 from the DTM 50 dataset were merged into one raster dataset using the mosaic tool in ArcGIS. Values for areas of overlap between tiles were set to the mean value of the overlapping pixels. The DEM was then reprojected from EUREF 89 UTM zone 33N to WGS 1984 UTM zone 33N coordinate system with a cell size set to 500 x 500 m and the extent set to line up with the climatic rasters. Bilinear resampling was used during the reprojection. This reprojected DEM was used as one of the variables in the distribution models, and it was also used to calculate aspect and slope. Slope was calculated in degrees (range 0-90) as was aspect (range 0-360, where 0 and 360 represent North-facing aspect). For modelling, the cosine of the aspect in degrees was used to make the aspect variable represent the magnitude of “northness”.

2.4.2. Species occurrence data

Georeferenced species occurrence data for the three focal species were downloaded from Artskart (downloaded 15.10.2017) and added to ArcGIS (Artsdatabanken, 2017a, 2017b, 2017c). The coordinates of the species occurrence records were projected to the coordinate system WGS 1984 UTM zone 33N in order to overlay them on the climatic and topographic raster data. Only occurrence records inside the rectangular study area extent were retained for modelling.

2.4.3. Pre-selecting predictors

A correlation analysis was done in R-studio to pre-select the variables to be used as predictors in the models. Specifically, the Pearson correlation coefficient was calculated for all pairs of predictor variables across the study area. Pairs or groups of variables with high internal correlations ($|\text{Pearson } r| > 0.7$) were reduced to a single variable. Elimination of strong correlation structure in the predictor data improves model fitting, simplifies the interpretation of the model, and increases the reliability of model predictions in a different spatial or temporal context. Specifically, coefficients may be biased among highly correlated variables, and variable selection may approach random selection. In addition, if the high correlation does not hold true in a new space or time, the model will produce biased predictions (Guisan et al., 2017). By pre-selecting predictors for the models it is also possible to prescribe which of the highly correlated predictors are most ecologically meaningful to use in the model, based on prior knowledge of the species' autoecology.

Among the topographic and climatic predictors that were checked for high correlation, a high correlation was found among several of the predictors (see Appendix, Figure A 1). Bio13, bio16, bio19, bio14, bio12, bio17, bio18 (Table 1) and elevation was a group of highly correlating variables, were bio19 was selected as a predictor in the models. Bio19 is precipitation in the coldest quarter, meaning that it is the only predictor that can be related to snow conditions, and was selected since snow cover is a limiting factor for alpine plants. Bio8, bio2, bio4, bio7, bio1, bio15, bio10 and bio5 was another group of highly correlated variables. All of these, however, were strongly negatively correlated with the previous group of correlating variables and were therefore left out of the models. The last group of highly correlated variables was bio6,

bio11 and bio9, which are all temperature related. Bio6, which is the mean temperature of coldest month, was selected as a predictor since it's a temperature variable that provides a cold extreme. Finally, the variables bio3, aspect and slope were not highly correlated with any of the other variables, and were all included as predictors in the model.

<i>Environmental index</i>	<i>Code</i>	<i>Description</i>	<i>Unit</i>	<i>Source</i>
Climatic variables	Bio3	Isothermality (Bio2/Bio7)*100	Dimensionless	http://www.worldclim.org
	Bio6	Min temperature of coldest month	Degrees Celsius*10	http://www.worldclim.org
	Bio19	Precipitation of coldest quarter	Millimeters	http://www.worldclim.org
Topographic variables	Slope	Slope	Degrees	Derived from DTM
	Aspect	Aspect	Cos (degrees)	Derived from DTM

Table 2: The five pre-selected predictor variables used in the Maxent models.

2.5. Species distribution modelling

All species distribution models (SDMs) were developed using the Maxent software (version 3.4.1) for distribution modelling. Maxent uses a maximum entropy algorithm designed for distribution modelling that relates species occurrence data to a set of environmental predictors. One important advantage Maxent offers compared to other modelling methods, is that its designed for use with presence-only data together with environmental information for the study area to predict species' relative occurrence rate (Phillips, Anderson, & Schapire, 2006). This is practical since absence data is difficult to obtain, and was not available for Jotunheimen either. The Maxent distribution is calculated over a set of background cells which represents the variety of environmental conditions present in the data. As a default setting, Maxent uses a sample of 10.000 random background cells, and the distribution is then calculated over the union of the background cells and the sample of the species being modelled (Phillips et al., 2006).

The feature types – or transformation types – allowed in the models were linear features, quadratic features and hinge features. These feature types are described in Phillips et al. (2006) and the Maxent help page as follows: “Linear features constrain the output distribution for each species to have the same expectations of each of the continuous environmental variables as the sample locations for that species. A linear feature is simply one of the continuous environmental variables. Quadratic features (when used together with linear features) constrain the output distribution to have the same expectations and variance of the environmental variables as the samples. A quadratic feature is the square of one of the continuous environmental variables. Hinge feature is derived from a continuous environmental variable. It is like a linear feature, but it is constant below a threshold value”.

Response curves were created for all models. The output format used for all models was raw, which corresponds to the relative occurrence rate. Relative occurrence rate is a meaningful measure when population size is unknown, and refers to the probability that a cell within the study area contains presence samples (Merow, Smith, & Silander, 2013).

Distribution models were trained using the pre-selected predictors under current climatic conditions and projected to the two different RCP scenarios using the same predictors but under future climate conditions. For each species, two distinct models and associated RCP projections were produced. The first used randomly selected background locations, while the second used a target group as selected background locations, as described in further detail below. In both cases all presence locations were added to the background. Finally, all model outputs were imported to ArcGIS for further interpretation and analysis

<i>Model</i>	<i>Species</i>	<i>Scenario</i>	<i>Background points (nr. of points)</i>
Pf-T	<i>Poa flexuosa</i>	Training	Random (10 000)
Pf-45	<i>Poa flexuosa</i>	RCP4.5	Random (10 000)
Pf-85	<i>Poa flexuosa</i>	RCP8.5	Random (10 000)
Rg-T	<i>Ranunculus glacialis</i>	Training	Random (10 000)
Rg-45	<i>Ranunculus glacialis</i>	RCP4.5	Random (10 000)
Rg-85	<i>Ranunculus glacialis</i>	RCP8.5	Random (10 000)
Ts-T	<i>Trisetum spicatum</i>	Training	Random (10 000)
Ts-45	<i>Trisetum spicatum</i>	RCP4.5	Random (10 000)
Ts-85	<i>Trisetum spicatum</i>	RCP8.5	Random (10 000)
Pf-T-TG	<i>Poa flexuosa</i>	Training	<i>Poa</i> (886)
Pf-45-TG	<i>Poa flexuosa</i>	RCP4.5	<i>Poa</i> (886)
Pf-85-TG	<i>Poa flexuosa</i>	RCP8.5	<i>Poa</i> (886)
Rg-T-TG	<i>Ranunculus glacialis</i>	Training	<i>Ranunculus</i> (919)
Rg-45-TG	<i>Ranunculus glacialis</i>	RCP4.5	<i>Ranunculus</i> (919)
Rg-85-TG	<i>Ranunculus glacialis</i>	RCP8.5	<i>Ranunculus</i> (919)
Ts-T-TG	<i>Trisetum spicatum</i>	Training	<i>Trisetum, Anthoxanthum, Melica</i> (740)
Ts-45-TG	<i>Trisetum spicatum</i>	RCP4.5	<i>Trisetum, Anthoxanthum, Melica</i> (740)
Ts-85-TG	<i>Trisetum spicatum</i>	RCP8.5	<i>Trisetum, Anthoxanthum, Melica</i> (740)

Table 3: The models produced in Maxent and there specifications.

2.5.1. Sampling bias

It is highly likely that the occurrence data for the study area is biased. Collecting efforts are known to be influenced by accessibility, meaning that occurrence data often are highly correlated to the nearby presence of roads, rivers or other access points. (Reddy & Dávalos, 2003). In addition, sampling intensity and sampling methods are likely to be varied throughout the study area since the occurrence data is based on records dating back almost a century. Sampling bias in occurrence data can lead to overrepresentations of certain environmental conditions, which again can lead to uncertainties in the species' characterization of the environmental niche (Loiselle et al., 2008). With the goal to correct for the potential sampling bias and improving model accuracy I produced a second model for each species using a target group as selected background locations, rather than randomly selected background locations (Table 3). This method was originally described by Ponder, Carter, Flemons, and Chapman (2001). By using a target group which is likely to be captured by either the same collection methods or collectors as the focal species as background

locations, target group background selection aims to select background locations where the focal species is more likely to be truly absent rather than present but unsampled. This works as a surrogate for absence data, which is nearly impossible to obtain in the real world given the ad hoc nature of collection effort.

For each species the target group consisted of all species within the same genus as the focal species. For example, all species from the genus *Ranunculus* were used as a target group for *R. glacialis*. For *T. spicatum* two additional genera were also included as a target group in order to get a sufficient number of background point to characterize the study area. Specifically, the genera *Trisetum*, *Anthoxanthum* and *Melica* were used as a target group for *T. Spicatum*. Occurrence records within the study area for each of the target groups were downloaded from Artskart (downloaded 16.02.2018) (Artsdatabanken, 2018a, 2018b, 2018c). The presence location coordinates were converted to raster files with the same extent and resolution as the predictor data, where cells containing at least one target group presence were assigned the value 1 and cells without target group presence were assigned No Value. For the second set of models the relevant target group raster file was added as a bias file in the software instead of using the default 10.000 random background locations.

2.5.2. Threshold

In order to calculate the reduction in area of suitable habitat a threshold value is needed to translate continuous model predictions in the form of relative occurrence rate into binary presence-absence predictions. The threshold value determines the boundary between predicted presence and absence of the modeled species. The highest possible value that omitted less than 5 % of the recorded presence in the training data (omission < 5 %) was used as the threshold for each model. This threshold gives relatively larger areas of predicted presence than most other common threshold selection methods and was used in order to avoid underestimation of the future distribution of the species and to give conservative estimates of habitat reduction. This user specified threshold is recommended by Freeman and Moisen (2008) when the goal is to predict all potential habitats and map with high sensitivity is required. This threshold provides a map with a sensitivity of 0.95. The threshold values were calculated using R-studio (Appendix, Table A 4).

2.6. Interpretation and analysis

2.6.1. GIS analysis

All of the Maxent model predictions were analyzed and visualized using ArcGIS. The total area of suitable habitat was calculated for each model from binary predictions by taking the number of presence cells multiplied by the cell size. The elevational range and mean elevation of the area predicted to contain species presence was gathered using zonal statistics in ArcGIS. The level of habitat fragmentation was calculated by converting the binary raster data into vector data. Specifically, areas of predicted presence were converted into polygons. The attribute tables of the vector data provided statistics on the number of patches and the mean patch size for each species, under each model, in the different scenarios.

According to ecological theory species optimum is found somewhere in the middle of its total elevational range, and the outer boundaries of a suitable habitat is considered less than optimal or even marginal (Thuiller et al., 2008). In order to determine how much of the suitable habitat that is likely to be marginal for the focal species, I have calculated the amount of marginal habitat or edge habitat (hereafter only

referred to as edge habitat) that was located within 500 meters from the low elevation habitat edge. The edge habitat was calculated using ArcGIS. By using the buffer and clip tools, the part of the suitable habitat that was within 500 meters (1 cell width) of a boundary between predicted presence and predicted absence was isolated and its total area was calculated. This was done for each model result.

For each species-model combination, the absolute and percent change in predicted suitable habitat area was calculated for the different future scenarios using Microsoft Excel.

3. Results

For each species two sets of models are presented in the results; the first set of models uses random background locations, while the second set of models uses a target group as background locations.

3.1. Maxent models

The equation to calculate the predicted value (raw output) of the Maxent model is given as:

$$P(x) = \exp(c1 * f1(x) + c2 * f2(x) + c3 * f3(x) ...) / Z$$

Here $c1$, $c2$, $c3$ etc. represents the coefficients for each model while $f1$, $f2$, $f3$ etc. are the corresponding features, or transformed variables. The predicted value (P) of the model is calculated independently for each raster cell. Z is a scaling constant, referred to here as the linear predictor normalizer (Table A 1, Table A 2 & Table A 3 in Appendix).

3.1.1. Model performance

The area under the receiver operating characteristic curve (AUC) values, calculated using the training data are higher for the models with a random background (Table 4). The average difference between the two sets of models were 0.079. Between species, the two *P. flexuosa* models have the highest AUC value in both model sets, while *T. spicatum* models have the lowest.

<i>Species</i>	<i>Model</i>	<i>AUC</i>
<i>Ranunculus glacialis</i>	Random background	0.773
	Target group background	0.668
<i>Poa flexuosa</i>	Random background	0.841
	Target group background	0.768
<i>Trisetum spicatum</i>	Random background	0.720
	Target group background	0.659

Table 4: AUC values for the training data.

