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Understanding the Ecology of Three Mixed Northern Hepatic Mat Species at Regional Scale through Species Distribution Modelling, and Local Scale through Growth Measurements and Micro-Climatic Assessment

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Summary

Good knowledge of a species' distribution and ecology is important for a successful management. The distribution of species is determined by many factors, among climate and topography determining their potential distribution. Other factors such as dispersal mode further affects their actual distribution through the ability to disperse and establish in suitable habitats. In this thesis, the ecology of three species belonging to the nationally and globally rare mixed northern hepatic mat community is assessed in two separate studies, at a regional scale through species distribution modelling (SDM), and at a local scale for *Scapania nimbosa* Taylor through micro-climatic comparison of presence and absence sites in addition to growth measurements. The results from the second study indicate that *S. nimbosa* grows approximately 4.68 ± 2.25 mm during one growth season. In the fist study, the SDM for both *Anastrophyllum donnianum* (Hook.) Steph., *Scapania ornithopodioides* (With.) Waddell and *S. nimbosa* predicted highly suitable areas outside the known geographical range at the south-western Norwegian coast, although the model for *S. nimbosa* could not be interpreted with confidence. It was not possible to find any difference in micro-climate between presence and absence sites for *S. nimbosa*. These results indicate that all three species are limited by dispersal rather than habitat in Norway, with suitable absence sites both at a regional scale, and also at a local scale for *S. nimbosa*. *Anastrophyllum donnianum* seems to be limited from reaching highly suitable areas in northern Norway due to a barrier of unsuitable climate mainly due to insufficient summer rain. This area may become suitable if climate change leads to an increase in summer precipitation along the Norwegian coast. *Scapania ornithopodioides* is absent from northern Norway despite the presence of highly suitable habitats continuously scattered throughout large parts of the western coast. The results suggest that both *A. donnianum* and *S. ornithopodioides* prefer high rain frequency and high amount of summer rain, and medium summer temperatures peaking at approximately 10 $^{\circ}C$. This is consistent with the current understanding of the ecology for these two species. Areas that stand out as interesting for the search of potentially undiscovered populations include northern Norway, the Fosen Peninsula and the Lofoten Islands. Highly suitable areas may also be appropriate for translocation of turfs or plant fragments with the aim of increasing the abundance and geographical range of threatened species. Other studies indicate that *in situ* regeneration from plant fragments of several mixed northern hepatic mat species is likely to be successful. This is especially relevant for *S. nimbosa*, which is vulnerable due to a small geographical range in Norway and due to limited dispersal abilities, which may lead to a contraction of actual distribution and abundance in the face of climate change.

Samandrag

God forståing av utbreiing og økologi til artar er viktig for ein vellykka forvaltning. Utbreiing av artar er bestemt av fleire faktorar, blant anna klimatiske og topografiske variablar som påverkar den potensielle utbreiinga. Andre faktorar, slik som form for spreiing, påverkar vidare den faktiske utbreiinga gjennom evna til å spreie og etablere seg i gunstige habitat. I denne masteroppgåva vil økologien til tre artar som høyrer til det globalt og nasjonalt sjeldne plantesamfunnet ”mixed northern hepatic mat” undersøkast på ein regional og ein lokal skala i to separate studiar. Den første studien har som mål å lage artsutbreiingsmodellar, medan den andre samanliknar mikroklima mellom lokalitetar der torntvebladmosen *Scapania nimbosa* Taylor finnast, og tilsynelatande passande lokalitetar der arten ikkje finnast, i tillegg til å sjå på vekst hos arten. Resultata frå den andre studien indikerar at torntvebladmosen veks omkring 4.68 ± 2.25 mm i løpet av ein vekstsesong, men dette er truleg eit underestimat, og variasjonen er stor blant ulike individ. I den første studien predikerar artsutbreiingsmodellane for praktdraugmosen *Anastrophyllum donnianum* (Hook.) Steph., prakttvebladmosen *Scapania ornithopodioides* (With.) Waddellalle og torntvebladmosen at det finst gunstige habitat i store områder utanfor den kjende utbreiinga til artane langs vestkysten, sjølv om modellen for torntvebladmosen ikkje kan tolkast med sikkerheit. Praktdraugmosen ser ut til å vere hindra i å nå gunstige habitat nord i Noreg på grunn av ei barriere av ugunstig habitat grunna for lite nedbør om sommaren. Dette området kan verte gunstig for arten dersom klimaendringar fører til meir sommarnedbør langs Norskekysten. Prakttvebladmosen er fråverande frå områda nord i Noreg trass tilgang på gunstige habitat spreidd jamt langs størsteparten av Norskekysten opp til Lofoten. Både praktdraugmosen og prakttvebladmosen ser ut til å føretrekke store nedbørsmengder om sommaren, høg nedbørsfrekvens gjennom vekstsesongen og middels høge sommartemperaturar, fortrinnsvis rundt 10 $^\circ C$. Dette stemmer overeins med det vi allereie veit om økologien til desse to artane. Områder som stikk seg ut som interessante med tanke på å oppdage potensielt uoppdaga, nye populasjonar inkluderar Nord-Noreg, Fosenhalvøya og Lofoten. Slike områder med gunstig habitat kan også vere passande til transplantasjon av tuer eller plantefragment, med det formål å auke storleiken på populasjonar og den geografiske utbreiinga til trua artar. Andre studiar indikerar at *in situ* regenerering av plantefragment er sannsynlig å vere vellykka for fleire artar som høyrer til ”mixed northern hepatic mat” plantesamfunnet. Dette er særleg aktuelt for sjeldne artar som torntvebladmosen, som er spesielt sårbar grunna ei smal utbreiing i dag som kan bli mindre under klimaendringar, og grunna begrensa spreiingsevne.

Contents

1. Introduction

At a global and regional scale, climate is the main ecological factor determining plant distributions, while topographic and biotic factors tune the distribution at a local scale (Dahl, 2007). Global climatic conditions vary systematically, which is reflected by the distribution of plant species. In south-north direction and along the elevational gradient, the variation in vegetation is mainly linked to warmth during the growing season (zones). In Europe, the variation in vegetation from west to east is linked to the degree of oceanicity. High oceanicity is characterized by mild winters, cool summers, high humidity, much and frequent precipitation, and high cloudiness - features that to a large extent is due to the proximity to the ocean (Moen, 1999). Species that show a similar distribution pattern at a regional scale are grouped together in floristic elements (Schofield, 1992; Takhtajan, 1986). Species of the same floristic element are thought to share distribution patterns because they are limited by the same climatic variables, but with a difference in sensitivity (Dahl, 2007). The oceanic element is of particular interest in this thesis, whose definition and climatic limitations have been discussed by for instance Dahl (2007); Hodd and Skeffington (2011*b*); Ratcliffe (1968); Störmer (1969). The mixed northern hepatic mat community, which is the focus in this thesis, is found within the eu-oceanic sub-element (Dahl, 2007). The use of ecologically relevant environmental variables in species distribution models can help us increase our understanding of species' distribution and ecology, which is important for a successful management of species and plant communities.

