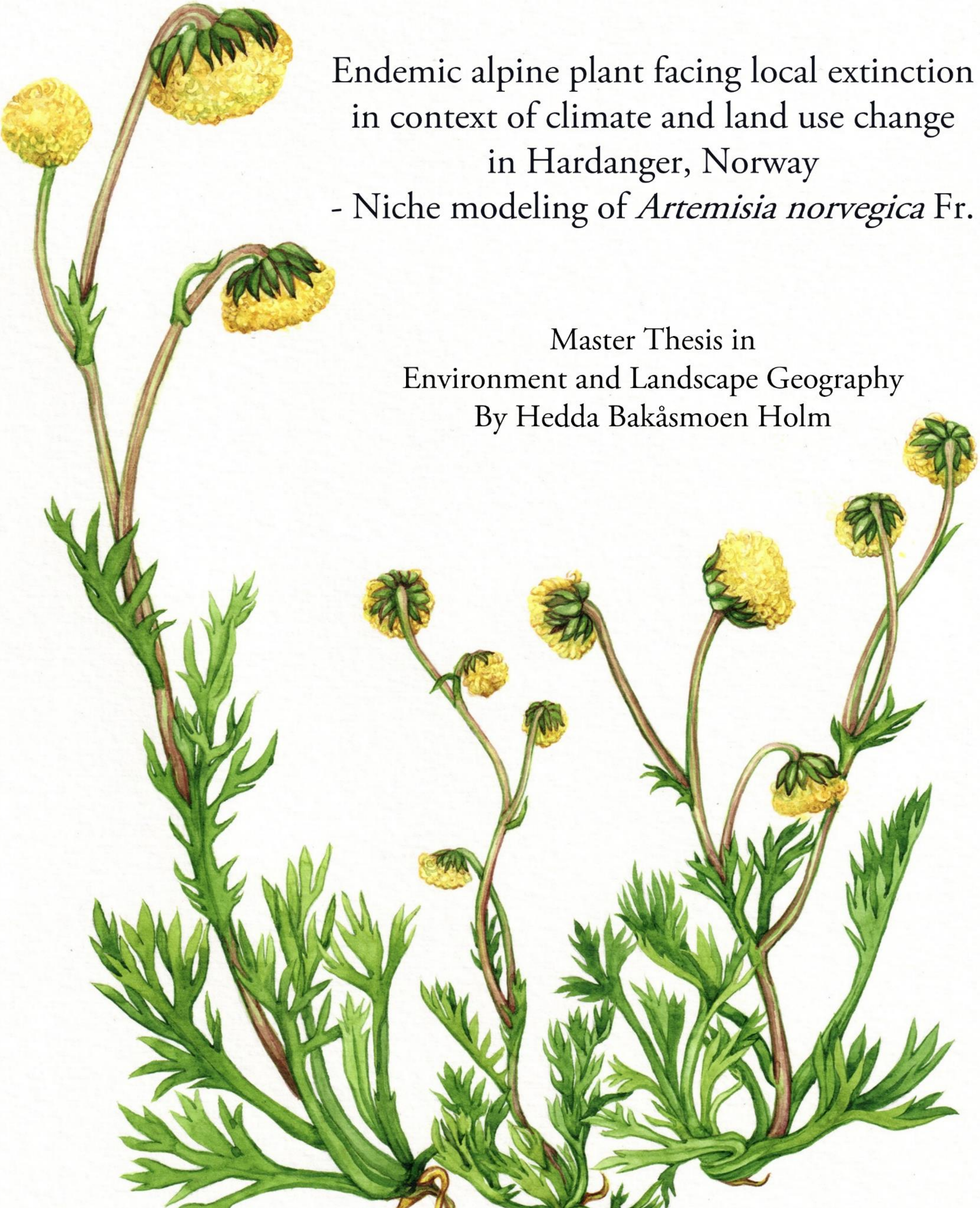
Endemic alpine plant facing local extinction in context of climate and land use change in Hardanger, Norway
- Niche modeling of *Artemisia norvegica* Fr.

Master Thesis in
Environment and Landscape Geography
By Hedda Bakåsmoen Holm



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Front page figure: Botanical watercolour by Anna Farba, 2021, of *Artemisia norvegica* (Fr.), with rights of usage.

Sustained by previous discoveries, we can go forth into the future, and by foreseeing the consequences of phenomena, we can understand once and for all the laws to which nature subject itself. In the midst of this research, we can achieve an intellectual pleasure, a moral freedom that fortifies us against the blows of fate and which no external power can ever reach.

- von Humboldt and Bonpland (2009, p. 75)

Abstract

Based on Hutchinson's niche theory, species need to move in space to stay within their climate niche during climate change. This thesis tests whether an upward range shift has occurred for *Artemisa norvegica* (Fr.) during the last 90 years at Dovre (main population). The thesis hypothesises that the lapse rate has decreased with warmer climates during the last three normal periods (1930-2020) due to climate change and elevational-dependent warming (EDW), i.e. a more rapid warming at a higher elevation than low-land. The main aim is to use the niche model based on data from Dovre to evaluate whether a subpopulation of *A. norvegica* at Mt Vassli in Hardanger is becoming locally mountain-top extinct. Two hypotheses were tested: extinction caused directly by warming or by the upward elevational movement of *Betula pubescence* that may outcompete *A. norvegica* for light based on the understanding of thermophilization.

Generalized linear model (GLM) was used on frequency data (number of occurrences per 100-m elevation) and logistic regression on presence-absence data to estimate temperature optimum and tolerance range for the three normal climate periods and the total. The datasets were organised according to the three normal climate periods of 1931-1960, 1961-1990 and 1991-2020. Lapse rates for each normal period were calculated by linear least square regression between climate stations data, and EDW was interpreted from these results. An ordination was done on earlier vegetation data from Dovre, Hardanger, and new data (including subpopulation in Hjelmeland), which revealed two alpine ridge type habitats, and one habitat in screes and cliff.

EDW of lapse rates varied in relevance between the two types of climates. It was confirmed for the Dovre area, whereas not detected in Western Norway. *A. norvegica* has moved upwards in the past 90 years at the average speed of 2.5 meters per year. Consequently, its elevation optimum has ascended, however its temperature optimum has increasingly become cooler. *B. pubescens* also moved to higher elevations nationally and locally at Mt Vassli.

Climate projections imply that the future temperature optimum of the target species is at a higher elevation than what Mt Vassli can facilitate. Thus, this subpopulation may become locally mountain-top extinct as there is no land to track its niche.

A. norvegica is known to have a high heat tolerance, and therefore the temperature is not necessarily expected to be a mortal factor, but *B. pubescence* is mowing upwards nationally and locally at Mt Vassli, thus the light-demanding alpine ridge plant *A. norvegica* may be outcompeted for light.

Acknowledgements

This thesis has been fueled with coffee and a passion for biogeography. Today we know the phrase "to drink from the bitter wormwood cup" to imply something negative. However, in ancient Rome, wormwood wine was given to the victorious! As I hand in my thesis, I feel like the latter. The road to this accomplishment has not been without moments of bitterness. However, the people around me have given me the motivation and support I needed to make the process overall sweet. So, to these people, I owe a special thanks! First and foremost, my supervisor Ole Reidar Vetaas – thank you for the inspiration for the thesis and for your steadfastness, guidance, academic challenges and understanding. Benjamin Aubrey Robson – thank you for your inspiration and help with the UVA. Magne Sætersdal – thank you for showing me Mt Vassli and her unique plant. Also, thanks to everyone at the Department of Geography and my co-students for support and laughs.

To my dearest friends Vilde, Monika and Sunniva! Thank you so much for always being there for me, especially Sunniva, who housed me during fieldwork. But most of all, I am grateful for the never-ending love and encouragement from my family, Mamma, Far and Ingeborg. This thesis is just as much yours.

Hedda Bakåsmoen Holm

Hedda Bakåsmoen Holm

Bergen, 14th November 2021

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Abbreviations and acronyms

ANO	Spatially representative nature monitoring program for terrestrial ecosystems, or "Arealrepresentativ naturåvervåkning" (ANO) in Norwegian
BP	Before Present
c	Maximum probability of occurrence
CA	Correspondence Analysis
CO_2	Carbon dioxide
DCA	Detrended Correspondence Analysis
DEM	Digital Elevation Model
DTM	Digital Terrain Model
EDW	Elevation-Dependent Warming
Fr.	Fries
GBIF	The Global Biodiversity Information Facility
GHG	Green House Gasses
GLM	Generalized Linear Model
GPS	Global Positioning System
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature
km	kilometre
m	Metre
MAP	Mean annual precipitation
Masl	Meters Above Sea Level
MAT	Mean Annual Temperature
mm	millimetre
Mt	Mountain
n.d.	no date
NAO	North Atlantic Oscillation
NRS	National responsibility Species
NT	Near Threatened
R^2	Coefficient of determination, also used for deviance
RCP	Representative Concentration Pathway
s.d.	Standard deviation
Subsp.	subspecies
t	Tolerance
u	Optimum
UAV	Unmanned Aerial Vehicle
UTM	Universal Transverse Mercator
var.	variety
VU	Vulnerable
YD	Younger Dryas

1. Introduction

The world is 1.09°C warmer today than in 1900, and the consequences are far-reaching (Intergovernmental Panel on Climate Change [IPCC], 2021). Although species geographical range limits are in flux over time, anthropogenic climate change compels a universal redistribution of life on Earth (Pecl et al., 2017, p. 1). In order to compensate for the warmer climate, many species are moving towards the cooler edge of their distribution. Hence, species must ascend to colder regions in order to track their environmental niche. Thus, we now see a global range shift of species either poleward or to higher elevations, in the estimated speed of 6.1 km northward or 6.1 meters ascending elevation for every decade (Parmesan & Yohl, 2003). In other words, the temperature of their habitat stays the same, but species are geographically moving (Pecl et al., 2017).

The overall upward shift in alpine vegetation is recorded in long- (Klanderud & Birks, 2003) and short-term studies (Pauli et al., 2005; Erschbamer, 2007). In the Alps, the increase of species richness of 11 % correlates with warmer local temperatures (Pauli et al., 2005). Over five years, there was a more significant increase in species richness in a higher than lower elevation in the Dolomites (Erschbamer, 2007), indicating an invasion of thermophile vegetation. In Norway, Klanderud & Briks (2003) found a considerable change in species composition and distribution across elevation over the last 70 years despite relatively small temperature changes. Among the plants studied in Jotunheimen, 53.5 per cent of species examined were found at higher elevations than 60 years ago, equating to an upward migration of 1.2 m per year. On the contrary, Chapin et al. (1995) have revealed a 30 to 50 per cent decrease in species richness over nine years in correlation to warmer temperatures in the arctic tundra. Additionally, other authors have registered a downward specie range shift (e.g. Crimmins et al., 2011; Kopp & Cleland, 2014; Bhatta et al., 2018).

Species range shift is expected to continue in correspondence with the advancement of climate change (Ramming et al., 2010). However, unlike animals, individual plants cannot migrate and are stuck in their geographical habitat, which is continuously becoming less suitable to their environmental niche. Furthermore, due to mountains general cone shape, there is a clear limit when moving upwards. Thus, alpine plants face range constrictions and possibly "mountain-top extinction" (Colwell et al., 2008, p. 260) as they ride "the escalator to extinction" (Urban, 2018, p. 11871) in the endeavour to track their environmental niche. Additionally, there is less room to escape thermophile competitors, such as mountain birch (*Betula pubescens* subsp. *Czerepanovii*), creeping upwards (thermophilization) (Vanneste et al., 2017).

There is evidence of overheating as a mortal factor for plants (Dahl, 1951). Some cold-adapted plants are not able to survive in warmer conditions and will overheat and wither. Dahl (1951, p. 22) made observations of alpine plants expiring in the warmer low-land climate of Oslo Botanical Garden, Norway. Alpine plants like "*Salix herbacea, Ranunculus glacialis, Lactuca alpina, Ranunculus platanifolius, Rhododendron lapponicum*" dried out, where the leaves became yellow or brown before losing them, and they did not produce seeds. Furthermore, the plants mentioned only seemed to thrive during early spring or late autumn and would not survive for more than a few years in this *ex situ* location. In other words, heat and overheating are abiotic factors that make survival outside an alpine plant's temperature tolerance challenging. Additionally, Larcher et al. (2010) demonstrate that high heat and water stress lead to alpine plants' leaf damage. However, they conclude that overall alpine plants show relatively high heat tolerance.

Moreover, for alpine plants, increased habitat unsuitability is happening at a faster rate. Compared to the lowland areas, mountains are experiencing a greater degree of warming, a phenomenon named elevation-dependent warming (EDW) (Pepin et al., 2015; Rangwala et al., 2010). Thus, alpine vegetation is regarded as particularly sensitive to climate change due to diminishing suitable area, with generally longer generation time and incoming competitors (thermophilization) (Pauli et al., 2005; Gottfried et al., 2012; Lenoir & Svenning, 2015; Vanneste et al., 2017; Verrall & Pickering, 2020). Consequently, climate change is awaited to affect the alpine regions in a fundamental way.

Observation shows cryophilic plants respond to warming temperatures differently and individually (Walker et al., 2006), where some respond better than others (Rumpf et al., 2018). As a result, it is still unknown which species are likely to become endangered in the following warmer decades. Broad-scale distribution maps have been generated to answer this dilemma, but these studies are often criticised for either under – or overestimating the threat of climate change to alpine plants (Pearson & Dawson, 2003; Thuiller, 2004; Guisan & Thuiller, 2005). Consequently, multiple researchers have requested fine-scaled models regarding species distribution and climatic fluctuations, particularly in mountainous locations (Randin et al., 2009; Austin & van Niel, 2011; Franklin et al., 2013). It is uncertain if species can follow their environmental niche efficiently in response to changing climate conditions, but fine spatial sampling resolution will be needed if they do. Thus, climatic niche modelling for individual species is a well-established fine-scale method determining climate tolerance and possible responses to climate change (Vetaas, 2002; Austin & van Niel, 2011).

In order to investigate climate changes' impact on alpine vegetation, this thesis examines the Norwegian sagewoth, *Artemisia Norvegica* Fries subsp. *norvegica* (hereafter *A. norvegica*). This is a potential threatened alpine and endemic *sensu lato* plant that is restricted in a few particular mountainous areas in Norway, such as Dovre, Austmannshovudet in Hjelmeland and Hardanger. More than 90 per cent of the global population is found in Norway. However, two small populations are known outside Norway; the Ural Mountains in Russia and Scotland. Whereas *A. norvegica* referred to outside Eurasia, most notably in North America, is another species in the *Artemisia* genus, *A. Arctica* (Riggins & Seigler, 2012). One of the unique locations of *A. norvegica* in Norway is on top of Mt Vassli in Hardanger. Based on the aforementioned reasoning, this population is at risk of being pushed off the top. Accordingly, this site of *A. norvegica* offers a unique insight into the possible future for alpine plants facing climate change.

Because temperature is a powerful determinant of species distribution and the primary explanatory variable in this thesis, it is essential to establish fine-scale temperature estimates and the lapse rate (the rate of temperature change with elevation). As mentioned, due to EDW, mountains are disproportionally affected by climate change compared to lowland, where altitudes experience increased warming (Pepin et al., 2015; Rangwala et al., 2010). Consequently, the lapse rate decreases as the temperature in the mountains approach lowland temperatures. Thus, the ecological impact is that species must move further to compensate. This thesis will explore this phenomenon by investigating the local changes in temperature and lapse rate over the last three normal periods and analyse the development of the lapse rate in light of climate changes and EDW.

In this study, the conceptual framework is based on niche theory (Hutchinson, 1957) and gradient analyses (Whittaker, 1967; Austin, 1985; ter Braak & Prentice, 1988) to assess and predict the effects of climate change on *A. norvegica* in the last century and into the future with climate change. The past 90 years of distribution patterns are analysed in light of Breshears et al. (2008) predictions of distribution responses. The niche model is based on data from the *A. norvegica* main population in Dovre obtained from Artskart.

1.2 Main aim and research questions

From a niche perspective, this thesis explores the three disjunct subpopulations of *A. norvegica* in Norway to assess the probability of future extinction in Hardanger and the past movement in Dovre. The aims are addressed by exploring the geographical distribution of *A. norvegica* by time and elevation, with appropriate temperature (lapse rate) to time, location, and elevation. Thus, three biographical aspects of *A. norvegica* are in focus: distribution in time (temporal), elevation (geographical) and temperature (environmental niche). The thesis will also examine how the local lapse rate has changed with climate change over the last 90 years. Moreover, the observed habitat of *A. norvegica* is described. Finally, the aims are addressed by answering and testing the following research questions.

Within the context demonstrated above, this thesis will investigate the research questions as follows:

I) How and to what degree is elevation-dependent warming occurring in the last three temperature normal periods?

II) How and to what degree has the *A. norvegica* population in Dovre responded climatically and geographically the last 90 years?

III) How and to what degree is *A. norvegica* in Hardanger a candidate for local extinction?

1.3 Thesis structure

Chapter 2 clarifies the core concepts that this thesis builds on.

Chapter 3 introduces the various characteristics of the study sites, followed up by a presentation of the target species. Eventually, the chapter ends with a description of the analytical path used to collect and analyse data.

Chapter 4 offer the results according to the analytical route described in the previous chapter.

Chapter 5 presents interpretations and discusses the results within the conceptual framework presented in chapter 2 and in the context of other authors research in the field.

Chapter 6 succinctly addresses the research questions.

Chapter 7 ultimately concludes the thesis by summing up significant findings and proposing some suitable conservation management guidelines.

2. Conceptual Framework

Hutchinson's niche (1957) is the core concept of this thesis (Fig. 2.1). Austin (1985) linked Hutchinson niche concept to the continuum concept, where the environmental niche for a species is represented by a unimodal response curve along the environmental gradient. This niche can be elucidated by the theory of gradient analysis (ter Braak and Prentice, 1988). Lastly, the expected range shift along the temperature-elevation gradient is understood in light of Breshears et al. (2008) distribution interpretations.

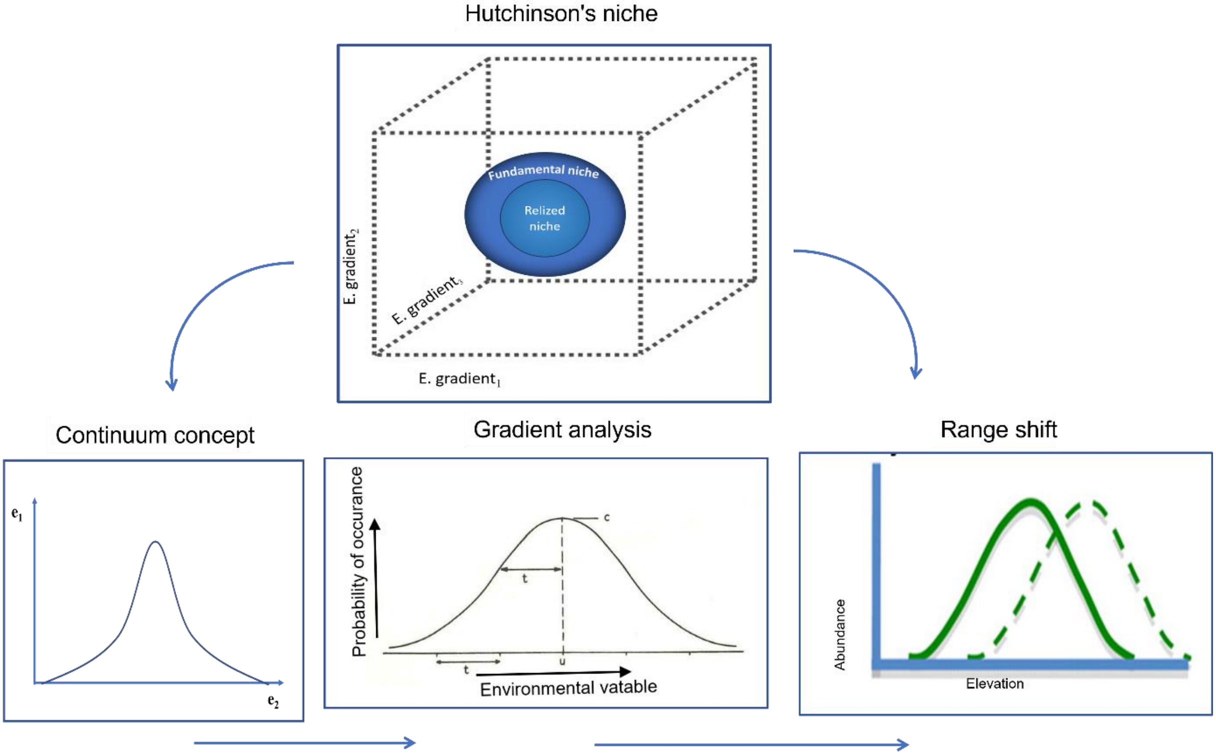

Figure 2.1 Visual overview of the conceptual framework used in the present thesis. Hutchinson's niche theory (Guisan et al., 2017, p. 36) is at the top, illustrating its central role within the thesis and the following concepts. The lowest level is the continuum concept (Austin, 1985), gradient analysis (ter Braak & Looman, 1995, p. 42) and range shift (Bershears et al., 2008, p. 11592), all based on Hutchinson's niche.

2.1 The Niche

Within biogeography, the niche is one of the main tools in explaining species distribution by establishing range limits (Wiens, 2011). However, although recognised as an essential component in understanding species distribution patterns, the niche concept is inconsistently used within the field (Pulliam, 2000; Sales et al., 2021). These discrepancies have resulted in several parallel definitions, further obscuring the concept to the point where some authors wish to avoid the concept calling it "a term perhaps best left undefined" (Bell, 1982, in Sales et al., 2021, p. 4) and some desire to "ditch the niche" altogether (McInerny & Etienne, 2012a, p. 2096). Nevertheless, going forth a precise, unambiguous usage of the niche concept is the foundation for good research, and it has become an agenda for many authors to find a coherent definition of the niche (e.g. Vetaas, 200; McInerny & Etienne, 2012a, b, c; Pocheville, 2015; Sales et al., 2021).

Niche has mainly been used in three parallel ways based on either Grinnell (1917), Eltons (1927) and Hutchinsons (1957) definitions. Grinnell (1917) linked species to their location, where the niche is all factors of a given location, including abiotic, biotic, and competitors. Thus, the niche is the same as habitat in geographical space, making the niche a property of the environment (Sales et al., 2021). On the other hand, Elton's (1927) niche concept focuses on what species are doing, i.e. the ecological role, placing them in relation to each other within trophic levels and energy translocations in ecosystems. Accordingly, the niche is not explicitly related to the geographical space but rather a species ecological role in a community (Sales et al., 2021). Whereas Hutchinson (1957) defined niche as a property of the species, resulting in a revolution in ecology. He described a niche as a multidimensional space, or an "*n*-dimensional hypervolume", characterised by different environmental factors that facilitate a species population to continually exist over generations. Hutchinson (1957) made an essential distinction between the theoretical fundamental, or potential, niche and an established sub-set of this environmental space, referred to as the realised niche (Vetaas, 2002).

The fundamental niche is environmentally suitable space within the tolerance of the species, based on abiotic requirements, making it an abstract space of potential existence. In comparison, the realised niche is limited by biotic interactions (e.g., competitors, herbivores, pollinators) and geographical barriers resulting in a subset of the fundamental niche (Fig. 2.2) (Vetaas, 2002; Guisan et al., 2017). Thus, Hutchinson includes the competitive exclusion principle formulated by Gause (1934, in Sales et al. 2021), which implies that species with equivalent environmental requirements could not perpetually co-exist over a long time. In short, niche overlap is not sustainable, where it eventually would lead to the local extinction of one of the two species.

An ecological question regarding plants individual inability to move is whether plants can adapt, or evolve, to current climate change (Jump & Peñuelas, 2005). The concept of niche conservatism implies that a species will not vary significantly in its environmental demands (niche) over generations (Wiens, 2011). To be specific, a species inherits a genetic code to a particular climate tolerance (Vetaas et al., 2018). Thus, niche conservatism implies that species are limited to their environmental range, thus dictating their possible geographical distribution.

Moreover, this concept also implies that species are at equilibrium with the climate, distributed across its climatically suitable area (Araújo & Pearson, 2005; Pili et al., 2020). Consequently, species genetic heritage contributes to understanding its biogeography (Wiens, 2011). In sum, a species' fundamental niche stays the same, but the geographical prevalence can change and shift over time due to environmental changes.

Utilising gradient analysis, the concept of niche stands at the core. By adopting the Hutchinson approach of niche, a species' geographical ranges are used to estimate their environmental niches (Austin, 1985), allowing the researcher to manipulate a factor of the environment, such as climate, and predict species range responses (Araújo & Person, 2005; Townsend Peterson et al., 2011). Therefore, this thesis will use Hutchinson's understanding of the niche and make predictions of range response to climate change based on estimates of the temperature niche of *Artemisia norvegica* Fr. (hereafter referred to as *A. norvegica*).

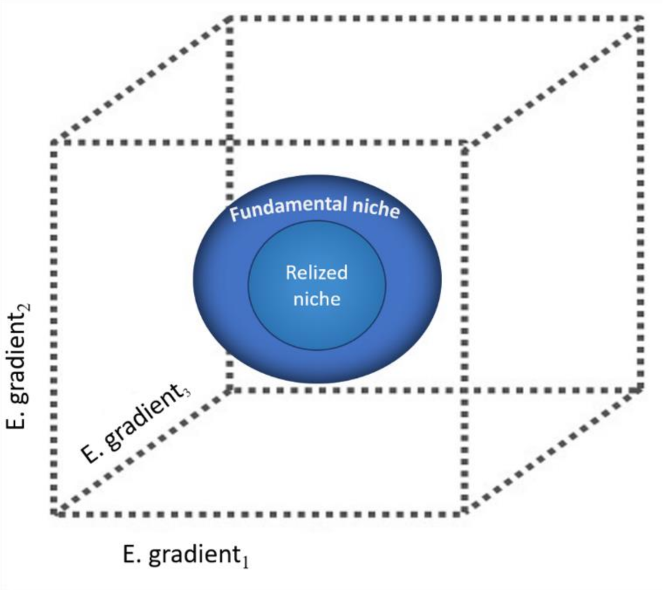

Figure 2.2 Illustrating a model of Hutchinson niche concept limited to a three-dimensional environmental niche. The fundamental environmental niche contains the realised niche. The realised niche is limited in range due to negative interactions, e.g., biotic factors, but have a self-sustaining population, R ≥ 1. Source: inspired by Guisan et al. (2017, p. 36), made by the author.

2.2 Meta-population, source-sink dynamics and the niche

A species has one environmental niche (Chase & Leibold, 2003), yet the geographical distribution is in most cases disjunct or non-continuous, referred to by Hanski (1998) as metapopulations. Pulliam (2000) incorporated the metapopulation concept into the niche concept and metapopulation theory, and demonstrated that source populations are within the realised niche, whereas sink populations may form populations outside the realised niche if dispersion is unrestricted. Referring to Hutchinson's (1957) niche division, sink populations exist within the fundamental niche but outside the realised niche due to insufficient reproduction to maintain a self-sustaining population.

2.3 Continuum concept and the niche

Austin (1985) linked the continuum concept to the niche. The concept assumes species variance with abundance is associated with the environmental gradient in a more or less bell-shaped response, e.g. temperature (physiological optima, cf. Ellenberg, 1954, in Austin, 1976, 1980). An interval of optimal conditions is realised along the environmental gradient, and it is expected that species have the most abundance or fitness at this interval, called the optimum (Fig. 2.3) (Austin, 1985). Likewise, a decrease in abundance and performance further from the optimum. Just as the fundamental niche, this gradient is abstract, where the graphical expression portrays the "abstract dimensions of an ecological space" (Austin, 1985, p. 40). As a result, the limitations of a species' ecological niche may be revealed by its geographical range (Sexton et al., 2009; Reddin et al., 2016). While the physiological response (fundamental niche) is assumed as Gaussian response, the ecological response (realised niche) is affected by topographic and biotic limitations thus might be less symmetric or skewed (Austin, 1985).

Sometimes there is confusion between abstract terminologies in ecology, e.g. fundamental niche or continuum concept, and geographical, physical prevalence, where the two concepts are not differentiated. For example, the abstract dimension of the environmental gradient represents the species' relative location that correlates to the environment and does not have a spatial relationship to the plant location (Dyakov, 2010). However, the elevation transects of a mountain with a lapse rate and subsequently close to a steady linear decline of temperature offer a zonation in geographical space that reflects a graphical environmental gradient, with a negative correlation between temperature and elevation.