3.1.2. Variable importance

The predictor bio19 was of greatest importance in all the Maxent models (except for *R. glacialis* in the models with random background) (Table 5). Bio6 is almost equal to bio19 in the models with a random background, but loses importance – or contributes less – in the models with a target group background. Bio19 is the only predictor that gains importance as bio6 contributes less. The biggest difference in predictor contributions between background types is found in the models of *T. spicatum*, where the contribution of the predictor slope varies from 15.5 in the models with random background, to 0 in the models with a target group background. Bio3 and aspect have a low contribution in all the Maxent models, with small differences between the two models sets and between the three species.

<i>Species</i>	<i>Model</i>	<i>Predictor</i>	<i>Permutation importance</i>
<i>Poa flexuosa</i>	Random background	bio3	1.5
		bio6	44.4
		bio19	45.0
		aspect	3.4
		slope	5.7
	Target group background	bio3	0.0
		bio6	20.2
		bio19	75.3
		aspect	3.8
		slope	0.7
<i>Ranunculus glacialis</i>	Random background	bio3	2.0
		bio6	46.5
		bio19	43.5
		aspect	1.4
		slope	6.6
	Target group background	bio3	2.0
		bio6	31.3
		bio19	66.2
		aspect	0.3
		slope	0.2
<i>Trisetum spicatum</i>	Random background	bio3	2.4
		bio6	29.3
		bio19	52.0
		aspect	0.7
		slope	15.5
	Target group background	bio3	1.3
		bio6	17.6
		bio19	75.7
		aspect	5.4
		slope	0.0

Table 5: The contribution of each predictor used in the Maxent models, measured by permutation importance.

3.1.3. Species response

The modeled species respond differently to the variables used as predictors in the models. A difference in the response curves was found between the models with a random background and the models with a target group background.

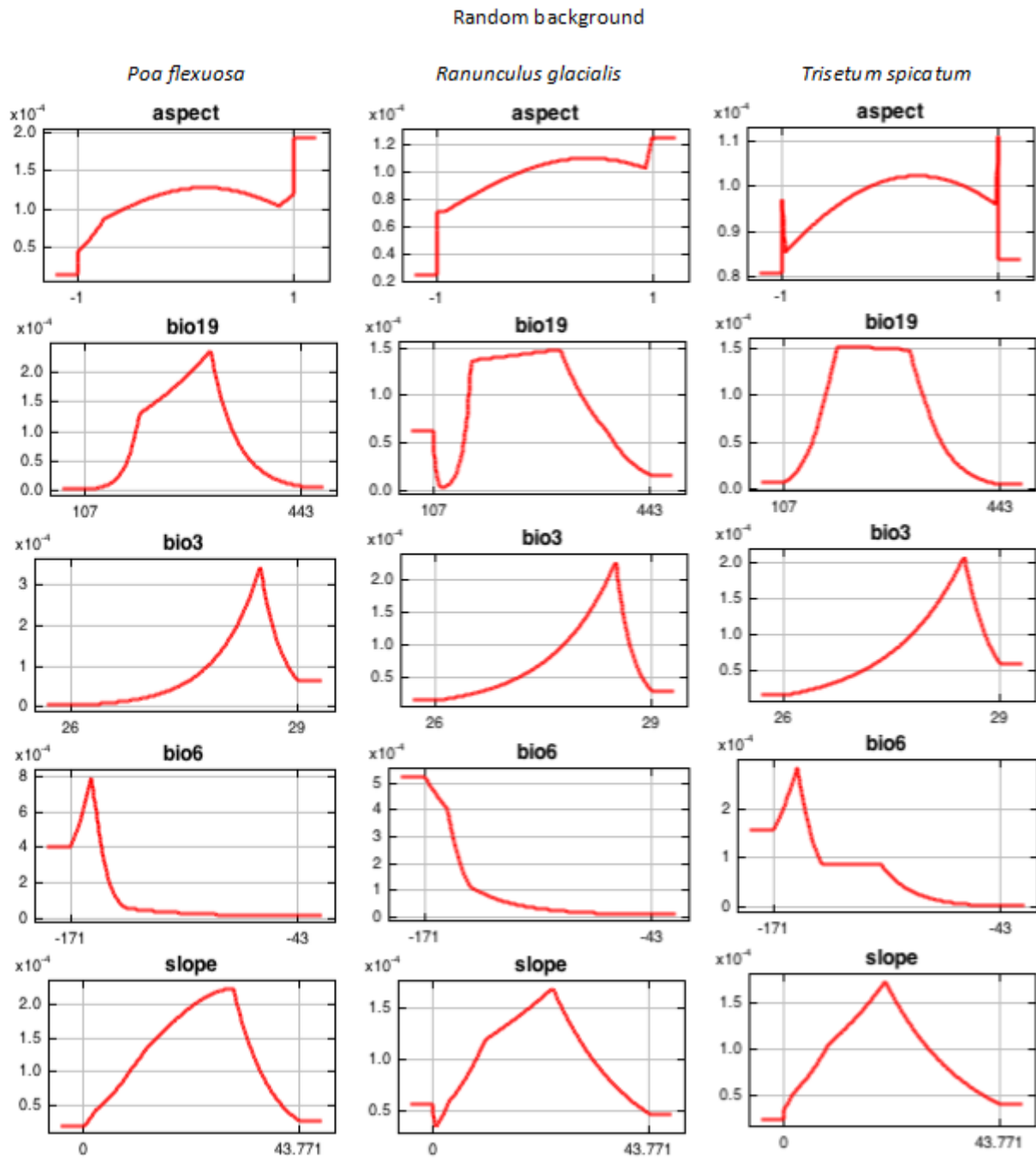


Figure 3: The species response to the environmental variables used as predictors in the models using a random background.

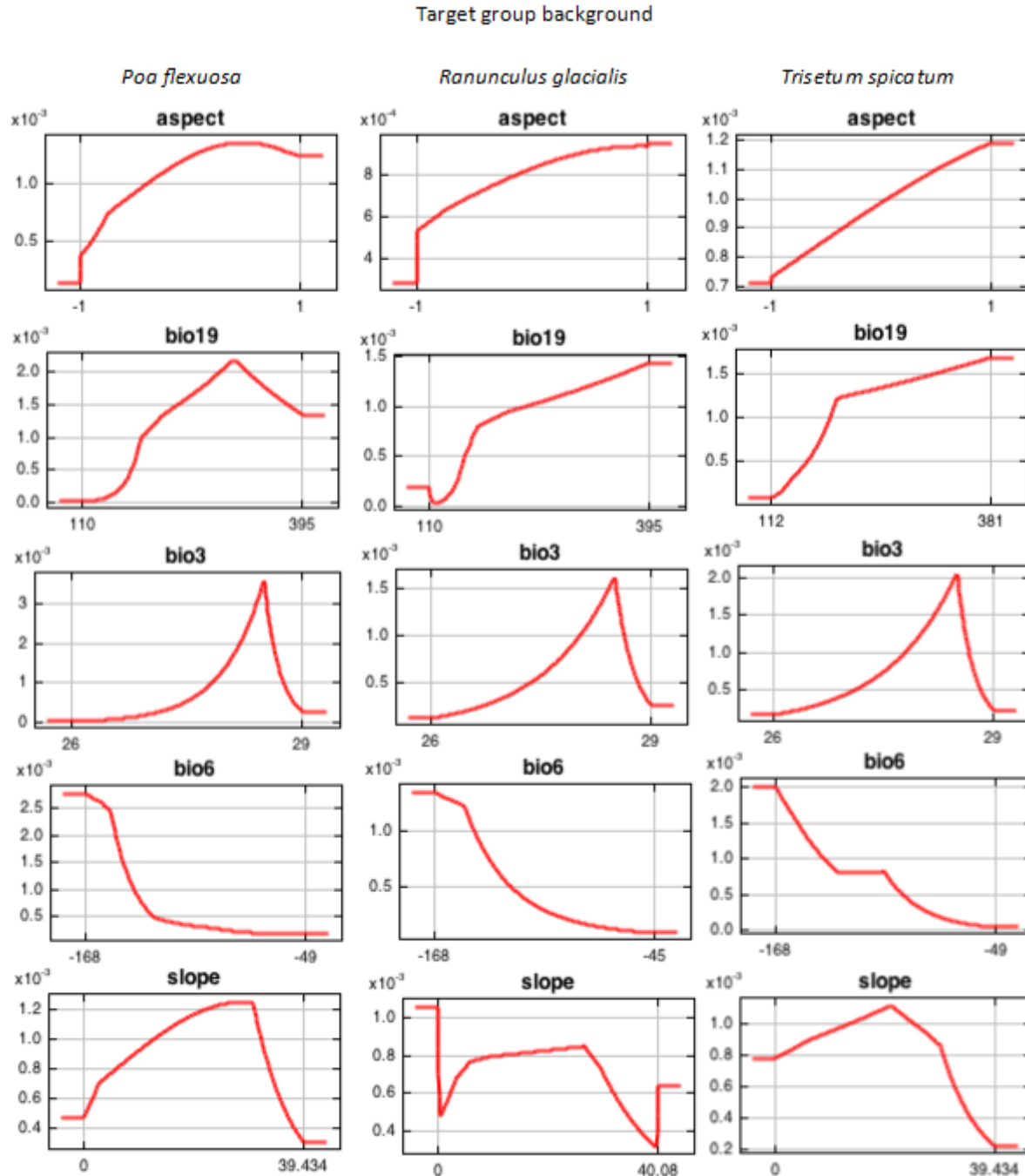


Figure 4: The species response to the environmental variables used as predictors in the models using a target group background.

For the predictors bio19, bio6 and slope the environmental range (y-axis) is different between the two model sets. Bio19 and bio6 – the two most influential variables in the models – tend to have a local optima in the models with a random background (Figure 3), while they show a more monotonic increase (bio19) or decrease (bio6) – without local optima – in the models with a target group background (Figure 4). The local optima observed in bio19 in the models with a random background is very similar for all species. *P. flexuosa* is the only species showing signs of having a local optima in response to bio19 in the models with

a target group background. In the models with a random background, bio6 is the variable with the largest variance in response between species. This variance was however minor, with small differences in the range on the y-axis, and small variations in the response curves. In the response to aspect, the local optimum shifts from being closer to zero in the first set of models to closer to one in the models with sampling bias correction. The response to bio3 is nearly identical in all models.

3.2. Distributional changes

3.2.1. Changes in habitat size

Based on topographical and climatic conditions (with a cell resolution of 500 x 500 m), all species were projected to lose suitable habitat under the two climate change scenarios (Figure 5 & Figure 6). The reduction in area of suitable habitat is greater in the models using a random background, compared to the models using a target group background (Table 6 & Figure 7). A larger reduction in suitable habitat was also found under the RCP8.5 scenario compared to the RCP4.5 scenario in all model results. The average size of current predicted distribution was 63 % of the study area (random background), and 67 % (target group background). The average projected loss of suitable habitat in the models using a random background under the RCP8.5 scenario was 4 030 374 km², which represents 70 % of predicted current distribution. In comparison, the average loss of suitable habitat in the same scenario in the models with a target group background was 2 324 142 km² or 38 % of predicted current distribution.

<i>Model</i>	<i>Suitable habitat (km²)</i>	<i>Reduction in suitable habitat (km²)</i>	<i>Reduction in suitable habitat (%)</i>
Pf-T	5131599	-	-
Pf-45	2119634	3011965	58.7
Pf-85	1167848	3963751	77.2
Rg-T	5681621	-	-
Rg-45	2293192	3388429	59.6
Rg-85	804540	4877081	85.8
Ts-T	6454030	-	-
Ts-45	4483666	1970364	30.5
Ts-85	3203739	3250291	50.4
Pf-T-TG	5125021	-	-
Pf-45-TG	4186138	938883	18.3
Pf-85-TG	3711004	1414017	27.6
Rg-T-TG	6041893	-	-
Rg-45-TG	3728967	2312926	38.3
Rg-85-TG	2235002	3806891	63.0
Ts-T-TG	7125745	-	-
Ts-45-TG	6300712	825033	11.6
Ts-85-TG	5374226	1751519	24.6

Table 6: The current prediction and the projected changes in suitable habitat size under climate change scenarios RCP4.5 and RCP8.5 for the year 2070.

The absolutely largest reduction in area of suitable habitat was projected for *R. glacialis* under the RCP8.5 scenario in the models using a random background, for which the total area of suitable habitat was projected to be reduced by 85 % (Table 6). In the models using a target group background, the reduction in area of suitable habitat under the same scenario was projected to be 63%. *P. flexuosa* was projected to have 77 % reduction in suitable habitat under the RCP8.5 scenario in the models using a random background, while the reduction was 27 % under the same scenario in the models using a target group background (Table 6). *T. spicatum* was projected to have the lowest reduction in area of suitable habitat of the species modeled, in both model sets, and under both RCP scenarios modelled. The reduction under the RCP8.5 scenario was 50 % in the models with a random background and 24.6 % in the models with a target group background (Table 6).