1.1 Species distribution models

Species distribution modelling (SDM) has become an increasingly popular tool within the field of ecology and conservation biology (Guisan and Thuiller, 2005; Pearson, 2007) as well as other disciplines. Many software for modelling species distributions have been developed, such as GARP, BIOCLIM, MARS and Maxent (Franklin, 2010). The general concept of SDMs is that based on available occurrence data of a species of interest and relevant environmental layers, the model identifies the environmental space that the species occur in, and thereafter identifies where these environments are located in geographical space, as illustrated in Figure 1. These areas are considered suitable for the species, often expressed as a probability of finding the species or habitat suitability, or as a discrete suitable/unsuitable predictions (Pearson, 2007). SDMs both provide information on which environmental variables are most important in explaining the distribution in addition to explicitly prediction the distribution in space. Which distribution (actual or potential) the model predicts depends on the input to the model. To understand the scope of SDMs, it is important to understand the link between the environmental space in which the SDMs operate, and the geographical space in which the distribution of the species is expressed, as illustrated in Figure 1. The fundamental niche (Hutchinson, 1957) refers to the environmental space in which the species could exist and persist. However, biotic factors and geographical and historical factors usually limits a species' distribution to only part of this range, which would then correspond to their occupied niche in environmental space. Plotting the fundamental and occupied niche in geographical space would correspond to the potential distribution and actual distribution. The degree to which a species is at equilibrium with the environment, and to what degree the actual distribution has been sampled is important to consider when making SDMs, since the models use the sampled occurrence data to predict the potential distribution. If the occupied niche only covers part of the fundamental niche (non-equilibrium), then the potential distribution will be underestimated. Likewise, if only part of the actual distribution has been sampled, then the potential distribution will be even more under-estimated. Thus, the model will not be able to predict the full extent of neither the actual nor the potential distribution, and will only be an approximation. In this study we aim at predicting the potential distribution of three study species. It is suspected that all three species to a varying degree are limited by dispersal, and it is likely that the range of the occupied niche has not been sampled. Such limitations have to be considered when interpreting the results from SDMs (Pearson, 2007).

1.2 The mixed northern hepatic mat community

The mixed northern hepatic mat community, is characterized by a group of large, leafy liverworts restricted to this community, in addition to a group of more widespread species (Table 1), which grow intermixed with mosses and dwarf shrubs mainly in oceanic mountain heath (Ratcliffe, 1968). This include the three species concerned in this study, *Anastrophyllum donnianum* (Hook.) Steph., *Scapania ornithopodioides* (With.) Waddell and *S. nimbosa* Taylor. The mixed northern hepatic mat community has a northern Atlantic distribution in Europe where it is confined to the most oceanic parts of Norway, the Faeroe Islands, the British Isles and Ireland (Dahl, 2007; Ratcliffe, 1968). The most species rich communities are found in the Scottish highlands (Hodd and Skeffington, 2011*b*). Many of the mixed northern hepatic mat species have a disjunct distribution typically with occurrences in north-western North-America, eastern Himalayas and eastern Asia, while others are more widespread (Schofield and Crum, 1972). The community follows humidity factors, amount of rainfall and rain frequencies, which are thought to be the main controlling factors of its distribution. The community also seem to favour cool summer temperatures, and mild winters (Dahl, 2007; Ratcliffe, 1968). While these climatic variables mainly control the distribution of the mixed northern hepatic mat species at a regional scale, the habitat suitability at a local scale is dependent on the topography for obtaining the micro-climate that these species depend on. The community is confined to sites with specific combinations of elevation, aspect, slope contributing to high humidity through low solar radiation, shelter from wind, frequent rainfall and cloudiness (Hodd and Skeffington, 2011*b*). This typically means that the community is found in north-west to east facing well-drained slopes in the northern boreal to low alpine zones, often associated with prolonged snow cover where the liverworts are protected from winter frost (Ratcliffe,

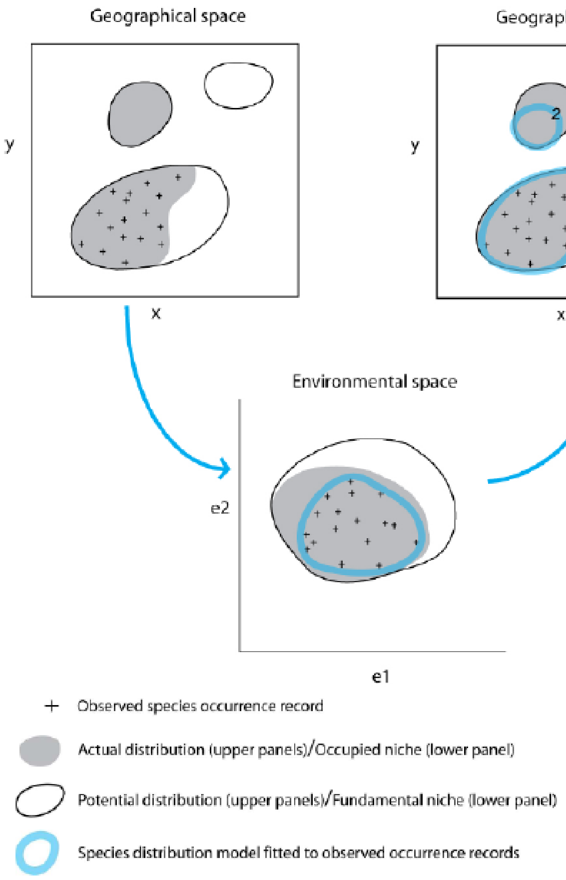

Figure 1: The theoretical framework behind SDM (from Pearson 2007), illustrated as a hypothetical example of the modelling of a species. Top panels illustrate the potential distribution (circles) actual distribution (grey area) in geographical space. Bottom panel illustrate the fundamental niche (circle) and the occupied niche (grey) in environmental space. Sampled occurrence sites are marked as ”+” in all panels. Area 2 represents an occupied but unsampled area, and area 3 represents an unoccupied but suitable area. The SDM uses the information abut the environment in the occurrence sites (blue circle in bottom panel) to predict the distribution in geographical space (blue circles in top right panel). The model succeeds in predicting part of the actual distribution and part of the unoccupied potential distribution.

Table 1: Species characteristic of the mixed northern hepatic mat community highlighted in bold, and species frequently found growing in this community. Species found in Norway, and those on the Norwegian red list are indicated. The table is based on Flagmeier *et al.* (2014); Hassel *et al.* (2010).

Species	Found in Norway	Red list status
Adelanthus lindbergianus Mitt.		
Anastrepta orcadensis (Hook.) Schiffn.	x	
Anastrophyllum alpinum Steph.		
Anastrophyllum donnianum (Hook.) Steph.	x	VU
Anastrophyllum joergensenii Schiffn.	x	EN
Barbilophozia atlantica (Kaal.) Müll.Frib.	x	
Barbilophozia floerkei (F.Weber et D.Mohr) Loeske	x	
Bazzania tricrenata (Wahlenb.) Lindb.	x	
Bazzania pearsonii Steph.		
Diplophyllum albicans (L.) Dumort.	x	
Herbertus borealis Crundw.		
Herbertus hutchinsiae (Gottsche) A.Evans	x	NT
Herbertus noreus D.G. Long, D. Bell & H.H. Blom	x	VU
Lepidozia pearsonii Spruce	x	
Mastigophora woodsii (Hook.) Nees		
Mylia taylorii (Hook.) Gray	x	
Plagiochila carringtonii (Balf.) Grolle		
Plagiochila spinulosa (Dicks.) Dumort.	x	VU
Pleurozia purpurea Lindb.	x	
Scapania gracilis Lindb.	x	
Scapania nimbosa Taylor	x	EN
Scapania ornithopodioides (With.) Waddell	x	

1968). The mixed northern hepatic mat species typically grow beneath an open canopy of *Calluna vulgaris* (L.) Hull in dwarf shrub heath, but are known to occur in wide range of habitats such as montane heath, snowbeds, alpine grasslands and scree (Hodd and Skeffington, 2011*b*; Ratcliffe, 1968).