2.4 Temperature, elevation and the niche

Elevation resembles the thermal gradient (Körner, 2007). Thus, elevation in itself is not of direct relevance for the physiology of plants. However, due to solid correspondence between elevation, temperature and species distribution, it is accepted that the elevation gradient is observed in these relations (Whittaker, 1967). Thus, this thesis will use the temperature – elevation gradient, referring to the combined environmental and geographical gradient, to explore the temperature niche of *A. norvegica*.

The main explaining factor of alpine plant distribution is the temperature (Woodward & Williams, 1987; Austin et al., 1990; Scherrer & Körner, 2011). Enzymes regulate many parts of a plant's life, e.g. photosynthesis, and are sensitive to temperature. Thus, the temperature will effectively restrict plant distribution and vegetation type because enzymes cease to function correctly in high or low temperatures (e.g. weather extremes and Shelford's Law of Tolerance, Fig. 2.3). Thus, the temperature is a regulating gradient, regulating the plant life functions (Cox & Moore, 2010).

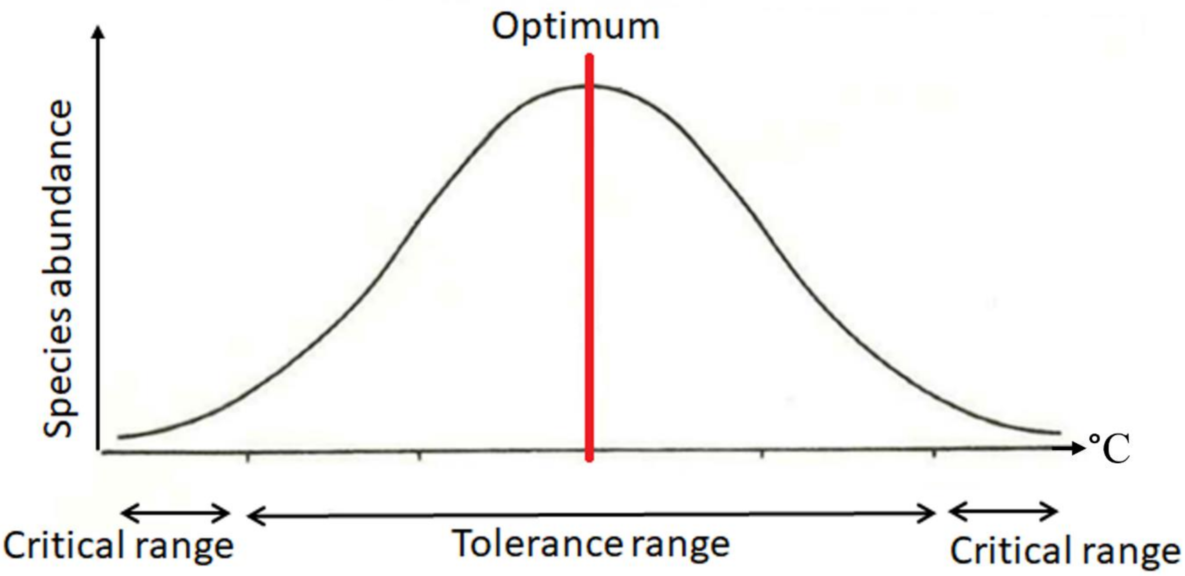

Figure 2.3 Response curve of the effects of an environmental factor, here in temperature (°C), on the abundance of a species. Optimum represent optimal conditions where abundance or fitness is expected to be the highest. Outwards from optimum are less suitable conditions but tolerable conditions resulting in lower levels of abundance and fitness. Furthest from optimum are critical levels of the environmental gradient where the species have problems surviving. Source: based on ter Braak & Looman (1995, p. 42), inspired by Helaouët and Beaurand (2009, p. 1237), modified by the author.

Moreover, the range of plants is believed to be limited by "low-temperature threshold for mortality" to the cooler edge and biotic interactions to the warmer edge (Woodward & Williams, 1987, p. 191; Kopp & Cleland, 2014). The physiological tolerances to low-temperature stress are believed to play a more significant role in determining higher elevational or latitudinal range boundaries as species have a clear lower temperature limit where death is present. At the same time, biotic interactions are thought to play a more prominent role in determining lower elevational or latitudinal range margins. In other words, a species minimum temperature tolerance controls the distribution upwards and poleward, while competition controls the southward and lower elevation limit (Woodward & Williams, 1987), a phenomenon named the Dobzhansky-MacArthur hypothesis (Lynn et al., 2021).

Across a mountain, the non-uniform terrain makes up different microclimates (Oke, 1987). Multiple factors affect the temperature in microclimates (e.g. wind speed profiles, humidity, albedo, surface roughness, etc.), but the amount of radiation that a surface receives is generally the significant predictor (Oke, 1987). Two main factors determine radiation received, azimuth and slope, on a local scale (not including latitude). Authors have pointed out the importance of understanding microclimates in climate change projections in ecology (Ulrey et al., 2016; Körner & Hiltbrunner, 2021), especially when there is a discrepancy between the temperature data gathered by climate stations (usually 2 meters above the ground) and temperatures experienced by lower statured plants, e.g. *A. norvegica*. Additionally, microclimates have been understood as possible indicators of refugia during climatic changes (Randin et al., 2009; Speziale & Ezcurra, 2015; Körner & Hiltbrunner, 2021). Refugium has earlier been a place of safe havens during glaciation or periods unsuitable regional climates where species have been able to survive (Cox & Moore, 2010). This thesis will investigate microclimates at Mt Vassli by using climate loggers placed out at different aspects (North, South, and at the top).

2.5 Gradient analysis and the niche

In order to relate environmental gradient to individual species response (Gleason, 1926) or population size, direct gradient analysis is often applied (Whittaker, 1967; ter Braak & Prentice, 1988). The species abundance or probability of occurrence is shown as a function of the observed environmental variable (Austin, 1985), e.g. by Generalized Linear Modelling (ter Braak & Prentice, 1988). This approach reveals a response curve for species along the environmental gradient, including the species optima and tolerance ranges, and is considered a species realised niche (Austin, 1985; Vetaas, 2000a; ter Brakk & Prentice 1988). Concerning changes in the environmental gradient, such as thermal energy, the response will be affected, referring to range shifts. Breshears et al. (2008) offer different interpretations in species response to climate change.

2.6 Range shift and the niche

Geographic range shift due to climate change is empirically proven in plants and animals (Thomas, 2010; Parmesan & Yohl, 2003; Lenoir et al., 2008; Lenoir & Svenning, 2015). Furthermore, Breshears et al. (2008, p. 11591) predict three possible distribution patterns of range shifts: "march", "lean", or "crash" (Fig. 2.4).

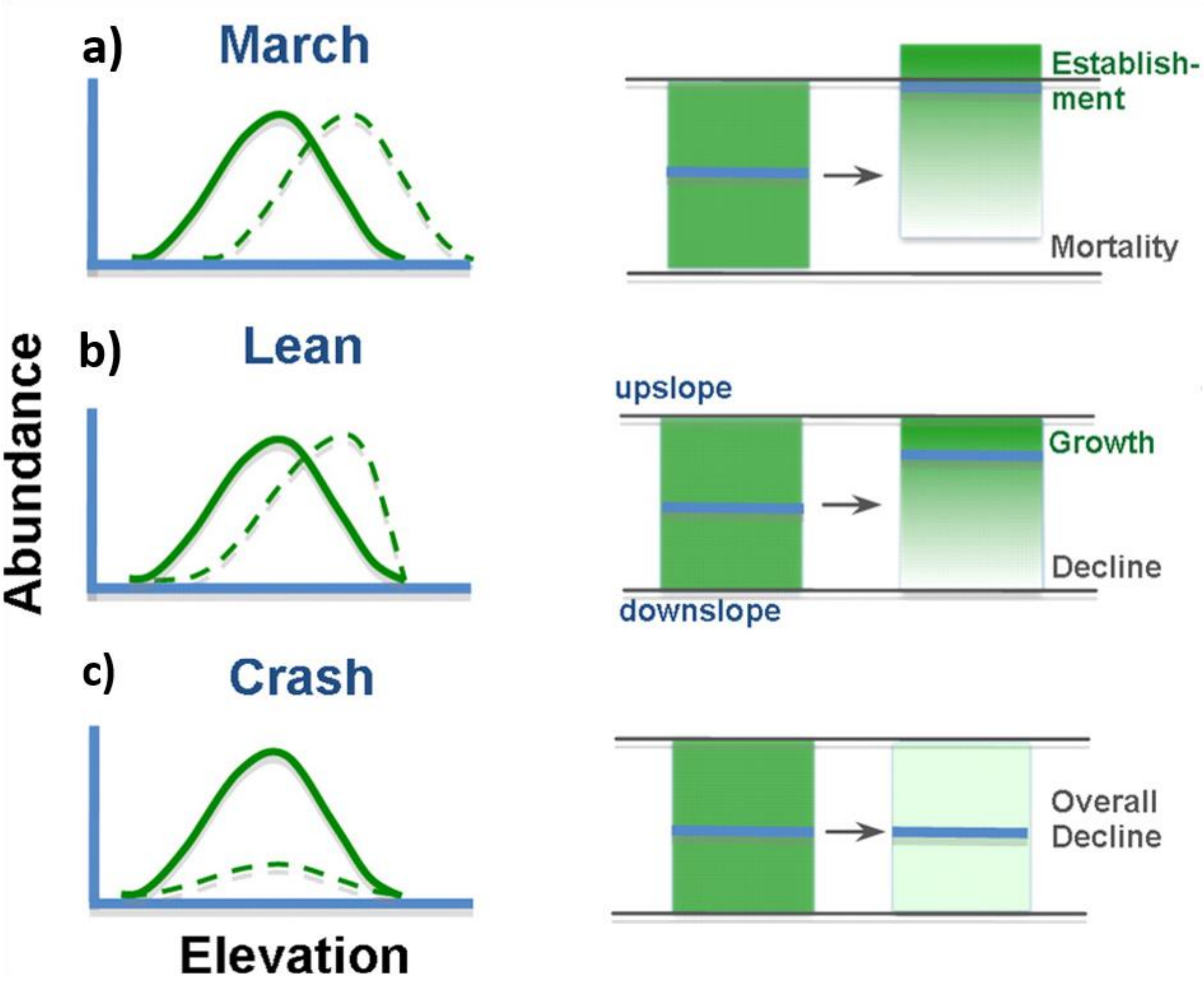

Figure 2.4 The three types of predicted distribution changed along the elevation gradient due to climate change as a result of changing patterns of establishment, growth and mortality. a) "March" refers to the expected upslope shift of species establishment, where range and optimum changes appropriately with a warmer climate. b) "Lean", where the range of plant in question stays the same, but with a tendency to higher growth/establishment rate higher up and higher mortality at lower elevation. c) "Crash" refers to a drastic decline in the population with a high mortality rate throughout the species range. Source: Breshears et al., 2008, p. 11592, modified by the author.

The "march" change in distribution pattern is the general expectation of species following their temperature niche correspondingly to higher elevations with warmer temperatures, as the high edge of distribution becomes more favourable. Conversely, the lower edge becomes less suitable, and higher mortality is expected. Thus, species are predicted to "march" upwards, with the trailing edge following the leading edge (e.g. Rumpf et al., 2019). In contrast, the "lean" change in distribution pattern predicts that the range stays the same but with a shift in optimum (Suwal & Vetaas, 2017). Lastly, the "crash" scenario refers to when climate warming results in a severe overall decrease in population.

Furthermore, extinction might result from range restriction and overall high mortality (Lenoir & Svenning, 2015). Lenoir & Svenning (2015) offer an additional two distribution scenarios, "retract" and "expand", in response to climate change. The former distributional response is expected for low mobility plants where optimum stays the same, but the overall range retracts in both directions. The latter is an expected response by plants with high persistence where the range expands in both directions of the temperature- elevation gradient.

2.7 Thermophilization and the niche

As stated, competition is a key concept in understanding plants geographical distribution within their fundamental niche. The concept of thermophilization can further help understand the out-competing dynamics cold-adapted alpine plants are facing. By combining the competitive exclusion with the empirically proven range change, thermophilization describes a pattern of species turnover where thermophile species increase and expand their range in beat with climate change at the expense of cryophile species (Gottfried et al., 2012; Vanneste et al., 2017). This is reflected in studies showing an increase and ascension in warm-adapted species and a corresponding decline in cold-adapted plants in mountains elevations (Gottfried et al., 2012). In other words, following their temperature niche "new" area becomes more suitable for warm-adapted species geographically overlapping and out-competing the alpine specialists. In Norway, *Betula pubescens* subsp. *czerepanovii* (N.I. Orova) Hämet-Ahti (commonly named mountain birch, hereafter *B. pubescens*) forms subalpine forest, and constitute the border to the alpine zone (Ryvarden, 2010). Thus, the accession of this tree would shadow out the low lying and light-demanding alpine vegetation. This upper forest line can be understood as the evicting factor of species belonging to the alpine zone, e.g. *A. norvegica*. Even though there is an ongoing discussion whether the trend of ascending *B. pubescens* in Norway is a result of climate change or changes in land use (Hofgaard, 1997; Larsson, 2004; Bryn, 2008; Rannow, 2013; Bryn & Pothoff, 2018), this thesis will explore *B. pubescens* forest expansion in relation to *A. norvegica* as the main competitor for light.

3. Materials and Methods

3.1 Materials

3.1.1 Study areas

Data from three different areas have been collected: Mt Vassli in Hardanger, Austmannshovudet in Hjelmeland, and the Dovre area. Characteristics for these three sites follows below, with a synopsis provided in Table 3.1.

Table 3.1 Overview of essential characteristics of study sites; Mt Vassli in Hardanger, Austmannshovudet in Hjelmeland, and the Dovre area.

Studt site	Masl	Climate	MAT	MAP	Vegetation
Mt Vassli	800 - 1055	slightly oceanic (O1)	0.3	1771	Low alpine
Austmannshovudet	600 - 860	highly oceanic (O3h)	8.3	2237	Low alpine
Dovre	0 - 1800	Oceanic to continental	3.3	547	Low, middle, high alpine

Masl = elevation (m), Climate = climate at site, MAT = Mean annual temperature (°C), MAP= Mean annual precipitation (mm), vegetation=type of vegetation.

Physiography

Mt Vassli, Hardanger

On the west coast of Norway, the mountain Mt Vassli is located in the Jondal district, now part of Ullensvang municipality in Vestland county. The peak is rounded and stretches from about 800 metres to 1055 masl (UTM32 6688157N 357588E). Mt Vassli (1035 masl) is a part of the Folgefonn peninsula's highland region (Moe et al., 1994), where the bedrock is riddled with zones of weakness and cracks reflected in the local topography (Fig. 3.1a) (Bakkestuen et al., 2001). Thus, varying terrain with valleys and plateaus surround Mt Vassli; the mountain Josteinen (1344 masl) is located to the east with the lower-lying plateau Krenglehaug between them. The study area is close to the sea at approximately 5 km (airline) from the Hardangerfjord to the north-west.

Austmannshovudet, Hjelmeland

Austmannshovudet is located in Hjelmeland district, Rogaland County (6567816N 353387E) (Fig. 3.1b), in the south-western corner of the Vormedalsheia landscape conservation area (Roalkvam, 1986). This study site elevates from approximately 600 masl and up to the mountain Austmannshovudet, at 860 masl. Austmannshovudet has a south-west facing cliff with extensive scree beneath. The farm Ritland is located to the south-east, and some shielings lie by the lake Ritlandstjørnet at the foot of the Austmannshovudet cliff to the east (Riis et al., 2011; Arnesen & Strøm, 2015).

Dovre area

The third study site is in the mountainous area of Trollheim, Dovre and Sunndal, where over 90 per cent of *A. norvegica* grow (in this thesis referred to as the Dovre area) (Artsdatabanken, n.d.). In all, the *A. norvegica* population stretch over a space of approximately 5 800 km^2 (Fig. 3.1c). The eastern terrain is characterised by broad valleys and rounded mountains, reaching heights up to 2 286 mals (Mt Snøhetta), with lowlands and valleys overlaid with quaternary deposits, e.g. moraines from the last glaciation. In comparison, the western topography has a more dramatic alpine relief with deeply cut glacial valleys (Trollheimsutvalet, 1980).

Geology

Mt Vassli, Hardanger

The geology of the Folgefonn peninsula's northern portion is of Precambrian age (Moe et al., 1994). Just at Mt Vassli, a stripe of basalt runs through the bedrock, whereas the surrounding area mainly consists of andesite, metagabbro and quartzite (Fig. 3.2). Compared with the tree latter bedrock types, basalt is soft and favourable to plant growth (Moe et al., 1994). Mt Vassli has little of quaternary deposits and is mostly a bear mountain (NGU, 2017). Therefore it is the bedrocks' properties and chemical content that significantly impact the flora (Arensen & Strøm, 2015).

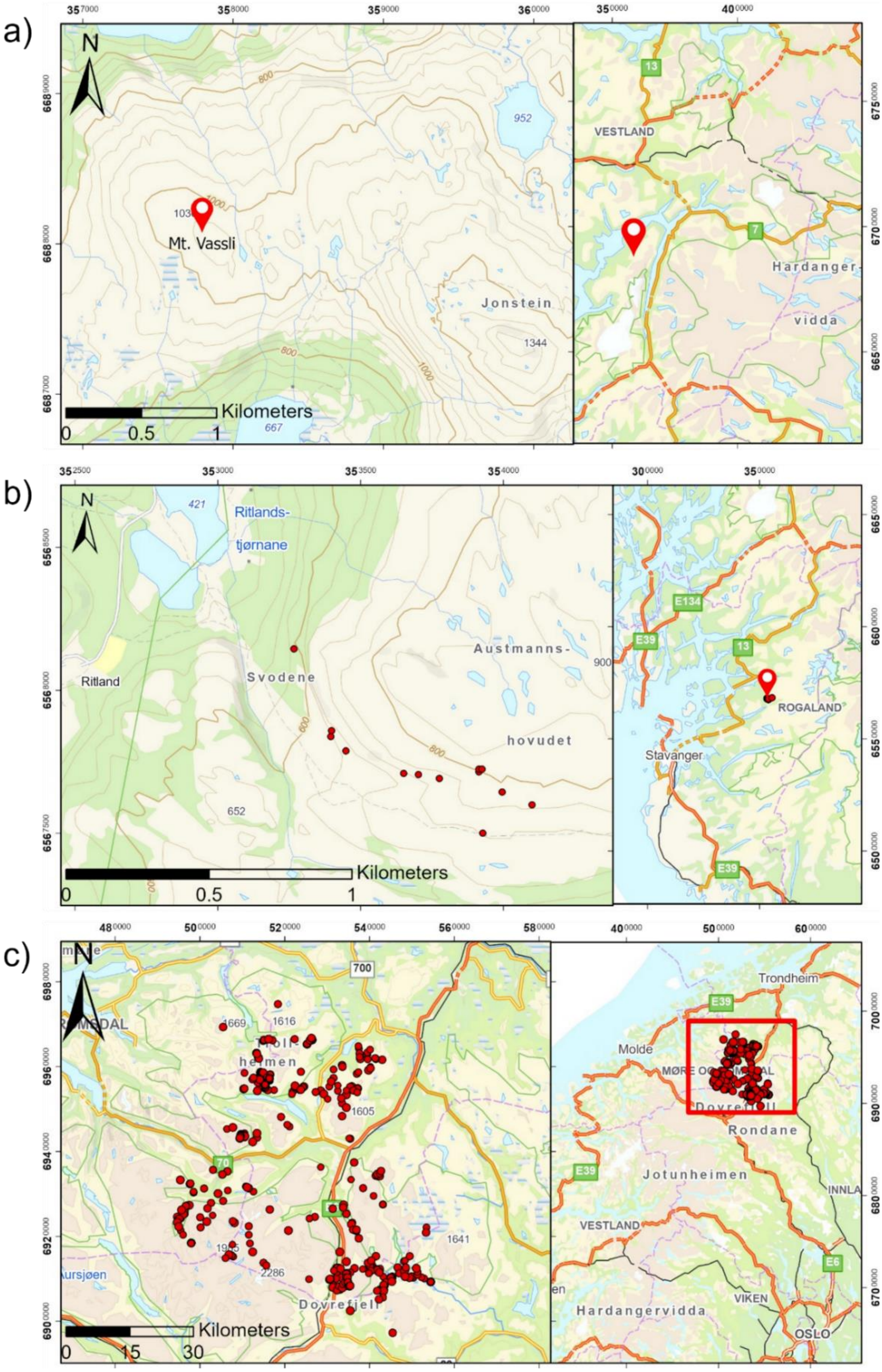

Figure 3.1 Topography maps of the study sites in the current thesis. a) Mt Vassli, Hardanger, b) Austmannshovudet, Hjelmeland with red points of earlier Artemisia norvegica occurrences, c) Dovre area with red points of occurrence of Artemisia norvegica used in the thesis niche modelling. Source: Basemap from Geodata Online; occurrence points from Artskart.artsdatabanken.no (2020).

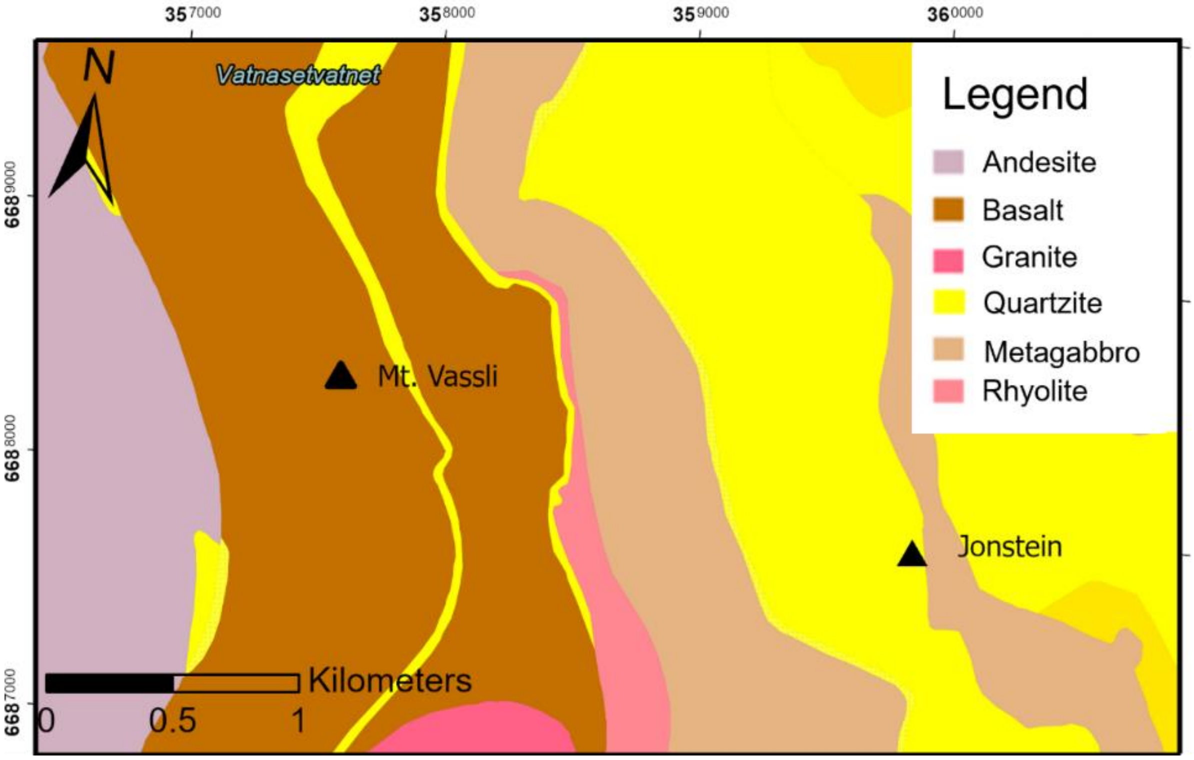

Figure 3.2 Geological map of Mt Vassli, Hardanger. Source: NGU (2009)

Austmannshovudet, Hjelmeland

Geologically, Austmannshovudet is a part of the newly discovered Ritlands crater. It was formed by a meteorite impact 540 million years ago, thus having unique geology. Today, the crater remains is a 2.5 km wide circular depression approximately 350 meters deep (Selbekk, 2021). Mica-schist makes up the lower part of the study area, and above it, a wide band of sandstone runs through the cliffside, or crater wall, south-west of Austmannshovudet. In contrast, the top of Austmannshovudet consists of nutrient-poor gneiss (Riis et al., 2011; Arnesen & Strøm, 2015; Marker & Slagstad, 2018). According to Arnesen & Strøm (2015), the calcareous mica-shist and sandstone provide a basis for high-pH leachate, which affects the adjacent vegetation. Lately, in a geological sense, glacial activity has eroded the high mountain areas and left sparse means for vegetation (Nasjonalparkstyre, 2012). For the most part, there are small amounts of quaternary deposits; a bare mountain covered by turf, and the larger screes at the foot of Austmannshovudet to the south-west (Arnesen & Strøm, 2015).

Dovre area

Dovre's bedrock has a mosaic of bedrock types (Trollheimsutvalet, 1980). Principally, there is a west and east division. The western side is old (Precambrian) bedrock, withered and nutrient-poor, consisting of gneiss and garnet mica-slate. In contrast, to the east, the ground is younger (Cambrosiluric) with higher levels of nutrients, where mica-slate and greenstone dominates (Drivdalen, n.d.; Trollheimsutvalet, 1980; Jordal & Gaarder, 2005). The quaternary deposits to the west have significant volumes of withered debris. While to the east, the deposits have been moved away by glaciers and left as sizeable continuous moraines and block fields (Vold, 1982; NGU, 2017).

Climate

Mt Vassli, Hardanger

The interaction of the local terrain determines the weather at Mt Vassli, affected by proximity to high mountains, the Hardangerfjord, and the nearby glacier Folgefonna (Lundstad et al., 2018). The closest weather station to this study area, which records temperature and precipitation, is at Folgefonna ski centre (1212 masl). Table 3.2 gives an overview of the weather station's newest climate normal (1991-2020), where the mean annual temperature is 0.3°C and receives mean annual precipitation of 1771 mm (eKlima, 2021)—resulting in a transition between markedly oceanic (O2) and slightly oceanic (O1), with a growing season of approximately 170 to 180 days (Moen, 1999). The area experience strong winds from the west and south-west but relatively small currents from the other celestial directions (Appendix Aa).

Table 3.2 Overview of mean temperature (°C) and precipitation (mm) for the standard period 1991-2020 from "Folgefonna skisenter" station (Station no. SN49085, 1212 masl). Source: eKilm.no (2021)

Mean	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
Temperature (°C)	-5.4	-5.8	-4.6	-1.5	2.3	5.7	7.4	7.4	4.5	1.4	-2.1	-5.2	0.3
Precipit-ation (mm)	184	113	158	105	74	87	105	131	193	216	198	202	1771

Austmannshovudet, Hjelmeland

Lyseboten is the closest climate station to the Austmannshovudet study site that records both temperature and rainfall. The climate station registered a mean annual temperature of 8.3°C and mean annual precipitation of 2237 mm, during the latest normal period, see Table 3.3, categorising the climate as "highly oceanic" (O3h) (Moen, 1999). Although the climate is oceanic, the temperature difference between winter and summer is 14.1°C. These climate conditions support a growing season of approximately 160 to 170 days (Moen, 1999). In general, the area is not exposed to strong air currents (Appendix Ab).

Table 3.3 Overview of mean temperature (°C) and precipitation (mm) for the normal period 1991-2020 from Lyseboten station (station no. SN45350, 5 masl). Source: eKilma.no (2021)

Mean	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
Temperature	2.0	1.6	3.4	7.4	10.8	13.6	15.6	15.7	12.6	8.5	5.3	2.6	8.3
Precipitation	226	227	184	107	93	102	122	164	197	236	249	285	2237

Dovre area

The Dovre area contains an oceanic and continental climate, where the western part is oceanic, while the eastern side is mainly continental (Moen, 1999). The amount of rainfall throughout the year is the most significant difference between the two climates, shown in Tables 3.4 and Table 3.5. The Surnadal-Sylte climate station represents the oceanic climate, receiving a considerable amount of precipitation (1250 mm/year), whereas the Drivadalen climate station (547 mm/year) represents the dryer continental climate. Even though Surnadal has an oceanic climate, the temperature difference between the warmest and coldest months is 17.6°C. In the Dovre region, the growing season varies. It can be as short as 110 days in the continental climate and as long as 170 days near the coast (Moen, 1999). Strong winds from the south-west are recorded at Kongsvoll, in the study area's middle southern part (Appendix Ac).