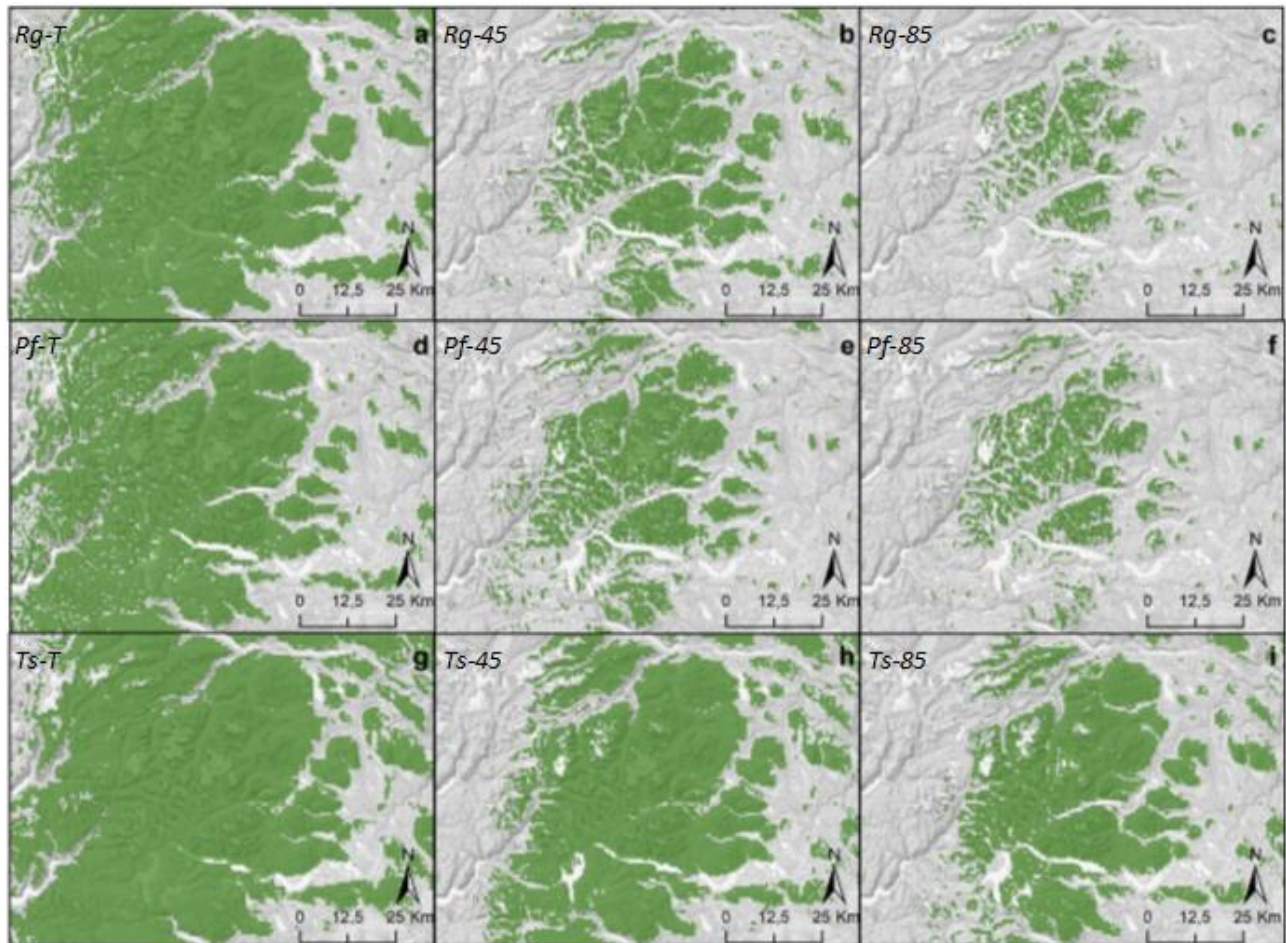


Figure 5: Maps of the current predictions and the projected changes in suitable habitat (green areas) from models using a random background. The maps are portraying the predicted current distributions and the projected future distributions under RCP4.5 and RCP8.5 for (a)(b)(c) *R. glacialis*, (d)(e)(f) *P. flexuosa* and (g)(h)(i) *T. spicatum*.

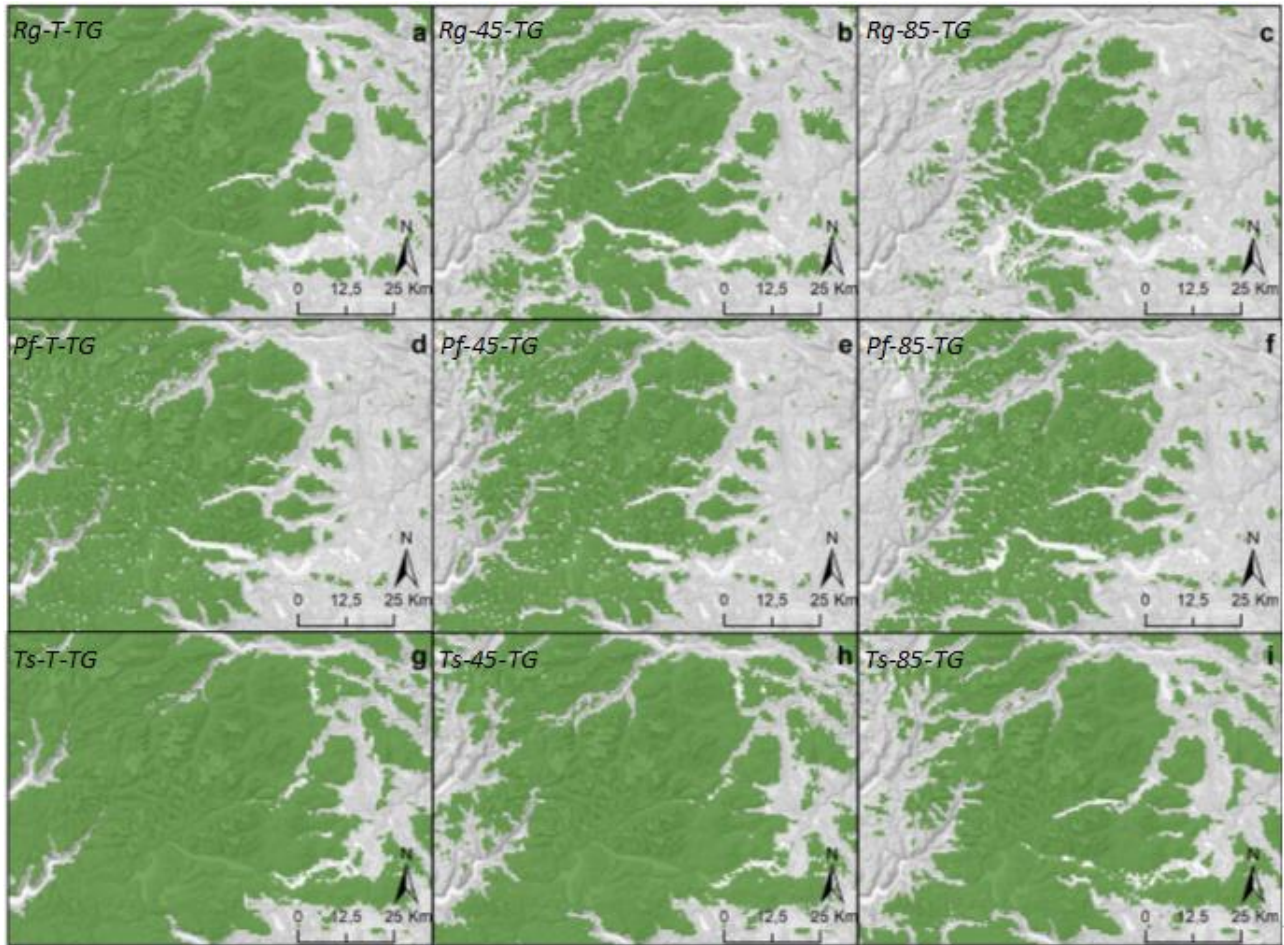


Figure 6: Maps of the current predictions and projected changes in suitable habitat (green areas) from models using a target group background. The maps are portraying current predicted distributions and the projected future distributions under RCP4.5 and RCP8.5 for (a)(b)(c) *R. glacialis*, (d)(e)(f) *P. flexuosa* and (g)(h)(i) *T. spicatum*.

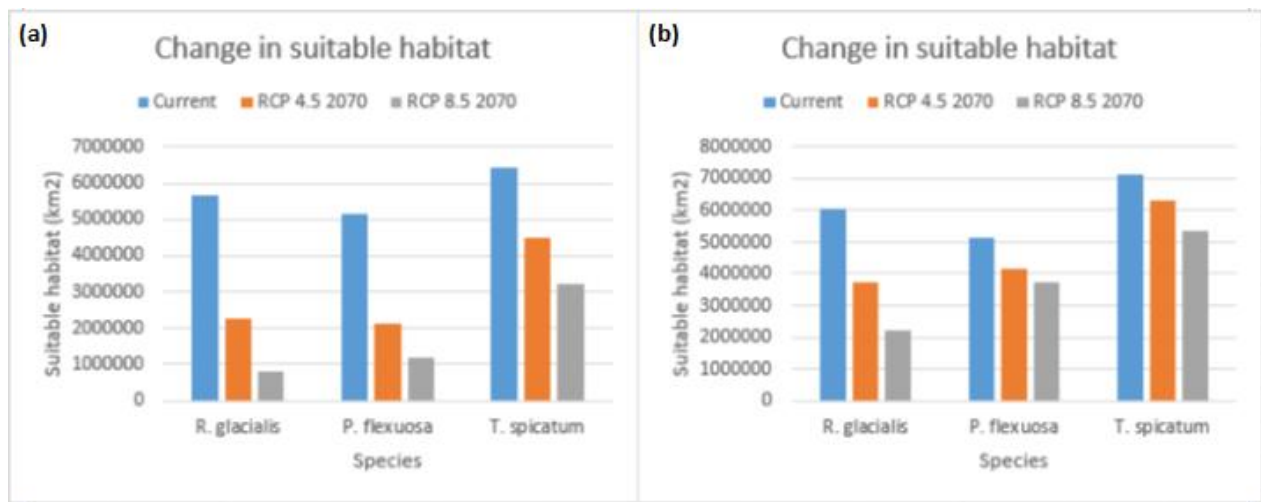


Figure 7: The projected absolute reduction in suitable habitat under climate change scenarios RCP4.5 and RCP8.5 from (a) models using a random background and (b) models using a target group background.

3.2.2. Changes in elevational range

All species was projected to disappear from their lowest elevations in both RCP scenarios modeled, and in both model sets (Table 7 & Figure 8). Except for *T. spicatum* in the models using a random background under the RCP8.5 scenario, all species was projected to remain at their highest elevations. In other words, the upper elevational boundary remained constant, as all species already were predicted to occur at the highest elevation under current conditions.

In the models with a random background, the biggest reduction in elevational range was found under the RCP8.5 scenario, with an average reduction of 524 m. The average reduction in elevational range under the same scenario, in the models with a target group background was 484 m. *R. glacialis* was the only species that was projected to have a larger reduction in elevational range in the models using a target group background, with a reduction of 868 m under RCP8.5 (Table 7). The biggest difference between species was found between *R. glacialis* and *P. flexuosa* in the models with a target group background under the RCP8.5 scenario with a difference of 656 m.