1.3 Dispersal and distribution

To understand the current distribution of species, both at a regional and local scale, it is important to have knowledge about dispersal capacity. All species characteristic of the mixed northern hepatic mat community are dioicous (Damsholt, 2002; Paton, 1999), and have never been observed with sporophytes in Europe, with the exception of *A. donnianum* very rarely (Paton, 1999). Some species, such as *S. ornithopodioides* and *S. nimbosa*, do on rare occasions produce asexual propagules such as gemmae, but this is mostly lacking (Damsholt, 2002; Paton, 1999). Thus, it is assumed that the typical mixed northern hepatic mat species mainly rely on other means of vegetative dispersal such as fragmentation for dispersal and maintenance of local populations (Flagmeier, 2013). The disjunct worldwide distribution exhibited by many of the hepatic mat species does however suggest that they produced spores at an earlier stage in history, at which they also probably were more widespread (Schofield and Crum, 1972). Spores have been shown to travel over long distances in other species (Muñoz *et al.*, 2004; Sundberg, 2013), which makes this a possible explanation. A study by Flagmeier (2013) shows a high genetic diversity in the mixed northern hepatic mat species *Anastrophyllum alpinum* Steph., also supporting this hypothesis. The current presumably low potential for long-distance dispersal, and the potential change in climate since they previously had the possibility of spore dispersal, makes a non-equilibrium with the suitable habitat likely today, both at a regional and local scale. The genetic study on *A. alpinum* suggests that asexual vegetative dispersal is of little importance for dispersal at a regional scale, but important for maintaining local populations of (Flagmeier, 2013). Bryophytes with restricted dispersal are likely to be dispersal limited rather than habitat limited (Löbel *et al.*, 2006), especially when the suitable habitat is fragmented. Studies on rarity and life history strategies suggests that species that rarely or never reproduce sexually or by asexual propagules are most likely to be rare (Laaka-Lindberg *et al.*, 2000). Many mixed northern hepatic mat species are both considered rare (ECCB, 1995; Hassel *et al.*, 2010), and suitable habitats are fragmented in the landscape due to strict topographic requirements (Ratcliffe, 1968). Dispersal limitation seems to be the case for several species, such as *Herbertus hutchinsiae* (Gottsche) A.Evans in Scotland (Flagmeier *et al.*, 2013) and *S. nimbosa* in Norway (Jordal and Hassel, 2010). Thus, the distribution of some of the mixed northern hepatic mat species in Europe do to large extent seem to be shaped by a limited dispersal capacity.

1.4 Threats

There are several sources of threats for the mixed northern hepatic mat community, most of them anthropogenic. The community is especially vulnerable to disturbance since many of the characteristic species have restricted distribution, very specific habitat requirements and few means of effective long-distance dispersal (Hodd and Skeffington, 2011*b*). The most widely recognized threat to the mixed northern hepatic mat community is overgrazing by sheep (Hodd and Skeffington, 2011*a*). This has led to a severe degradation of the mountain vegetation, and has led to decreased frequency many places, especially in Ireland (Holyoak, 2006; Long, 2010). The most well-documented example is in the Twelve Bens of Connemara in Ireland where *Plagiochila carringtonii* (Balf.) Grolle is presumed lost from one of two known Irish sites, and *Adelanthus lindbergianus* Mitt. has been reduced from once abundant to only occur in one small site (Long, 2010). Overgrazing by livestock is likely the main reason for the observed reduction of dwarf shrub such as *Calluna* and increase in grazing-tolerant graminoid generalists in the liverwort-rich oceanic montane heaths in Scotland, which is considered less optimal for the hepatic mats (Flagmeier *et al.*, 2014). High abundance in red deer has also shown to reduced the *Calluna* cover through grazing and trampling, with the same negative cascading effect (Moore and Crawley, 2015). High livestock abundance also increase the risk of erosion, and cause nitrogen enrichment, which is highly toxic to many bryophytes (Long, 2010). Overgrazing may also threaten the Norwegian mixed northern hepatic mat communities in some localities (Jordal and Hassel, 2010), since the populations of red deer and roe deer have increased along the western coast of Norway the last 60 years (Austrheim *et al.*, 2008). Other threats are due to more direct human activities. In Norway, *S. nimbosa* was thought to be extinct due to mining activities in the only known locality. It was however found again some years later, but many of the populations are still threatened by habitat reduction due to construction of roads, water pipes and power lines in the area (Jordal and Hassel, 2010). In Scotland and Ireland, muriburning has also been recognized as a source of threat in some areas (Rothero, 2003).

In addition to direct anthropogenic driven threats, climate change is also expected to have an impact on the mixed northern hepatic mat (Flagmeier *et al.*, 2014). In Ireland, the community was projected have an increase in potential distribution with a shift northwards, but the actual distribution was projected to decrease due to low dispersal abilities (Hodd *et al.*, 2014). Possible effects of climate change along the Norwegian south-western coast include more fluctuating climate during the winter, warmer summers and more autumn precipitation (Hanssen-Bauer *et al.*, 2003). More unstable winters may lead to less protection from snow-cover, which again may increase the chance of drying out or the risk of experiencing severe frost events. Warmer summers may lead to an increase in tree cover and rise of the tree line due to a warmer climate and less intense grazing pressure in some areas in Norway (Speed *et al.*, 2010). A shift in potential range is likely to have implications for population viability, since the mixed northern hepatic mat species have very poor dispersal capacity (Flagmeier, 2013).

1.5 Conservation

The characteristic mixed northern hepatic mat species are in Europe restricted to south-western Norway, the Faeroe Islands, Ireland and Great Britain (Damsholt, 2002), and are of international importance. Several of them are red listed both in Norway (Hassel *et al.*, 2010) and in Europe (ECCB, 1995). The Norwegian populations are the northern limit of the geographical range in Europe. This underlines the conservation responsibility Norway has for this community. The limited dispersal capacity of the mixed northern hepatic mat species may inhibit their possibility to spread to new regions in response to climate change. For a successful management it is critical to have good understanding of the ecology of the constituent species, and have sufficient knowledge about the potential and actual distribution. A combination of local scale and regional scale ecological studies contribute to a good understanding of the ecology of the community.

1.6 Aims

This thesis aims at increasing our understanding of the ecology of the mixed northern hepatic mat community both at a regional and local scale through two separate studies. The first study investigates the regional scale ecology through species distribution modelling of three mixed northern hepatic mat species in Norway, *A.donnianum*, *S. ornithopodioides* and *S. nimbosa*. The second study aims at increasing our knowledge of the ecology of *S. nimbosa* at a local scale through comparing micro-climatic variables in presence sites and in seemingly suitable absence sites, in addition to measuring growth during one growth season. The results is presented as two separate manuscript drafts.