Table 3.4 Overview of mean temperature (°C) and precipitation (mm) for the normal period 1991-2020 from Drivadalen station (station no. SN63820, 680 masl). Source: eKilm.no (2021)

Mean	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
Temperature	-3.4	-3.9	-2.0	2.0	6.3	9.9	12.5	11.6	8.1	2.8	-1.0	-3.1	3.3
Precipitation	34	29	28	30	31	93	72	83	41	43	29	28	547

Table 3.5 Overview of mean temperature (°C) and precipitation (mm) for the normal period 1991-2020 from Surnadalen – Sylte station (station no. SN64760, 5 masl). Source: eKilma.no (2021)

Mean	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
Temperature	-2.7	-2.2	0.4	4.8	9.1	12.5	14.9	14.2	10.1	4.4	0.0	-1.7	5.3
Precipitation	101	70	92	78	75	101	103	124	137	131	99	133	1250

Vegetation and fauna

Mt Vassli, Hardanger

The Folgefonn peninsula's vegetation reflects the general nutrient-poor bedrock, slightly oceanic climate, and significant elevation variations (Lundbo, 1991; Bakkestuen, 2001). Located just above the subalpine *Betula pubescens* forest, the vegetation is typical for an alpine ridge (Appendix Ba) (Dahl et al., 1986; Moe et al., 1994).

B. pubescens forest upper edge is considered the dividing line between forest vegetation and the low alpine vegetation in Norway (Ryvarden, 2010). According to Moe et al. (1994) *B. pubescens* forest reaches up to 850 masl on the southern side and 750 masl on the northern side of Mt Vassli. However, the local forest lines are challenging to determine since snow cover, small mires, and changes in land usage manipulate the extremities (Moe et al., 1994; Bryn & Potthoff, 2018). Above the forest line lies heather-rich low alpine ridge vegetation with sparse and varying snow cover. The snow cover varies by topography, whereas in some small areas, it persists into late summer surrounded by marshes and snow-bed vegetation (Moe et al., 1994).

Because the topography and vegetation above the forest line do not provide much fodder or shelter wildlife is scarce. Deer is common among the dominant herbivores, while elk are considered stray animals. Additionally, a herd of about 50 reindeer is found in the northern parts of the Folgefonna peninsula (Overvoll, 2008).

Austmannshovudet, Hjelmeland

Vegetation at Austmannshovudet is similar to that of Mt Vassli (Appendix Bb). Above the forest line at Austmannshovudet, the general vegetation of the area is as boreal heather, with cliffs and scree at the *A. norvegica* habitat (Arnesen & Strøm, 2015). The landscape is affected by grazing sheep, and the forest line is thus artificially low, at about 700 masl. Various nutrient-demanding alpine plants are found here due to the schist and alkaline bedrock, among *A. norvegica*, such as: " [*Primula scandinavica, Potentilla nivea, Arenaria Norvegica, Carex rupestris, Veronica fruticans Jacq., Gymnadenia conopsea, Convallaria majalis and Anthyllis vulneraria*] " (Paulsen, 1987, p. 8). Based on this rich flora Roalkvam (1986, p. 42) proclaims the area of Austmannshovudet as "the most protection worthy alpine plant areas in Rogaland [county]".

Among the larger wild herbivores at Austmannshovudet are deer, roe deer, reindeer, and elk. Deer and roe deer are considered stray animals, while elk have a permanent population. Reindeer graze in the Vormedalsheia landscape protection area throughout the summer and winter (Roalkvam, 1986; Nasjonalparkstyre, 2012).

Dovre area

Due to its size, the Dovre region includes different types of vegetation (Appendix Bc), such as subalpine forests and typical vegetation for low, middle, and high alpine zones. The vegetation in the mountains of Oppland municipality, which contain the main population of *A. norvegica* in Dovre, is mainly divided between *B. pubescens* forests and the alpine zone. The latter can be divided into low, middle and high alpine vegetation zones. In Oppdal, the upper *B. pubescens* forest boundary differs according to exposure and terrain, but usually lies between 900 and 1000 masl (Gjærevoll, 1979). The low alpine region is characterised by small shrubs and heather plants. The boundary between low and middle alpine is typically interpreted by the elevation at which blueberries cease to grow, an area usually just covered by graminoids. The high alpine vegetation is sparse, as this zone in Southern Norway usually begins at 1800 masl (Gjærevoll, 1979; Ryvarden, 2010). Due to differences in bedrock structure, Gjærevoll (1979) notes a variation in vegetation between the eastern and western mountains in this area, whereas the easter mountains have a richer flora, containing plants such as *Dryas octopetala*. As previously mentioned, strong winds are typical in this region, and the harsh wind conditions result in varying snow cover during winter, and Vold (1982) states that *A. norvegica* is most abundant on the wind-exposed ridges.

In Dovre, deer, roe deer, reindeer and elk are the main wild herbivores. The reindeer heard has approximately 1500 individuals, but their numbers fluctuate (Michelsen et al., 2011). More interesting, a herd of wild musk ox live here, an animal native to northern America and Greenland. The musk ox was introduced to the Dovre region in the 1910s. Their numbers have varied through the years, becoming extinct during World War II, but reintroduced again afterwards. Today their numbers are stable and slightly increased to a heard of about 250 individuals. During spring, they come down from the mountains and graze in the *B. pubescens* forest and usually stay on the western side of Driva valley (Bretten, n.d.; Østbye, 2020; Michelsen et al., 2011; Statsforvalteren i Trøndelag, 2018).

Land use

Mt Vassli, Hardanger

Due to the discoveries of a 9000-year-old homestead, we know the Folgefonna peninsula has been home to humans since the stone age (Bergsvik, 2008). Later, in conventional farming, farmers relied on efficient and intensive mountain pasturing to make the most of the land. As a result, transhumance has been an essential aspect of conventional farming. However, due to modernisation in the farming sector, transhumance operations significantly declined after the 1950s. Nevertheless, today, Mt Vassli and the adjacent areas are still used for sheep pasturing, with relative low grazing pressure. Sjusete and Botnen were two adjacent shielings south of Mt Vassli, but transhumance operations ceased during the twentieth century (Losnegård, 2003).

Jondal is one of five national park villages in Norway. A national park village is a town that serves as a gateway to a national park, in this case, the Folgefonna National Park, and provides tourist services (Sulen 2019). Folgefonna, Norway's third-largest mainland glacier, lies at the heart of the national park (Folgefonna, n.d.a). Summer skiing and a restaurant are available at Fonna Glacier Ski resort, a common destination for locals and tourists alike (Folgefonn, n.d.b). Mt Vassli is adjacent to the national park, thus it is part of a more extensive network of hiking paths, including hunting opportunities (Bakkestuen et al., 2001). The top of Mt Vassli is categorised in the municipality area plans of Ullensvangs as a "consideration area" with the intention to preserve the natural environment (Ullensvang kommune, 2021).

Austmannshovudet, Hjelmeland

There are no documented records of early human settlements in the Austmannshovudet region, most likely owing to the lack of such research in this area (Nasjonalparkstyre, 2012). Aside from that, there is a newer history of land use in the district, most notably at Ritland farm, located just south-west of the study area. The farm was presumed founded in the mid-eighteenth century and abandoned in the 1960s (Sandvik, 2017). Today, the area continues to serve as rangeland for sheep, but with very little grazing pressure (Nasjonalparkstyre, 2012). In addition, a hiking path passes through the area and leads to Melands Grnahei, a tourist association cabin with 710 lodgings in 2003, alluding to the area's hiking frequency (Johanson, 2003). Additionally, the Vormedalsheia landscape preservation allows hunting small and large game (Paulsen, 1987; Nasjonalparkstyre, 2012).

Dovre area

"United and loyal until the mountains of Dovre crumble"[1]

In Dovre, conventional farming emerged after the Black plague and depended on the mountain vegetation to collect fodder and transhumance practices at summer shielings (Haugland, 2002). However, by the 1950s, the number of farms in Dovre declined by more than half. However, farms in Oppdal (in the middle of the Dovre area) are specialised in cow and sheep husbandry, which has led to active use of mountain rangeland, and is still an essential resource for local farmers (Haugland, 2002).

There are two national parks within the Dovre area and a few protected areas. The main ones are Dovrefjell – Sunndalsfjella- and Dovre National Park, and Knutshø- and Trollheim landscape conservation areas.

Oppdal has more holiday homes than permanent households, suggesting that tourism is prevalent in the study region. Tourism is directly linked to the mountain and offers events and experiences synonymous with this nature, with a focus on skiing, bicycling, and hiking (Oppdal masterplan, 2013; Statistisk sentralbyrå, 2020; Statistisk sentralbyrå, 2021). In addition, hunting has always been a valuable resource for locals and as a tourist attraction (Haugland, 2002).

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[1] The Eidsvoll-oath: "United and loyal until the mountains of Dovre crumble" was proclaimed when the first Norwegian constitution was written in 1814, illustrating Dover’s place in the Norwegian’s consciousness. The mountains of Dovre have a symbolic value to Norway’s identity, constituting "the eternal, permanent and secure" (Mardal, 2017; Dovrefjell nasjonalparkstyre, n.d.).

3.1.2 Climate change and temperature

Climate change scenarios

> "[W]arming in the climate system is unequivocal"
>
> - IPCC, 2014a, p.ii

Climate is constantly changing and has varied considerably in the Holocene (last 12 000 years) (Fig. 3.3). For instance, between 9 to 6 000 years BP, the average temperature was 1.5°C to 2°C warmer than the reference period of 1961-1990. It is presumed that this led to the upper forest line of *B. pubescens* and *Pinus sylvestris* reaching about 60 to 100 meters higher than today in western Norway. Additionally, pollen records of *P. sylvestris* indicate that the tree existed at 1200 masl on Harangervidda 9000 BP (Nesje et al., n.d.; Bjune, 2005; Bryn & Potthoff 2018). In contrast, the last millennium (from 1350 to 1850) has experienced a cooling period, named The Little Ice age, resulting in expanding glaciers (Rafferty & Jackson, 2016). These changes were part of natural fluctuations, whereas the current surge in mean temperature is due to Anthropocene pollution of greenhouse gasses (GHG) (Fig. 3.4) (IPCC, 2014a), in particular CO_2 that has increased drastically since the 1970s. However, this development of Anthropocene climate change is not uniform across the globe and is more pronounced at higher latitudes and higher elevations (IPCC, 2014b; Pepin et al., 2015). The latter, elevation-dependent warming (EDW), is a phenomenon that affects the lapse rate as well (cf. p. 26).

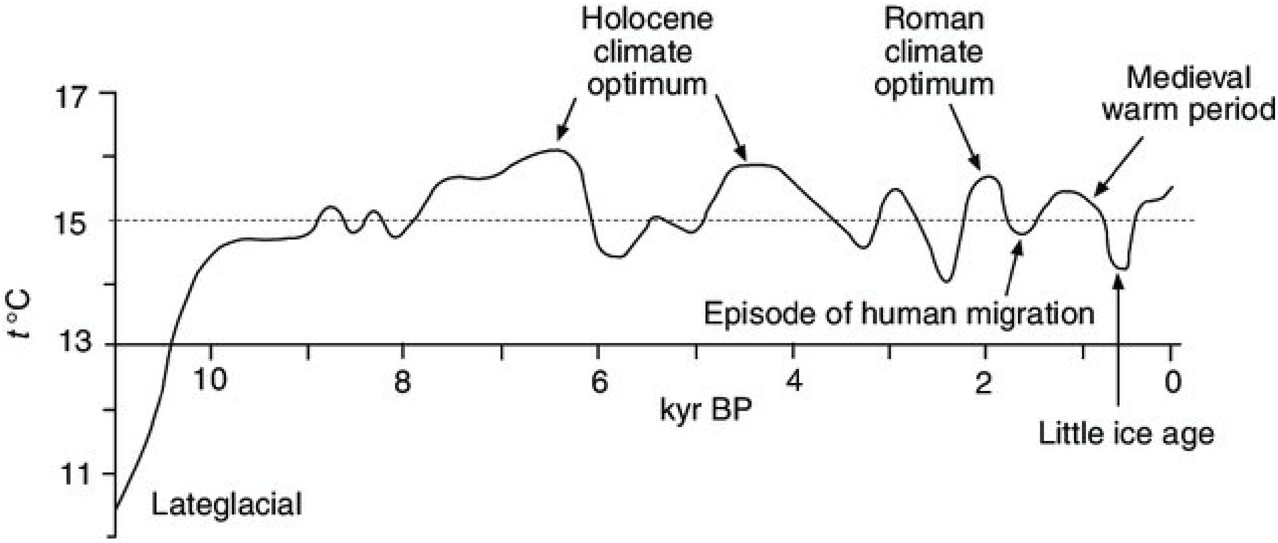


Figure 3.3 Reconstructed average temperature (°C) variances during the Holocene in the Northern hemisphere. Source: Borgatti & Mauro (2013, p. 309).

IPCC has made climate projections based on prospective GHG emissions, "Representative Concentration Pathways" (RCP). These projections simulate temperature changes based on different estimates in the advancement of GHG and aerosols levels in the atmosphere until 2100. This thesis uses two RCP, the moderate and the most extreme estimate, RCP4.5 and RCP8.5, respectively. RCP4.5 predictions are based on a weak but stable increase of GHG until 2040 and, after that, a sharp decrease in emissions, often referred to as the "optimistic scenario" (He et al., 2019). This development equates to approximately a 2°C temperature increase relative to 1850-1900 temperature levels globally.

Artsdatabanken is in charge of the Norwegian red list (following The International Union for Conservation of Nature [IUCN] guidelines). They suggest using the RCP4.5 scenario when evaluating the degree of risk a species is threatened by climate change, as the 2°C increase is considered moderate and Artsdatabanken do not want to make "dooms day prophecies" (Artsdatabanken, 2020, p. 18).

On the other hand, the RCP8.5 scenario, also referred to as "business as usual" or the "pessimistic scenario", is based on a continued surge of emissions following the emission trend from the last decades. This projection results in a threefold increase of CO_2 emissions within 2100 and a likely temperature rise of more than 4°C on a global level (Hanssen-Bauer, 2015; He et al., 2019).

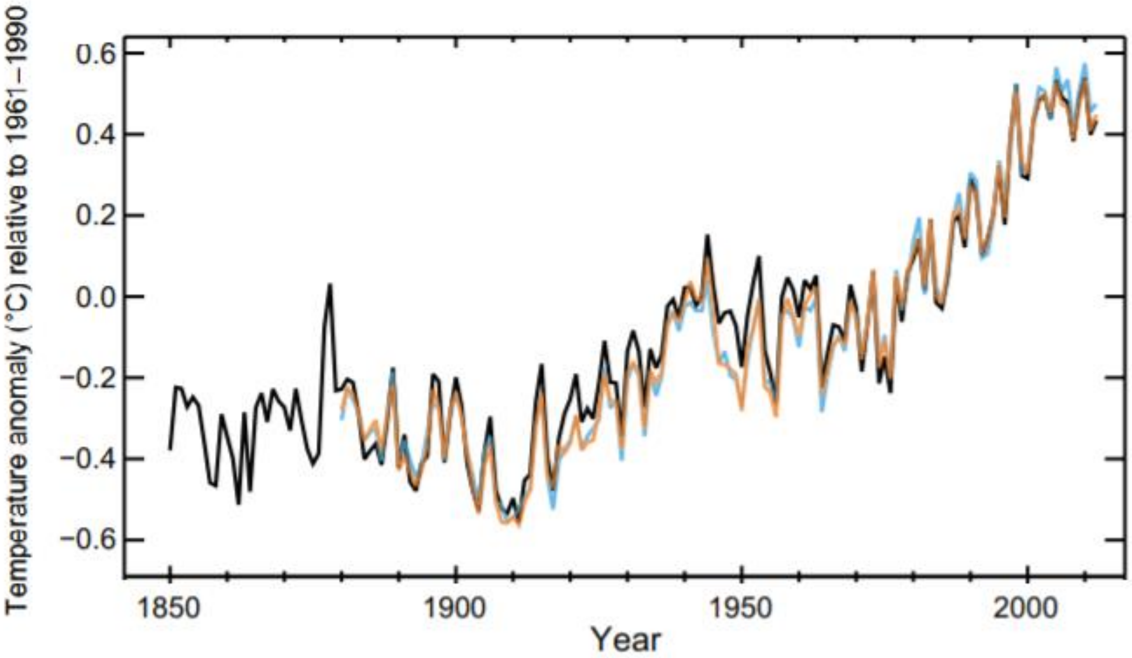


Figure 3.4 Observed global annual mean values combined land and ocean surface temperature (°C) anomalies, from 1850 to 2012 from three data sets. Source: IPCC, 2014b, p. 6, modified by the author.

It is essential to downscale the climate projections appropriately because the temperature does not rise uniformly across the globe, as mentioned. Hanssen-Bauer et al. (2015) present such a downscaling of IPCC's climate scenarios to Norwegian national levels, where the RCP4.5 scenario equates to a national general temperature increase of 2.7°C and the RCP8.5 equates to 4.5°C by the end of the twenty-first century (Hanssen-Bauer et al., 2015). Furthermore, there is a south to north and west to east gradient in relative temperature change, where the most significant warming is expected in Norway's north and east (Engen-Skaugen et al., 2007). By downscaling the national predictions, Lundstad et al. (2018) offer climate projections for the Hardanger municipality Ullensvang. They project the average local temperature increase of 2.3°C (RCP4.5) and 3.9°C (RCP8.5) by 2100. Table 3.6 summarises the estimated median temperature increase for each season and annual for the two relevant RCP scenarios at Ullensvang municipality.

Table 3.6 Estimated median temperature (°C) increase for RCP4.5 and RCP8.5 in Ullensvang by 2100 based on reference period 1971-2000. Source: Lundstad et al. (2018, p. 19)

Period	RCP4.5	RCP8.5
Year	2.3°C	3.9°C
Winter	2.4°C	4.1°C
Spring	2.3°C	3.8°C
Summer	2.2°C	3.6°C
Autumn	2.5°C	4.1°C

Climate change contributes to change in precipitation patterns (Trenberth, 2011), and Lundstad et al. (2018) project a mean annual precipitation increase of 6 per cent RCP4.5 and 12 per cent with RCP8.5 for the region of Sunnhordaland. Table 3.7 gives an overview of these expected changes in precipitation for each season of the Sundhordaland region. Even though precipitation is expected to increase, snow cover is expected to decrease (Lundstad et al., 2018).

Table 3.7 Estimated precipitation change in per cent from reference period 1971-2000, for the region of Sundhodaland in 2100. Source: Lundstad et al., 2018, p. 24

Period	RCP4.5	RCP8.5
Year	6	12
Winter	3	16
Spring	8	13
Summer	5	7
Autumn	4	12

Local lapse rate

Temperature, in general, declines with altitude. This phenomenon is called a lapse rate and signify the rate of temperature decline "per unit of altitude change" (Meyer, 1992, p. 72). It is usually expressed as temperature decline per 100-meter altitude ascension. Due to Boyls' law, a decrease in air pressure by altitude results in a decrease in temperature, and the standard lapse rate is considered to be -0.65 °C per 100 meters in altitude increase (Dingman, 2008; Dunlop, 2008). However, moist air releases more latent heat, thus having a more moderate lapse rate than dry air (Dingman, 2008; Ahrens, 2012).

A study (Bruun, 1957) on lapse rates in different regions of Norway concluded that the standard of -0.65 °C is not representative to calculate different annual mean temperatures across Norway. Instead, local lapse rates produce more accurate temperature measures (Tveito & Førland, 1998). Including moisture, other factors affect lapse rates, such as "atmospheric conditions, […], albedo of the ground surface, local and regional topography, time of day, season, and the nature and source of predominant air masses" (Meyer, 1992, p. 72). Therefore, the lapse rate of an area is constantly changing. To even out these fluctuations and make site relevant lapse rates, Meyer (1992) suggests using mean temperatures from standard climate measuring stations over 30 years (normal periods) (Meyer, 1992). These data can be regressed against elevation (masl), where the regression coefficient represents the lapse rate. In generating local lapse rates, Meyer (1992, p. 73) recommend using climatic records from stations within "1-2° of latitude and 1-5 ° of longitude" of each other, preferably with a high topographic relief of more than 750 meters. These instructions have been guiding measures in providing local lapse rates in this thesis.

Calculations of lapse rates were executed for two areas representing the continental climate in Dovre and oceanic climate in Western Norway, using climate data from two weather stations per area (Pepin, 2001; Trivedi et al., 2007). Pepin (2001, p. 5) conducted research on lapse rates in Northern England found that lapse rates estimated from two stations had a matching lapse rate to estimates done by twenty-two stations, thus found the former lapse rate as a "fair representation" for the area in question. The meteorological database service of eKlima.no was used to find climate normal from appropriate climate stations (Appendix C). Climate stations were selected based on Mayers (1992) previous instructions and long-term measures over the last three normal periods.

Climate change and elevation-dependent warming (EDW)

In the light of climate change, studies show a steeper increase in temperature warming in higher elevations than in the lowland (Pepin et al., 2015; Rangwala et al., 2010). This is due to the characteristic of mountains that contributes to increased net flux of energy along elevation. Pepin et al. (2015) list four essential factors contributing to this phenomenon called elevation-dependent warming (EDW): albedo, clouds, water vapour and aerosols.

These factors contribute to a steeper warming rate in alpine regions than the global average. Overall temperatures in the lowland and higher elevations will approach each other with climate change. Consequently, EDW is expected to decrease the lapse rate in negative correlation with the higher temperatures of climate change in the last century and into the future. Thus, the effects of EDW are essential to consider as it affects the rate of change in mountain ecosystems and biodiversity concerning climate change (Joshi et al., 2018).

The lapse rate for Dovre and Western Norway's will be calculated by linear regression for each normal period of 1931-1960, 1961-1990 and 1991-2020, and a hypothesised correlation with temperature trends will be tested. Furthermore, the Dovre and Western Norway lapse rates will make up local mean annual temperatures (MAT) at different elevations, locations and time periods. These sites and time-specific temperatures will be added to the occurrence data of *A. norvegica* in the calculation of the modelled niches. This is done to get the most accurate temperatures for each data point so that the temperature niche modelled for each period is climatically fine-scaled. Using normal periods avoids "snapshots" of focal species allocation but rather reflects their distribution trend in relation to the climate of the period.

The past three normal periods temperatures, 1931-1960, 1961-1990 and 1991-2020, will be evaluated in light of expected Anthropocene climate change impact. Temperatures are anticipated to have increased and are explored by establishing average temperature at 0 masl for Dovre and Western Norway, utilizing least square regression of the same climate data used to calculate lapse rate. These results will also serve as a backdrop for evaluating past developments in EDW. Additionally, estimates of the elevation at freezing point, where MAT quals 0°C, is calculated in the same manner. This is done to illustrate how EDW affects the elevational movement of MAT.

Moreover, the difference in normal period temperatures and change in lapse rate is used to calculate lapse rates for the two RCP scenarios, RCP4.5 and RCP8.5. This projection is based on a linear understanding of EDW, which the concept is not, but it allows making a logical projection of future lapse rate, as what drives EDW is highly complex (Palazzi et al., 2019).

The normal period of 1961 – 1990 served as a reference, as this period has the biggest overlap to the reference period (1971 – 2000) used by Lundstad et al. (2018). The 1961-1990 normal period was the coldest period out of the three normal periods examined and may result in a more conservative prediction.

3.1.3 Target species

Artemisia Norvegica

The target species *Artemisia Norvegica* Fr. subsp. *norvegica* is a perennial flower herb in the aster family, with the common name Norwegian mugwort ("Norsk malurt" in Norwegian). This calciphilous and heliophyte flower is a part of the low- and middle alpine vegetation, found on dry and windy ridges, preferably in well-drained soil, gravel or scree. It is usually found with typical ridge vegetation consisting of "heather, graminoids, mosses and lichens" (Moe et al., 1994, p. 19), and in *Racomitrium lanuginosum* mats. *A. norvegica* is most frequently encountered at around 1100 mals, but individuals are registered as low as 200 masl, and up to 1810 masl (Skridalskollen, Oppdal) (Gjærevoll, 1990; Gjærevoll & Jørgensenbakke, 1987; Ryvarden, 2010).

Other than the locations in Norway, *A. norvegica* grows in Scotland and the Ural Mountains. *Artemisia arctica* Less., sometimes wrongly referred to as a subspecies of *A. norvegica* as subsp. *saxatallis (Basser) H.M. Hall & Clements*, has an extensive distribution across Northern America. This mix-up persists in some literature (e.g. Douglas et al., 1989; Mitchell, 2006; Shultz, 2006; Koser, 2019; The Global Biodiversity Information Facility [GBIF], n.d.; Artemisia norvegica, 2021) due to Hall and Clemets (1923) work on the North American flora, classifying many distinct *Artemisia* taxons under a broad *A. norvegica* label. Moreover, it has resulted in an incorrect picture of the global distribution of *A. norvegica* (Fig. 3.5). Hultèn (1954) comments on Hall and Clemets (1923) mistakes and makes a morphological distinction between the Eurasian (paleartic ecoregion) *A. norvegica* and the North American (neartic ecoregion) *A. Arctica*, the latter having longer and narrower inflorescence and smaller blossom heads. In contrast, Douglas et al. (1989, p. 44) describe Hultèns distinctions as "inadequate", and they call it bewilderment of *A. norvegicas* distribution when the plant is referred to as *A. artica* in North America. However, Riggins and Seigler (2012) put this discussion to rest when they explored the molecular phylogentic of the *Artemisia* genus. They concluded that North American *A. Arctica* is distinct from the Eurasian *A. norvegica* subsp. *norvegica*, based on multiple saplings. Thus, this misunderstanding is an example of the

Wallace shortfall, which refers to inadequate or incomplete knowledge of species distribution (Townsend Peterson et al., 2011).

A. norvegica grows to be 10 to 25 cm, with green, smooth, finely split leaves in a low rosette, close to the root or a bit up the flower stalk. It has a powerful rot that makes it possible to establish itself in cliff ledges. The fertile individuals have hairy flower stalk with yellow spherical, compressed, and nodding flowers spreading their seeds by wind (Fig. 3.6) (Gjærevoll et al., 1987; Vold, 1982). Their generation time is approximately ten years, and their main form of reproducing is by vegetative propagation (Artsdatabanken, n.d.). Thus, the range of its dispersion is limited.

Figure 3.5 Wrongful illustration of global Artemisia norvegica Fr. *distribution by GBIF (n.d.). The yellow dots represent the assumed occurrence of the plant. Source: GBIF (n.d.)*

Figure 3.6 Botanical illustration of Artemisia norvegica Fr. subsp. norvegica. Source: Gjærevoll et al., 1987, p. 163

In general, *A. norvegica* is not recognised as a fastidious plant and has a broad ecological range (Gjærevoll, 1990). The temperature range is extensive, as the plant is found from 200 to 1800 masl. *A. norvegica* is occurs chiefly on more alkaline bedrock (Artsdatabanken, n.d.; Gjærevoll & Jørgensen, 1987), but Vold (1982) discovered that the plant is also found in more acidic soil (pH from 4.2 to 7.1), but never in soil with much humus (Vold, 1982; Gjærvoll, 1990). As an alpine plant, it has a strong dependence on light because the growing season is short in the mountains, and Vold (1982) informs that the plant is never found growing in shadow. Thus, this fact affects its ability to withstand competition from higher statured plants, as *A. norvegica* can be overshadowed. It is not certain how much *A. norvegica* is grazed on by wild or domestic animals. Moe et al. (1994) presume the fertile individuals are severely grazed, whereas Vold (1982) only observed a few individuals that had signs of grazing. Nevertheless, *A. norvegica* is found where sheep and wild herbivores pasture and transhumance activity has existed for hundreds of years. Thus, grazing activity takes place where *A. norvegica* grows, but the direct effect is uncertain. However, Arnesen & Strøm (2015) conclude that the plant at Austmannshovudet is not affected by grazing or overgrowth as it "grows on rocks and ledges in steep terrain" (Arnesen & Strøm, 2015, p. 7).