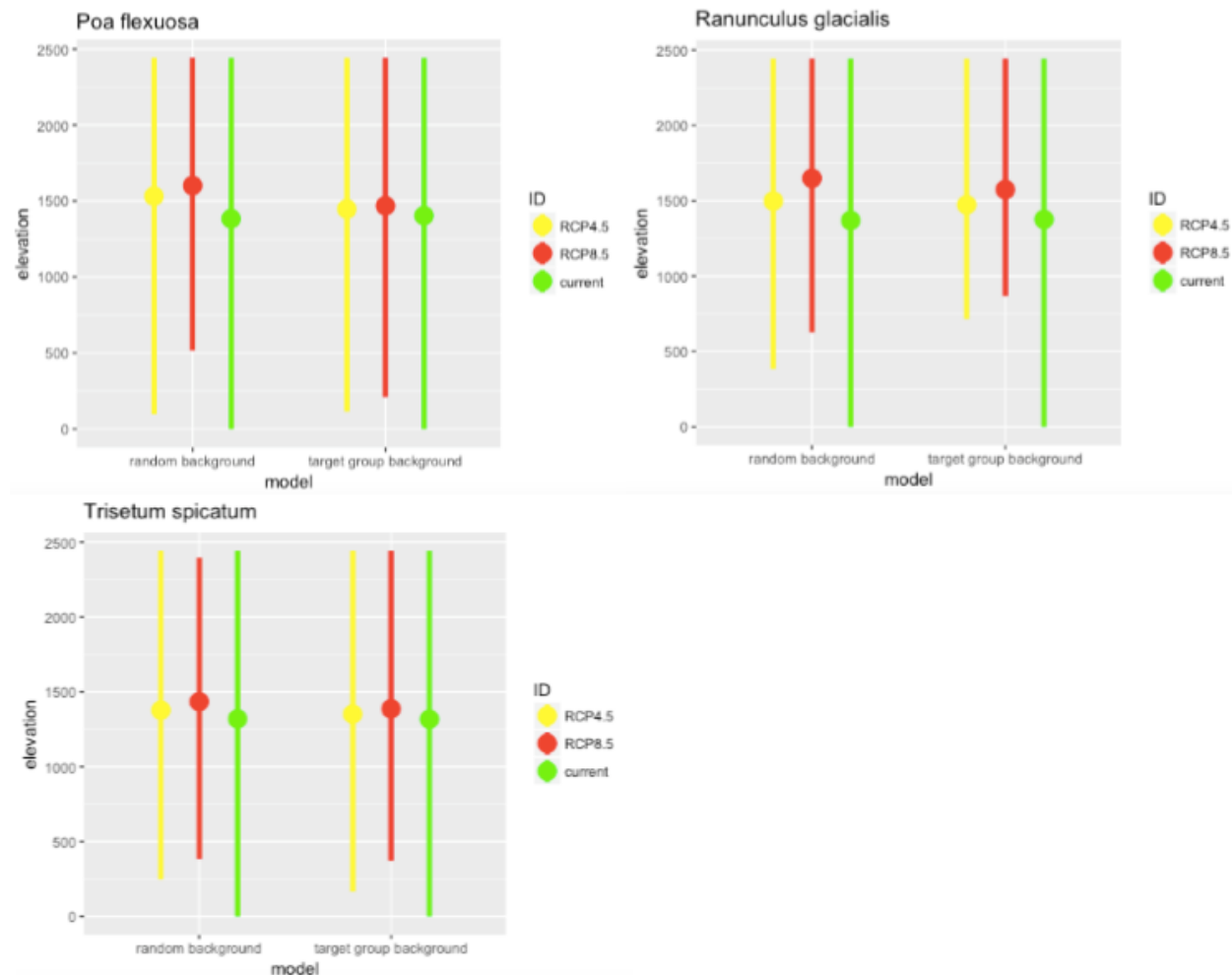


Figure 8: The projected changes in the species elevational range under climate change scenarios RCP4.5 and RCP8.5.

The mean elevation of the area predicted as suitable was projected to increase for all three species under both the scenarios modeled (Table 7). The increase was highest in the models using a random background for all three species with an average increase of 111 m under the RCP4.5 scenario and 204 m under the RCP8.5 scenario. In comparison, the average increase in mean elevation in the models using a target group background was 58 m under the RCP4.5 scenario and 110 m under the RCP8.5 scenario. *R. glacialis* was projected to have the biggest increase in mean elevation in both sets of models with a 280 m increase in the models with a random background and 198 m in the models using a target group background under the RCP8.5 scenario. The smallest change in mean elevation was projected for *T. spicatum* in all scenarios except for the RCP8.5 scenario (target group background).

<i>Model</i>	<i>Minimum elevation</i>	<i>Maximum elevation</i>	<i>Elevational range</i>	<i>Mean elevation</i>	<i>Elevational range contraction</i>	<i>Change in mean elevation</i>
Pf-T	0	2442	2442	1384	-	-
Pf-45	99	2442	2343	1532	99	148
Pf-85	517	2442	1925	1602	517	218
Rg-T	0	2442	2442	1369	-	-
Rg-45	384	2442	2058	1498	384	129
Rg-85	627	2442	1815	1649	627	280
Ts-T	0	2442	2442	1320	-	-
Ts-45	248	2442	2194	1378	248	58
Ts-85	384	2396	2012	1435	430	115
Pf-T-TG	0	2442	2442	1404	-	-
Pf-45-TG	115	2442	2327	1448	115	44
Pf-85-TG	212	2442	2230	1469	212	65
Rg-T-TG	0	2442	2442	1376	-	-
Rg-45-TG	715	2442	1727	1473	715	97
Rg-85-TG	868	2442	1574	1574	868	198
Ts-T-TG	0	2442	2442	1318	-	-
Ts-45-TG	168	2442	2274	1352	168	34
Ts-85-TG	374	2442	2068	1387	374	69

Table 7: The current predictions and the projected changes in elevational range and mean elevation for all species under climate change scenarios RCP4.5 and RCP8.5. All numbers are given in meters.

3.2.3. Habitat fragmentation

Number of patches of suitable habitat was projected to increase for all species, and the mean patch size projected to decrease for all species in both scenarios and in both model sets (Table 8). The change in number of patches was greater between the two model sets than between the two scenarios. The number of patches increased the most in the models with a random background. The difference in mean patch size was also larger between the two sets of models than between scenarios. The mean patch size for the current distribution was predicted to be largest in the models with a target group background. The reduction in mean patch size was projected to be largest under the RCP8.5 scenario in both model sets. The projected reduction was 93 975 km² (70 %) in the models using a target group background and 32 754 km² (82 %) under the RCP8.5 scenario.

R. glacialis showed the biggest reduction in mean patch size in both sets of models, and under both RCP scenarios. The biggest reduction in mean patch size was a 92.8 % (35 986 km²) reduction found in the models using a random background under the RCP8.5 scenario.

3.2.4. Edge habitat

The share of edge habitat, defined as the area within a 500 m buffer from the habitat edge, was projected to increase for all species (Table 8 & Figure 9). Across scenarios, the share of edge habitat was largest in the models with random background. The largest share of edge habitat was projected under the RCP8.5 scenario with an average of 67.9 % of the suitable habitat defined as edge for all three species. In comparison, the average share of edge habitat predicted under the same scenario in the models with a target background set was 31 %.

The largest increase in edge habitat was projected for *R. glacialis*, with a 65.3 % increase in edge habitat in the models using a random background, and a 25 % increase under the same scenario in the models using a target group background. The smallest increase in edge habitat was projected for *T. spicatum* in both sets of models and under both RCP scenarios. (See Figure A 2 & Figure A 3 in Appendix)

<i>Model</i>	<i>Number of Patches</i>	<i>Mean patch size (km²)</i>	<i>Reduction in mean patch size (km²)</i>	<i>Reduction in mean patch size (%)</i>	<i>Edge habitat (km²)</i>	<i>Edge habitat (%)</i>
Pf-T	171	30198	-	-	1604675	31.1
Pf-45	314	6696	23502	77.8	1221779	58.1
Pf-85	260	4430	25768	85.3	906971	78.7
Rg-T	147	38798	-	-	1252518	22.0
Rg-45	265	8612	30186	77.8	1209255	53.0
Rg-85	277	2811	35986	92.8	680136	87.3
Ts-T	129	50186	-	-	1131767	17.5
Ts-45	171	26290	23895	47.6	1342164	29.9
Ts-85	234	13678	36507	72.7	1206106	37.7
Pf-T-TG	43	120160	-	-	1301279	25.2
Pf-45-TG	83	50799	69360	57.7	1371490	32.5
Pf-85-TG	95	39298	80861	67.3	1359323	36.4
Rg-T-TG	53	114113	-	-	723819	12.0
Rg-45-TG	122	30536	83576	73.2	1072459	28.8
Rg-85-TG	176	12590	101523	89.0	830324	37.5
Ts-T-TG	43	165943	-	-	739343	10.4
Ts-45-TG	98	64360	101582	61.2	965342	15.3
Ts-85-TG	81	66401	99541	60.0	1030567	19.2

Table 8: The projected level of habitat fragmentation. Showing changes in number of patches, mean patch size and share of edge habitat for all species under climate change scenarios RCP4.5 and RCP8.5.

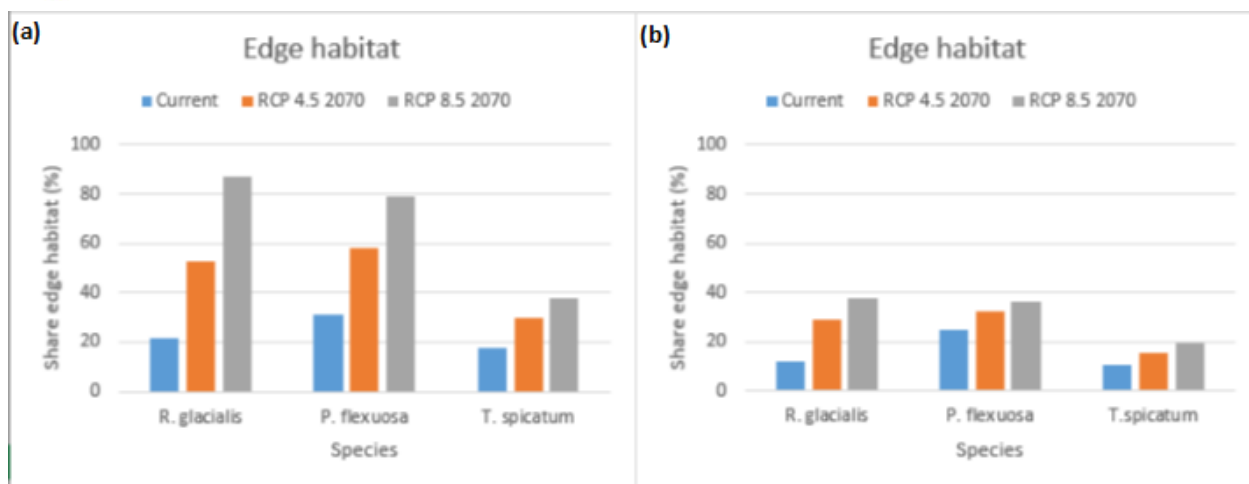


Figure 9: The predicted current and the projected future changes in share of edge habitat for all species under climate change scenarios RCP4.5 and RCP8.5 from (a) models with a random background and (b) models with a target group background.

4. Discussion

4.1. Maxent models

All models perform markedly better than a random prediction according to their AUC values. They provide 'fair' predictive ability ($0.70 < \text{AUC} < 0.90$) after a scale by Halvorsen (2013), and in a five grade scale developed by Araújo, Pearson, Thuiller, and Erhard (2005) they fall in the two categories 'fair' accuracy ($0.70 < \text{AUC} < 0.80$) and 'good' accuracy ($0.80 < \text{AUC} < 0.90$). This demonstrates that the selected predictors in the models account for a fair amount of variation in the occurrence of these species, and suggests that these predictors are ecologically meaningful. However, these AUC values were calculated using the same presence only data used to train the models. It would have been better to evaluate the models predictive abilities using an independent data set. Since the amount of presence data for the focal species within the area was limited, all available presence data was used to train the models. Sampling of an independent data set to test the models predictive ability would have been preferable, but not realistic given the limited time – and the time of year – for this study.

The presence records used in this study are dating back a century, and with little knowledge about the sampling effort and the sampling methods used, it is highly likely that these records are biased. This is why the second set of models attempts to correct for this sampling bias using a target group as background locations. In biased presence data, certain environmental conditions suitable for the species will be overrepresented, resulting in a model that might project too much reduction in suitable habitat under new conditions. The presence data used here are likely biased by accessibility from roads, lower lying areas and towards the national park located within the area. This bias might have led to an underestimation of future suitable habitat size under the different climate change scenarios. Some studies have showed that using a target group as background to correct for this bias have improved model accuracy and performance (Phillips et al., 2009; Ranc et al., 2017). In the study by Ranc et al. (2017) the effects of sampling bias correction was tested in a geographically biased virtual species system. They found that relative

occurrence area was the most important factor driving species vulnerability to sampling bias, meaning that widespread species were more affected and more likely to benefit from sampling bias correction compared to narrow ranging species. The species used in this study showed a high relative occurrence rate (> 50 %) within the study area which was the motivation for using a target group to correct for sampling bias. A concern associated with using a target group background is that the predictions are made focusing only on a small part of the geographic, and thus environmental space that contains presence samples compared to a random background that takes background locations from the entire study area (Phillips et al., 2009). The limited number of background locations (pseudo-absence) (Table 3) used in this study lead to lower AUC values in the models using a target group background compared to the models using a random background (Table 4). VanDerWal, Shoo, Graham, and Williams (2009) showed that drawing pseudo-absence from a small part of an area could produce incorrect models. Simultaneously, pseudo-absence drawn from too large of an area can lead to artificially inflated AUC values and predictions of species distributions as well as potentially producing less informative response curves. These errors will be propagated when projections are made onto a new set of environmental variables, and thus provide misleading results (VanDerWal et al., 2009).

A target group that covered a wider range of environmental conditions in the area would likely have produced models with a performance closer to the models with a random background. However, selecting an appropriate target group proved difficult given the lack of knowledge about the collection efforts in the area. By selecting from the same genus as the focal species, the assumption was that the collector who sampled a species from the target group also would have collected the focal species if it was present. From the presence records used, it can be seen that several of the same institutions have collected the focal species and species from the target groups. This, and the fact that records are collected within the same alpine area, makes it likely that the focal species would have been collected if it were present in a target group location. Then again, some of the collection effort can be part of studies that are studying a restricted number of species, and the focal species from this study might not have been collected. For example, a study that focuses on the sampling of *Poa alpina* is likely to exclude any occurrences of *Poa flexuosa* at the same location. In addition to lower performance statistics, the low number of background locations used to determine the distributions compared to the size of the study area, suggests that the target group represents a narrow portion of the total range of environmental conditions found within the area. This restricted background are likely to have led to an “over” correction for the sampling bias. This could mean that the models using a target group background overestimates the amount of suitable habitat. Assuming that there is some sampling bias in the data, then the truth, by definition, would lie somewhere in between the models with no correction and the models with over-correction. To further evaluate which of the two model sets are more accurate, an independent unbiased data set would be needed to check model performance.