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Dispersal limitation or habitat limitation in three mixed northern hepatic mat species? Insight from species distribution modelling

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Abstract

In order to successfully manage species and plant communities, it is important to have a good understanding of the ecology and distributions. Species distribution modelling (SDM) is a useful tool to increase our understanding of the distribution of species and their ecological requirements at a regional scale. Through SDMs, this study aims at predicting the potential distribution in Norway of three mixed northern hepatic mat species, *Anastrophyllum donnianum* (Hook.) Steph., *Scapania ornithopodioides* (With.) Waddell and *S. nimbosa* Taylor, which are restricted to the most oceanic parts of north-western Europe. The models can be used to assess whether these species are limited by dispersal or suitable habitat, in addition to identifying which climatic factors are most important in determining their distribution. Maxent models were made using target-group background data, and five environmental coverage layers. All three species seem to be limited by dispersal rather than suitable habitats in Norway, although the model for *S. nimbosa* is associated with uncertainty. *Anastrophyllum donnianum* seems to be limited from reaching highly suitable areas in northern Norway due to insufficient summer rain in areas in between. If climate change leads to an increase in summer precipitation, this area may become more suitable. *Scapania ornithopodioides* is absent from northern Norway despite the presence of highly suitable habitats scattered along the coast. Both *A. donnianum* and *S. ornithopodioides* seem to prefer high rain frequency and summer rain, and medium summer temperatures peaking at approximately 10 $°C$, which agrees with our current understanding of the ecology for these two species. Both species seem to be limited from southern Norway due to too high summer temperatures. If climate change leads to higher summer temperatures, their range may be even more contracted in the southern parts. Areas of interest for the search of potentially undiscovered populations include northern Norway, the Fosen Peninsula and the Lofoten Islands.

Keywords: Species distribution modelling, Maxent, target-group background, mixed northern hepatic mat, dispersal limitation, limiting factors, MESS, conservation.

1. Introduction

Understanding species' distribution and the factors determining this is a fundamental question in plant ecology and conservation biology. The last decade there has been an enormous development in species distribution modelling (SDM) techniques and an increased availability of environmental coverage data (Franklin, 2010; Hijmans *et al.*, 2005). This allow for testing the effect of relevant environmental variables on species' distributions, as well as explicitly predicting the distribution of species in space. Such models can be useful in guiding filed surveys to improve success (Bourg *et al.*, 2005), as well as supporting conservation decisions (Guisan *et al.*, 2013; Hodd *et al.*, 2014).

In the hyper-oceanic mountainous areas along the western coast of Norway, the European fringe populations of species of the rare mixed northern hepatic mat community is found (Ratcliffe, 1968). Many of the constituent species are of high conservation value, both in Norway (Hassel *et al.*, 2010) and in Europe (ECCB, 1995). In order to conserve and manage the community, it is important to understand its distribution and climatic requirements. The mixed northern hepatic mat community has been described by several authors, who have related their distribution to macro-climatic variables (Dahl, 2007; Hill and Preston, 1998; Ratcliffe, 1968; Störmer, 1969). However, only a few attempts have been made to explicitly model the distributions of the constituent species (Hodd *et al.*, 2014).

The mixed northern hepatic mat community is characterized by a small group of dominating, large, leafy liverworts, in addition to a set of species that frequently grow in the hepatic mats without being restricted to, or characteristic of this community (Ratcliffe, 1968). The most species rich mixed northern hepatic mat communities within Europe are found in the Scottish highlands, but many species are found more widespread in the British Isles, Ireland, the Faeroe Islands and in south-western Norway (Damsholt, 2002; Paton, 1999; Ratcliffe, 1968). Many of the characteristic mixed northern hepatic mat species have disjunct populations in north-western North America, eastern Himalayas and western Asia (Schofield and Crum, 1972). The community has a north-western distribution in Europe, which is characterized by an oceanic climate. In Norway, the characteristic mixed northern hepatic mat species have a south-western distribution, where they are found within the most oceanic sections (Figure 1). The association with highly oceanic regions reflects the climatic requirements, most importantly assumed to be high rain frequency and humidity, cool summer and mild winters. Topographic variables such as aspect, slope and elevation are also assumed to play an important role in creating the right micro-climatic conditions (Ratcliffe, 1968).

Liverworts may disperse both sexually through spores, or asexually through specialized propagules or from plant fragments (Vanderpoorten and Goffinet, 2009). It has been suggested that dispersal limitation often is the cause of rarity in dioicous bryophytes with rare or no sexual or specialized asexual dispersal (Flagmeier *et al.*, 2013; Söderström and During, 2005). The species characteristic of the mixed northern hepatic mat community fall within this category, since most of them have never been observed with sporophytes, and only a few produce gemmae on rare occasions, including *Scapania ornithopodioides* (With.) Waddell and *S. nimbosa* Taylor (Damsholt, 2002; Paton, 1999). This means that dispersal of fragments attached to animals or spread by wind presumably is the most important mean for dispersal and for maintaining local populations today (Flagmeier, 2013). Spores may however have been more important at an earlier stage in history, which may at least partly explain the disjunct worldwide distribution exhibited today (Schofield and Crum, 1972). This is supported by several studies which show that spores may travel long distances (Muñoz *et al.*, 2004; Sundberg, 2013). High genetic variation in the mixed northern hepatic mat species *Anastrophyllum alpinum* Steph. also suggest that it has reproduced sexually after it came to Scotland (Flagmeier, 2013). Still, a non-equilibrium with the suitable habitat is likely for many of the characteristic mixed northern hepatic mat species in Norway today, both at a local and regional scale, due to a currently low potential for long-distance dispersal, and because the range of suitable habitats might have changed since they previously had the possibility of spore dispersal. The oceanic climate along the Norwegian coast (Moen, 1999) stretches far outside the currently known geographical range of the characteristic mixed northern hepatic mat species, which suggests that there are areas with potentially unoccupied suitable sites in Norway (Figure 1). In this study, the potential distribution of the three mixed northern hepatic mat species *Anastrophyllum donnianum* (Hook.) Steph., *S. ornithopodioides* and *S. nimbosa* will be modelled along the Norwegian coast. The aims of this study are to:

1. Estimate habitat suitability for *A. donnianum*, *S. ornithopodioides* and *S. nimbosa* along the Norwegian coast.
2. Assess whether the distributions of these three species are constrained by suitable habitat or dispersal in Norway.
3. Identify which environmental variables are the most important in predicting their potential distribution, and what habitat preferences the species have.
4. Suggest new areas for surveys with the aim of finding potentially undiscovered populations.

2. Method

2.1 Study area and study species

The western coast of Norway is characterized by a fjord landscape, with steep mountains rising up from the sea to more than 1500 meters some places. The mountains are typically more rounded and lower at the outer coast and higher further inland, where they also often have a more alpine structure. At the outer coast, the tree-line varies from 400-500 meters in south-western Norway and down to 200-300 meters as you move up along the coast and pass the Lofoten Islands. Further inland, the tree-line increases 900-1000 meters south-western parts of the study area (Moen, 1999). The high topographic variability with a steep elevational and thereby climatic gradient across relatively short distances allow for high heterogeneity in niches and nature types (Jordal and Hassel, 2010). Most of the Norwegian western coast has a climate characterized as highly (O3) and markedly (O2) oceanic sections as described by Moen (1999) (Figure 1B), which typically means mild winters, cools summers and high humidity through high and frequent rainfall and high cloudiness (Crawford, 2000).