A. norvegica is listed on the Norwegian Red List from 2015 as near threatened (NT) (Solstad et al., 2015) after IUCN criteria due to a more than 15 per cent reduction of the population in the last 30 years (Artsdatabanken, n.d.). This is a demotion from the 2010 Red list, which categorised the plant as vulnerable (VU) based on having a small population or small habitat area (Solstad et al., 2010). Additionally, the focal species has more than 90 per cent of its population in Norway, categorising it as a national responsibility species (NRS) for Norway (Henriksen & Hilmo, 2015). Based on this fact, Nature Diversity Act (2009, § 23 letter b) gives a legal basis for giving species, such as *A. norvegica*, extra protection as a priority species, limiting the activities that can be carried out in its habitat (Bugge, 2019). The agenda of NRS labelling is to coordinate conservation efforts and to ensure local populations survival in a global context by committing nations to responsibility for biodiversity (Kukkala et al., 2019).

Disjunct distribution in space and time

Explaining *A. norvegica* disjunct distribution falls within the biographical controversy about plant migration and the history of flora in the North Atlantic. In Norway, this discussion begins with contemplations around the isolated occurrences of rare alpine plants concentrated within a few locations in Norway, especially in the mountainous areas of Dovre (Gjærevoll, 1963;

Westegaard et al., 2019). Some of the rare plants, among *A. norvegica*, are "*Taraxacum dovrense, Poa artica* subps. *Elongate* and subps. *Depauperate*, and *Pedicularis oederi*" (Gjærevoll, 1963, p. 279). Consequently, two principal theories have emerged; the overwintering theory and the tabula rasa theory (Ægisdóttir & Þórhallsdóttir, 2004), but some find these proposals unnecessary (e.g. Birks, 1996; Gabrielsen et al., 1997).

In short, the overwinter theory (sometimes referred to as nunatak theory or glacial survival theory) argues that some rare alpine plants have survived *in situ* the last glaciation, close to where the population is situated today, in ice-free refugia such as nunataks (Brochmann et al., 2003). Thus, it is expected to find a concentration of rare alpine plants in, or close to, such refugia making the plants glacial relics (Birks, 1996; Ægisdóttir & Þórhallsdóttir, 2004; Cox & Moore, 2010). This theory rests on the notion that not all of Norway was covered by the inland ice sheet during the Younger Dryas (YD), where some high-elevation areas protruded from the glaciers, like the Jensens Nunataks on Greenland today (Mangerud, 1973). Consequently, this hypothesis implies that an ice-free area equals opportunities for survival during glaciations. Recent research on genetic variation in the alpine plant *Carex scirpoidea Michx* subsp. *Scirpoidea*, with similar unique distribution, support glacial survival in Norway and regards it as most the feasible explanation (Westergaard et al., 2019).

The tabula rasa theory's alternative approach connotates that these alpine plants are not glacial relics but post-glacial immigrants. Compared to the previous hypothesis, this theory is based on the Scandinavian region being covered in ice during the YD, obliterating all life beneath it (Ægisdóttir & Þórhallsdóttir, 2004). However, parts of the North Sea continent could have housed alpine flora, as it was presumably sea- and ice-free. So, when the ice retreated, a clean slate, or tabula rasa, for plant life presented itself. Thus, all plant life in this region stems from migration after the last ice age from outside of Scandinavia (Ægisdóttir & Þórhallsdóttir, 2004). Regarding rare alpine plants, they established themselves in Norway during the early deglaciation as pioneers in a still cold climate. Afterwards, their geographical location has been pushed upward into the mountains in order to follow the temperature niche as the climate became warmer.

Prior to discovering *A. norvegica* in Hjelmeland and Jondal, the overwintering hypothesis was the standing account of *A. norvegica* then unicentric distribution. However, the discovery of *A. norvegica* in Hjelmeland seeded doubt about the overwintering theory, an opposition furthered by the discovery in Hardanger. Additionally, geologist Mangerud (1973) believes that Hjelmeland, including Hardanger, was ice-covered. However, he agrees to a possible early deglaciated and consequently an early establishment of chrylophile pioneer plants (Roalkvam, 1986). In a similar line, Gjærevoll (1963) refers to Nordhagen (1936, in Gjærvoll, 1963) and suggests ice-free areas along the coast of Norway during the YD that would have served as a cradle for such flora. A notion supported by genetic studies on 20 000-year-old *Picea* and *Pinus* pollen in lake sediment from Andøye in Northern Norway concluded that trees were able to survive along the coast during the last glacial periods (Paraducci et al., 2012). Furthermore, Brochmann et al. (2009) offer northeast Russia, around the Ural Mountains, as a possible source for *A. norvegicas* Norwegian postglacial establishment. Nevertheless, whether *A. norvegica* is a glacial relic or a post-glacial immigrant, these explanations do not fully explain the current limited distribution of *A. norvegica*. However, Helle (2008) offers a visual interpretation of the glaciation scenario at Mt Vassli during the YD suggesting the possibility of a nunatak, thus a refugium, at the very top (Fig. 3.7).

Explaining species distribution and their geographical response to the climatic condition in space and time is at the heart of biogeography. However, the two aforementioned theories are not crucial to explain the current unique distribution of alpine species. The hypotheses above have been dubbed "redundant" (Birks, 1996, p. 332) and "superfluous" (Gabrielsen et al., 1997, p. 840), as it is empirically proved that "modern topography, geology, geography, and climate" (Birks, 1996, p. 336) are the absolute key variables deciding diversity and distributions of Norwegian alpine plants today, and not their potential glacial history. In other words, theories of the pre-or post-glacial establishment of *A. norvegica* do not have a sufficient explanatory effect on current distribution than conditions relating to the species environmental niche.

Paeoloecologists have produced pollen maps of from 13 000 BP to 10 000 BP, illustrating the presence of the *Artemisia* genus in Norway. However, there are none or uncertain presence from 9 500 BP to 5 000 BP (Huntly & Birks, 1983), indicating that *Artemisia* in Norway existed just after the last glacial maximum. Thus, the maps give reason to believe Artemisia have later migrated into Scandinavia. However, the pollen maps of the *Artemisia* genus cannot be used to say something specific about the *A. norvegica* species.

Moreover, phylogentic studies of the *Artemisia* genus show that the genus's oldest lineage, Norvegica/Hetrophyllae (which *A. norvegica* is a part of) and Dracunulus, arrived in North America from its place of origin in North-Centra Asia over 28 million years ago. Afterwards, the Bering land bridge has been a vital route for the dispersal of *Artemisia* in the northern hemisphere, and has served as a route for the genus dispersal in multiple waves throughout different climatic conditions (Riggins & Sigler, 2012). Thus, indicating that *A. norvegica* may have a complex history of multiple movements across the Northern Hemisphere. However, the last 10 000 years of existence and dispersion within Norway have left only the three known locations within the country. So, whether *A. norvegica* is a glacial relic or a later migrant is "a secret the plant will keep" (Vold, 1982, p. 117).

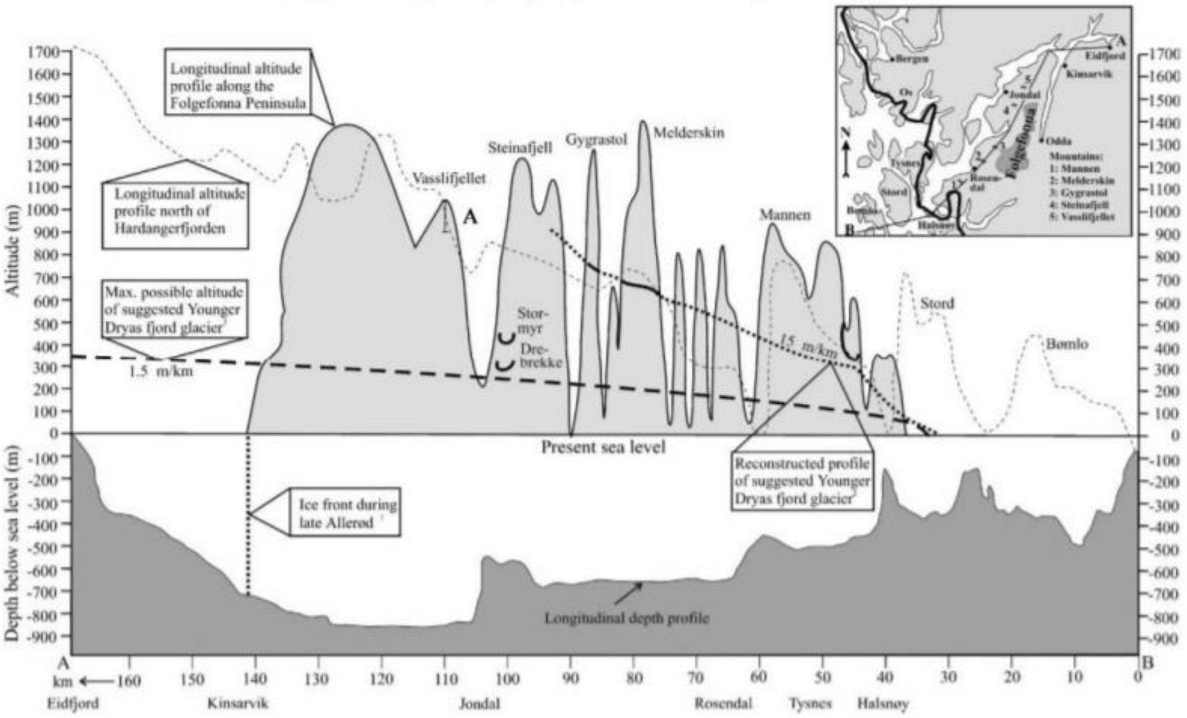


Figure 3.7 Illustrating different glacial scenarios in Hardanger during Younger Dryas. The lower bold dotted line and the fine higher line are different reconstructions of how high the ice sheets went. The A indicates the elevation interval where Artemisia norvegica exists. Source: Helle, 2008, p. 24

Forrest and tree line in Norway

As mentioned, in Norway, the upper line of *B. pubescens*, constitutes the border between forest and alpine vegetation. The forest line is defined by trees above 2 meters in height and a minimum distance of 15 meters between them (Arnesen et al., 2020). Up to 30 meters above this established forest line are some companionless trees that make up what is known as the tree line (Aarnes, 2019; Arnesen et al., 2020). These definitions were used as guidelines in fieldwork for establishing the empirical forest- and tree-line at Mt Vassli. The tree-line is recognised as more responsive to climate changes and thus used as an indicator of climate change, as the forest line has a slower response (Arnesen et al., 2020).

On a regional scale, the forest line does vary and is lower northward and closer to the coast, but also differ in response to local-scale variables such as topography, wind exposure, aspect, disturbances and land usage (Holtimer & Broll, 2005; Arnesen et al., 2020). Thus, two approaches for defining the forest line are differentiated: climatic forest line and empirical forest line (Aarnes, 2019). First, the climactic forest line is understood as the upper border of where *B. pubescens* forest *can* grow, regulated by climatic conditions (Aarnes, 2019; Arnesen et al., 2020), equating to the fundamental niche. Here, the temperature during the growing season is recognised as the limiting factor, where *B. pubescens* does not survive a tetra term (combined mean temperature of June, July, August and September) colder than 8°C in continental climate or 10°C in oceanic climate (Aarnes, 2019). Second, the empirical forest line, also called the actual forest line (realised niche), is the forest line that can be observed. Consequently, in researching changes of the *B. pubescens* forest line as an ascending barrier to *A. norvegica*, this thesis will establish both the climatic and the empirical forest line at Mt Vassli.

3.2 Method

> "[A]ll good detective work was a mere matter of method"
>
> – Captain Hastings quoting his good old friend
> Hercule Poirot (Christie, 1920, p. 19)

This sub-chapter explains the methods used to evaluate the likelihood of extinction of the *A. norvegica* subpopulation in Hardanger. Data input, occurrence data, and environmental predictors are presented and described, including descriptions of statistical analyses applied (Fig. 3.8). Followed by an explanation of different methods used to assess *B. pubescens* forest and tree line, microclimates at Mt Vassli, and habitat size of *A. Norvegica*.

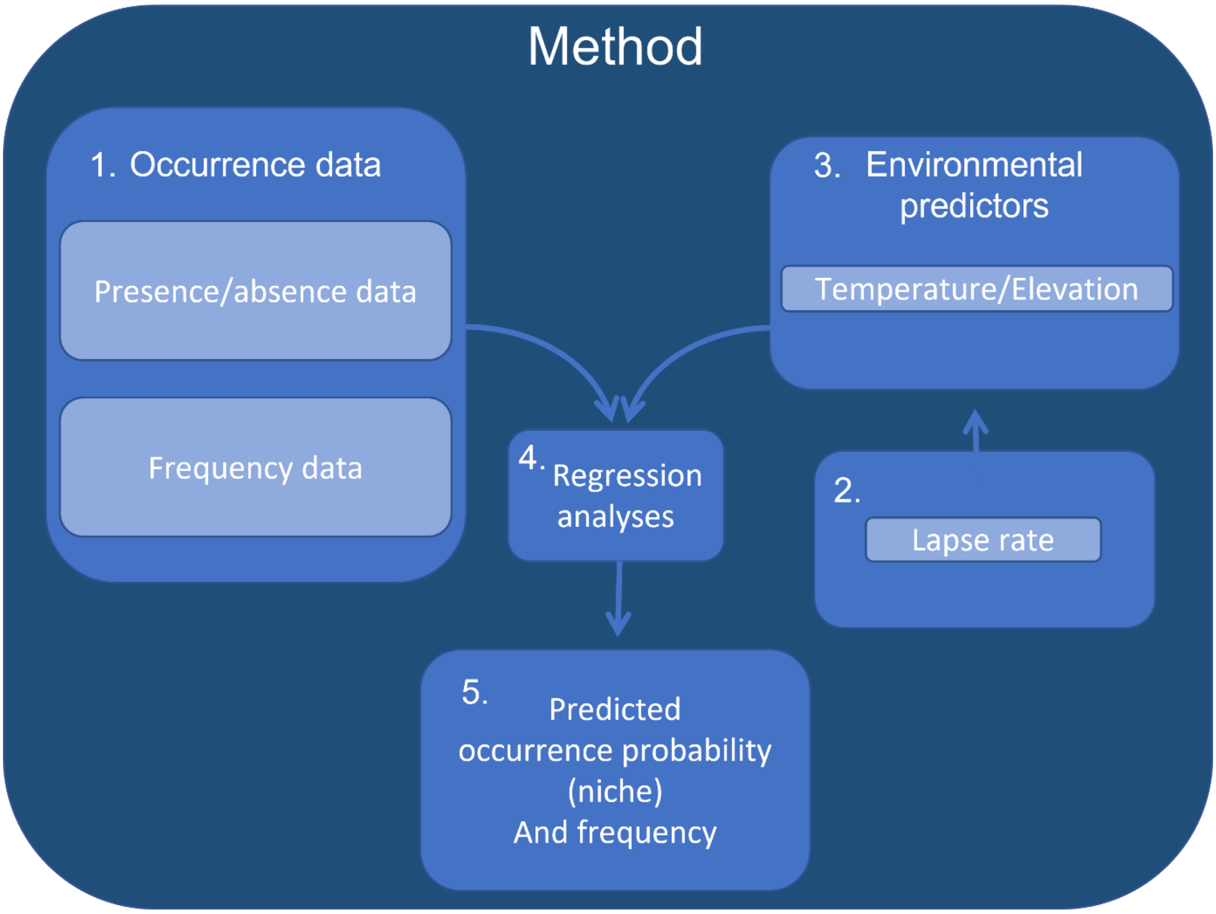


Figure 3.8 Model of method design used in the present study. The first step (1.) was gathering the occurrence data of Artemisia norvegica from Artsdatabenken and dividing them into datasets of presence/absence and frequency. Second, (2.) lapse rate was calculated to the appropriate area and time and estimating the (3.) relevant environmental variables (temperature/elevation). Fourth step (4.), regression analyses were used to estimate (5.) the likelihood of occurrence and frequency.

3.2.1 Statistical analysis

Three stages were used to complete the data analysis, each a distinct type of examination. First, the lapse rate for the two broad areas was found by least square regression with the aforementioned guidelines (cf. p. 26). Thus, two different lapse rates were produced, one for the continental climate in Dovre and one for the oceanic climate, combining Mt Vassli and Austmannshovudet, referred to as Wester Norway for the three different normal periods. Second, correspondence analysis (CA) was conducted to describe the species composition between the different geographical areas of *A. norvegica* populations and to explore how the habitats relate to each other. Finally, the lapse rate was used to convert the occurrence-masl data to occurrence-temperature data used in the subsequent regression analyses.

Generalized linear model (GLM) regression was applied to relate *A. norvegica* to temperature and estimate optima. This approach was also conducted on *B. pubescens* presence data. Additionally, least-square regression was applied to all of the occurrences, for each species, to establish a trend of masl per year.

Correspondence analysis

Floras (Gjærevoll & Jørgensen, 1987; Ryvarden, 2010) describe the habitat of *A. norvegica* as dry, wind-exposed mountain ridges, and most often on calcareous bedrock. These descriptions will be explored in this thesis by means of correspondence analysis (CA), plot analysis and field observations. Utilising CA is an investigative approach to species composition in ecological space and classifying the habitat of the focal species. The outcome of the CA-analysis is an ordination plot in which all species or plots are designated as points. Closely related species in terms of environmental preferences or plots with similar species composition are represented by points near each other. This kind of ordination plot may be used to identify the underlying environmental gradient (ter Braak, 1995). Thus, the environmental meaning of the CA-axes in the CA graph can be interpreted as they are reflected in the species composition in ecological space (Correa-Metrio et al., 2014). The length of the axes represents the plot scores denoted in standard deviation (s.d.). With Gaussian response as the backbone of CA, the resulting graph has four s.d. Thus, plots that differ with close to four s.d. will have few to no species in common (ter Braak, 1995). In other words, the Chi-square distance between the plots represents their difference or similarity in species composition and response to environmental factors (Correa-Metrio et al., 2014).

CA is used in this thesis to descriptively understand and interpret the relations between the communities of *A. norvegica* in the three different study sites and further understand their common environmental responses. A preliminary Detrended CA (DCA) analysis was done to estimate the gradient length in s.d. units (Hill & Gauch, 1980). This analysis gave 4.2 s.d. units long gradient. Furthermore, the data plots did not result in the sometimes-occurring arch in the CA-graph. Thus, applying a DCA-analysis for the plot ordination was unnecessary, and a standard CA-analysis was executed with log-transferred of species abundance and down weighting of rare species. Canoco software programme version 4.5 (ter Braak & Smilauer, 2012) was used to carry out the CA analysis.

Species recorded in plot analysis were used in the CA ordination. Sixteen plots divided between the three areas of interest (six at Mt Vassli, six at Autmanshuvudet, four at Søndre Knutshø, Dovre) were produced during fieldwork. Soil samples were collected for each plot during fieldwork with the intention to measure soil pH. However, due to the Covid situation, access to a lab was limited as an external scientist, and there were no funds for commercial service. In addition, plots from earlier work on *A. norvegica* were supplemented. All five plots from Mt Vassli in Moe et al. (1994) paper was included, and additionally, two randomly chosen plots from four relevant vegetation type (eight in total) by Vold (1982) based in Dovre were added.

Plots of 1 × 1 m were used, and all vascular plants were recorded, and a percentage of cover registered coverage. Plot size affects the amount of species counted, and the size of the plant might influence the evaluated degree of cover the plant occupies. The conversion of different plot sizes used and units for the degree of coverage might also be a source of error.

However, there may be differences between vegetation stud*ies* and the vegetation stud*ied*. Whereas differences in the vegetation stud*ied* can most obviously result from the differences in the areas climate, geology, plant history, biotic interactions, land use, etc. Whereas the difference in vegetation stud*ies* at the same sites can have a more human artefact. Whenever conducting habitat observation, a "snapshot" in ecological time is observed. The species composition differences observed in the same area but in different years are bound to differ as vegetation is not a static subject. Moreover, plots analysis and habitat observation are inherent to the Wallacean shortfall.

Species occurrence data

Occurrence data of the target species was gathered from the Artsdatabanken database. Artsdatabankens feature Artskart collaborates with the Norwegian Global Biodiversity

Information Facility (GBIF), and the service offers geographical UTM locations of species occurrences. Artskart provided 482 presence data of *A. Novegica* from Dovre (Artskart.artsdatabanken.no, 2020), and 2443 presence points of *B. pubecens* gathered from the whole of Norway (Artskart.artsdatabanken.no, 2021). ArcGIS Pro software was used to find the z-value, or masl, of each point, where the Digital Terrain Model (DTM) serving as a reference was sourced from Kartverket (2007).

The Dovre population served as the model population in establishing *A. norvegica*s temperature niche and optima. The 482 occurrence data points of *A. norvegica* from Atrskart was used after fileting out occurrences with low coordinate precision. Different conditions of the coordinate precision were made for the tree period intervals (1931-196, 1961-1990, 1991-2020), the two earliest periods filtered out occurrences with a coordinate precision outside a precision of 1 to 1 000 meters, whereas the latest period had 1 to 100 m precision. This was done to obtain a representative number of occurrences of the species and due to better location measures only in the later years. The occurrence information gathered was grouped into two datasets presence and presence-absence, while *B. pubescens* occurrences were solely grouped in presence datasets. The *B. pubescens* present datasets only included occurrence with a precision of 1 to 100 m as this criterion yielded sufficient occurrences.

The second-hand source such as the occurrence points received Artskart relies on others peoples expertise and consequently their biases. Occurrence data from Artskart origin from contributors such as universities, museums, interest groups, consultants, and natural science institutes, where the contributor is responsible for the information following the established format of Darwin Core (Artsdatabanken, 2016). However, whenever dealing with ecology, the Wallaces shortfall might be affecting studies result, as is the case of the global GBIF database who wrongly referred to *Artemisia arctica* as *A. norvegica* in northern America. Thus, this thesis might have included but also excluded misidentified species occurrences by using these second-hand data.

Generalized linear model and predicted occurrence probability

Regression analysis is a technique that is often used to determine the nature of the relationship between a continuous predictor variable and a categorical response variable. The datasets used consist of the different "temperature-elevation" and "presence-absence" variables. The temperature-elevation variable is continuous, and presence is a discreet response variable with a presence-absence measure. The datasets used in the Generalized linear model (GLM) were divided up into four groups with appropriate temperatures to period and location: 1931-1960, 1961-1990, 1991-2020 and 1931-2020. GLM with presence-absence datasets was undertaken with the three former periods, while the 1931-2020 served as a mean overall estimate and had a presence only dataset. As mentioned, occurrence data of *A. norvegica* was linked to the appropriate temperature in 100-mals intervals. Regarding the study's presence-absence data, the latter was created by random procedure evenly distributed absence points along the elevation gradient.

GLM was used with a logit link function and a binomial distribution to estimate the optimum, tolerance and coefficient of determination (R^2, here used for deviance) (Fig. 3.9) (Appendix D). The probability of occurrence at optimum was interpolated from the graph. The frequency analysis used a Poisson distribution of residuals, whereas the presence-absence analysis had binominal distributed residuals. A Chi-test was performed on each analysis to attain the p-value. R software programme version 4.0.3 (The R Development Core Team, 2020) was used to carry out the GLM regression analyses.

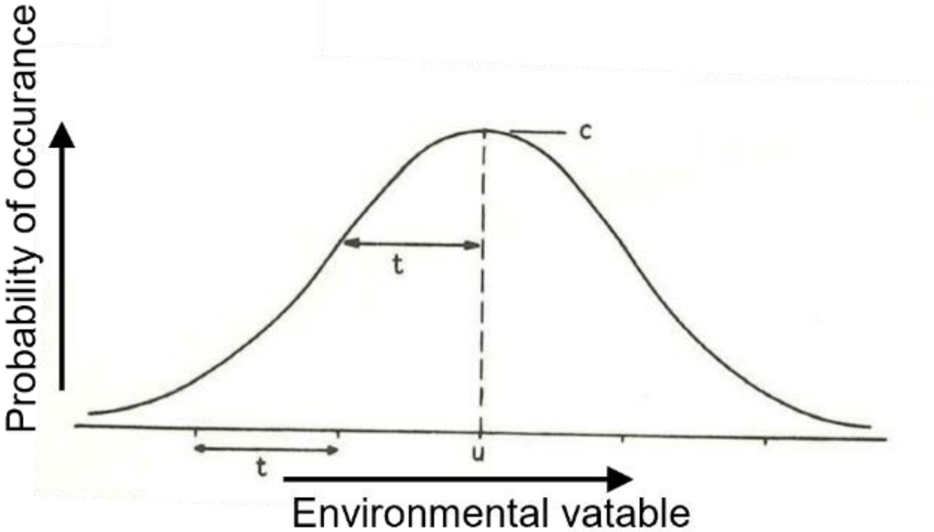


Figure 3.9 A Binominal Generalized Linear Model (GLM) species response curve indicating optimum (u), maximum probability of occurrence (c) and tolerance (t). Source: ter Braak and Looman, 1995, p. 42, modified by the author.

3.2.2 *Betula pubescens* forest and tree line

By using the 10°C tetra term limit and occurrence data, the climactic and empirical forest line of *B. pubescens* is explored. The empirical forest line works as a baseline for climatic predictions of the future expansion regarding the different emission scenarios, while the climactic forest line indicates the potential forest line. The current empirical forest line was established during fieldwork and by aerial imagery. The past empirical forest line is compared with the current to analyse the development of the forest line. During fieldwork at Mt Vassli, the forest- and tree-line was registered with a GPS based on the aforementioned definitions of forest- and tree-line. The altitude of the GPS used was calibrated at the benchmark at the top of Mt Vassli, to minimize errors in altitude measured.

Photointerpretation is a method that involves the usage of aerial images as a source to gather information about terrain (Andersen, 1985), such as vegetation and land use. By interpreting the same area from different years, differences and changes in vegetation cover can be detected. The temporal and geographical change in forest-line can be defined by recognising the patterns and forms in an aerial photo time-series (Andersen, 1985). The source site "Norge i Bilder" has digitised and georeferenced areal images in an open-access map. For the study site in Hardanger, "Norge i Bilder" offered aerial photos from 1971 and 2019 that were chosen to interpret the change in the forest line at Mt Vassli (Fig. 3.10). Differences in resolution can be a source of errors in interpretation between aerial photos (Lillesand et al., 2015), which is a relevant challenge when comparing pictures from 1971 and 2019.

As mentioned, occurrence data, 2 185 occurrences of *B. pubescens* between 1931 and 2020, provided by Artskart, were used in a GLM with frequency and masl as parameters to explore the *B. pubescens* development over the three normal periods of 1931-1960, 1961-1990 and 1991-2020 in masl. Occurrences below 100 masl were taken out of the analysis due to noise.

3.2.3 Microclimate and climate loggers

Mountains accommodate heterogeneity in microclimatic patterns (Scherrer & Körner, 2010; MacIean et al., 2021). Thus, there is deviance between temperature recorded by climate stations (sensors usually two meters above the ground) and the temperature experienced by low laying vegetation on alpine ridges (MacIean et al., 2021). In order to explore the microclimates experienced by *A. norvegica* at Mt Vassli, three climate loggers (TinyTag Plus 2) were used; one to the south-exposed slope (1039 masl, 50° inclination, UTM32 6688068N 0357656E), on the top of the mountain (1031 masl, 0° inclination, UTM32 6688091N 0357653E), and the last one on the north-western exposed slope (1001 masl, 30° inclination, UTM32 6688404N 0357482E). They were set up to record the temperature every three hours, i.e. eight times a day, and were covered in a white plastic bag to minimise the abortion of solar radiance and consequently reduce error in measurements. The data loggers were placed on the ground and lightly covered by some rocks to protect them from possible curious passers-by. The EasyView (11.0.9.50 Pro) software was used for climate logger calibration, reading and data analysis.