Threshold selection of continuous model output strongly influences predictions. Nenzén and Araújo (2011) found that the choice of threshold stood for 25 % of the variability in model results. This is a high variability considering that thresholds usually are determined subjectively (Freeman & Moisen, 2008), as is also the case in this study. Several studies argue that threshold selection should be determined based on the purpose of the study (Freeman & Moisen, 2008; Jiménez-Valverde & Lobo, 2007). Freeman and Moisen (2008) showed that species with poor model quality or low prevalence within the study area were more sensitive to the choice of threshold, resulting in greater variability between model results depending on

the threshold used. A default threshold of 0.5, often used in forest management, was shown to strongly underestimate the prevalence of the species (Freeman & Moisen, 2008).

Given the goal to determine the level of habitat reduction under climate change for the focal species, a user specified threshold that gives the highest possible specificity while not omitting more than 5 % of observed presence was chosen. The goal with the selected threshold was to avoid exaggeration of the habitat reduction by misclassifying true presence as predicted absence. This threshold is recommended by Freeman and Moisen (2008) when the goal is to predict all potential habitats. A threshold that maximizes training sensitivity plus specificity, which is one of the standard threshold selection methods in Maxent, was also considered for this study, but this threshold penalizes lower specificity (false positives) which is not appropriate when using presence only data to calculate the threshold. The specified threshold used in this study made more conservative projections of minimum suitable habitat.

4.2. Distributional changes

As expected, based on previous studies (Engler et al., 2011; Felde et al., 2012; Klanderud & Birks, 2003; Odland et al., 2010; Steinbauer et al., 2018) and ecological theory, the model results projects a significant loss of habitat for the focal species in the future under climate change. A study by Engler et al. (2011) projected that 25 % of the species modelled across European mountain ranges would lose all of their suitable habitat, and that half of the species would lose 80 % of their suitable habitat by 2070-2100. The Norwegian Scandes was found to be least vulnerable to climate change of the European mountain ranges, where less than 10 % of the species are projected to lose all suitable habitat (Engler et al., 2011). One possible explanation for this could be the expected increase in precipitation along with the climatic warming in the Scandes (Engler et al., 2011). These findings are similar to the projections in this study. However, my study uses a different set of climate change scenarios and a different spatial resolution, so a direct comparison is difficult. The spatial resolution used in my study was 500 m, while Engler et al. (2011) used climatic and topographic variables with a spatial resolution of 100 m. The coarse resolution used in my study could suggest that my projections overestimates habitat loss, but it could also mean that habitat loss is underestimated. Specifically, topographic variations not captured at the 500 meter scale could provide patches of suitable habitat in areas predicted to be unsuitable, but at the same time areas predicted as suitable are likely to contain unsuitable areas. Which of these effects outweighs the other is unknown. A finer resolution would have given more precise estimates of change.

The reduction in suitable habitat is strongly linked to the contraction of elevational range. This range contraction was only projected for the lower elevational boundaries, because all species were predicted to already occur at the highest elevations within the study area. This is due to the coarse resolution, which allows a species to be predicted to occur at the highest possible elevation if presence is found within a 500 meter cell located at the highest elevation. In addition to the previously observed range contraction of the lower elevational boundary (Klanderud & Birks, 2003; Odland et al., 2010), Felde et al. (2012) found that the upper limit shifted downwards for a few species, including *R. glacialis* and *T. spicatum*. They explained these findings with a prolonged snow cover at higher elevations. These findings is however not coherent with the findings of Klanderud and Birks (2003), which found that *R. glacialis* shifted their lower elevational range upwards and increased in abundance at higher elevations. A downward shift of the upper elevational boundary was not predicted for *R. glacialis* in this study. *T. spicatum* did however show sign of range contraction at the upper limit, with a downwards shift of 46 meters in the RCP8.5 scenario (Random

background). *T. spicatum* is the species with the lowest upper elevational boundary currently observed of the three focal species (Felde et al., 2012; Holten et al., 2011), which could suggest that it is more sensitive to snow cover than the other two. *R. glacialis* was projected to have larger elevational range contraction – and thereby lose more suitable habitat – than the other species. This indicates that the species currently found at the highest elevations will be affected the most by climate change.

The projected habitat fragmentation might compromise the species' reproductive success. This breaking up of habitat is associated with several negative effects such as reduced gene flow between populations, inbreeding within populations, increased genetic differentiation between populations, which again is associated with increased vulnerability (Young et al., 1996). The increased isolation between populations can also prevent rescue by immigration from other populations (Leimu et al., 2010), which can be linked to the limited dispersal abilities in alpine ecosystems (Körner, 2003). For *P. flexuosa* and *T. spicatum* the majority of seeds have been found to disperse less than 5 meters from its origin (Ryvarden, 1971), suggesting that fragmentation could isolate populations. However, if pollination still occurs between populations the short distance dispersal might not have severe negative effects. *R. glacialis* is also expected to have a restricted dispersal ability, but must be capable of long distance dispersal due to its broad geographical distribution which includes arctic islands (Schönswetter, Paun, Tribsch, & Niklfeld, 2003). The focal species in this study all have the ability to reproduce clonally, but sexual reproduction is considered the most important, especially for *R. glacialis* (Körner, 2003), which is pollinated by small flies which are weak pollinators (Wagner et al., 2010). Habitat fragmentation could affect pollinator behavior (Aguilar, Ashworth, Galetto, & Aizen, 2006), and the level of habitat fragmentation is projected to be strongest for *R. glacialis*. But in order to speculate around how this might affect the reproductive abilities of *R. glacialis* more knowledge about the spatial population dynamics and genetics in the area is needed.

The analysis of marginal habitat in this study was a heuristic way of examining how the amount of sub-optimal habitat as a proportion of the total habitat is likely to change. Here marginal habitat – or edge habitat – was calculated as all habitat within 500 meters from the habitat edge (1 cell size). This estimation of marginal habitat could also have been executed by isolating all cells that fall just above the threshold and in that way getting habitat that was environmentally marginal rather than geographically marginal. Even though we don't know what parts of the habitat could actually be considered marginal, this simple definition was used to get an idea of any changes in trend.

Towards the edge of suitable habitat growth and establishment is reduced, and growth efficiency-related mortality increases (Thuiller et al., 2008). The projections show that the share of edge habitat increases as the habitat gets more fragmented, which suggests that larger portions of the habitat could fall outside species optimum. As all models project the distributions to extend to maximum altitude the edge habitat was found at the lower elevations. In reality, observations suggest that the highest altitudes also are sub-optimal. The main limiting factor at lower elevations are thought to be competition from other species, and this is supported by studies showing that alpine plants can grow and reproduce at lower elevations through transplantation (Hautier, Randin, Stöcklin, & Guisan, 2009). The increased edge habitat could suggest that the species will be more prone to competition in these areas, and increased competition from other species is documented to affect *R. glacialis* negatively through reducing leaf size (Kulonen et al., 2017). In addition to resolution being an issue when determining the amount of edge habitat, the negative effects associated with edge habitats depends on the new competitor's abilities to spread upwards or track their environmental conditions.

Climatic warming has previously been identified as the main driver for changing distributions. Odland et al. (2010) however observed an increasing number of species associated with wetter habitats on mountain summits in a study conducted within the same study area used here. Another study by Felde et al. (2012), also located within the same study area, found that changes in precipitation rates were more pronounced than changes in temperature the last decade, suggesting that changing water dynamics and balance may be important drivers for the observed changes. In addition to these observational studies, Grytnes et al. (2014) found no positive correlation between warming and the upward range shift for alpine species, suggesting that temperature is not the main driver of the upward elevational shift observed in alpine areas. They go on to present a hypothesis that more melting snow and ice has revealed more areas for colonization as an explanation for why the observed patterns of upward shift is not directly linked to the climatic warming through the physiological effects of temperature on the plants. Another explanation could be that the interpolated surface air temperatures in the climate models will differ from the actual temperature alpine plants experience given their low stature (Grytnes et al., 2014).

In my results, bio19 (precipitation of coldest quarter) contributed the most to all models, followed closely by bio6 (minimum temperature of coldest month) in the models using a random background (Table 5). The variables aspect and slope showed low contribution in all models, which is expected since these variables only affect species indirectly. The high contribution of bio19 suggests that snow cover is strongly affecting the species distributions, which is meaningful since snow cover is a limiting factor for plant growth. The high correlation found between bio19 and the other precipitation variables (Figure A 1 in Appendix) also suggests that year round precipitation and the water dynamics in general within the area have a strong impact on the species distributions, as other studies have found.

In response to bio19 all species show a wide range in their local optima, suggesting that the species have a relatively wide tolerance for winter precipitation. As precipitation increases all species are negatively affected, but for *R. glacialis* the curve does not drop to zero suggesting it can tolerate the most extreme precipitation currently found within the area. The full response is however not ecological meaningful since it shows sign of an optimum at the low end of the precipitation scale, before dropping to zero and then rising to its absolute optimum as precipitation increases. This response is likely a case of model overfitting of the presence data by Maxent. In response to bio6, all species have a drop in response as the temperature gets warmer than -16 °C. The range in local optima is narrow in bio6 compared to bio19, which suggest that in this study area temperature is more of a limiting factor for the species than precipitation. It also suggests that the species will have a higher tolerance for increased precipitation than for the increased temperatures. This could support the findings of Engler et al. (2011) that the projected increase in precipitation in the Scandes will make this area less vulnerable to climate change compared to other European mountain ranges. Between the two model sets the main difference between the response curves is due to the low number of background locations used in the models with a target group background. This leads to a narrower environmental range in the response curves, resulting in different fitted responses.

To what extent the projected changes in suitable habitat come true depends on the species ability to track their optimal environment. In this study, species are only projected to lose habitat, meaning the projections doesn't account for any new areas that might open up for colonization. In reality it is likely that new areas will open up for the species as snow and ice melts in a warmer climate, like Grytnes et al. (2014) hypothesized. For alpine plants, their growth and dispersal abilities determines how fast they can track their optimal habitat. Opening of new areas can facilitate the focal species in tracking their optimal

environmental conditions. Strong wind often found in alpine areas, can also facilitate species to track their optimal habitat as it shifts upwards.

Species distributions are likely not to shift as fast as climatic conditions changes. Tracking of habitat takes time since plant growth – and thereby movement – is limited. Their tracking abilities can be further restricted through short distance dispersal, topography, increased habitat fragmentation or amount of soil available for them to grow in at high elevations. This time lag makes it likely that species will persist within areas even after they have become unsuitable. This is known as extinction debt, meaning species eventually will become extinct from an area due to changes that already have occurred (Kuussaari et al., 2009). Dullinger et al. (2012) found that almost half of the alpine species that was part of their study were likely to occupy areas classified as climatically unsuitable by the end of this century due to the delayed response. It is highly likely that the focal species in this study will persist outside areas classified as suitable in this study by the year 2070. One reason being the extinction debt within the area, another being that the coarse resolution of the models might not capture smaller patches of suitable habitat.

5. Conclusion

The results was produced for setting bounds on the magnitude of expected changes in vegetation in an alpine ecosystem of national interest.

All species in this study was projected to have an upward elevational shift under climate change, which leads to a reduction in suitable habitat and increased habitat fragmentation. In addition to having less area to occupy, the focal species might experience increased competition from lowland species, increased isolation between populations and having larger shares of their suitable habitat outside species optimum. The projections was different for the three species, and the high alpine specialist *R. glacialis* was projected to be affected the most of the focal species. This suggests that species currently found at the highest elevations are the most vulnerable to climate change. These projections support previous findings that alpine species will be negatively affected by the upward elevational shift predicted under climate change.

At this scale, and in this study area, precipitation was found to be the environmental variable that affected the species distributions the most, followed by temperature. This supports previous findings that water dynamics is an important driver of distributional changes in alpine habitats along with temperature. The expected increase in precipitation and rising temperatures are likely to be the causes of the upward elevational shift for the focal species.

The expected distributional changes will change the alpine vegetation cover as we know it today in Jotunheimen, leading to a changed composition of the ecosystem. To further evaluate the performance of these projections and to establish whether the models using a random background or the models using a target group background are more accurate, sampling of an independent and unbiased data set is needed.