The known distribution of the study species is presented in Figure 1A. *Scapania ornithopodioides* is relatively widespread along the western coast, while *A. donnianum* is somewhat more restricted with a central distribution in the north-west of the western coast and some scattered occurrences further south. *Scapania nimbosa* is the most restricted of these three species, only known from a small area in the north-western part of the western coast (Norwegian Biodiversity Information Centre, 2015).

We suspect that suitable habitats exist for these three species within the whole O2 and O3 section as described by Moen (1999), even though the known geographical range covers only part of these areas in Norway. For this reason, we defined the areas within these two section as the study area, delimited by a polygon with all municipalities (Norwegian Mapping Authority, 2006) containing such climate (Figure 1B). Consequently, predictions were extrapolated into new areas within the same environmental range and the same time frame as the sampled training data. This is a model-based interpolation to unsampled sites, which is considered as relatively reliable, given that the input data and settings of the model is reasonable, and that correlation between predictor variables are relatively stable across the study area (Elith and Leathwick, 2009).

2.2 Modelling method

The objectives were addressed by making species distribution models (SDM) using maximum entropy models (Maxent version 3.3.3; *http : //www.cs.princeton.edu/ schapire/maxent/*). Maxent is machine learning method specially designed for presence only (PO) data (Phillips *et al.*, 2006, 2004), and it has become very popular with more than 1000 published applications since 2006 (Merow *et al.*, 2013). It has shown to perform very well compared to many other modelling methods (Elith and Leathwick, 2009), even when the sample size is small (Hernandez *et al.*, 2006). The modelling was carried out in R (R Core Team, 2014) using the dismo package (Hijmans *et al.*, 2014). Apart from that, ArcMap was also used for data treatment and for making maps (ESRI, 2012). SDMs require two types of input data: occurrence data, both presence and background data, and environmental coverage data.

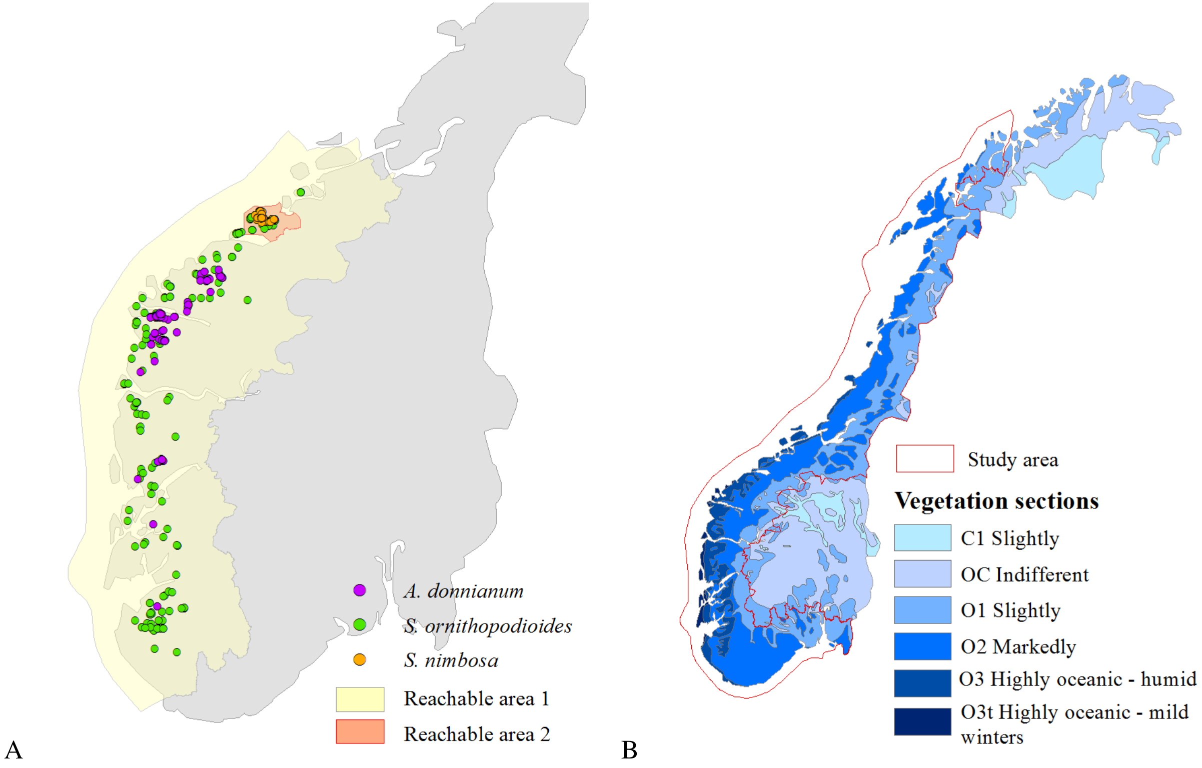


Figure 1: A: Distribution of the presence records used in the model for *A. donnianum* (purple dots), *S. ornithopodioides* (green dots) and *S. nimbosa* (orange dots). Reachable area 2 (red) applies to *S. nimbosa*, and reachable area 1 (peach) applies to the two other species. The reachable areas restrict the range from which target-group background (TGB) data and random background (BG) data are collected from. B: The study area (red line) restricts the geographical range in which predictions were made. The study area was defined as all municipalities which contain areas of markedly (O2) or highly (O3 and O3t) oceanic section as defined by Moen (1999).

2.2.1 Species occurrence data

Presence data. Occurrence data for the study species was downloaded from Norwegian Biodiversity Information Centre (2015). Both museum collections and observations were used, since the study species are easily recognized by anyone likely to know about them. As the aim of this study was to predict the current habitat suitability, records from 1950 or older were excluded from the analysis, since these localities might not represent suitable climates any longer. Duplicates were removed from the data-set. The records were controlled manually by comparing their location with the description, and moved to the correct location or removed. In particular records before 1990 and records with a slope of 0, which were potentially placed on water, were thoroughly checked. Finally, a subset of the cleaned data set was discarded under the correction of sample bias (see below). The final datasets for *A. donnianum*, *S. ornithopodioides* and *S. nimbosa* had 173, 611 and 165 records respectively (Table 1).

Table 1: Number of presence, target-group background (TGB) and random background (BG) points used in the models. The TGB and BG data is the basis for the difference between the two model types.

	A. donnianum	*S. ornithopodioides*	*S. nimbosa*
Presence	173	611	165
TGB	4200	4200	733
BG	7869	7869	665

Background data. Maxent is designed for modelling species distribution based on presence-only (PO) data (Phillips *et al.*, 2006). Instead of using absence data, Maxent uses a set of background data randomly selected from across the landscape, and uses this information to contrast the environment of the landscape to the environment at the presence sites. Maxent assumes that the species is at equilibrium with the suitable environment within the range which the random background data is generated from. The choice of the range from which background data is generated will thus have implications for ecological assumptions and the predicted outcome of the model (Elith *et al.*, 2011; Merow *et al.*, 2013). We expected that our study species are not at equilibrium with the environment, and therefore restricted the background data to the areas where the species could have reached if the environment was suitable (reachable areas). The reachable areas of *A. donnianum* and *S. ornithopodioides* was constructed by removing all municipalities from the study area south and north of the extreme occurrences, with one municipality in buffer. The reachable areas for *S. nimbosa* was defined as those municipalities with occurrences, and one municipality in buffer around (Figure 1A).