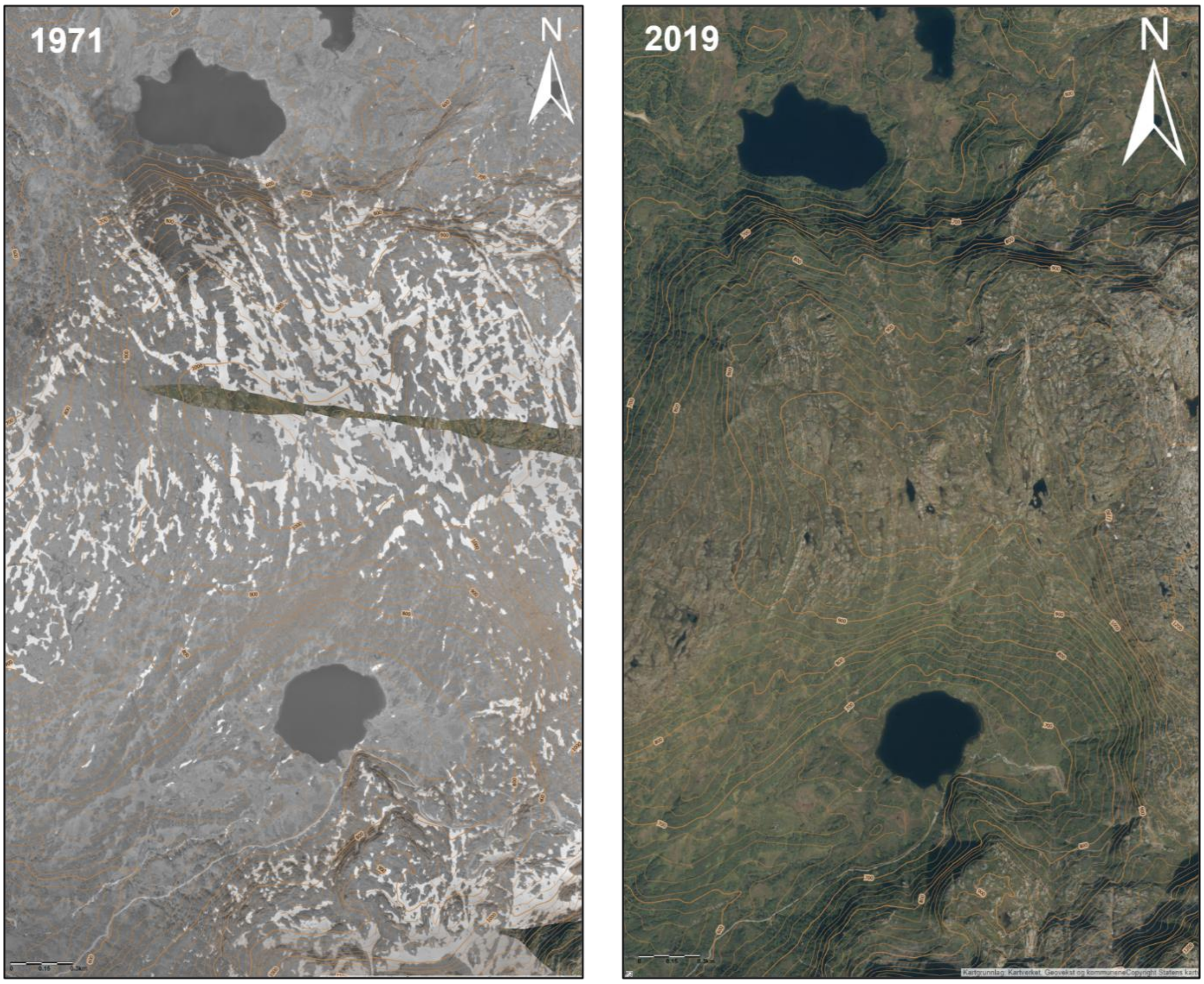


Figure 3.10 Aerial imagery of Mt Vassli, Hardanger, in 1971 (left) (Norge i Bilder, 2017) and 2019 (right) (Norge i Bilder, 2020).

3.2.4 Species observations

As a part of gathering a fundamental understanding of *A. norvegica* at each site, species observations of the focal plant were registered by GPS coordinates. Later these points from the MtVassli population were overlayed on a bedrock map to illustrate the correlation between focal species distribution and bedrock composition. At Austmannshovudet and Mt Vassli extensive search for A. Norvagica individuals were conducted. However, the Dovre area was too large to comprehensively explore, and field work was limited to Søndre Knutshø.

3.2.5 Calculation of area by elevation and 3D model

A species optimum and range will depend on the area available (McCain, 2009). Due to the general clonal shape of mountains, the elevation bands do not cover the same surface area, as the surface area decreases with elevation. Consequently, an area-correction of the distribution of *A. norvegica* is needed. Area of each 100 masl interval of Dovre, and 50 mals interval at Mt Vassli was calculated using ArcGIS Pro software. The same DTM used to find the elevation (z-values) of the species occurrence data was used in this endeavour. The terrain model has a 50 × 50 m grid. The relative amount of presence of the focal species was divided on the relative amount of area available, resulting in proportional distribution of *A. norvegica* in each elevation band.

I order to visually evaluate the topography of Mt Vassli at a fine-scale 3D model, or dense point cloud, was produced by using a drone or UAV (Unmanned Aerial Vehicle) (DJ Mavic Mini). The drone was manually operated at a roughly 60-meter altitude of the ground surface, with approximately 70 per cent overlap of the pictures taken, and the camera angled straight down (90°). The resulting images were processed in Agisoft Metashape software to make the dense point cloud. This process is based on the principles of photogrammetry and Structure from Motion technology, where a series of overlapping photos are used to determine the parallax between image pairs, and subsequently produce topographic data such as a dense point cloud or Digital Elevation Model (DEM). The images are recorded with information of camera geometry, position and altitude, enabling the construction of a topographical model of the area (Micheletti et al., 2015; Novotny, 2019).

4. Results

4.1 Habitat observations

Three types of habitats were observed between the three study sites. In both Dovre and at Mt Vassli *Artemisia norvegica* Fr. had a habitat on ridges with either more acid-tolerant or chalcophile cohabitants, and at Austamanshovudet, the habitat was defined by cliff and screes.

A. norvegica was found within 39 hectares ranging from 836 masl to 1062 masl at Mt Vassli, Hardanger, and recorded at 206 points (Fig. 4.1). Most individuals occur as rosettes, usually small but plentiful, commonly found together (Fig. 4.2). The fertile individuals also occurred in small groups (Fig. 4.3). In other words, areas of infertile rosettes with a few fertile individuals and areas with a high density of fertile individuals were grouped separately. As such, *A. norvegica* was found in patches within those 39 hectares. When the recorded points were overlaid on a bedrock map, it showed that *A. norvegica* was only observed on basalt bedrock (Fig. 4.4). Along the elevation gradient, the distribution of *A. norvegica* is relatively even, though none were found under 836 masl, despite a vigorous search. The plant was mainly found at the top and to the north of the mountain. The focal species only occurred on well-drained, exposed ridges. Some are situated in mats of *Racomitrium lanuginosum,* often together with *Carex bigelowi*, presumably containing low levels of pH (Fremstad & Elven, 1987). Moreover, *A. norvegica* did also cohabit with plants such as *Silen acaulis* and *Saxifraga oppositifolia*, two plants indicating higher levels of pH (Fremstad & Elven, 1987). However, non of the types of habitats contained much hummus but had some raw humus. Even though the area is frequented by pasturing sheep and different wild herbivores, *A. norvegica* was registered to have been grazed on at only one location.

At Austmannshovudet, Hjelmeland, the search for *A. norvegica* was challenging because the primary habitat is a vertical cliff expanding over 100 meters (cf. Fig. 3.1b, p. 15). At this site, some *A. norvegica* were found within 13 hectares along an elevational range of 656 to 853 mals (Fig. 4.5). Here the largest individuals with a high rate of flowers were located on the cliff, clinching to small cracks (Fig. 4.6). These individuals grow in steep south-facing slopes (inclination 30-90 degrees). Other individuals were found beneath this cliff in older screes (Fig. 4.7). In general, these latter ones were smaller and had a lower rate of fertile individuals. Furthermore, *A. norvegica* was not the favourite fodder for the nearby grazing sheep, as none of the individuals had signs of grazing.

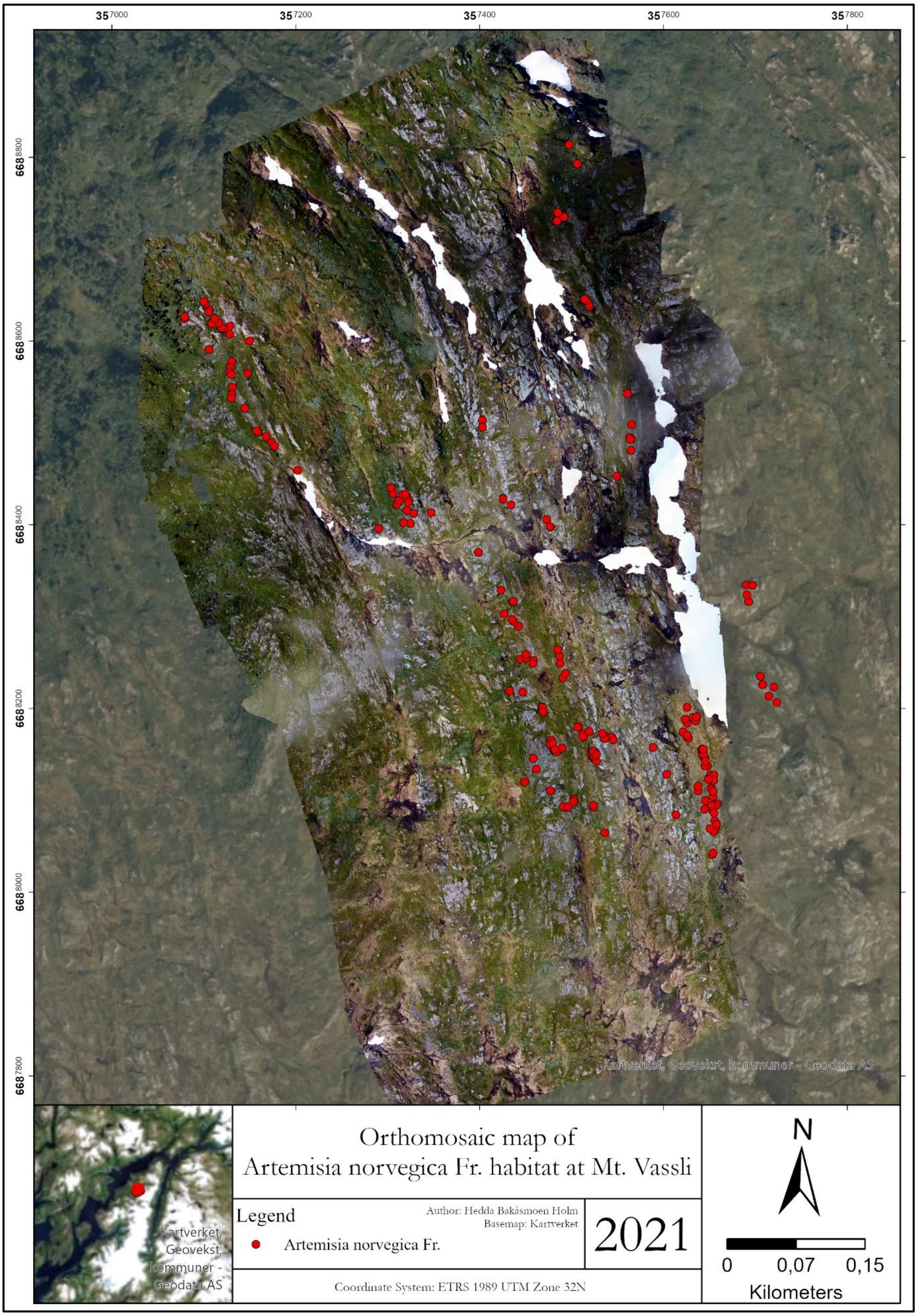


Figure 4.1 Orthomosaic map of Artemisia norvegica habitat at Mt Vassli, Hardanger with the registered point of A. norvegica observations.

Figure 4.2 Picture of rosettes of Artemisia norvegica at Mt. Vassli, Hardanger

Figure 4.3 Picture of fertile group of Artemisia norvegica at Mt. Vassli, Hardanger

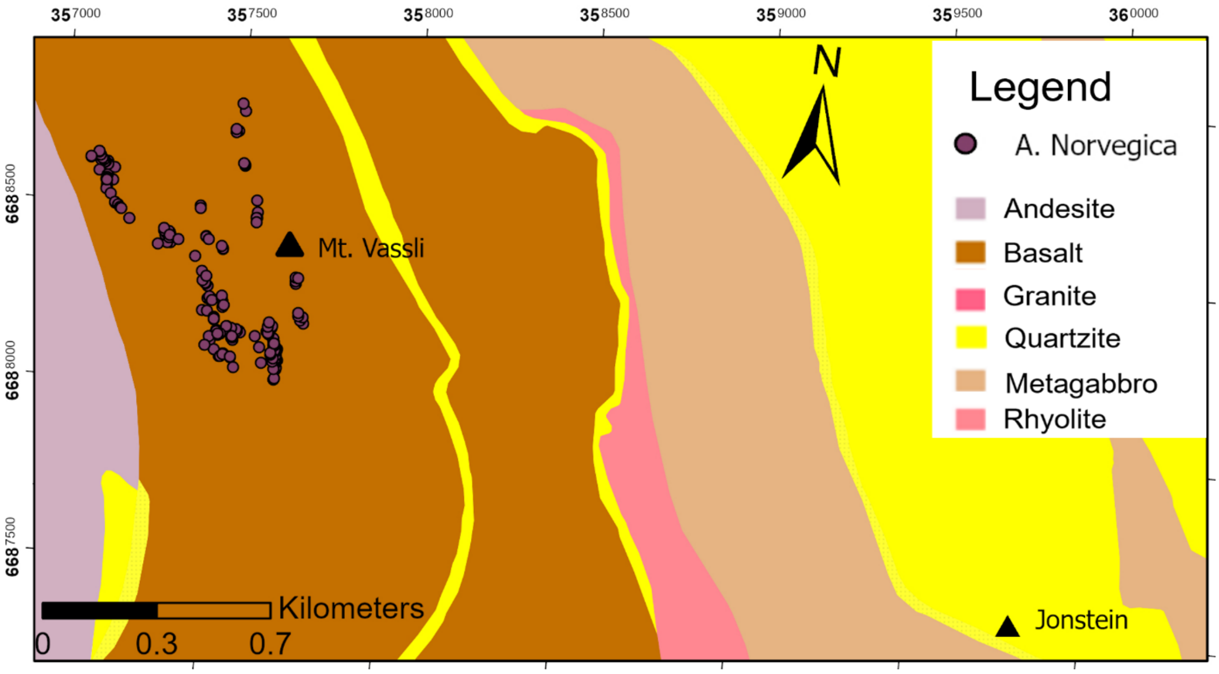


Figure 4.4 Record points of Artemisia norvegica at Mt. Vassli, Hardanger, on a bedrock map. Source: Bedrock map from NGU (2009)

The range of *in situ A. norvegica* stretches from 1185 to 1664 masl at Syndre Knutshø, Dovre (Fig. 4.8). The lowest of the findings, at 925 masl, are some individuals' *ex-situ* in an old botanical garden in connection to Kongsvoll Alpine Garden. Considerable amounts of *A. norvegica* were registered at the 1400 masl interval. At Syndre Knutshø *in situ A. norvegica* occurred in mainly two forms. The first type was in large tufts, with multiple flowers and larger leaves in the stony block field (Fig. 4.9). The second type was more chusion like with low lying leaves and fewer flowers with shorter stalks (Fig. 4.10). Only the latter formation had signs of grazing.

Overall, the most pronounced morphological difference between the three subpopulations was the flowers stalks' height. The Søndre Knutshø population usually never had flower stalks over 10 cm, while at Austmannshovudet and Mt Vassli the stalks generally grow to over 15 cm (Fig. 4.11).

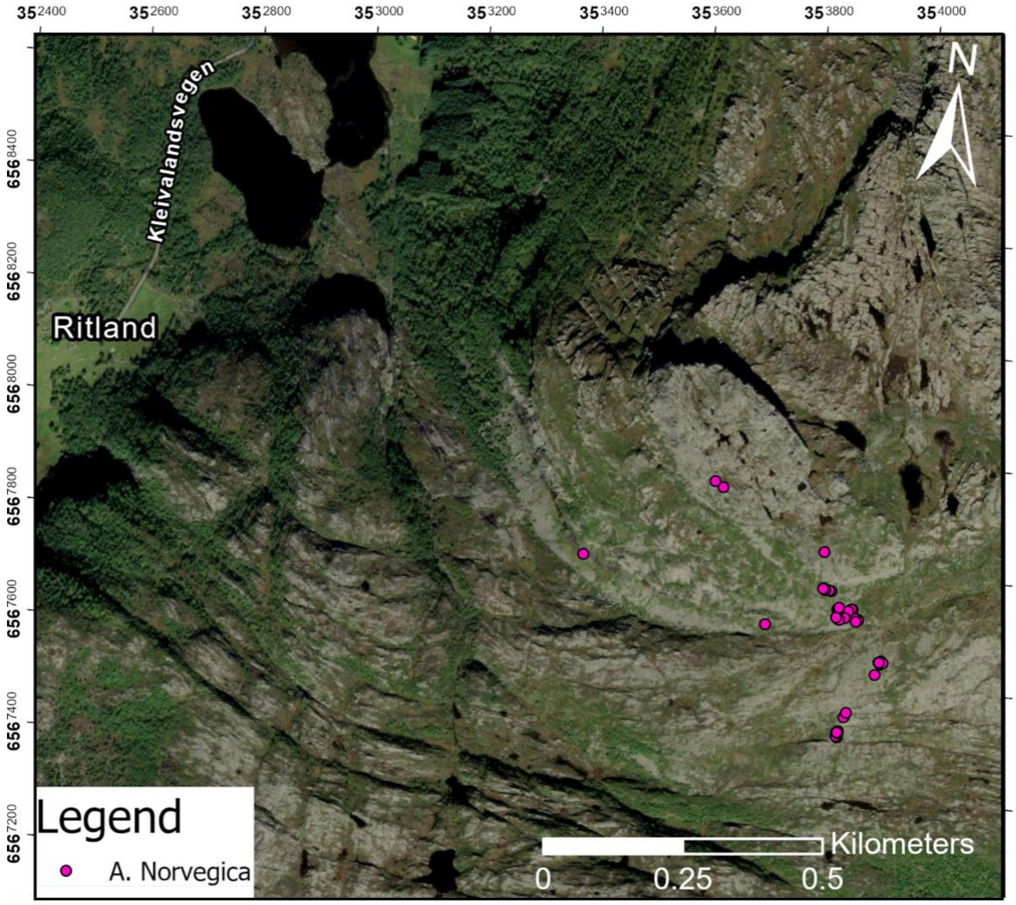


Figure 4.5 Registered points of Artemisia norvegica at Austmannshovudet, Hjelmeland. Source: basemap from Geodata Online

Figure 4.6 Artemisia norvegica in the cliff of Austmannshovudet, Hjelmeland

Figure 4.7 Artemisia norvegica (in the top left corner) on scree with Dryas octopetala at Austmannshovudet, Hjelmeland

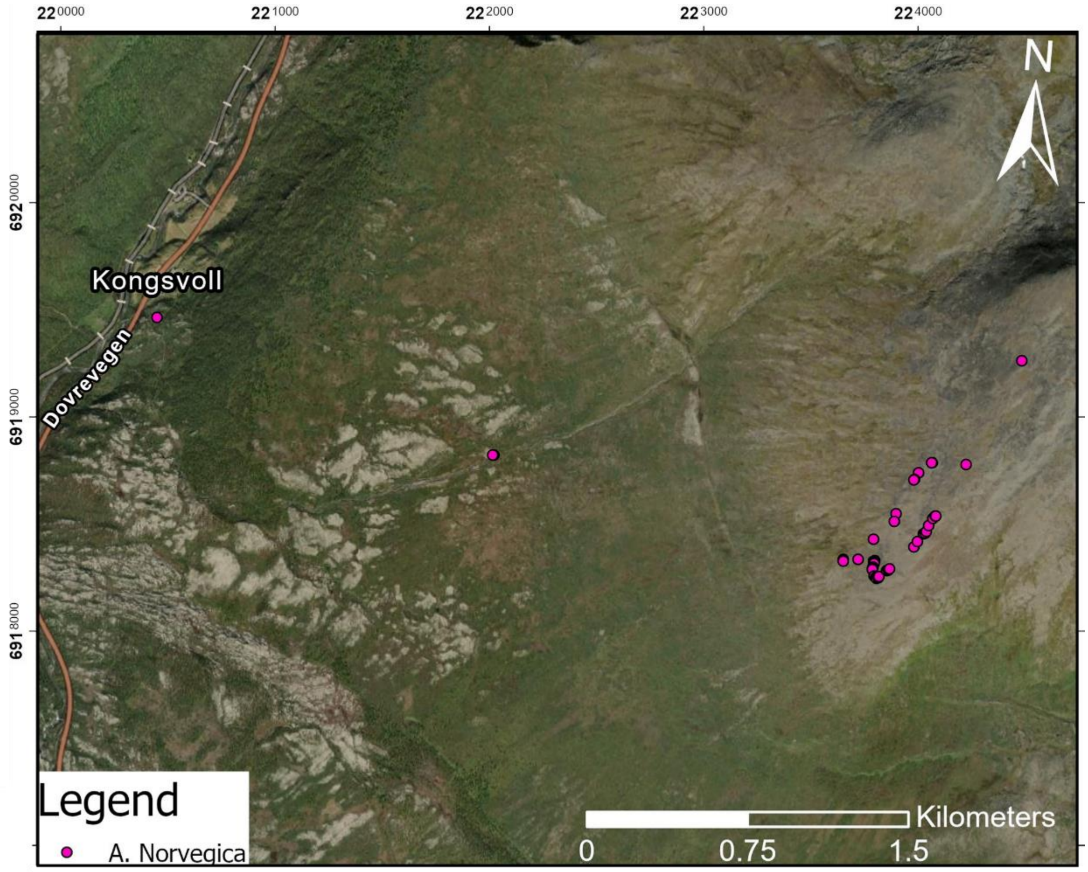


Figure 4.8 Registered points with Artemisia norvegica at Søndre Knutshø, Dovre. Source: basemap from Geodata Online

Figure 4.9 Artemisia norvegica tuft in block field at Syndre Knutshø, Dovre

Figure 4.10 Large mat formation of Artemisia norvegica at Søndre Knutshø, Dovre

Figure 4.11 Samples of Artemisia norvegica flower stalks at Mt Vassli (Hardanger), Austmannshovudet (Hjelmeland) and Søndre Knutshø (Dovre) (from left to right).

4.2 Species composition at the locations: Correspondence analysis

The sampled plots (29) contained 52 vascular plants in addition to *A. norvegica* (Appendix E). All 52 species were used in the Correspondence Analysis (CA), thus contributing to the characterisation of the species composition from the three sampling locations. Table 4.1 summarises the CA-analysis statistics. CA-axes 1 and 2 have almost equal eigenvalues, suggesting they both account for nearly the same variation in species composition. Furthermore, the environmental gradients underpinning the compositional turnover along CA-axes 1 and 2 represent approximately one-quarter of the variance between the plots.

Three groups of vegetation are identified in the CA diagram (Fig. 4.12), more or less in correspondence with the aforementioned habitats observed. The first CA- diagram divide plots from Austmanhovudet with the cliff-scree vegetation to the top right corner, and Mt Vassli and Dovre calcareous and more acidic ridge vegetation to the left. Plots from Dovre and Mt Vassli are intermingled but do divide up into two forms of habitat. One group is characterised by calciophile herbs, e.g. *Saxifraga oppositifolia*, *S. nivalis*, and *Silene acaulis*. In comparison, the other group is dominated by heather plants such as *Empetrum hermaphroditum*, *Calluna vulgaris* and *Arctostaphylos alpinus*. As mentioned, plots from Austmannshovudet form their distinct group in the top right corner of the diagram.

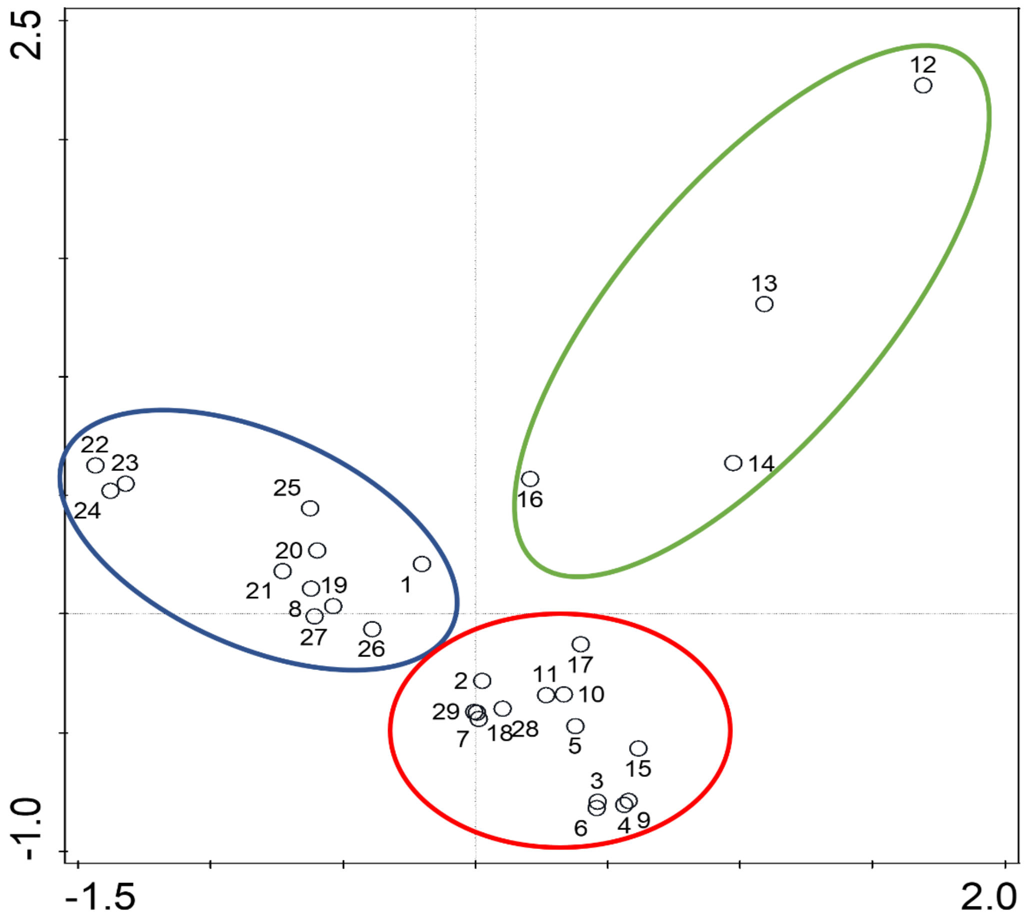


Figure 4.12 Correspondence Analysis (CA) plot showing the distribution of plots in relation to the CA-axes 1 and 2, where the blue ring indicates the vegetation of heather with herbs, the red group is heather, and the green group is the habitat at Austmannshovudet, Hjelmeland.

Interpretation of the ordination plot indicates that the CA-axis 2 reflects the pH level of the plots. The more acidic tolerant vegetation is on the negative side of the axis, and more calcareous demanding plants are higher on the CA-axis 2. This is indicated by the species associated with calcareous conditions, e.g. *Dryas octopetala*, *Kobresia simpliciuscula*, *Salix reticula*, *Carex rupestris*, that are in the chart's upper half. While the negative part of the CA-axis 2 contains plots that consist of species found in less nutrient-rich soils, e.g. *Agrostis mertensii*, *Arctostaphylos alpinus*, *Loiseleuria procumbens* and *Calluna vulgaris*.

The CA-axis 1 may assumingly be interpreted as a moisture gradient, where snowbed plants represent the moister conditions and plants associated with alpine ridge vegetation represents dryer conditions. Out of the 52 species, 39 were recognised as belonging to ridge-, leeward or snowbed vegetation. 17 species were identified as characteristic to only ridge vegetation, 15 to ridge and leeward vegetation, 7 typical to leeward vegetation, and 1 exclusively known to be distinct to snowbed vegetation (*Agrostis mertensii*, found in plot 2, 3, 17, 18) (Fremstad & Elven, 1987). Overall, species that represent these three types of vegetation are found throughout the plots. Although all the plots containing *A. mertensii* are located on the right side of the CA-axis 1, which indicate higher moisture levels, however, there is no clear ridge-snowbed gradient in the species composition.

Table 4.1 Results of correspondence analysis (CA).

CA	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.4822	0.4164	0.2988	0.2663
Explained variation (cumulative)	13.95	25.99	34.63	42.33

4.3 Regional change in temperature

As per Anthropocene climate change, the overall temperature increased during the last 90 years. However, not linearly as demonstrated by temperatures at 0 masl for Dovre and Western Norway, as Table 4.2 illustrates. For Western Norway, this reference temperature at 0 masl has slightly decreased between 1931 – 1960 and 1961 – 1991 normal periods by 0.3°C but increases with 1 °C in the newest normal period (1991-2020). In Dovre, the temperature stays the same for the two earliest normal periods, 1931 to 1991, at 5.3°C. Comparatively, the latest temperature increased by 0.8 °C (1991-2020).