6. References

- Aguilar, R., Ashworth, L., Galetto, L., & Aizen, M. A. (2006). Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology Letters*, *9*(8), 968-980. doi:10.1111/j.1461-0248.2006.00927.x
- Andrén, H. (1994). Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review. *Oikos*, *71*(3), 355-366. doi:10.2307/3545823
- Araújo, M. B., Alagador, D., Cabeza, M., Nogués-Bravo, D., & Thuiller, W. (2011). Climate change threatens European conservation areas. *Ecology Letters*, *14*(5), 484-492. doi:10.1111/j.1461-0248.2011.01610.x
- Araújo, M. B., Pearson, R. G., Thuiller, W., & Erhard, M. (2005). Validation of species–climate impact models under climate change. *Global Change Biology*, *11*(9), 1504-1513. doi:10.1111/j.1365-2486.2005.01000.x
- Artsdatabanken. (2017a). *Occurrence data Poa flexuosa*. Made available by: Naturhistorisk Museum - UIO, Agder Naturmuseum, NTNU - Vitenskapsmuseet, Norsk botanisk Forening, JBJordal. Downloaded from artskart.artsdatabanken.no, 2017-10-15.
- Artsdatabanken. (2017b). *Occurrence data Ranunculus glacialis*. Made available by: Naturhistorisk museum – UIO, Agder naturmuseum, NTNU – Vitenskapsmuseet, Biofokus, Universitetet for Miljø- og biovitenskap, Miljølære.no, MFU, Arkeologisk museum UiS, Universitetsmuseet i Bergen UiB, Ecofact, Tromsø museum – Universitetsmuseet, Norsk botanisk forening, JBJordal. Downloaded from artskart.artsdatabanken.no, 2017-10-15.
- Artsdatabanken. (2017c). *Occurrence data Trisetum Spicatum*. Made available by: Naturhistorisk museum – UIO, Agder naturmuseum, NTNU – Vitenskapsmuseet, Norsk institutt for naturforskning, Biofokus, MFU, Arkeologisk museum – UiS, Universitetsmuseet i Bergen – UiB, Miljølære.no, Ecofact, Tromsø museum – Universitetsmuseet, Norsk botanisk forening, JBJordal. Downloaded from artskart.artsdatabanken.no, 2017-10-15.
- Artsdatabanken. (2018a). *Occurrence data Poa*. Made available by: Norsk botanisk forening, Biofokus, JBJordal, NTNU – Vitenskapsmuseet, MFU, Naturhistorisk Museum – UiO, Norsk institutt for naturforskning, Universitetsmuseet i Bergen, UiB, Agder naturmuseum, GBIF. Downloaded from artskart.artsdatabanken.no, 2018-02-16.
- Artsdatabanken. (2018b). *Occurrence data Ranunculus*. Made available by: Norsk botanisk forening, Biofokus, JBJordal, NTNU – Vitenskapsmuseet, Naturhistorisk museum – UiO, Norsk institutt for naturforskning, GBIF, Norsk institutt for vannforskning MFU, Universitetsmuseet i Bergen – UiB. Downloaded from artskart.artsdatabanken.no, 2018-02-16.
- Artsdatabanken. (2018c). *Occurrence data Trisetum, Anthoxanthum and Melica*. Made available by: Norsk botanisk forening, Biofokus, JBJordal, NTNU – Vitenskapsmuseet, Naturhistorisk museum – UiO, MFU, Norsk institutt for naturforskning, Universitetsmuseet i Bergen – UiB, Agder naturmuseum, Tromsø museum – Universitetsmuseet. Downloaded from artskart.artsdatabanken.no, 2018-02-16.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*(4), 365-377. doi:10.1111/j.1461-0248.2011.01736.x
- Bogaert, J., Farina, A., & Ceulemans, R. (2005). Entropy increase of fragmented habitats: A sign of human impact? *Ecological Indicators*, *5*(3), 207-212. doi:10.1016/j.ecolind.2005.02.002
- Botkin, D. B., Saxe, H., Araújo, M. B., Betts, R., Bradshaw, R. H. W., Cedhagen, T., . . . Stockwell, D. R. B. (2007). Forecasting the Effects of Global Warming on Biodiversity. *BioScience*, *57*(3), 227-236. doi:10.1641/B570306
- Chapin, F. S., & Shaver, G. R. (1985). Individualistic Growth Response of Tundra Plant Species to Environmental Manipulations in the Field. *Ecology*, *66*(2), 564-576. doi:10.2307/1940405
- Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, *333*(6045), 1024-1026. doi:10.1126/science.1206432
- Choler, P., Michalet, R., & Callaway, R. M. (2001). Facilitation and Competition on Gradients in Alpine Plant Communities. *Ecology*, *82*(12), 3295-3308. doi:10.1890/0012-9658(2001)082[3295:FACOGI]2.0.CO;2
- Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichet, T., Friedlingstein, P., . . . Wehner, M. (2013). Long-term Climate Change: Projections, Commitments and Irreversibility. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley (Eds.), *Climate Change 2013: The*

Physical Science Basis. Contribution of Working Group 1 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

- Cornelissen, J. H. C., Callaghan, T. V., Alatalo, J. M., Michelsen, A., Graglia, E., Hartley, A. E., . . . Aerts, R. (2001). Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology*, 89(6), 984-994. doi:10.1111/j.1365-2745.2001.00625.x
- Cubasch, U., Wuebbles, D., Chen, D., Facchini, M. C., Frame, D., Mahowold, N., & Winter, J.-G. (2013). Introduction. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group 1 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.
- Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N., Guisan, A., . . . Hülber, K. (2012). *Extinction debt of high-mountain plants under twenty-first-century climate change (SOM)*.
- Engler, R., Randin, C. F., Thuiller, W., Dullinger, S., Zimmermann, N. E., Araujo, M. B., . . . Guisan, A. (2011). 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, 17(7), 2330-2341. doi:10.1111/j.1365-2486.2010.02393.x
- Felde, V. A., Kapfer, J., & Grytnes, J.-A. (2012). Upward shift in elevational plant species ranges in Sikkilsdalen, central Norway. *Ecography*, 35(10), 922-932. doi:10.1111/j.1600-0587.2011.07057.x
- Flato, G., Marotzke, J., Abiodun, B., Braconnot, P., Chou, S. C., Collins, W., . . . Rummukainen, M. (2013). Evaluation of Climate Models. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group 1 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.
- Forman, R. (1995). *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge: Cambridge University Press.
- Freeman, E. A., & Moisen, G. G. (2008). A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecological Modelling*, 217(1), 48-58. doi:10.1016/j.ecolmodel.2008.05.015
- Geological Survey of Norway. (2018a). NGU. *Løsmassekart*. Retrieved from <http://geo.ngu.no/kart/losmasse/>
- Geological Survey of Norway. (2018b). NGU. *Berggrunnskart*. Retrieved from <http://geo.ngu.no/kart/berggrunn/>
- Gjærevoll, O. (1989). *Mountain flowers of Scandinavia*. Trondheim: Bruns bokhandels forlag.
- Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J. L., . . . Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2, 111. doi:10.1038/nclimate1329
- Grytnes, J. A., Kapfer, J., Jurasinski, G., Birks, H. H., Henriksen, H., Klanderud, K., . . . Birks, H. J. B. (2014). Identifying the driving factors behind observed elevational range shifts on European mountains. *Global Ecology and Biogeography*, 23(8), 876-884. doi:10.1111/geb.12170
- Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). *Habitat Suitability and Distribution Models: With Applications in R*. Cambridge: Cambridge University Press.
- Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I. T., . . . Buckley, Y. M. (2013). Predicting species distributions for conservation decisions. *Ecology Letters*, 16(12), 1424-1435. doi:10.1111/ele.12189
- Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, 135(2), 147-186. doi:10.1016/S0304-3800(00)00354-9
- Halvorsen, R. (2013). A strict maximum likelihood explanation of MaxEnt, and some implications for distribution modelling. *Sommerfeltia*, 36(1), 1-132. doi:10.2478/v10208-011-0016-2
- Hanssen-Bauer, I., & Førland, E. J. (1998). *Annual and seasonal precipitation variations in Norway 1896-1997*. (27/98 Klima). Norwegian Meteorological Institute Retrieved from file:///C:/Users/180607/Downloads/MET-report-27-1998.pdf.
- Hanssen-Bauer, I., & Nordli, P. Ø. (1998). *Annual and seasonal temperature variations in Norway 1876-1997*. (25/98 Klima). Norwegian Meteorological Institute Retrieved from file:///C:/Users/180607/Downloads/MET-report-25-1998.pdf.

- Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, 12(10), 1040-1049. doi:10.1111/j.1461-0248.2009.01355.x
- Hautier, Y., Randin, C. F., Stöcklin, J., & Guisan, A. (2009). Changes in reproductive investment with altitude in an alpine plant. *Journal of Plant Ecology*, 2(3), 125-134. doi:10.1093/jpe/rtp011
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965-1978. doi:10.1002/joc.1276
- Holten, J. I., Aune, E., Tveito, O., Dyrddal, A., Etzelmüller, B., & Johansen, B. (2011). *Altitudinal distribution patterns of alpine plants: Studies along a coast-inland transect in southern Scandes, northern Europe*. Trondheim: Tapir academic press.
- Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B., & Hermy, M. (2002). Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters*, 5(4), 525-530. doi:10.1046/j.1461-0248.2002.00346.x
- Jiménez-Valverde, A., & Lobo, J. M. (2007). Threshold criteria for conversion of probability of species presence to either–or presence–absence. *Acta Oecologica*, 31(3), 361-369. doi:10.1016/j.actao.2007.02.001
- Jump, A. S., & Peñuelas, J. (2005). Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, 8(9), 1010-1020. doi:10.1111/j.1461-0248.2005.00796.x
- Jørgensen, R. (1933). Karplantenes høidegrenser i Jotunheimen. *Nyt magasin for naturvitenskaberne*, 72, 1-128.
- Klanderud, K., & Birks, H. J. B. (2003). Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *The Holocene*, 13(1), 1-6. doi:10.1191/0959683603h1589ft
- Kulonen, A., Imboden, R. A., Rixen, C., Maier, S. B., Wipf, S., & Diez, J. (2017). Enough space in a warmer world? Microhabitat diversity and small-scale distribution of alpine plants on mountain summits. *Diversity and Distributions*. doi:10.1111/ddi.12673
- Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., . . . Steffan-Dewenter, I. (2009). Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology & Evolution*, 24(10), 564-571. doi:10.1016/j.tree.2009.04.011
- Körner, C. (2003). *Alpine Plant Life: Functional Plant Ecology Of High Mountain Ecosystems*.
- Leimu, R., Vergeer, P., Angeloni, F., & Ouborg, N. J. (2010). Habitat fragmentation, climate change, and inbreeding in plants. *Annals of the New York Academy of Sciences*, 1195(1), 84-98. doi:10.1111/j.1749-6632.2010.05450.x
- Lenoir, J., Gégout, J.-C., Marquet, P., Ruffray, P., & Brisse, H. (2008). *A Significant Upward Shift in Plant Species Optimum Elevation During the 20th Century* (Vol. 320).
- Lid, J., Lid, D. T., & Elven, R. (2005). *Norsk flora*. Oslo: Norske Samlaget.
- Loiselle, B. A., Jørgensen, P. M., Consiglio, T., Jiménez, I., Blake, J. G., Lohmann, L. G., & Montiel, O. M. (2008). Predicting species distributions from herbarium collections: does climate bias in collection sampling influence model outcomes? *Journal of Biogeography*, 35(1), 105-116. doi:10.1111/j.1365-2699.2007.01779.x
- Matthews, J., & Whittaker, R. (1987). *Vegetation Succession on the Storbreen Glacier Foreland, Jotunheimen, Norway: A Review* (Vol. 19).
- Merow, C., Smith, M. J., & Silander, J. A. (2013). A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*, 36(10), 1058-1069. doi:10.1111/j.1600-0587.2013.07872.x
- Mossberg, B., & Stenberg, L. (2012). *Gyldendals Store Nordiske Flora*. Oslo: Gyldendal Norsk Forlag.
- Nenzén, H. K., & Araújo, M. B. (2011). Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling*, 222(18), 3346-3354. doi:10.1016/j.ecolmodel.2011.07.011
- NIBIO. (2018). *Norsk Institutt for Bioøkonomi: Kilden karttjeneste*. Retrieved from https://kilden.nibio.no/?X=6843735.15&Y=139033.92&zoom=6&lang=nb&topic=arealinformasjon&bgLayer=graatone_cache&layers_opacity=0.75
- Nordhagen, R. (1943). *Sikkildal og Norges fjellbeiter: en plantesosiologisk monografi*. Bergen: A. S. John Griegs Boktrykkeri.
- Norwegian Meteorological Institute. (2018a). *Månednormaler Fanaråkki*. (923506). Retrieved from http://sharki.oslo.dnmi.no/portal/page?_pageid=73,39035,73_39049&_dad=portal&_schema=PORTAL.
- Norwegian Meteorological Institute. (2018b). *Månednormaler Sikkildal*. (923511). Retrieved from http://sharki.oslo.dnmi.no/portal/page?_pageid=73,39035,73_39049&_dad=portal&_schema=PORTAL.