The type of background data used in a model, will also have implications for the underlying assumptions of the model. An alternative to the randomly chosen background (BG) data is to use target-group background (TGB) data. It consists of the occurrence data of a group of species likely to be recorded with the same method or by the same collectors as for the species of interest (Ponder *et al.*, 2001). Using TGB data has shown to improve model performance compared to a randomly selected background data (Phillips and Dudík, 2008) or pseudo-absence data (Mateo *et al.*, 2010). One reason is that it is likely to reflect a more correct picture of the environment where the species do not occur (Mateo *et al.*, 2010), given that the species is at equilibrium within the sampled area. Another reason is that it will contribute to correct for the sample bias, as the TGB data will reflect the same sample bias as the presence points, which in theory will cancel each other out (Phillips *et al.*, 2009).

In this study, two models were made for each species: one using the randomly generated background (BG) data from the reachable areas, the other using the TGB data. For the TGB data, the occurrence records (both observations and museum collects) from the taxon Marchantiophyta from Norwegian Biodiversity Information Centre (2015) were used. Since Maxent is designed to use background data (which also include points in presence sites), the presence data were not excluded from the TGB data (Mateo *et al.*, 2010). The TGB data were treated the same way as the presence records, although the manual control was restricted to records with slope of 0° (because they were potentially on water). The final dataset had 4200 records from the reachable area of *A. donnianum* and *S. ornithopodioides*, and 733 records from the reachable area of *S. nimbosa* (Table 1). The Marchantiophyta (liverworts) was considered a good representation for the TGB data because anyone collecting or recording liverworts would presumably also find and collect or record the study species. One consequence of this choice was that areas that are generally unsuitable to liverworts were under-represented in the model. This weakness has to be kept in mind. The two types of models made in this study, from now on referred to as TGB-models and BG-models, should be interpreted in two slightly different ways:

TGB This model estimates habitat suitability in contrast to areas suitable to liverworts generally.

BG This model estimates habitat suitability in contrast to the environment in the reachable area in general.

Sample bias. Unevenly distributed (clustered) presence records may reflect a real difference in density, but is usually due to sampling bias. The result is that environments from sparsely sampled areas are under-represented in the model, thus the presence points are unlikely to represent the true frequency of environments in which the species occur. This can greatly affect the predicted outcome of the models (Elith *et al.*, 2010). To reduce the effect of sample bias, the presence and TGB data were sub-sampled by randomly select one occurrence record within each 25×25m grid cell. In addition, as mentioned above, it has been argued that the use of TGB will help correcting the sample bias, as they are likely to reflect the same sample bias as the presence records (Phillips *et al.*, 2009).

2.2.2 Environmental coverage data

When making SDMs it is important to use existing knowledge and theory to select variables that are ecologically relevant for the modelled species. Using a range of available, but unimportant variables can give misleading predictive results which are hard to assign any ecological meaning, partially due to correlation between variables. Particularly with small data sets, there is a risk of the model to select irrelevant variables, which can greatly affect the predicted outcome (Mac Nally, 2000). The use of variables that indirectly affect distribution in models (distal variables) may lead to erroneous results if the correlation to the variable that directly affect the distribution (proximal variable) vary in space or time (Austin, 2002). Proximal variables should therefore as far as possible be used. It is also recommended to avoid using highly correlated variable pairs in the model, even though it is suggested that machine learning methods such as Maxent deal with this quite well (Merow *et al.*, 2013). The Pearson correlation coefficient between the variables was calculated in R (Table A1 in the Appendix). Selection between correlated variables (Pearson correlation coefficient $\geq$ 0.6) was based on knowledge of the species' ecological requirements. In addition, a jackknife test (Section 2.2.3 based on a 10-fold cross-validation (Section 2.2.3) was used to make sure that the area under the curve (AUC) of the receiver operating characteristic (ROC) curve would not increase when removing any of the variables in the model.

With this in mind, the predictive variables in the candidate set was based on existing knowledge from of the hepatic mat community (Dahl, 2007; Hodd and Skeffington, 2011; Ratcliffe, 1968). Four climatic and three topographic variables were considered for analysis: mean summer temperature, mean January temperature, mean summer rain, rain frequency, elevation, aspect and slope. Two topographic and three climatic variables ended up in the models based on the argumentation below (Table 2).

The restricted distribution of the hepatic mat species to oceanic areas suggests that they are dependent on a wet climate. Their distribution closely follow humidity factors, amount of rainfall and rainfall frequencies. It is assumed that it is the continuous dampness of the climate that is of importance. For this reason, it has been argued that the number of days with precipitation in a year is a better parameter than the total amount of precipitation. This will lead to a constant humid atmosphere, which again lead to low evaporation and transpiration, especially in the mountains (Ratcliffe, 1968). Ratcliffe (1968) found that *S. nimbosa* is restricted to areas with more than 200 ”rain” days, and *S. ornithopodioides* and *A. donnianum* are found in areas with 180-200 ”rain” days. In the drier localities, he found that the mixed northern hepatic mat species were associated with prolonged snow cover, which probably reduces the exposure to and the effect of the drought periods. In this study, we wanted to use a parameter which reflects the wetness of the climate during the period that the species are not protected by the snow. It was represented as the number of days with $\geq$1 mm precipitation in the growth season divided by the length of the growth season. The growth season was in this case defined as the days without snow cover. We have called this variable rain frequency. In addition, we suspected that the amount of precipitation also will affect the wetness of the climate, especially during the summer. Thus, we also included the variable summer rain in the model, defined as precipitation during the warmest quarter (Hijmans *et al.*, 2005).

Temperatures can have an indirect effect on liverworts through the effect on humidity and wetness. Warmer air will increase evaporation, especially in vegetation exposed to direct solar radiation. Generally, the cooler the climate, the wetter it becomes (Dahl, 2007). But temperature does also usually have a direct effect on plants. The distributional patterns suggests that the hepatic mat species are limited by an intolerance to high summer temperatures (Ratcliffe, 1968). This was the reason for including the mean summer temperature variable in the model, which is defined as the mean temperature of the warmest quarter (Hijmans *et al.*, 2005). Many species with a western distribution are also limited by cold winter temperatures, which also appear to be true for some of the hepatic mat species. Since mean January temperature and mean summer temperature has a correlation coefficient of 0.65, it was desirable to exclude one of the variables. The real effect of winter temperatures on the liverworts will be complicated because they are protected by the snow during long periods of the winter. Thus, mean January temperature was excluded from the candidate set.