Table 4.2 The simulated average temperature (°C) at 0 masl for Dovre and Western Norway.

	1931-1960	1961-1990	1991-2020
Dovre	5.3	5.3	6.1
Western Norway	5.4	5.1	6.1

4.4 Changes in lapse rate

A decrease in the lapse rate was hypothesised due to elevation-dependent warming (EDW). The change in lapse rate of Dovre confirms this rationale, whereas the lapse rate for Western Norway rejects it, see Table 4.3. In comparing the different lapse rates of Dovre in time, they correspond to the general warming and the cold period of 1961-1990, as hypothesised. In other words, when general temperature increases, the lapse rate decrease, and vice-versa. At Dovre, the lapse rate has overall decreased, from -0.61 to -0.53. To illustrate this geographically, the elevation at freezing temperature, has correspondingly crept upwards, from 870 masl to 1161 masl. Dovre has a steeper decline in temperature by elevation than Western Norway, and the difference between the two places is continuous. In Dovre EDW is detectable. The lapse rate is becoming slightly less steep in comparison to the measured temperatures; the coldest period (1961-1990) has the steepest decline in temperature by elevation and results in colder temperatures in a higher elevation than 1931-1960, even though the starting point is the same (5.3°C at sea level). The latest normal period has a higher temperature at sea level, and a slacker decrease in temperature in elevation increase gained.

On the other hand, in Western Norway, there is an overall increase in lapse rate, thus rejecting the hypothesis. Between 1931-1960 and 1991-2020 normal period the lapse rate increases, with the 1961-1990 period only slightly higher by 0.01°C than the 1991-2020 period. Elevation of freezing point has moved in correspondence with these changed lapse rates, resulting in a movement within a range of 183 meters during the last three normal periods.

Western Norway had a 1°C change between the two last periods, resulting in a lapse rate change of 0.01°C. Thus, the future lapse rates in 2100 of the two RCP scenarios adds 0.023°C (RCP4.5) and 0.039°C (RCP8.5) to the lapse rate closest to the reference period that the two projections are based upon, in this case, the normal period 1961-1990. Thus, the future lapse rate would be -0.583°C (RCP4.5) and -0.599°C (RCP8.5), see Table 4.3. Therefore, the geographical change of the freezing point, for the two scenarios, is at 1275 masl (RCP4.5) and 1551 masl (RCP8.5). Appendix F lists the lapse rate converted to MAT at the appropriate place, elevation and time, including the projected MAT in 2100 at Western Norway.

Table 4.3 Lapse rates (-°C/100m) *for two areas; Dovre and Western Norway, for the last three normal periods; 1931-1960, 1961-1990 and 1991-2020, and RCP scenarios at 2100 for western Norway. Including the elevation with MAT of 0°C.* ***1931-2020*** *illustrate the overall mean.*

	Dovre		Western Norway	
Time period	Lapse rate (°C)	0°C MAT at masl	Lapse rate (°C)	0°C at masl
1931-2020	-0.59	940	-0.57	964
1931-1960	-0.61	870	-0.56	973
1961-1990	-0.62	860	-0.59	869
1991-2020	-0.53	1161	-0.58	1052
RCP4.5: 2100			-0.583	1269
RCP8.5: 2100			-0.599	1502

4.5 Local microclimate at Mt Vassli

At Mt Vassli the climate loggers reveal microclimatic differences between the different aspects, most apparent during the summer (Figs. 4.13 & 4.14). Likewise, during the winter months (December, January, February), the average day temperature varied considerably from 2.1°C down to -11.6°C day average. During the tetra term, the daily average diverged with 16.1°C between the coldest and warmest days. Moreover, the tetra term average differed between the three aspects at 10.9°C (North), 11.79°C (South) and 11.12°C (top). These distinct measures were also present in MAT 2.9°C (North), 3.8°C (South) and 3.2°C (top). Thus, there are microclimatic differences between the three aspects at Mt Vassli. As expected, the southern exposed site was the warmest and the northern the coldest, while the top location generally experienced temperatures between the two former. Appendix G leads to an overview of the recorded temperatures.

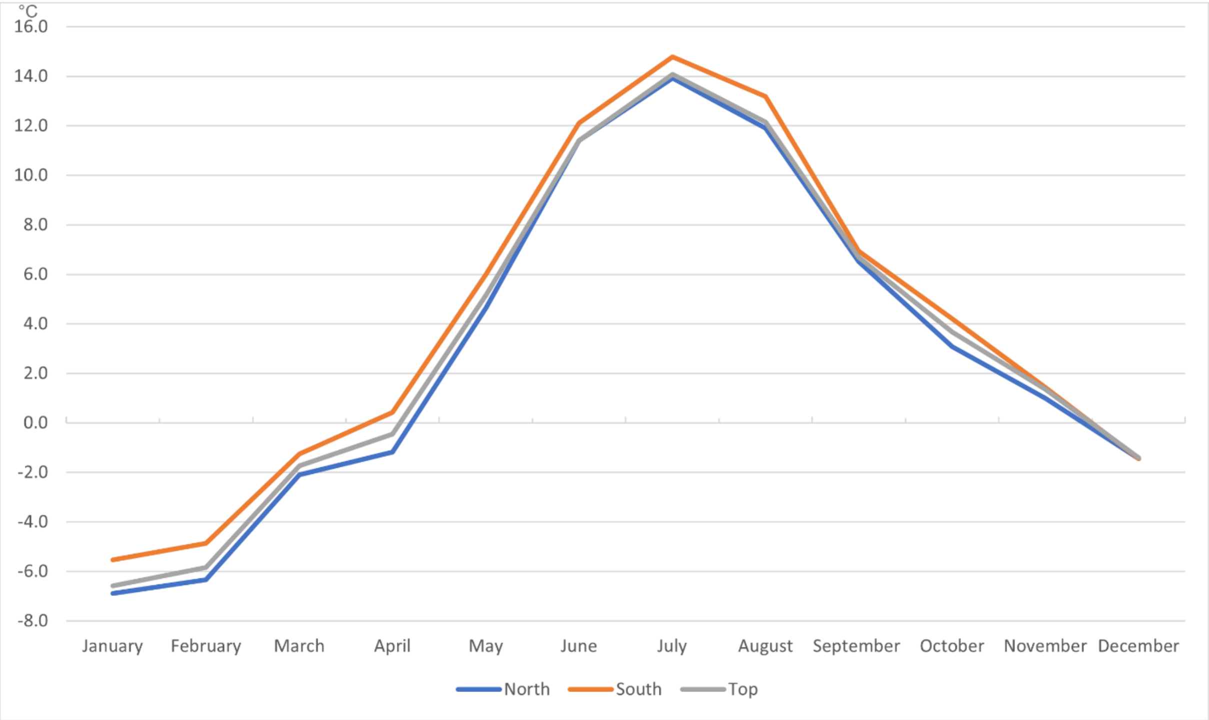
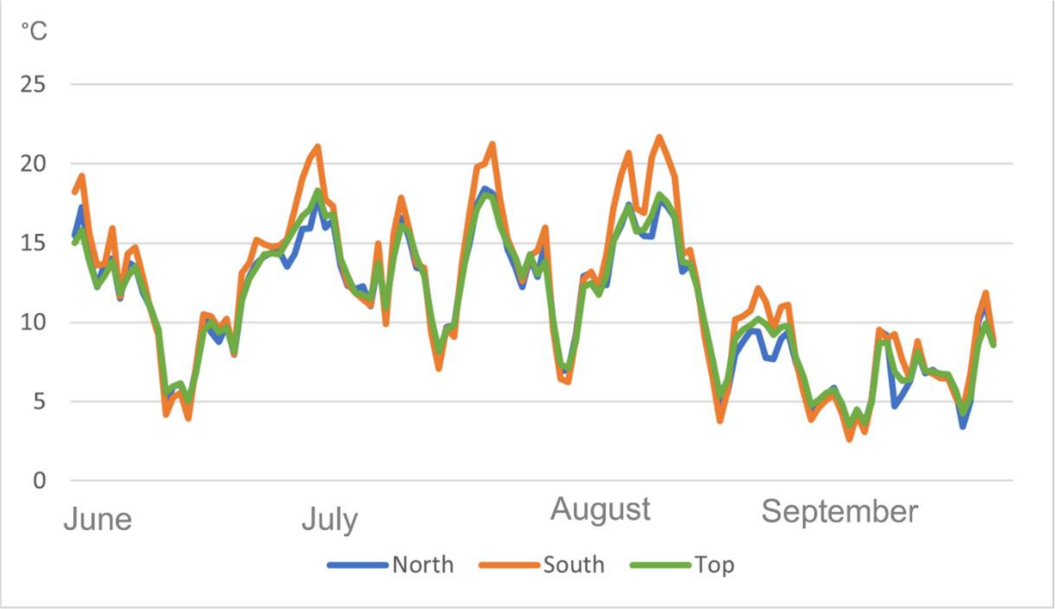


Figure 4.13 Microclimate differences throughout a year on Mt Vassli, Hardanger. Average month temperature (°C) on the northern and southern side, and at the top.



Figur 4.14 Tetra term at Mt Vassli, Hardanger. Daily temperature (°C) average throughout June, July, August and September on the northern and southern side and at the top of the mountain.

4.6 *Artemisia norvegica* response optima and range

The linear regression of *A. norvegica* occurrences data over the 90 years confirms the hypothesis of upward movement. During this period, *A. norvegica* has had a steady increase, beginning at 975 masl and ending at 1205 masl (Fig. 4.15). Thus, resulting in an increase of 230 meters, or an average of 2.5 meters per year (in the relevant period).

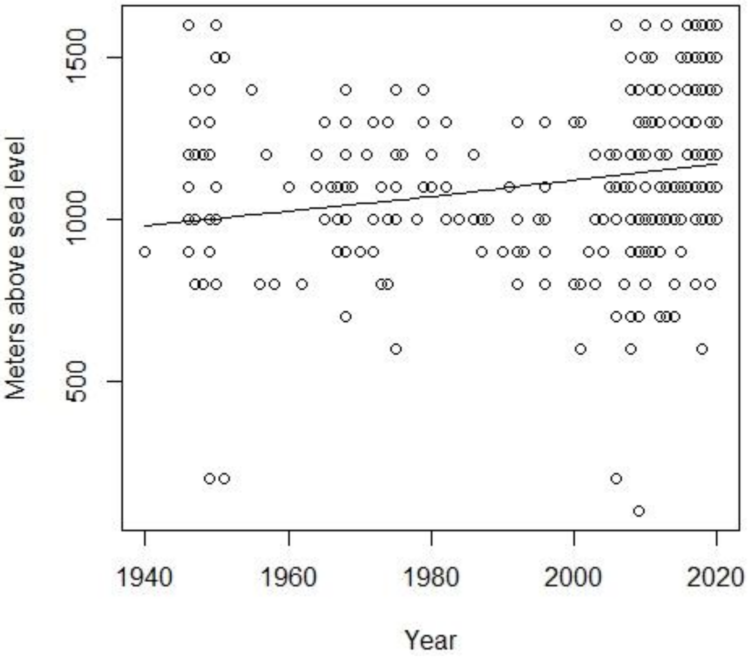


Figure 4.15 Linear regression of occurrences of Artemisia norvegica (subpopulation in Dovre) against time in the period of 1931-2020 ($p < 0.001$), illustrating a general increase in elevation of occurrences.

GLM on frequency data from Dovre (1931-2020) estimated the optima at 0.02°C, equivalent to 945 masl at Dovre, with an empirical range between 100 and 1600 masl, see Table 4.4 (Fig. 4.16a).

GLM estimated varying temperature optima between the three normal periods; see Table 4.4 (Fig. 4.16b, c, d). Comparing the tree periods results illustrates a steady increase in temperature optimum in the last 90 years. Between the first and latest normal period, this optimum has increased by 0.27°C, but with minor changes between the two earliest periods. The tolerance interval does not vary greatly between the different optimum calculations, except the tolerance interval of 1931-1960, which is the largest. The converted temperature optima and tolerance illustrates the same trends of increased elevation optima. However, the middle period had a slight decline of 2 m from the former period.

Moreover, the empirical range of *A. norvegica* has somewhat differed between the three periods, with the middle period being the shortest: 600-1400masl (1961-1990). In contrast, the oldest and the latest period has the most extensive range and are nearly identical at 200-1600 masl (1931-1960) and 100-1600 masl (1991-2020).

In the Chi-squared test, all *A. norvegica* GLM analyses, except one, showed $p < 0.001$. However, the GLM of the period 1931-1960 had a $p < 0.01$. This might be due low number of occurrences (n=51) and multiple elevation intervals lacking occurrences.

Table 4.4 Modelled optimum and tolerance (temperature (mean annual temperature (MAT (°C)) and elevational (MASL)) response of Artemisia norvegica Dovre population by Generalized Linear Model (GLM) to mean annual temperature (°C). D_{tot}:frequency indicates GLM results on frequency per 100 m elevation band from 1931-2020. D_{60}:binary, D_{90}:binary and D_{20}:binary depict the GLM results on presence/absence data for each normal period 1931-1960, 1961-1990 and 1991-2020, respectively.

			MAT		MASL	
	Probability	R^2	Optimum	Tolerance	Optimum	Tolerance
D_{tot}:frequency		0.817	0.02	± 0.12	945	± 21
D_{60}:binary*	0.6	0.962	-0.21	± 0.34	904	± 57
D_{90}:binary	0.72	0.902	-0.29	± 0.25	902	± 41
D_{20}:binary	0.86	0.903	-0.417	± 0.2	1229	± 39

*Probability= Probability of finding species at optimum interpolated from graph. R^2=Coefficient of determination, here variance in deviance. *$p < 0.01$, all other results have $p < 0.001$.*

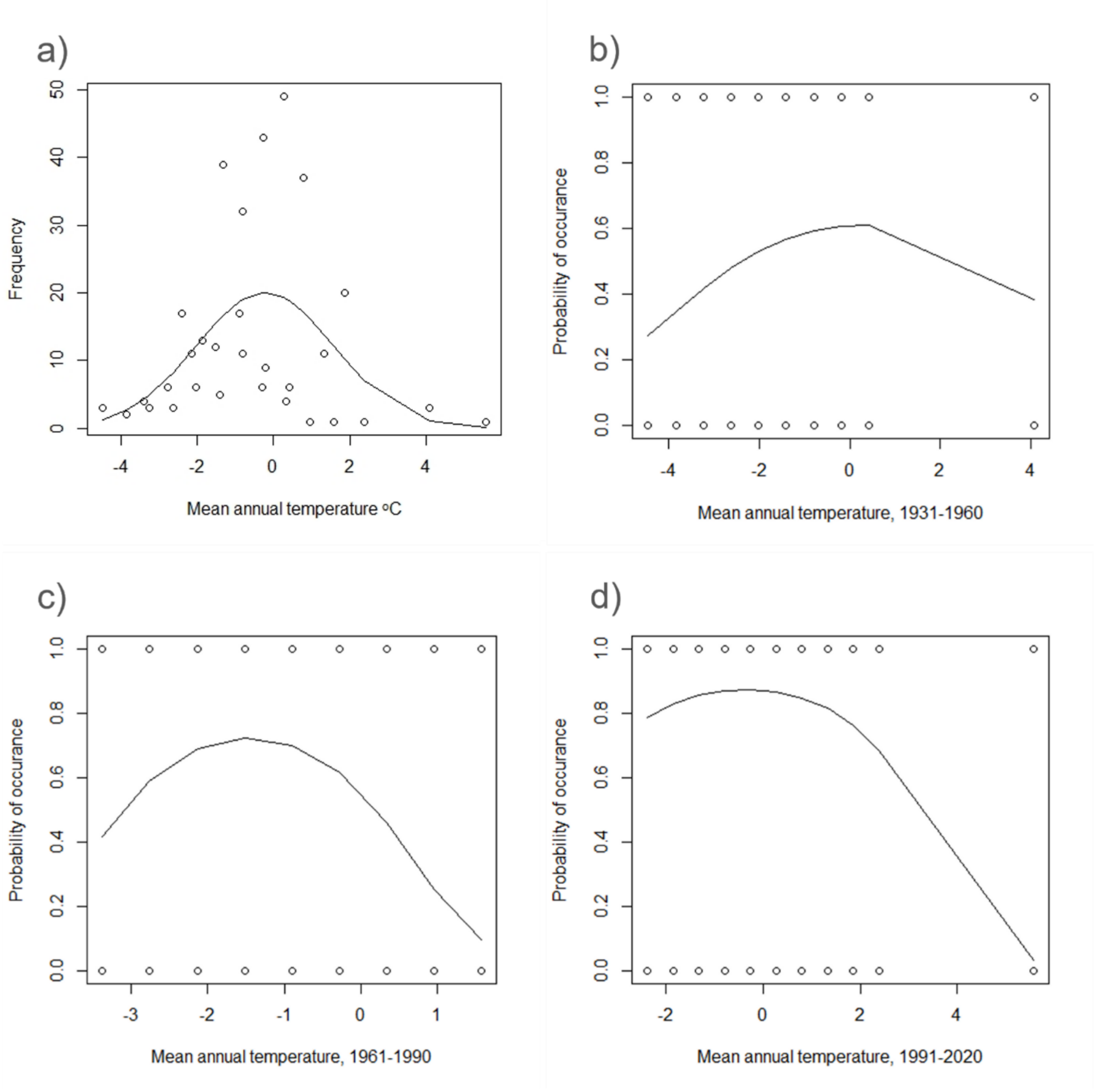


Figure 4.16 Response curves of Artemisia norvegica (Dovre population) estimated with Generalized Linear Model (GLM). Response curve a) illustrates the frequency by 100 masl interval to temperature (°C) of the period 1931-2020 ($p < 0.001$). The other models illustrates different periods of presence-absence based GLM indicating the probability of occurrence to temperature (°C) at different time periods; b)1931-1960 ($p < 0.01$), c) 1961-1990 ($p < 0.001$) and d) 1991-2020 ($p < 0.001$).

4.7 Area of population

Calculating the elevation area by 100-meter interval at Dovre and Mt Vassli discloses varying surfaces area by elevation, as expected in alpine regions (Appendix H). In Dovre approximately 60 per cent of the surface is between 800 and 1400 masl, while at Mt Vassli 56 per cent lies between 800 and 1000 mals.

The area-correction of *A. norvegica* occurrences in Dovre presented in Table 4.5 illustrates that the relative clustering of *A. norvegica* to elevation surface area primarily lies between 1400 and 1600 masl. Accordingly, this site-corrected optimum lies higher and colder than the modelled optima. This optimum corresponded with the observations at Syndre Knutshø where *A. norvegica* was most abundant at the 1400 mals interval.

Table 4.5 Relative distribution of *Artemisia norvegica* to the surface area to 100 masl intervals in elevation of the Dovre area.

Masl	500	600	700	800	900	1000	1100	1200	1300	1400	1500	1600
Rel. *A. Nor*	0.07	0.0	0.05	0.9	0.42	1.39	2.05	1.36	1.29	2.48	1.28	2.3

Rel. *A. Nor*= relative distribution of *A. norvegica*

An Unmanned Aerial Vehicle (UAV) survey over the top and northern sides of Mt Vassli (where *A. norvegica* was present) allowed the area to be studied in 3D (cf. Fig. 4.1, p. 44, which is a DTM of the dense point cloud produced, see Appendix I for address to published 3D model). The model illustrates a relatively flat top of the mountain with snow beds still prevalent in early July and alluding to small grooves in the mountain top topography.

4.8 *Betula pubescens* response

It was hypothesised that the *Betula pubescens* forest and tree line is ascending. This hypothesis was confirmed by steady upward movement of *B. pubescens* in the last century (Fig. 4.17a). The elevation optima have moved from 659 to 676 masl between 1931 – 1960 (Fig. 4.17b) and 1991 – 2020 (Fig. 4.17c), respectively. Whereas optimum 1961-1990 (Fig. 4.17c) period was at 601 masl, and the overall elevation optimum was 736 masl (1931-2020) (Fig. 4.18). The GLM analyses on frequency data for each normal period had a unimodal, skewed response where the right tail of the curve becomes longer by each period (Fig. 4.17b, c, d). Only one normal period was not significant at $p < 0.001$, as the 1930-1960 period was significant at $p < 0.05$. Overall, there is an overlap in the range between *A. norvegica* and *B. pubescens* (Fig. 4.18).

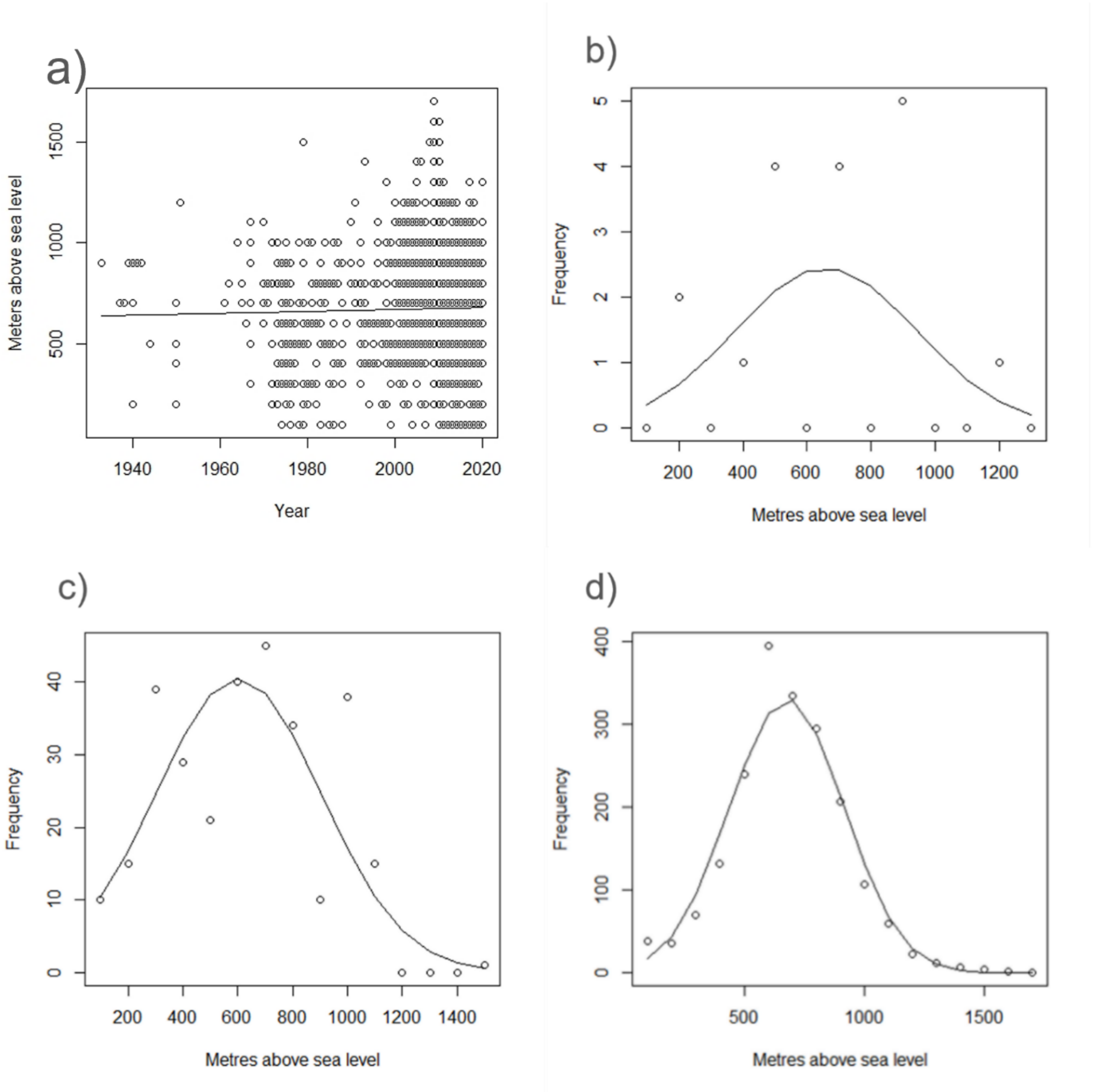


Figure 4.17 Response of Betula pubescens with a) linear regression of occurrence against time in the period of 1931-2020 ($p < 0.001$). The Generalized Linear Model (GLM) response curve that illustrates the frequency of B. pubescens by 100 masl interval to elevation at different periods; b)1931-1960 ($p < 0.05$), c) 1961-1990 ($p < 0.001$) and d) 1991-2020 ($p < 0.001$).

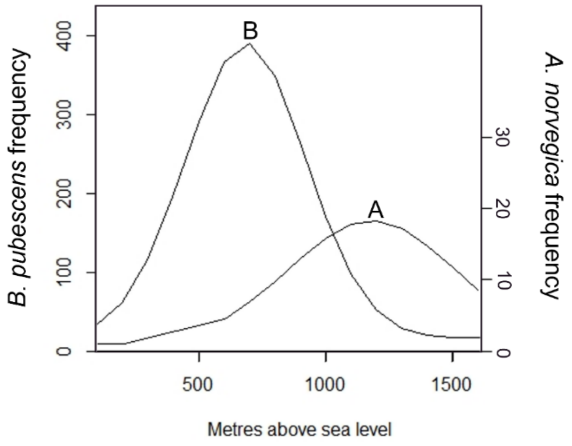


Figure 4.18 Overlapping frequency response of B) Betula pubescens 1931-2020 ($p < 0.001$) and frequency response of A) Artemisia norvegica 1931-2020 ($p < 0.001$) to masl.

Analyses of empirical forest lines at Mt Vassli by aerial imagery between 1971 and 2012 show an upward forest line movement. The forest line in 1971 was at approximately 710 masl on the northern side and 800 masl on the southern aspect. While in 2019, the forest line was at 760 (northside) and 840 masl (southside). Forest- and treeline were registered at 897 masl (Fig. 4.19) and 917 masl (Fig. 4.20) on the southern side during fieldwork. The Northern side had a rough terrain making it difficult to obtain accurate forest and tree line measures. Current empirical forest line indicates an upward range shift of the mountain birch of almost 50 meters in the past 50 years at Mt Vassli. This was backed up by a local hiker who remarked that since he put up a family cabin on the northern side of Mt Vassli by the lake Vatnaset in the 1970s, he has observed a steady forestation of Mt Vassli the past 50 years, similar to the aerial photo interpretation.

Additionally, one small pine (*Pinus sylvestris* L.) was found at Dåren, just 1.5 km west of Mt Vassli at 885 masl (Fig. 4.21).

Figure 4.19 Topmost forest line of Betula pubescens. Multiple trees growing close together at 897 masl on the southside of Mt. Vassli, Hardanger (UTM32 6687425N , 0358470E).

Figure 4.20 Topmost Betula pubescens observed on the south side of Mt. Vassli, Hardanger at 917 masl (UTM32 6687472N , 0358443E).

Figure 4.21 Pinus sylvestris observed at Dåren, Hardanger at 885 masl. Pen for scale (UTM32 6687228N , 0356412E).

5. Discussion

> " [A] good biogeographer is also a prudent one"
> – Vuilleumier (1999, p. 98)

In light of relevant theory and other studies in the field, this chapter discusses the main results concerning the thesis research questions. While others have confirmed climate change (see IPCC, 2021), this thesis supports this fact. Regarding the less studied climatic phenomenon of EDW, a correlating response of lapse rate with temperatures changes was hypothesised. This was both rejected and confirmed. *Artemisia norvegica* Fr. was expected to have had a range shift with temperature increase, which was confirmed. The plant elevational optimum has changed according to theory, but so has its optimum temperature, in contrast to theory. *Betula pubescens*) was also predicted to ascend the past 90 years, and this notion was also confirmed. Following, these results are discussed and explored, beginning with species composition.