- Odland, A., Høitomt, T., & Olsen, S. L. (2010). Increasing Vascular Plant Richness on 13 High Mountain Summits in Southern Norway since the Early 1970s. *Arctic, Antarctic, and Alpine Research*, 42(4), 458-470. doi:10.1657/1938-4246-42.4.458
- Parmesan, C. (2006). *Ecological and Evolutionary Responses to Recent Climate Change* (Vol. 37).
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37. doi:10.1038/nature01286
- Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J. L. B., . . . Grabherr, G. (2012). Recent Plant Diversity Changes on Europe's Mountain Summits. *Science*, 336(6079), 353-355. doi:10.1126/science.1219033
- Pearman, P. B., Guisan, A., Broennimann, O., & Randin, C. F. (2008). Niche dynamics in space and time. *Trends in Ecology & Evolution*, 23(3), 149-158. doi:10.1016/j.tree.2007.11.005
- Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190(3), 231-259. doi:10.1016/j.ecolmodel.2005.03.026
- Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications*, 19(1), 181-197. doi:10.1890/07-2153.1
- Ponder, W. F., Carter, G. A., Flemons, P., & Chapman, R. R. (2001). Evaluation of Museum Collection Data for Use in Biodiversity Assessment. *Conservation Biology*, 15(3), 648-657. doi:10.1046/j.1523-1739.2001.015003648.x
- Ranc, N., Santini, L., Rondinini, C., Boitani, L., Poitevin, F., Angerbjörn, A., & Maiorano, L. (2017). Performance tradeoffs in target-group bias correction for species distribution models. *Ecography*, 40(9), 1076-1087. doi:10.1111/ecog.02414
- Reddy, S., & Dávalos, L. M. (2003). Geographical sampling bias and its implications for conservation priorities in Africa. *Journal of Biogeography*, 30(11), 1719-1727. doi:10.1046/j.1365-2699.2003.00946.x
- Root, T., Price, J., Hall, K., Schneider, S., Rosenzweig, C., & Pounds, A. (2003). *Fingerprints of global warming on wild animals and plants* (Vol. 421).
- Roque, B. B., Koptur, S., & Sah, J. P. (2017). The Effects of Habitat Fragmentation on the Reproduction and Abundance of *Angadenia berteroi*. *Plant Ecology*, 10(2), 340-348. doi:10.1093/jpe/rtw024
- Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., . . . Imeson, A. (2008). Attributing physical and biological impacts to anthropogenic climate change. *Nature*, 453, 353. doi:10.1038/nature06937
- Ryvarden, L. (1971). Studies in Seed Dispersal 1. Trapping of Diaspores in the Alpine Zone at Finse, Norway. *Nordic Journal of Botany*, 18, 215-226.
- Scherrer, D., & Körner, C. (2011). Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, 38(2), 406-416. doi:10.1111/j.1365-2699.2010.02407.x
- Schönswetter, P., Paun, O., Tribsch, A., & Niklfeld, H. (2003). Out of the Alps: colonization of Northern Europe by East Alpine populations of the Glacier Buttercup *Ranunculus glacialis* L. (Ranunculaceae). *Molecular Ecology*, 12(12), 3373-3381. doi:10.1046/j.1365-294X.2003.01984.x
- Settele, J., Scholes, R., Betts, R. A., Bunn, S., Leadley, P., Nepstad, D., . . . Taboada, M. A. (2014). Terrestrial and Inland Water Systems. In C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (Eds.), *Climate Change 2014: Impacts, Adaptation and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group 2 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 271-359). Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.
- Snøtun, M. (2011). Jotunheimen Nasjonalpark. *Jotunheimen og Utladalen Nasjonalparkstyre*. Retrieved from <http://www.nasjonalparkstyre.no/Jotunheimen/Verneomrade/Jotunheimen/>
- Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., . . . Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*. doi:10.1038/s41586-018-0005-6
- Thuiller, W., Albert, C., Araújo, M. B., Berry, P. M., Cabeza, M., Guisan, A., . . . Zimmermann, N. E. (2008). Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, 9(3), 137-152. doi:10.1016/j.ppees.2007.09.004

- Thuiller, W., Lavorel, S., Araújo, M., Sykes, M., & Prentice, I. (2005). *Climate change threats to plant diversity in Europe* (Vol. 102).
- Totland, Ø., & Alatalo, J. M. (2002). Effects of temperature and date of snowmelt on growth, reproduction, and flowering phenology in the arctic/alpine herb, *Ranunculus glacialis*. *Oecologia*, 133(2), 168-175. doi:10.1007/s00442-002-1028-z
- VanDerWal, J., Shoo, L. P., Graham, C., & Williams, S. E. (2009). Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? *Ecological Modelling*, 220(4), 589-594. doi:10.1016/j.ecolmodel.2008.11.010
- Wagner, J., Steinacher, G., & Ladinig, U. (2010). *Ranunculus glacialis* L.: successful reproduction at the altitudinal limits of higher plant life. *Protoplasma*, 243(1), 117-128. doi:10.1007/s00709-009-0104-1
- Walther, G. R. (2010). *Community and ecosystem responses to recent climate change* (Vol. 365).
- Wilson, S. D., & Nilsson, C. (2009). Arctic alpine vegetation change over 20 years. *Global Change Biology*, 15(7), 1676-1684. doi:10.1111/j.1365-2486.2009.01896.x
- Woodward, F. I. (1987). *Climate and plant distribution*. Cambridge: Cambridge University Press.
- WorldClim. (2005a). *CCSM4 RCP4.5*. by www.worldclim.org; Hijmans et al. 2005. Int J. of Clim 25: 1965-1968. Is licensed under a Creative Commons Attribution-ShareAlike 4.0 International License.
- WorldClim. (2005b). *CCSM4 RCP8.5*. by www.worldclim.org; Hijmans et al. 2005. Int J. of Clim 25: 1965-1968. Is licensed under a Creative Commons Attribution-ShareAlike 4.0 International License.
- WorldClim. (2005c). *Current climatic conditions*. by www.worldclim.org; Hijmans et al. 2005. Int J. of Clim 25: 1965-1968. Is licensed under a Creative Commons Attribution-ShareAlike 4.0 International License.
- Young, A., Boyle, T., & Brown, T. (1996). The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology & Evolution*, 11(10), 413-418. doi:10.1016/0169-5347(96)10045-8

7. Appendix

7.1. Coefficient values

<i>Poa flexuosa</i>					
Random background			Target background		
Variable	Feature	Coefficient	Variable	Feature	Coefficient
aspect	linear	-0,108	aspect	linear	0,177
aspect	quadratic	-0,228	aspect	quadratic	-0,199
aspect	reverse hinge	-0,516	aspect	reverse hinge	-0,980
aspect	reverse hinge	-1,134	aspect	reverse hinge	-0,053
aspect	forward hinge	0,136	bio3	linear	0,034
aspect	forward hinge	0,586	bio6	linear	0,000
aspect	forward hinge	-0,117	bio6	quadratic	2,093
bio3	linear	0,000	bio6	forward hinge	-0,891
bio3	quadratic	1,274	bio6	reverse hinge	-0,089
bio6	linear	-0,879	bio6	forward hinge	-0,205
bio6	quadratic	5,326	bio19	linear	0,268
bio6	reverse hinge	0,201	bio19	reverse hinge	-0,247
bio6	reverse hinge	-1,317	bio19	reverse hinge	-0,793
bio6	forward hinge	-0,070	bio19	reverse hinge	-0,222
bio6	forward hinge	1,107	bio19	reverse hinge	-1,084
bio6	reverse hinge	0,019	bio19	forward hinge	-0,023
bio19	linear	0,513	bio19	forward hinge	-0,118
bio19	reverse hinge	-2,262	bio19	reverse hinge	-1,568
bio19	forward hinge	-0,488	bio19	reverse hinge	-0,215
bio19	forward hinge	-0,963	bio19	forward hinge	-0,332
bio19	forward hinge	-0,975	bio19	reverse hinge	-0,140
bio19	reverse hinge	-1,390	bio19	forward hinge	-0,031
slope	linear	1,705	slope	linear	0,235
slope	reverse hinge	-0,042			
slope	reverse hinge	-0,104			
slope	forward hinge	-0,979			
slope	reverse hinge	-0,124			
slope	forward hinge	-0,290			
slope	reverse hinge	-0,020			
slope	forward hinge	-0,058			
Linear predictor normalizer		6.785	Linear predictor normalizer		2.304

Table A 1: Coefficient values for *P. flexuosa*, used for calculating the models predicted value.

Ranunculus glacialis

Random background			Target background		
Variable	Feature	Coefficient	Variable	Feature	Coefficient
aspect	linear	0,043	aspect	linear	0,069
aspect	quadratic	-0,169	aspect	quadratic	-0,008
aspect	reverse hinge	-0,082	aspect	reverse hinge	-0,170
aspect	reverse hinge	-0,500	aspect	forward hinge	0,171
aspect	reverse hinge	-0,743	aspect	forward hinge	0,052
aspect	forward hinge	0,017	bio3	linear	0,148
aspect	reverse hinge	-0,017	bio3	quadratic	0,301
aspect	forward hinge	-0,809	bio6	linear	0,000
aspect	reverse hinge	0,059	Bio6	quadratic	0,426
aspect	forward hinge	0,011	bio6	forward hinge	-1,509
aspect	forward hinge	0,438	bio6	reverse hinge	-0,095
aspect	forward hinge	0,018	bio6	forward hinge	-0,147
aspect	reverse hinge	0,040	bio6	forward hinge	-0,349
aspect	forward hinge	0,226	bio6	reverse hinge	-0,019
aspect	forward hinge	0,018	bio19	linear	0,322
aspect	forward hinge	0,133	bio19	reverse hinge	-0,515
aspect	reverse hinge	0,010	bio19	reverse hinge	-0,224
bio3	linear	0,806	bio19	reverse hinge	-0,608
bio3	quadratic	0,356	bio19	reverse hinge	-0,228
bio3	forward hinge	-0,071	bio19	reverse hinge	-0,163
bio6	linear	-0,887	bio19	reverse hinge	-0,481
bio6	quadratic	3,893	bio19	reverse hinge	1,934
bio6	reverse hinge	-0,271	bio19	reverse hinge	1,042
bio19	linear	0,000	bio19	reverse hinge	-0,357
bio19	quadratic	-0,437	bio19	reverse hinge	-0,812
bio19	reverse hinge	-0,632	bio19	reverse hinge	-0,088
bio19	forward hinge	-0,651	slope	linear	0,000
bio19	reverse hinge	1,619	slope	quadratic	-0,063
bio19	reverse hinge	-0,576	slope	reverse hinge	0,187
bio19	reverse hinge	2,136			
bio19	reverse hinge	-3,071			
bio19	forward hinge	-0,115			
bio19	forward hinge	-0,319			
bio19	reverse hinge	1,013			
bio19	reverse hinge	0,418			
slope	linear	1,436			
slope	reverse hinge	-0,005			
slope	reverse hinge	0,409			
slope	forward hinge	-0,296			
slope	forward hinge	-0,173			

slope	reverse hinge	0,054		
slope	forward hinge	-0,179		
slope	reverse hinge	-0,120		
slope	forward hinge	-0,301		
slope	reverse hinge	-0,036		
slope	reverse hinge	0,036		
slope	reverse hinge	-0,051		
slope	forward hinge	-0,101		
Linear predictor normalizer		4.710	Linear predictor normalizer	0.981

Table A 2: Coefficient values for *R. glacialis*, used for calculating the models predicted value.

<i>Trisetum spicatum</i>					
Random background			Target background		
Variable	Feature	Coefficient	Variable	Feature	Coefficient
aspect	linear	-0,012	aspect	linear	0,198
aspect	quadratic	-0,165	aspect	quadratic	0,009
aspect	reverse hinge	0,080	bio3	linear	0,458
aspect	reverse hinge	-0,088	bio3	quadratic	0,077
aspect	reverse hinge	0,035	bio6	linear	0,000
aspect	reverse hinge	-0,166	bio6	quadratic	0,458
aspect	forward hinge	-0,194	bio6	forward hinge	-1,450
aspect	forward hinge	0,053	bio6	forward hinge	-1,856
aspect	reverse hinge	0,006	bio19	linear	0,139
aspect	reverse hinge	0,023	bio19	reverse hinge	-0,188
bio3	linear	0,436	bio19	reverse hinge	-0,218
bio3	quadratic	0,466	bio19	reverse hinge	-0,537
bio3	forward hinge	0,289	bio19	reverse hinge	-0,760
bio6	linear	0,000	bio19	reverse hinge	-0,067
bio6	quadratic	1,158	bio19	reverse hinge	-0,525
bio6	forward hinge	-3,526	slope	linear	0,140
bio6	reverse hinge	-0,219	slope	reverse hinge	-0,064
bio6	reverse hinge	-0,553	slope	forward hinge	-0,519
bio6	reverse hinge	0,427			
bio6	reverse hinge	0,265			
bio6	forward hinge	-0,620			
bio19	linear	0,000			
bio19	quadratic	-0,688			
bio19	reverse hinge	-0,058			
bio19	reverse hinge	-0,959			
bio19	reverse hinge	-0,754			
bio19	reverse hinge	-0,159			
bio19	forward hinge	-0,443			

bio19	forward hinge	-1,252	
bio19	forward hinge	-1,193	
bio19	reverse hinge	-0,550	
bio19	reverse hinge	-0,115	
bio19	reverse hinge	-0,083	
slope	linear	1,981	
slope	reverse hinge	-0,671	
slope	reverse hinge	-0,024	
slope	reverse hinge	-0,043	
slope	forward hinge	-0,433	
slope	reverse hinge	-0,047	
slope	forward hinge	-0,916	
slope	forward hinge	-0,494	
slope	reverse hinge	-0,050	
Linear predictor normalizer		2.574	Linear predictor normalizer 1.154

Table A 3: Coefficient values for *T. spicatum*, used for calculating the models predicted value.