The experienced micro-climate for the liverworts will not only depend on macro-climatic factors. The topographic properties at a local scale will also affect the wetness/humidity and temperature in a specific site. Most importantly, both temperature and evaporation rate will be higher in slopes exposed to direct solar radiation. The hepatic mat species are known for thriving best in north-west to east facing relatively steep slopes in montane areas (Ratcliffe, 1968). It could be argued that solar radiation would be the most proximal and best variable to reflect the effect of solar radiation, but this is not available. Therefore, the variables slope and aspect were included in the models instead. Elevation can often be a good predictor of the distribution, but it is a distal variable which is important through affecting the variables of actual ecological importance (Phillips *et al.*, 2006). The response to elevation is also likely to vary in space. In Eide municipality in Norway, the average elevation of *S. nimbosa* increases by 140 m from the coastal localities to the most inland localities (Jordal and Hassel, 2010). Elevation is also correlated to many of the variables in the candidate set. Therefore elevation was not included in the models.

To sum up, the variables in the models (Table 2) included: rain frequency; summer precipitation; mean summer temperature; slope; and aspect. The same variables were used for all three species, since they are thought to be limited by the same variables, although the response was expected to be somewhat different. Maps of the climatic and topographic layers are presented in Figure 2 and Figure 3.

2.2.3 Model settings

Maxent's default settings were used apart from the exceptions mentioned in the following section.

Model smoothing. In order to avoid over-fitting, the model was smoothed by increasing the beta-multiplier. It is desirable that the regularization is large enough to avoid over-fitting, but small enough to not loose real correlative patterns (zero-inflation; Elith *et al.*, 2006). There is no straight forward way to decide how smooth a model should be, so the method applied by Elith *et al.* (2010) and recommended by Merow *et al.* (2013) was used. Many different beta-multiplier values were tested, starting at 2.5, and the effect visually

Table 2: Description of the variables included in the models and ecological importance. Year denotes the period from which the rasters derives from. All rasters were projected and treated in WGS 1984 UTM Zone 33N projection, and were cropped by the study area layer in Figure 1B. *Growth season was defined as number of days with snow depth=0 cm.

Variable	Description	Ecological importance	Resolution	Range	Year	Reference
Rain frequency	Number of days with > 0 mm precipitation during the growth season × growth season^{-1}*.	High humidity is one of the most characteristic features of the oceanic climate. It is affected by the rain frequency...	1 km^2	0.40–1.88	1990-2014	Derived (Norwegian Meteorological Institute and NVE, 2014*a*,*b*)
Summer rain	Precipitation (mm) in warmest quarter.	... and the amount of precipitation among other things. The distribution of the hepatic mat species closely follow these variables (Dahl, 2007).	30 seconds ($\sim$1 km^2)	14.5–64.3 mm	1950-2000	(Hijmans *et al.*, 2005)
Mean summer temperature	Mean temperature in warmest quarter ($^\circ C$).	Liverworts of the western element seem to be limited by high summer temperatures (Ratcliffe, 1968).	30 seconds ($\sim$1 km^2)	2.0–16.3 $^\circ C$	1950-2000	(Hijmans *et al.*, 2005)
Slope	Degrees inclination of slope	Hepatic mat species prefer steep, well-drained slopes where the shade effect is good...	25×25 m	0° to 85°	2001	Derived from (Norwegian Mapping Authority, (Norge Digitalt)
Aspect	360° divided into cardinal and intercardinal directions.	...and are almost exclusively found in NW to E facing slopes (Ratcliffe, 1968).	25×25 m	1=N; 2=NE; 3=E; 4=SE; 5=S; 6=SW; 7=W; 8=NW; Flat	2001	Derived from (Norwegian Mapping Authority, (Norge Digitalt)

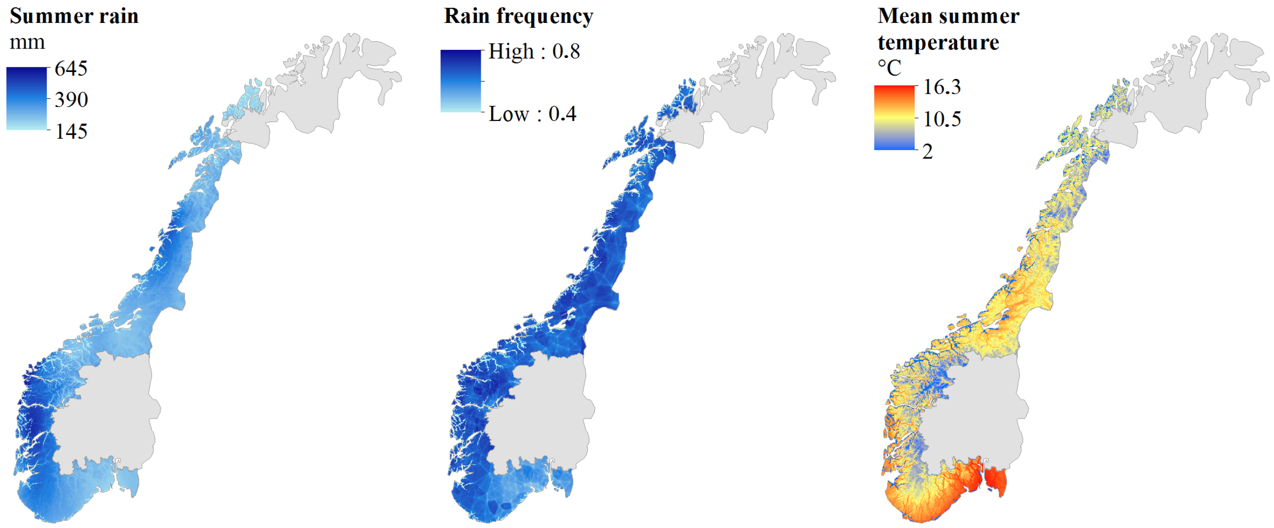


Figure 2: Map of the climatic variables within the study area. See Table 2 for description.

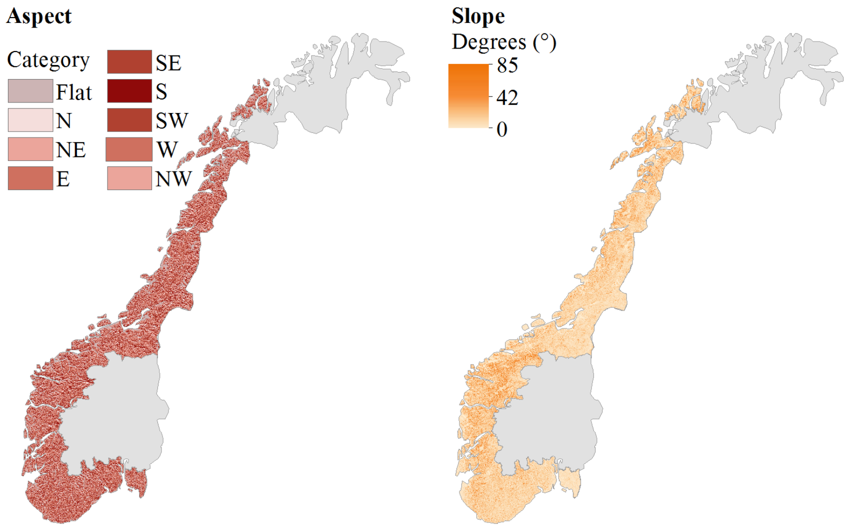


Figure 3: Map of the topographic variables within the study area. See Table 2 for further description.

assess by looking at the smoothness of the response curves (Figures 10 and A5). A beta-multiplier that removed locally complex patterns was chosen: 2 for *A. donnianum* and *S. ornithopodioides*; 1.5 for *S. nimbosa*).