5.1 Species composition in *Artemisia norvegica* community

The results of the ordination indicated a distinction between levels of pH in the plots included. Whereas a moisture gradient only could be alluded to, and thus will not be reflected on further. Combining the Correspondence Analysis (CA) diagram, plot analysis and field observations three habitat groups were recognised; ridges with chalcophile cohabitants, ridges dominated by plants tolerant to soil with low pH, and cliffs and screes. The latter was found at Austmannshovudet (Hjelmeland), and the two former were found at Mt Vassli (Hardanger) and Dovre. These characteristics are in somewhat accordance with other authors reports on the same vegetation; in Scotland (Blakelock, 1953), at Austmannshovudet (Arnesen & Strøm, 2015; Ryvarden & Kaland, 1968), at Mt Vassli (Holtan, 2007) and at Dovre (Gjærevoll, 1990). Whereas Gjærvoll (1990) and Holtan (2007) recorded *Dryas octopetala* at Mt Vassli and the Dovre area, the typical calciphilous plants were only observed at Austmannshovudet during fieldwork, in accordance with Ryvarden and Kaland (1968). Moreover, according to Gjærevoll (1990), *Campanula uniflora* is a typical cohabitant with *A. norvegica* in Dovre, whereas it was not observed during fieldwork at Søndre Knutshø (Dovre). The CA-analysis diagram exhibited that the habitat at Austmannshovudet formed a district group. The uniqueness of the Austmannshovudet habitat might be the result of the area being categorised by Arnesen and Strøm (2015) as an active landslide with a large scree fan, similar to the observations during field work with the addition of the cliff habitat. In comparison, the areas Søndre Knutshø and Mt Vassli do not have this type of terrain.

The observed habitat with *R acomitrium langinosum*, a moss indicating moderate levels of pH 4.0-5.0 (Fremstad & Elven, 1987), at Mt Vassli contradicts the previous report of Holten (2007), who only refers to the mountain's vegetation as calciphilous ridge vegetation. However, the vegetation observed supports Moe et al. (1994), who observed this additional habitat with acidic soil. However, as *A. norvegica* is mostly described as a calciphilous plant, the occurrence with *R. langinosum* habitat might be understood by source-sink theory (Pulliam, 2000). Where *A. norvegica* in basalt habitat spreads seeds to the *R. langinosum* mats where the focal species is able to sprout and form a sink population, but perhaps not thrive. Alsos et al. (2007, 2015) indirectly supported this theory on a larger scale, who found that arctic plants have high dispersal abilities, but the plants are limited when establishing a sustainable population due to unsuitable environmental conditions.

More interestingly, Blakelock (1953) offers a short description of the *A. norvegica* var. *Scotia* habitat in Scotland. He describes the medium of which the plant lives as exposed and on dry gravel, gravely soil or piles of sandstone, similar to the Norwegian habitats of Dover's block field and the scree at Austmannshovudet. Moreover, he refers to some plants that are typical of a *A. norvegica* var. *Scotia* community in Scotland, who are also found in the plots analysed; *Alchemilla alpina, Antennaria dioica, Solidago virgaurea, Salix herbacea, Carex sp*. and *R. lanuginosum*. Whereas *A. alpina* and *A. dioica* are found in all three of the study sites, *S. herbacea* is found in Dovre and Mt Vassli. Whereas *S. virgaurea* is only found in the Austmannshovudet plots. Thus, the three locations of *A. norvegia* var. *norvegica* and the var. *Scotica* show similar preferences of habitat and with similar cohabitants. However, Hultén (1954) is adamant about keeping the two different subspecies distinct from one another on the basis of their morphological differences. Additionally, he leaves no doubt in his comparison that var. *Scotica* has to be indigenous to Scotland.

Another species occurring at Austmannshovudet is the rear *Oxytropis campestris subsp. Scotia*. This plant only has two international occurrences; in the area of Austmannshovudet and in Scotland (Arnesen & Strøm, 2015; Sunding, 2020). Thus, two rear species have a similar disjunct distribution, an interesting correlation that can make one speculate about their possible conjoined distribution history.

5.2 Temperature, lapse rate and EDW developments

5.1.1 Development in temperature

The latest IPCC report (IPCC, 2021, p. 41) states that climate change *has* affected "every region across the globe". The results of the recent temperature increase in Dovre and Western Norway reflects this notion. Overall, there has been an increase of MAT of 0.08°C (Dovre) and 0.07°C (Western Norway) per decade in the last 90 years. Hanssen-Bauer (2005) found similar trends on a regional scale. Hanssen-Bauer (2005) compared temperature development between 1875 and 2004, which gave an increase of 0.06°C (Dovre and Trøndelag region, based on five stations) and 0.08°C (Western Norway, based on twelve stations) per decade. She comments on the colder period of the 1980s as "the coldest decade in [the] entire time-series" (Hanssen-Bauer, 2005, p. 14) due to great cold spells during the winters of this period.

Similarly, the results illustrate the same overall increase in temperature, with a colder or stable period between 1961 and 1990. Hanssen-Bauer (2005) indicates that the climate of Norway is affected by the North Atlantic Oscillation (NAO). This correlation is stronger in the winter and during colder periods, and more so for Western Norway than other regions. Consequently, NAO might explain these differences in temperatures between normal periods and between Norway's western and central parts.

5.1.2 Changes in recent local lapse rates

It was hypothesised that the lapse rate would decrease due to EDW dynamics. The local lapse rate of Dovre confirmed this hypothesis because the temperature change over the last three normal periods was higher at the alpine zone. In contrast, the estimated lapse rates for Western Norway rejected this hypothesis. However, both lapse rates diverge from the steeper global, or "the standard", lapse rate of -0.65°C (Ketzler et al., 2021; Tveito & Frøland, 1999) demonstrating that the application of local lapse rates is essential for fine-scale studies.

Other authors have found consistent empirical indications of EDW on regional (Joshi et al., 2018; Shi et al., 2021; Minder et al., 2018), national (Oyler et al., 2015) and global scale (Wang et al., 2014). Both Wang et al. (2014) and Joshi et al. (2018) grant humidity as a significant effect on EDW, where the moisture heat convection is a primary contributor. On the other hand, Joshi et al. (2018) explain that temperatures can stay relatively high due to high moisture content throughout the elevation gradient, decreasing the lapse rate. Pepin (2001) also reveal that cloud cover and strong wind shears contribute to steeper lapse rates. The Dovre area is characterised by a higher elevation than Western Norway as a whole. Thus, potentially more snow cover may affect EDW, as per Oyler et al. (2015), who documents a strong correlation between the snow-albedo feedback and EDW.

Moreover, most of Norway's coast does not experience snow cower or very little of it (Hanssen-Bauer et al., 2015). Thus, snow-albedo might not have a substantial effect in Western Norway. At the same time, NAO is not expected to significantly impact EDW (Pepin, 2001), in contrast to the regional temperature predicted by Hanssen-Bauer (2005) above. In the effort to unravel how Western Norway oceanic climate and topography has resulted in lapse rates that are different from EDW theory, the answer might lie in an intricate process of the aforementioned factors.

In sum, EDW is a complex mechanism and Pepin et al. (2015) caution about generalisation. At the same time, Oyler et al. (2015) warn about the generally overlooked EDW effects in research. Moreover, Wang et al. (2014, p. 99) add "the warming amplification in the high-elevations regions is an intrinsic feature of global warming in recent decades", further illustrating that the continuation of overlooking EDW might give misleading results when researching climate change effects in mountains.

5.1.3 The ecological implications of EDW

While many studies have empirically proven EDW in the mountains, few have explored the phenomenon's ecological effects (e.g. Joshi et al., 2018; Shi et al., 2021). The geographical effects of EDW were illustrated on the temperature-elevation gradient by specifying the masl at freezing point (MAT equal to 0°C) at the different lapse rates calculated.

Consequently, EDW will increase the length an alpine species must move upward to stay within their temperature niche. Shi et al. (2021) predict EDW will positively affect coniferous alpine trees' mass growth. Joshi et al. (2018) agree with this notion and add that the treeline will be affected. In the case of *A. norvegica*, it must stay close to the elevation with 0°C masl to stay within its temperature optimum and tolerance range. Thus, as demonstrated, EDW is further pushing this limit upwards in Dovre, and *A. norvegica* must move accordingly to stay within its niche.

5.3 *Artemisia norvegica* response shape and its implication

5.3.1 Target species and the temperature-elevation gradient

Viewing the distinctive bell-shaped response and the relatively high coefficient of determination (0.817), one can conclude that the frequency response illustrates that temperature significantly affects *A. norvegica* distribution. This corresponds with the theory on the relationship between alpine plants and temperature (cf. p. 9). Moreover, the frequency model illustrates a clear range, demonstrating that the likelihood of *A. norvegica* occurring outside these limits is low (Oksanen & Minchin, 2002).

Other research investigating species distribution along the temperature-elevation gradient has found similar results for other species (Austin et al., 1990; Vetaas, 2000b, 2002; Trivedi et al., 2007; Amissah et al., 2014; Suwal & Vetaas, 2017) with a strong response to the temperature – elevation gradient. This response can be interpreted along two dimensions. First, the probability of occurrence and abundance within the target area is highest at the optimum temperature. Secondly, the temperature range represents suitable environmental conditions (Sexton et al., 2009).

However, the area correction (cf. p. 42) resulted in a relative optimum different from the modelled optimum. The optimum site correction shows that relatively most of *A. norvegica* in Dovre is located at the 1400 interval, equivalent to -1.32°C. Converting this to elevation optimum to Mt Vassli, it would lie between 1200 and 1300 masl (by the latest normal period temperatures). This indicates that *A. norvegica* might have a cooler temperature tolerance than noted in the niche model, with a 1.3°C difference, alluding to its hidden past as a potential glacial relic. Furthermore, the site correction of optimum is about 200 mals higher than the top of MtVassli, implying that the population at Mt Vassli already lies at the warmer edge of its temperature tolerance.

5.3.2 *Artemisia Norvegica* and range shift predictions

Based on niche theory, niche conservatism and equilibrium, and range shift predictions, it was hypothesised that *A. norvegica* would geographically move its niche with changes in temperature over the last three normal periods. *A* change is indicated by the difference in *A. norvegica* optimum and empirical range. *A. norvegica* elevational optimum has continuously moved towards higher elevation, indicating a geographical optimum shift. In Western Europe, Lenoir et al. (2008) conducted long term studies (1905-2005) of alpine plants. They determined a general rapid (29 m a decade) upward shift in optimum elevation range in 118 out of 171 species. In this study, climate change was the main explanator of the observed changes in the alpine vegetation. Although the optimum elevation movement of *A. norvegica* is in accordance with Lenoir et al. (2008), it somewhat diverges with theory.

According to niche conservatism and equilibrium, the temperature optimum of *A. norvegica* was expected to stay the same, but it has changed. The temperature optimum of *A. norvegica* has gradually become cooler. Each period has separate occurrences with a corrected lapse rate; consequently, a difference in optimum is inevitable. However, the difference between the first and the latest period is notable and is still within one tolerance range of one another. It is especially the latest normal period that has deviant temperature optimum (cf. Table 4.4 p. 54) and is comparatively much cooler than the two more similar earlier optima. An explanation might be that *A. norvegica* has either earlier not been able to stay in its climatic equilibrium or that *A. norvegica* has disproportionally been pushed upwards the last 30 years. Plants are relatively effective in staying in equilibrium with climate conditions (Araújo & Pearson., 2005). Still, some are faster in response to environmental change than others (Rumpf et al., 2018). Rumpf et al. (2018) documented that along the mountain range of the European Alps, the most significant change in species range and abundance was at lower elevations. Svenning and Skov (2004) documented that *B. pubecens* was able to fill more or equal to 90 per cent of climatically suitable areas across Europe, illustrating the trees ability to disperse inside its fundamental niche. Thus, *A. norvegica* can have been outcompeted at its lower edge (temperature optimum pushed up) in the race of range shift, indicated by the overlapping ranges of *B. pubecens and A. norvegica* (cf. Fig 4.18, p. 57).

All the tree niche models (1931-1960, 1961-1990, 1991-2020) compared describe a movement of elevational optimum towards the cooler edge. Based on the predictions of Breshears et al. (2008) and Lenoir & Svenning (2015), alpine plants populations would either "march", "lean", "crash", "retract" or "expand" in response to climate change (cf. p. 11). Comparatively, it seems that *A. norvegica* has maintained its range between 1931-1960 and 1991-2020. Whereas the range retracted in the middle period, but the elevational optimum moved. Consequently, the "lean" responses apply to *A. norvegica* movement for the last 90 years. While a "march", "crash", "retract" or "expand" are not apparent interpretations. In other words, *A. norvegica* has *not* had a geographical range shift but an elevation optimum shift in contrast to range shift predictions. Conversely, Rumpf et al. (2019) found, on average, the same rate of movement at both edges in the European Alps. In other words, the "march" predictions are appliable to Rumpf et al. (2019) study and agreeable to range shift theory. The *A. norvegica* "lean" response can also be explained by better growth conditions at higher elevations and worse conditions at lower elevations.

5.3.3 *Artemisia norvegica* and other possible interactions

Another factor that can affect species growth and distribution along with climate change is increasing nitrogen and carbon dioxide (CO_2) availability (Theurillat & Guisan, 2001; Lenoir et al., 2008; Rumpf et al., 2018). Increased CO_2 is expected to result in more biomass production. In contrast, nitrogen can either increase growth or contribute to nitrogen saturation and consequently species loss and groundwater contamination (Hättenschwiler & Körner, 1998). While Hättenschwiler & Körner (1998) found inconclusive results on how CO_2 affected their research on the matter in montane spruce communities, nitrogen was likely to affect biomass production positively. As climate change leads to increased temperatures and nitrogen availability Klanderud (2008) conducted an experimental investigation on dry alpine *Dryas octopetala* heath in Finse, Hardanger Plateau. She found that nitrogen addition significantly affected *A. norvegica*-community plants such as *Poa alpina* and *Cerastium alpinum*. On the other hand, *Saxifraga oppositifolia* and *Antennaria dicica,* also located in plots with *A. norvegica*, decreased with warming and nitrogen additions. There are divergent responses to nitrogen among species in the *A. norvegica* community. Therefore, using these plants as proxies to understand whether *A. norvegica* is affected by increased nitrogen availability will be speculative.

Inquiring further on the matter of species range shift, other studies show that some species have had a recent downward range shift (Crimmins et al., 2011; Kopp & Cleland, 2014; Bhatta et al., 2018). Bhatta et al. (2018) primarily explain the general downhill movement of alpine plant assemblages by reduced grazing freeing up suitable land below. In comparison, Crimmins et al. (2011) elaborate on the climatic effects of precipitation to explain species downhill movement. The interaction between warmer climates and changes in precipitation patterns results in better water conditions further downhill in the study area of Sierra Nevada (Spain). Thus, species moved downhill to alleviate water stress. A conclusion Kopp and Cleland (2014) agree to, but ads the possible implications of sampling artefact when dealing with fieldwork where target species can be overlooked, i.e. the Wallaces shortfall. Even though there is general decrease in grazing pressure, it is more likely that other thermophile species have established themselves there, such as *B. pubescens*, before *A. norvegica*. Moreover, precipitation has not decreased in late years (Meterologisk institutt, 2020), including the fact that *A. norvegica* has high drought tolerance (Vold, 1982), a downhill range shift, as Crimmins et al. (2011) explains, seems improbable. However, the Wallace shortfall is always a relevant challenge for biogeographical studies.

5.4 *Artemisia norvegica* and the future

By applying the *A. norvegica* niche model produced of Dovre population data, the future of the Hardanger population can be explored. The results revealed that the temperature optimum of *A. norvegica* is 0.02°C, approximately equating to an elevation of 1030 masl in Western Norway (by 1991-2020 normal temperatures), just below Mt Vasslis highest point (1055 masl). This implies that today *A. norvegica* is within its optimum range at the uppermost limit of Mt Vassli.

Future climate scenarios with warmer temperatures imply that the elevation optimum of *A. norvegica* would be 1265 masl (RCP4.5) and 1499 masl (RCP8.5) by 2100 at Mt Vassli. Thus, there will be a loss of suitable habitat, and the habitat will become increasingly unsuitable with the advancement of global warming. Both the conservative and the pessimistic IPCC projections result in optimum beyond the range of Mt Vassli. Consequently, (following range shift predictions and niche equilibrium) climate change will send *A. norvegica* on the "escalator to extinction" (Urban, 2018) and become "mountaintop extinct" (Colwell et al., 2008). Other authors have found that high alpine plants with limited range might succumb to the same future (e.g. Gottfried et al., 1999; Guisan & Theurillat, 2000).

Guisan and Theurillat (2000) identified that most genuinely alpine plant species were predicted to lose their suitable habitat by the lowest warming predictions in the Swiss Alps, while some plants in the same vegetation band would likely experience increased distribution. Gottfried et al. (1999) came to the same conclusions in predicting the future for alpine plants found in the Austrian Alps, thus announcing "winners" and "losers" of climate change. On the one hand, Guisan and Theurillat (2000) found that *Carex curvula* would decrease in distribution under even the lowest predicted climate warming in the Swiss Alpes. At the same time, Gottfried et al. (1999) concluded that *C. curvula* would gain favourable habitat in the Austrian Alps. In short, predictions regarding species as either "winners" or "losers" of climate change is site-specific. Nevertheless, in the discussion of species range shift and climate change predictions, there is a general trend of terming species as either "winners" and "losers" of climate change (e.g. Gottfried et al., 1999; Erschbamer, 2007; Schöb et al., 2009; Kafash et al., 2018; Rumpf et al., 2018). Where generally, thermophile species are termed as "winners" and cold-adapted plants as "losers" (Rumpf et al., 2018).

A. norvegica is likely to be a loser in Hardanger, but it might be a winner at Dovre and Hjelmeland. Besides thermophilization and other threats discussed belove, authors (Gottfried et al., 1999; Guisan & Theurillat, 2000; Körner, 2009) point out a few characteristics that adhere to the alpine species as either "winners" or "losers". Plant species with large environmental tolerance, living mid-elevation, with large populations come better out of climate change predictions than small, fragmented, restricted specialised plants in high altitudes (alpine and nival). Thus, regarding the subpopulation of *A. norvegica* at Mt Vassli it is likely to become a climate loser. Even though the target species has a broad environmental tolerance, its population is relatively small and is restricted to the mountain top. Both Guisan and Theurillat (2000) and Gottfried et al. (1999) emphasise the advantage of being located mid-slope along the mountain elevation as areas above the current range will become suitable with climate change, a luxury this population does not have.

On the other hand, the larger population in Dovre might be considered as a climate "winner". Here *A. norvegica* has a large population spread over a large area, and more importantly, predominantly lies mid-slope. For example, at Syndre Knutshø (1690 masl) the greatest number of *A. norvegica* is located at 1400 masl, thus having area to move uphill. Moreover, as the Dovre population is large, it has a greater chance of surviving climate change as it is less vulnerable to genetic erosion than the Hardanger population.

The Austmannshovudet population is located in a southwest-facing cliff that receives much radiation. Thus, even higher temperatures might result in heat stress in the plant. However, this cliff is, and will always be, free from *B. pubescens* and herbivores. Assuming *A. norvegica* has a large temperature tolerance, its main antagonist is likely not to push it off the cliff at Austmannshovudet.

Additionally, other factors that are predicted to have novel responses to climate change can indirectly affect *A. norvegica*, such as pollinators. The alpine climate is more favourable to insect pollinators such as bumblebees, moths, and flies than in lower elevations (Inouye, 2020). As a result, these species will change their range with climate change as well. For example, today, the *Dombus alpinus*, a large alpine bumblebee, is found 100 meters higher up in the mountain than just ten years ago. Plants cannot keep up with such a quick ascent, thus losing possible pollinators (Forsgren et al., 2015).

Additionally, the connectivity of alpine pollinator populations is being pieced up by ascending thermophile trees. Accordingly, Inouye (2020) predicts new compositions of the plant-pollinator relationships. As a result, some new synergies will be created while others might go extinct. In other words, *A. norvegica* might lose pollinators it relies on. Especially as pollinators are more mobile and can follow their temperature niche with climate change to other mountains higher than Mt Vassli. However, these effects might not significantly impact *A. norvegica* propagation as Vold (1982) believes that *A. norvegica* mainly germinates vegetatively.

As sister taxa have similar climatic niches (Hof et al., 2010), a sister taxes environmental response can, by proxy, shed light on the focal plant. Three other taxa within the *Artemisia* genus, *A. rothrockii* (Kopp & Cleland, 2013), *A. genipi* (Erschbamer, 2007) and different subtypes of *A. tridentata* (Shaw et al., 2000; Perfors et al., 2003) have had their response to climate change evaluated. For *A. rothrockii* an increase in abundance was reported at the highest part of the elevation range as a response to warmer temperatures (Kopp & Cleland, 2013). In comparison, *A. tridentata* was expected to widen its range and increase growth in response to climate change (Shaw et al., 2000; Perfors et al., 2003). At the same time, *A. genipi* was evaluated to remain unaffected (Erschbamer, 2007). Assuming a similar environmental niche between congeneric taxa, the studies support previous understandings on the broad temperature tolerance of *A. norvegica* (Vold, 1982). Additionally, *A. norvegica* has had a similar range shift as *A. rothrockii*. Their abundance has increased in the higher elevations, but dissimilar as *A. norvegica* has not had a geographical range shift. By extension, the niche response might be similar, but the ability to establish is not.

Historically, when more significant fluctuations in climate have occurred, species either "adapt, move or die" (Faculty of Science - University of Copenhagen, 2018). Until now, this thesis has focused on the "move or die" part, but evolutionary change is a theoretical option. This thesis has adhered to niche conservatism; thus, this exploration is outside of the established framework. Nevertheless, it is an ongoing discussion regarding ecology and climate change (e.g. Skelly et al., 2007; Alsos et al. 2012; Cotto et al., 2017; Nogués-Bravo et al., 2018). Some studies show "microevolution" in plants in response to manipulations of climatic parameters in experimental studies (Bone & Farres, 2001; Skelly et al., 2007). Calculations of evolutionary rate and increased thermal tolerance show a possible increased temperature tolerance of 3.2°C over 10 generations (of a hypothetical plant with 5-year generation time) (Skelly et al., 2007). Outside of the strictly theoretical and experimentally isolated studies, species are not expected to genetically adapt to Anthropocene climate change (Skelly et al., 2007; Cotto et al., 2017).

Furthermore, due to loss of range, genetic corrosion is expected to increase in cryophile plants with climate change (Alsos et al., 2012). In studying alpine plants, Cotto et al. (2017)

found that the short-term adaption needed to acclimate to Anthropocene climate change is unlikely. Specifically, alpine plants with poor connectivity to other populations, extended lifespans and limited dispersal abilities will produce offspring that are increasingly not suited for the ongoing warming. Thus Cotto et al. (2017) predict first an extended stable phase of range stability followed by population collapse. In sum, hypothetically, plants can adapt to warmer temperatures. Still, the general conclusion is that Anthropocene climate change is advancing faster than what plants can adapt to (Skelly et al., 2007; Cotto et al., 2017). This might be the case for the *A. norvegica* population on Mt Vassli, which have a small range and mainly vegetative reproduction resulting in low genetic variability. Thus, whether adhering to niche conservatism or not, it might not be relevant when facing rapid climate change.

5.5 *Betula pubescens* response shape and its implication

B. pubescens was proposed as the antagonist to *A. norvegica* in the future with climate change based on the theory of thermophilization. Thus, it has been relevant to obtain insight into the tree's movement according to temperature change. The results indicate an upward advancement of *B. pubescens* on a national and local (Mt Vassli) scale, in accordance with theory and other studies (Kullman, 2001; Tape et al., 2006; Bryn, 2008; Bryn & Potthoff, 2017; Vanneste et al., 2017). However, studies (Bryn, 2008) show that climate warming is not the primary driver of *B. pubescens* movement, but the change in land use. *B. pubescens* range has moved upwards, implying the "expand" response (Breshears et al., 2008), as the species is presumably following its temperature niche. Currently, assuming the 10°C (tetra term) lower temperature limit of *B. pubescens*, the whole of Mt Vassli offers a suitable climatic habitat. Its possible climatic range dictates that the tree should already be established on the top of Mt Vassli, which has a microclimate tetra term of 11.12°C, if in equilibrium. Thus, there is a gap between the potential range (fundamental) and the tree line's actual (realised) range. Consequently, land use might have a substantial effect on *B. pubescens* distribution at Mt Vassli. Furthermore, *Pinus sylvestris* might also portray itself as an additional antagonist to *A. norvegica*, as one was observed at 885 masl not far from Mt Vassli.

Historically, there has been transhumance activities around Mt Vassli, at least since the 16th century (Kolltveit, 1953), but ceasing during the last century (Losnegård, 200). A visual analysis of the response curves of *B. pubescens* over the last three normal periods shows an increasing tail towards the colder edge of its empirical range. Further supporting notions that temperature might not be the main factor of *B. pubescens* range shift on a local scale in Norway (e.g. Bryn, 2008; Bryn & Potthoff, 2017).

However, Bandekar and Odland (2017) determine strong winds as a limiting factor to *B. pubescens* distribution, and Mt Vassli does receive strong winds from the south-west. Consequently, it can be derived that *B. pubescens* is not able to establish itself on the mountain top. Even though one can hypothetically explore such effects on *B. pubescens*, it is challenging to give a definitive answer on whether Mt Vassli experiences strong enough wind currents to expel the tree from establishment at the top of the mountain. While wind is not expected to deviate with climate change, snow cover might (Lundstad et al., 2018).

Karlsson et al. (2005) claim that *B. pubescens* seedlings depend on snow cover's insulating effect during winter. As snow cover results in stable temperatures, so the soil and plants beneath rarely freeze (Körner & Hiltbrunner, 2021). The climate loggers show significant variances in temperatures during wintertime, indicating thin or no snow cover at Mt Vassli. Consequently, the vegetation on the top of Mt Vassli has to tolerate harsh wind and low temperatures during winter. In addition, Lundstad et al. (2018) project less snow cover with the advancement of climate change in Hardanger. Conversely, the UAV-derived 3D model of Mt Vassli shows the topography accommodates snow beds during the summer. These areas might be allegeable in 2100 for *B. pubesences* establishment, as it is more likely that this area will be covered by snow during winter and cleared during summer in the warmer future. However, species that are adapted to live on windy ridges, e.g., *A. norvegica*, is expected to withstand the decreasing protective cover that snow offers (Körner & Hiltbrunner, 2021). In sum, *B. pubescens* establishment at the top might be limited by the lack of snow cover and strong winds.

Additionally, large pests outbreaks have been linked to a warmer climate that has affected the *B. pubescens* forest line in Northern Norway. The tree has experienced locally devastating attacks by moth larva (*Epirrita autumnata* and *Operophtera brumata*), resulting in mortality of up to 90 per cent (Forsgren et al., 2015). Hence, these attacks have led to a downward movement of the local *B. pubescens* forest line (Bryn & Volden, 2020).

5.6 The ecological implications of microclimates and refugium across time

The complex mountain terrain produces different microclimates, where slope and aspect dictate much of the temperature variations, as documented at Mt Vassli. However, it is generally accepted that mountains complex terrain results in microclimates, there is an ongoing discussion on whether these microclimates will be suitable as a refugium in a warmer future (Gottfried et al., 1999; Randin et al., 2009; Scherrer & Körner, 2011; Keppel et al., 2012; Speziale & Ezcurra, 2015; Ulrey et al., 2016). Whether Mt Vassli can be a suitable refugium for *A. norvegica*, adding to the population resilience, authors offer some characteristics to mountains and microclimates as essential for refugia, by which Mt Vassli can be evaluated. First, topographical complexity is granted as essential to the suitability for a mountain as a refugium (Randin et al., 2009; Opedal et al., 2015; Speziale & Ezcurra, 2015), as it offers different microhabitats. This is underlined by Opedal et al. (2015), who found an increase in species richness and species turnover by increased microclimate heterogeneity. Second, connectivity between suitable microclimates is related to greater chances of survival, especially within different elevations (Opedal et al., 2015; Speziale and Ezcurra, 2015).

Moreover, Ulery et al. (2016) concluded that the southern Appalachian Mountains (United States) currently suits the endemic *Geum radiatum* due to stable temperatures in the microhabitat. Referring to the temperature recordings, the northern side of Mt Vassli is on average 0.9°C cooler than the south side and thus might offer a cooler habitat. However, most of the *A. norvegica* population is predominantly already on the northern side or the top of Mt Vassli, and the expected temperature increases of 2.4°C (RCP4.5) and 3.9°C (RCP8.5) is greater than the 0.9°C buffer that the north side offers. Additionally, Mt Vassli is relatively flat but with a few furrows in the topography (cf. Fig. 4.1, p. 44, and 3D model in Appendix I). The furrows might result in microclimates that are not captured here. It has been stated that flat topography logically makes up minor differences in microclimates and has fewer buffering effects as a refugium (Opedal et al., 2015; Speziale and Ezcurra, 2015). Thus, the flatness of Mt Vassli indicates less heterogeneous terrain and less connectivity between microclimates, the two characteristics most important to a refugium.