7.2. Threshold values

<i>Species</i>	<i>Model</i>	<i>Threshold</i>
<i>Poa flexuosa</i>	Random background	2.7093e-05
	Target group background	5.2502e-04
<i>Ranunculus glacialis</i>	Random background	3.8354e-05
	Target group background	4.4503e-04
<i>Trisetum spicatum</i>	Random background	3.8420e-05
	Target group background	3.6290e-04

Table A 4: Threshold values used to convert relative occurrences to binary predictions.

7.3. Correlation matrix

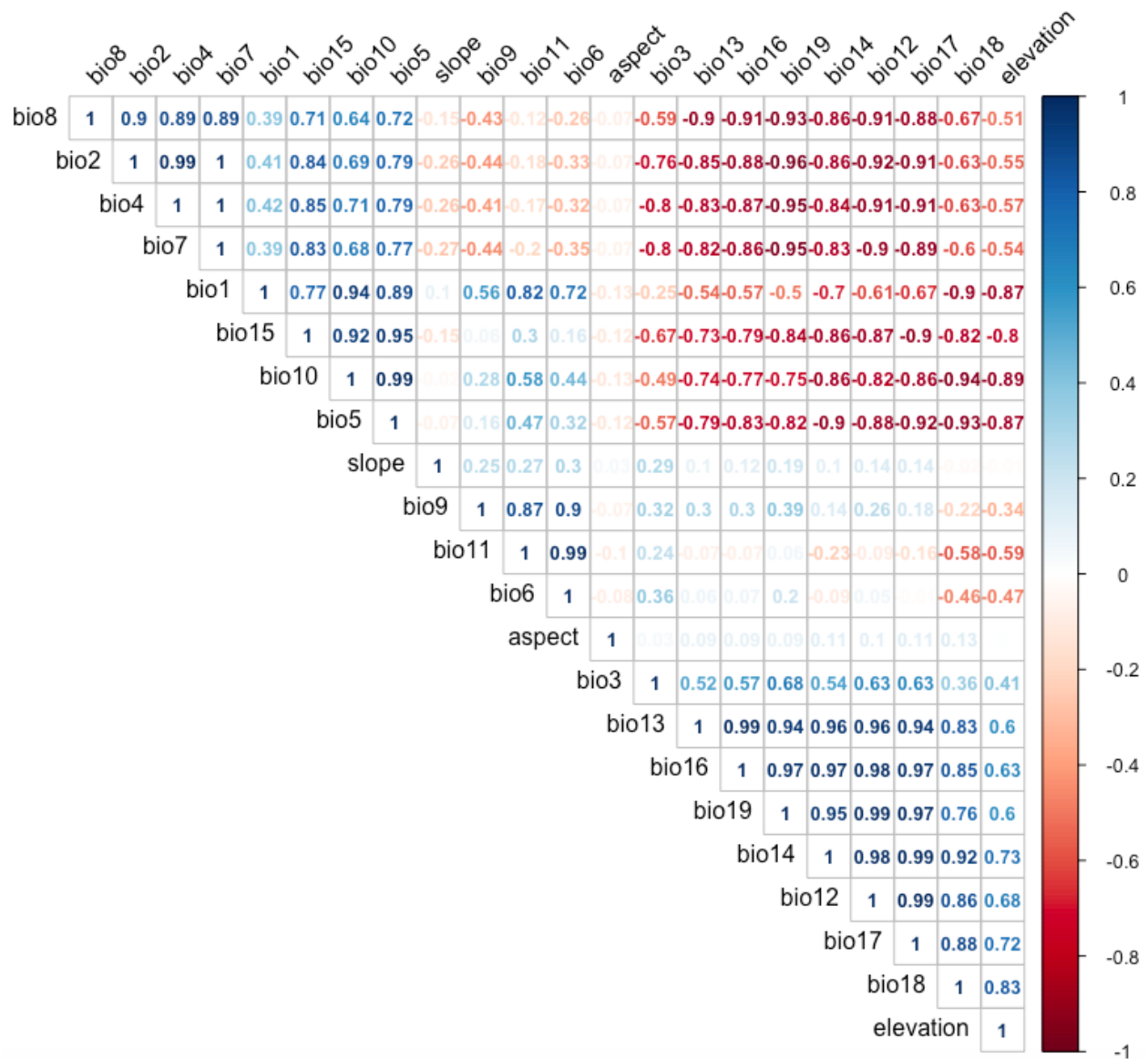


Figure A 1: The correlation matrix used to eliminate highly correlated variables within the study area. The correlation analysis was done using R-studio.

7.4. Edge habitat

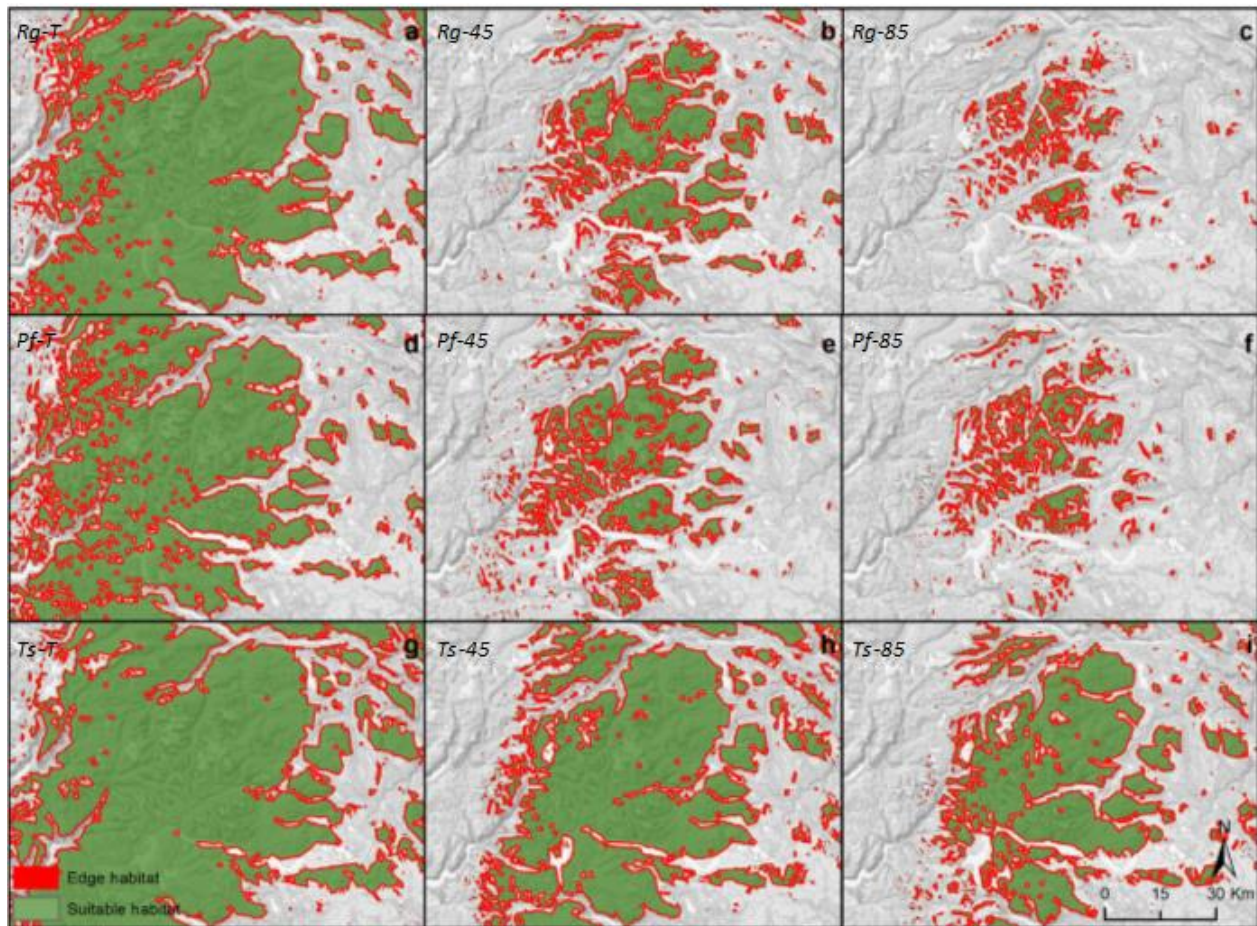


Figure A 2: Map showing the current predictions and the future projections under RCP4.5 and RCP8.5 of changes in suitable habitat with the estimated edge habitat from the models with a random background. The edge was calculated as all habitat within 500 meters from the habitat edge.

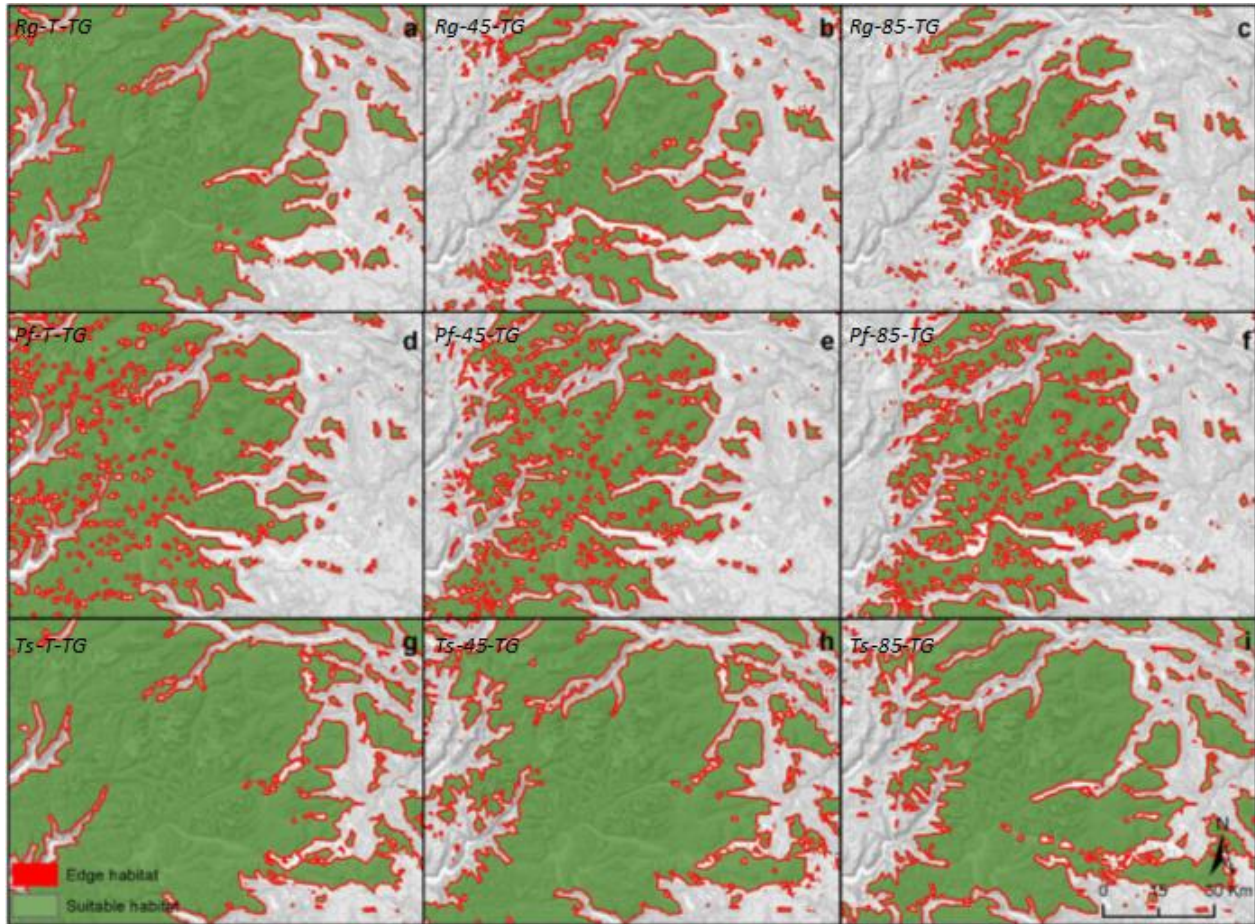


Figure A 3: Map showing the current predictions and the future projections under RCP4.5 and RCP8.5 of changes in suitable habitat with the estimated edge habitat from the models with a target group background. The edge was calculated as all habitat within 500 meters from the habitat edge.