The interaction of topography and bedrock chemistry also affect microclimates (Keppel et al., 2012; Opedal et al., 2015; Körner & Hiltbrunner, 2021). When adding the registered points of *A. norvegica* at Mt Vassli, no occurrences are outside the basalt type of bedrock (cf. Fig. 4.4, p. 45). Thus, when Moe et al. (1994, p. 20) writes, "the distribution [of *A. norvegica* at Mt Vassli] ceases abruptly despite the fact that there are apparently suitable adjacent habitats with "correct" vegetation types around", the answer might not lie in the surrounding vegetation but in the bedrock below. The more pH rich bedrock basalt than the quartzite surrounding it indicate that Mt Vassli might not be a micro*climatic* refugium but more of a micro*geological* refugium. Authors (Keppel et al., 2012; Opedal et al., 2015; Körner & Hiltbrunner, 2021) include geological heterogeneity as an important contributor to characterising microhabitats and refugia. For example, if *A. norvegica* was able to move to the higher neighbouring mountain Jonsteinen (1344 masl) it might not be able to establish itself there as the bedrock chemistry is different than at Mt Vassli.

Rather than evaluating possible refugia in relation to Anthropocene climate change, Keppel et al. (2012) and Speziale and Ezcurra (2015) explore future refugia by understanding the past. By identifying previous refugia, these authors call for conservation measures regarding such areas. Because, where species previously congregated and survived under unfavourable regional temperatures, refugia are expected to harbour species again amid projected climate change (Keppel et al., 2012). Whether Mt Vassli has accommodated *A. norvegica* during Younger Dryas relies on whether the mountain was deglazed or not. However, suppose we accept Helles (2008) illustration (cf. Fig. 3.7, p. 33) on Mt Vasslis glacial past. In that case, Mt Vassli might have served as a refugium during glacial periods and other climatic variances during the past 12 000 years, including the warmer periods, thus adding to the resilience of *A. norvegicas* in the warmer future. Thus, Mt Vassli gives a better chance for *A. norvegica* to survive the future warming period. However, as most of *A. norvegica* is already at the top and to the northern (cooler) side of the mountain, it might look like the target species has already retracted to its refugium or never left it.

5.7 Thermophilization and climate change predictions

> "[P]lants' competition for light and nourishment that limited their lives and growth"
> - von Humboldt's reflections while exploring South America
> (Wulf, 2015, p. 68)

Whereas "there is no competition for temperature" (Austin et al., 1990, p. 175), the rivalry for light can be the "first step toward local species extinction" (Walker et al., 2006, p. 1345). Even though this thesis has explored temperature as the primary explanatory variable for *A. norvegica*s distribution, it might not be this abiotic factor that threatens *A. norvegica* existence on Mt Vassli in a warmer world. *B. pubescens* was proposed as the antagonistic interaction to *A. norvegica* based on understanding the Dobzhansky-MacArthur hypothesis and thermophilization (cf. p. 9-10, 12). Consequently, it was hypothesised that *B. pubescens* would move upwards and outcompete *A. norvegica* at Mt Vassli, making it locally extinct.

As mentioned, the results indicate a national and local upward movement of *B. pubescens* and an optimum retraction from the lower elevation range of *A. norvegica*, indicating the dynamics of thermophilization (cf. Fig. 4.18, p. 57). Thus, supporting others research that found range shift will increase competition at the lower edges of alpine plants (Klanderud & Birks, 2003; Walker et al., 2006; Vittoz et al., 2009). Walker (2006) predicts that the competition for light might be the ultimate conflict that more specialised species might lose, because when vascular plants battle for light, trees and shrubs almost always prevails (Zimov et al., 1995; Vittoz et al., 2009). For example, Vittoz et al. (2009) report that climate change might indirectly limit future alpine plants because the "forest shadow will exclude the remaining alpine plants". These predictions align with other reports on thermophilization as already happening (Vanneste et al., 2017; Gottfried et al., 2012).

Tape et al. (2006) add nutrient availability to the equation of thermophilization and points out that shrubs, such as *Betula nana* and *B. glandulosa* (in their study), are more nutrient efficient than other cryophilic plants. Moreover, more nutrient-rich soil usually contributes to more competition (Nicklas et al., 2021). Thus, indicating that the bedrock composition that possibly is "keeping" *A. norvegica* at Mt Vassli might also invite competitors to its refugium.

A. norvegica is probably already at its refugium on the summit of Mt Vassli. Its temperature niche suggests that the population is currently within its optimal and tolerance range. According to the lowest RCP forecast (RCP4.5), Mt Vassli will no longer be as climatically suitable, indicated by the optimum and tolerance margins that would then be above the highest point of the mountain. Nevertheless, in general, overheating is not regarded as a mortal factor on a large scale, especially in comparison to the relative threat of competitors (Woodward & Williams, 1987, p. 191). By assuming *A. norvegicas* high-temperature tolerance, warming temperatures are likely not the executing factor. Even though *B. pubescens* can be hampered by harsh winds and decreasing snow cover the forest line advancement will overshadow and give *A. norvegiva* the boot of the top, as the target species is never found where the sun does not shine.

All things considered, in the future of global warming, it is not the temperature increase by itself that might make *A. norvegica* potentially locally extinct in Hardanger "but the plants' competition for light and nourishment" (von Humbolt, in Wulf, 2015, p. 68).

6. Conclusion

This thesis explored the temperature niche of *Artemisia norvegica* over the past 90 years by means of regression analyses of occurrence data. The main population of *A. norvegica* at Dovre has moved to higher elevations in the last 90 years. The range had stayed the same, whereas elevational optimum had moved higher, and temperature optimum had increasingly become cooler. The subpopulations of Dovre and Hjelmeland were acknowledged as "winners" of climate change, whereas the population of Mt Vassli is most likely a "looser" due to multiple factors. Firstly, the subpopulation at Mt Vassli is already at the top of the mountain. Thus, there is no more area to move upwards to track its niche in a warmer future. Second, higher surrounding mountains do not contain the bedrock composition (basalt) preferred by *A. Norvegica*. Thirdly, *Betula pubescens* possible ascendance and establishment at Mt Vassli represents the ultimate threat to *A. norvegica* in the future, as the alpine plant will be outcompeted for light. Additionally, with the climate change backdrop, dynamics of lapse rates and elevation-dependent warming (EDW) was considered and calculated with least squares regression. Even though the phenomenon was not regionally proved in Western Norway, it was established as ongoing in Dovre. Furthermore, the ecological consequences of EDW include a shift in species distribution as a result of climate change, with species moving proportionately further to maintain their climatic niche.

7. Summary

This thesis explored the temperature niche of *Artemisia norvegica* over the past 90 years employing lapse rate and regressions on occurrence data from the main population at Dovre. It was assured a stable range, but a movement of elevational optimum have to higher elevations and an increasingly cooler temperature optimum. However, the warmer temperatures of climate change is not a direct threat to this population.

The lapse rates did vary in response to climate warming over the past 90 years of Dovre, but not in Western Norway. Elevation-dependent warming (EDW) may increase the elevation a species has to move in order to track its temperature niche.

The subpopulation at Mt Vassli in Hardanger is dependent on whether *Betula pubesence* may establish itself at the top of Mt Vassli. The projected future climate of Mt Vassli will become increasingly unsuitable for the target species, as its niche and tolerance range will be higher than the top of the mountain. The microclimates at Mt Vassli might give *A. norvegica* a chance of survival as a refugium.

The plant is expected to be heat tolerant, and global warming may not have a lethal effect. However, the dominant subalpine forest tree, *B. pubescens*, is moving uphill towards the subpopulation of *A. norvegica*. This upward movement is probably mainly due to reduced grassing pressure because the practice of transhumance has almost disappeared as well as underpinning climate change. This thesis concludes that the competition for light makes *A. norvegica* a candidate for local extinction in Hardanger, an effect of land-use change and fortifying climate change.

A. norvegica is endemic *sensu lato* to Norway, and more than ninety per cent of its global population is found in the country. Therefore, the Norwegian government is responsible for preserving this target species and securing the plant from extinction. In terms of conservational measures, keeping *B. pubescens* away from the top of Mt Vassli may secure a vital subpopulation of *A. norvegica* in the future.

The thesis indicates that temperature- elevation gradient should be included in terrestrial ecosystems monitoring system (e.g. Spatially representative nature monitoring program for terrestrial ecosystems, or "Arealrepresentativ naturåvervåkning" (ANO) in Norwegian) (cf. Tingstad et al., 2019), which may elucidate on species range shift and climate change. For example, it can be advantageous to add transects along the elevation gradient as it would present an opportunity for valuable information regarding vegetations response to changes in land use, climate changes, and the effects of EDW.

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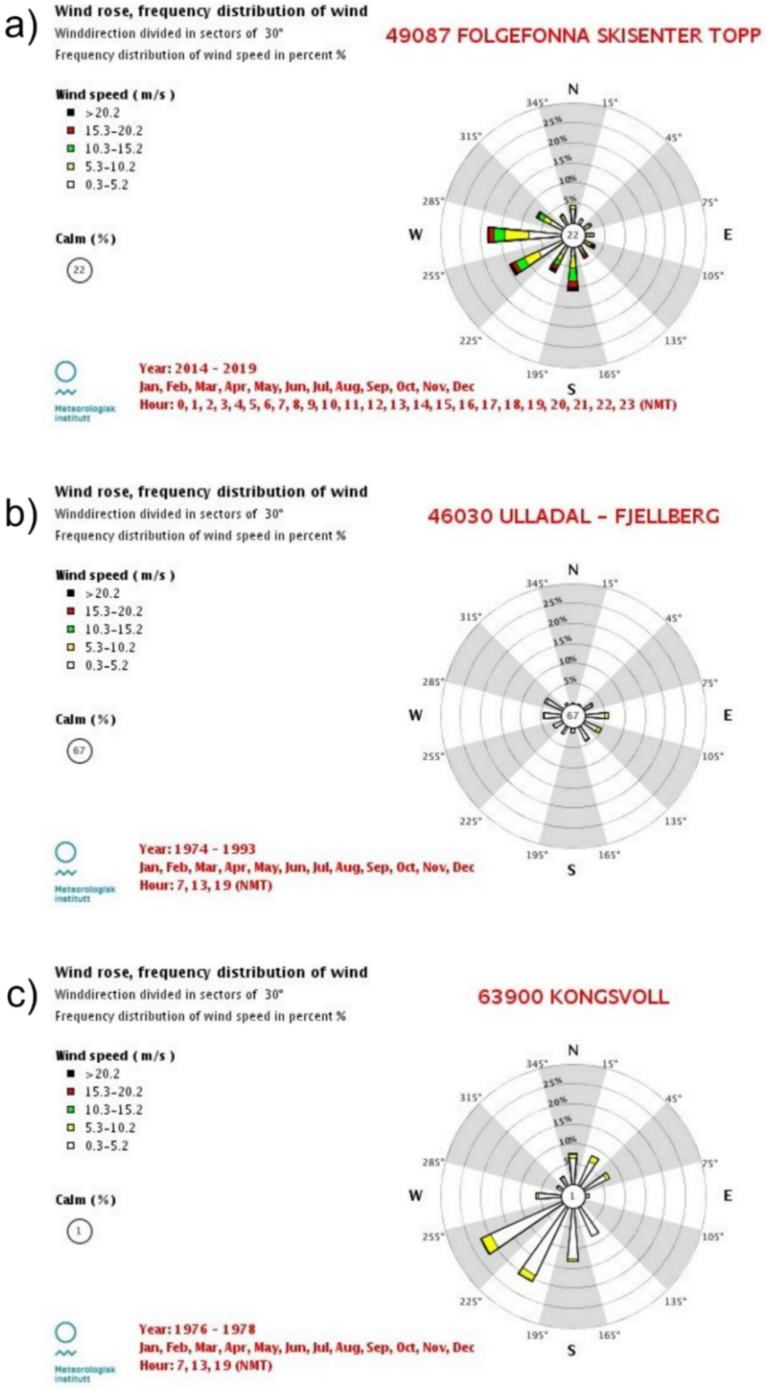
Appendices

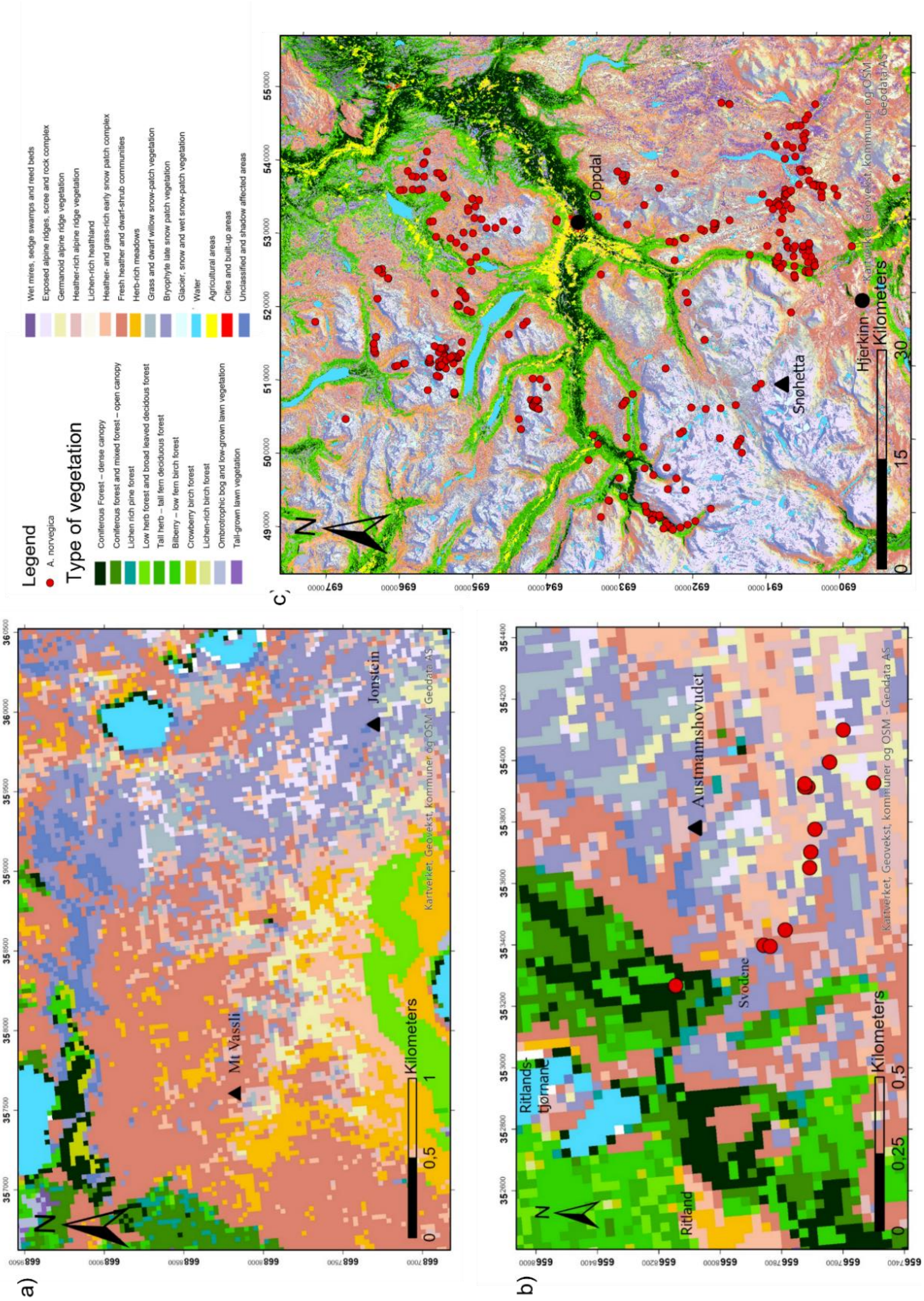
Appendix A: Wind roses

Wind roses illustrating the wind direction and speed distribution close to; a) Mt Vassli (Station Folgefonna skisenter Topp, no. SN49087, 1390 masl; b) Austmannshovudet (Station Ulladal – Fjellberg, no. 46030, 382 masl); c) Dovre (Station Kongsvoll, no. 63900, 885 masl). Source: eKlima.no (2021)



Appendix B: Vegetation maps

Vegetation map over a) Mt Vassli, Hardanger b) Autmannshovudet, Hjelmeland with earlier registered *Artemisia norvegica* Fr. occurrences, and c) Dovre with occurrence of *A. norvegica* used in current thesis niche modelling. This map is to course (30 × 30 m) to illustrate appropriate vegetation type for each fine scaled occurrence point. Source: SatVeg (2011); Artskart.artsdatabanken.no (2020).



Appendix C: Climate stations

Climate stations information and normal period mean average temperatures (MAT) used to calculate lapse rates. Sourced from eklima.no (2021).

Area of lapse rate	Climate station number	Climate station name	Latitude (UTM32)	Longitude (UTM32)	Masl (m)	Normal period MAT (°C)		
						1931-1960	1961-1990	1991-2020
Western Norway	25840	Finse	6719444.742	418099.727	1223	- 1.4	- 2.1	- 1
	55840	Fjærland - Skarestad	6813295.475	381095.839	10	5.4	5.1	6.1
Dovre area	16610 16600*	Fokstugu Fokstua*	68868834.954 6887445.580*	514934.647 514451.952*	973 952*	- 0.5	- 0.7	1
	69100	Værnes	7038259.882	596233.006	12	5.3	5.3	6.1

*Between the normal period of 1931-1960 and 1961-1990 the climate station Fokstua at Fokstugu Fjellstue was moved approximately 780 meters further up the hill, with a difference of 21 masl, and was renamed Fokstugu. In this thesis temperature from the former station was used for the 1931-1960 normal period, and the latter for 1961-1990 and 1991-2020 normal periods.

Appendix D: Formulas

Formulas used with GLM analysis to obtain optimum, tolerance and coefficient of determination (R^2, here deviance explained), based on ter Braak and Looman (1995).

$(\text{logit})\text{P} = b_0 + b_1\text{x} + b_2x^2$

P = presence, 0 or 1 (binominal)

x = elevation in masl (100 meters intervall) (continuous)

$b_{0,}$ b_1 and b_2 = parameters

optimum = $-b_2/(2b_{2)}$, where b_1 and b_2 are first and second-order polynomial coefficients

tolerance = $1/\sqrt{(-2b_2)}$

$R^2 = 1 - (residual\ variance/total\ variance)$

Appendix E: Artemisia Norvegica plot analysis

Species record used in CA-analysis. Coverage expressed as a percentage. Place code: V=Mt Vassli, Hardanger, H=Austmannshovudet, Hjelmeland, D=Dovre. Author code: M= Moe et al., 1994, A= Authour, Holm, fieldwork summer 2020, V=Vold, 1982.

Plot information:

Plot no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Place	V	V	V	V	V	V	V	V	V	V	V	A	A	A	A	A	A	D	D	D	D	D	D	D	D	D	D	D	D
Mat (°C)	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	1.73	1.73	1.73	1.22	1.73	1.22	-1.32	-1.32	-1.32	-1.85	-3.38	-4	-4	-3.38	-0.28	-2.14	-1.52	-1.52
Masl	1030	1030	1030	1010	1020	1021	1034	1027	1008	1043	1002	793	786	730	853	779	828	1430	1466	1466	1545	1430	1560	1520	1450	920	1220	1110	1160
Azimuth						70		150	245	180	182	170	190	170	148	165	180	230	230	252	270								
Exposure	Ø	Ø	Ø	NØ	.	NØ		S	SV	S	S	S	S	S	SW	S	S	SW	SW	SW	W	S	S	E	S	-	-	E	S
pH	6,6	6.2		4.8	4.7																	6.3	5.7	5.6	5.5	5.1	5.1	5.1	5.8
Source	M	M	M	M	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	V	V	V	V	V	V	V	V

<u>Plot table:</u>

Plot number		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Place		V	V	V	V	V	V	V	V	V	V	V	A	A	A	A	A	A	D	D	D	D	D	D	D	D	D	D	D	D
Source		M	M	M	M	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	V	V	V	V	V	V	V	V
Species name	**Abbreviation**																													
Agrostis mertensii	Agr_mer	0	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	2	5	0		0	0	0	0	0	0	0	0	0
Alchemilla alpina	Alc_alp	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0	0	0	2	0	0	0	0	1	0	0	0	0
Antennaria dioica	Ant_dio	0	5	5	2	0	5	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0
Arctostaphylos alpinus	Arc_alp	0	2	1	10	0	0	2	0	15	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	1
Arctostaphylos uva-ursi	Arc_uva	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Agrostis mertensii	Arg_mer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Avenella flexuosa	Ave_fle	0	0	0	0	0	0	0	0	0	0	0	2	2	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Betula nana	Bet_ana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0
Calluna vulgaris	Cal_vul	0	0	2	0	0		0	0	0	0	0	0	0	0	2	0	20	0	0	0	0	0	0	0	0	0	0	0	0
Campanula rotundifolia	Cam_rot	2	1	1	1	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Campanula uniflora	Cam_uni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0
Carex bigelowii	Car_big	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Carex rupestris	Car_rup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0
cassiope hypnoides	Cas_hyp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cerastium alpinum	Cer_alp	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0
Draba flanizensis	Dra_fla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Dryas octopetala	Dry_oct	0	0	0	0	0	0	0	0	0	0	0	0	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Empetrum hermaphroditum	Emp_her	0	1	5	5	0	2	0	0	5	0	0	0	0	10	10	0	2	0	0	0	0	0	0	0	0	2	0	2	4
Euphrasia wettsteinii	Eup_wet	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Festuca ovina	Fes_ovi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	1	1	0	0	0	1	2	1	1	1	1
Festuca vivipara	Fes_viv	5	10	2	2	1	0	2	0	5	2	0	2	2	0	0	0	2	0	0	2	2	0	0	0	0	0	0	0	0
Hieracium alpinum	Hie_alp	0	1	1	1	0	0	0	0	0	2	2	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0
Juniperus communis	Jun_com	0	0	0	0	0	0	0	0	0	0	0	30	2	10	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Juncus trifidus	Jun_tri	0	0	0	0	0	0	0	0	0	2	2	0	0	2	2	2	1	5	0	0	0	1	0	0	0	0	0	0	0
Kobresia myosuroides	Kob_myo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	10	10	2	3	0	0	0	0	0	0
Kobresia simpliciuscula	Kob_sim	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Loiseleuria procumbens	Loi_pro	0	0	10	10	5	2	0	0	0	2	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0
Luzula confusa	Luz_con	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	1	1	0	0	0	0	0
Luzula spicata	Luz_spi	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	2	2	0	0	1	1	0	0	0	1
Pedicularis oederi	Ped_oed	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Poa artica	Poa_art	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Poa flexuosa	Poa_fle	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Poa glauca	Poa_gla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Polygonum viviparum	Pol_viv	1	2	1	0	0	0	2	2	0	2	0	0	0	0	0	0	0	2	2	2	0	1	0	1	1	0	0	0	1
Potentilla crantzii	Pot_cra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Potentilla nivea	Pot_niv	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Rhodiola rosea	Rho_ros	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Rubus spp	Rub_spp	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salix herbacea	Sal_her	2	5	2	1	10	0	5	2	0	2	0	0	0	0	0	0		2	2	2	2	0	0	1	1	0	1	1	1
Salix polaris	Sal_pol	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Salix reticulata	Sal_ret	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Sassurea alpina	Sas_alp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Saxifraga nivalis	Sax_niv	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Saxifraga oppositifolia	Sax_opp	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
Sedum rosea	Sed_ros	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Silene acaulis	Sil_aca	1	0	0	0	0	0	0	2	0	0	0	0	2	0	0	0	2	2	2	0	5	1	1	1	1	0	0	0	0
Solidago virgaurea	Sol_vir	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalictrum alpinum	Tha_alp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Trisetum spicatum	Tri_spi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Vaccinium uliginosum	Vac_uli	0	0	0	1	5	0	0	0	0	5	0	0	5	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium vitis-idaea	Vac_vit	5	0	1	1	1	0	0	2	0	0	0	0	0	2	0	5	2	20	20	5	0	0	0	0	0	1	1	0	1

Appendix F: Lapse rates (°C) for Dovre and Western Norway

	Dovre				Western Norway					
masl	31-20	31-60	61-90	91-20	31-20	31-60	61-90	91-20	RCP4.5 2100	RCP8.5 2100
0	5.6	5.3	5.30	6.10	5.59	5.4	5.1	6.1	7.4	9
100	5.01	4.69	4.68	5.57	5.02	4.84	4.52	5.51	6.817	8.401
200	4.42	4.08	4.06	5.04	4.45	4.28	3.94	4.92	6.234	7.802
300	3.83	3.47	3.44	4.51	3.88	3.72	3.36	4.33	5.651	7.203
400	3.24	2.86	2.82	3.98	3.31	3.16	2.78	3.74	5.068	6.604
500	2.65	2.25	2.20	3.45	2.74	2.6	2.2	3.15	4.485	6.005
600	2.06	1.64	1.58	2.92	2.17	2.04	1.62	2.56	3.902	5.406
700	1.47	1.03	0.96	2.39	1.6	1.48	1.04	1.97	3.319	4.807
800	0.88	0.42	0.34	1.86	1.03	0.92	0.46	1.38	2.736	4.208
900	0.29	-0.19	-0.28	1.33	0.46	0.36	-0.12	0.79	2.153	3.609
1000	-0.3	-0.8	-0.90	0.80	-0.11	-0.2	-0.7	0.2	1.57	3.01
1100	-0.89	-1.41	-1.52	0.27	-0.68	-0.8	-1.28	-0.4	0.987	2.411
1200	-1.48	-2.02	-2.14	-0.26	-1.25	-1.3	-1.86	-1	0.404	1.812
1300	-2.07	-2.63	-2.76	-0.79	-1.82	-1.9	-2.44	-1.6	-0.179	1.213
1400	-2.66	-3.24	-3.38	-1.32	-2.39	-2.4	-3.02	-2.2	-0.762	0.614
1500	-3.25	-3.85	-4.00	-1.85	-2.96	-3	-3.6	-2.8	-1.345	0.015
1600	-3.84	-4.46	-4.62	-2.38	-3.53	-3.6	-4.18	-3.3	-1.928	-0.584
1700	-4.43	-5.07	-5.24	-2.91	-4.1	-4.1	-4.76	-3.9	-2.511	-1.183
1800	-5.02	-5.68	-5.86	-3.44	-4.67	-4.7	-5.34	-4.5	-3.094	-1.782
1900	-5.61	-6.29	-6.48	-3.97	-5.24	-5.2	-5.92	-5.1	-3.677	-2.381
2000	-6.2	-6.9	-7.10	-4.50	-5.81	-5.8	-6.5	-5.7	-4.26	-2.98
2100	-6.79	-7.51	-7.72	-5.03	-6.38	-6.4	-7.08	-6.3	-4.843	-3.579
2200	-7.38	-8.12	-8.34	-5.56	-6.95	-6.9	-7.66	-6.9	-5.426	-4.178

Appendix G: Temperatures (°C) from climate loggers

Recorded data (temperature in °C) from the climate loggers is published at this address (link): https://www.researchgate.net/publication/356129419_Appendix_G

Appendix H: Area of Dovre and Mt Vassli

Table of area (km^2) of each elevation interval in Dovre and Mt Vassli at Hardanger

	Dovre		Hardanger	
Masl intervall	km^2	%	Km2	%
1-99	48427,5	0.601		
100-199	49490	0.614		
200-299	81142.5	1.007		
300-399	104152.5	1.293		
400-499	229415	2.849		
500-599	444522.5	5.522	270	5.934
600-699	566890	7.042	407.5	8.956
700-799	587465	7.297	635	13.956
800-899	744290	9.245	1320	29.010
900-999	833177.5	10.350	1237.5	27.197
1000-1099	867845	10.780	680	14.945
1100-1199	837992.5	10.409		
1200-1299	820280	10.189		
1300-1399	690205	8.573		
1400-1499	488502.5	6.068		
1500-1599	298512.5	3.708		
1600-1699	193487.5	2.403		
1700-1799	102417.5	1.272		
1800-1899	29540	0.366		
1900-1999	7695	0.095		
2000-2099	2847.5	0.035		
2100-2199	1375	0.017		
2200-2278	352.5	0.004		

Appendix I: Dense point cloud

The topographic 3D model produced of Mt Vassli is published at this address (link): https://cloud.agisoft.com/shared/projects/449076c9-7925-41fa-a678-5230aad7bff1