Variable importance and habitat preference. To assess and rank the importance of the variables in each model, a jackknife test was conducted on the test data set. This test provides an indication of the importance of each variable by calculating the effect on the model gain when dropping variables from the model, and also when using each variable in isolation in the models. The gain is a measure of goodness of fit of the models. The higher the gain, the higher the average logistic output at the presence points compared to that at the background points. The variable which reduces the gain the most when removed from the models includes the most information which is not present in the other variables. The variable which has the highest gain when used in isolation contains the most useful information by itself. The last measure from the mean of a 10-fold cross-validation (see below) was used to rank variable importance within the models.

While the jackknife tests can identify the importance of the different variables generally, a map of the limiting factors as described by Elith *et al.* (2010) can show which factor is affecting the habitat suitability the most at any given site in the study area. This is a useful tool in order to understand the reason why certain areas are unsuitable. In each site in the study area, the value of each variable one at the time was changed from the value at that site to the mean value across the presence points. The variable which increased the habitat suitability the most when this was done was considered as the limiting factor in that site. This was done for all the TGB-models according to the instructions in the supported materials of Elith *et al.* (2010).

To assess habitat preference, or the response of the predicted habitat suitability on the variables used in the models, response curves were built. The aspect variable was defined as categorical with nine levels: Flat; N; NE; E; SE; S; SW; W; NW. Apart form that, Maxent was allowed to select automatically among all six feature classes which it offers: linear, quadratic, product, hinge, threshold and category (Elith *et al.*, 2011).

Spatial prediction maps. The default logistic output of Maxent was used to describe the habitat suitability. It was depicted as values ranging from 0 to 1 which were scaled so that 0.5 represents ”typical” conditions at the presence sites. This way, habitat suitability could be ranked as less or more suitable than the environment typical for the species in the presence sites within each model. Areas with habitat suitability $\geq$0.5 were considered highly suitable, although the actual number should not be compared between models and species (Bombosch *et al.*, 2014; Elith *et al.*, 2011; Phillips and Dudík, 2008).

Model evaluation. To evaluate the model performance, a 10-fold cross-validation was conducted. This method splits the occurrence data into ten sub-samples, where nine of the folds are used as training data, and the left out fold as test data. The model is run ten times, with each fold used as test data successively (Hastie *et al.*, 2009). The summarized statistics of the ten models are then used by Maxent to make the jackknife tests, response curves with error bars and mean AUC. The AUC was used to get an impression of the performance of each model, but it should be interpreted with care. It is a measure of how well the model is able to discriminate between presence and absence sites, and it has been argued that it provides information on how widely or restricted a species is within the range of the predictor variables (Lobo *et al.*, 2008). Further, it cannot be used to compare different models, due to different occurrence data sets. It is for instance expected that the TGB-models will have lower AUC compared with the BG-model for the same species, since the background points in the TGB-model already are in sites suitable for liverworts, while the background points in the BG-models are evenly distributed across the whole geographical and environmental range. Thus it is more difficult for the TGB-model to correctly predict presence and absence (Elith *et al.*, 2011). In this study, predictions were made outside the geographical range of the training data and into environments which were possibly different from the sampled area. Predictions into ”novel” environments are based on extrapolation in environmental space, and are associated with uncertainty. Predictions in such areas have to be interpreted with caution. MESS (Multivariate Environmental Similarity Surfaces) maps are a way of identifying these novel environments, which are areas where the values in the environmental variables lie outside the range of a set of reference points (in this case the presence and TGB/BG data). These areas will get negative values, and otherwise the value will be positive. The larger the positive value, the more similar the environment is compared to the environment at the presence locations. The MESS maps were used to identify areas with novel environments in which the predictions were considered as unreliable (Elith *et al.*, 2010).

3. Results

3.1 Prediction maps

Predicted habitat suitability for the three species across the study area is presented in Figures 4 to 6 for the TGB-models and in Figures A1 to A3 in the Appendix for the BG-models. The prediction maps illustrate habitat suitability relative to the suitable habitat for all liverworts in the TGB-models, and relative to the environment in the reachable area in general in the BG-models. For all three species, the models predict suitable habitats outside the current geographical range. At a regional scale, the predicted suitable habitat by TGB-model for *A. donnianum* seem to be split in two: one area covering the current distribution approximately between latitudes 58.5-62.5°N (although the southern part of this range is sparsely populated), and another large area between latitudes 64-67°N in northern Norway, in addition to some smaller areas in the Lofoten Islands at 69°N. The predictions by the TGB-model for *S. nimbosa* shows the same general pattern, although areas with habitat suitability ≥ 0.5 is much more sparse than for *A. donnianum*. The TGB-model for *S. ornithopodioides* predict suitable habitats more evenly spread out throughout the whole

Table 3: Ranked importance (1-5) of variables to each TGB-model based on the mean test gain obtained from a jackknife analysis when that variable is used in isolation; and mean AUC (bottom line) from a 10-fold cross-validation.

		Ordered variable importance.		
		A. donnianum	*S. ornithopodioides*	*S. nimbosa*
Variables	Summer rain	1	2	1
	Mean summer temp	2	1	2
	Rain frequency	3	3	4
	Slope	4	4	3
	Aspect	5	5	5
Mean AUC±SD		0.926±0.025	0.769±0.027	0.689±0.060

study area. Even though the areas with habitat suitability $\geq$0.5 seem quite continuous within the two suitable areas for *A. donnianum* and for *S. ornithopodioides* at a regional scale, they do on a local scale have a patchy distribution. For *S. nimbosa*, areas with habitat suitability $\geq$0.5 are even more rare and spread out. The two model types (TGB and BG) show the same general pattern both within the models for *A. donnianum* and for *S. ornithopodioides*. For *S. nimbosa* however, the TGB-model predicts higher suitability further inland between latitudes 62-64°N and 66-69°N compared to the BG-model. In the BG-model, the most suitable areas are skewed further south and towards the coast. Generally, the TGB-models are here considered as the most ecologically relevant and will therefore be the focus further in the results and discussion. Results for the BG-model is presented in the Appendix.

3.2 Variable importance

The ranked importance of the variables to the TGB-models is presented in Table 3 and is based on the jackknife test, presented in Figure 8. For *A. donnianum* and *S. nimbosa*, the two most important variables are summer rain and mean summer temperature respectively, although the difference is marginal. The ordered importance is switched for *S. ornithopodioides*. The third most important variable is rain frequency for *A. donnianum* and *S. ornithopodioides*, and slope for *S. nimbosa*. For all species, the least important variable is aspect.

While the ranking based on the jackknife test says something about which variables are the most influential on the model gain overall, this might vary in space, which is illustrated by the maps of the limiting factors in Figure 9. The general pattern for all species is that climatic variables dominate as the limiting factor in areas with low habitat suitability, while topographic variables dominate as the limiting factor in areas with high habitat suitability. Why an area has low habitat suitability can be interpreted by comparing the values of the limiting factors in this area with the values of the respective variable in areas with high habitat suitability (Figure 2 and 3). For *A. donnianum*, too high mean summer temperatures stand out as the main reason for low habitat suitability in the south and south-eastern parts of the study area, and some parts in the north. Too little summer rain is the main

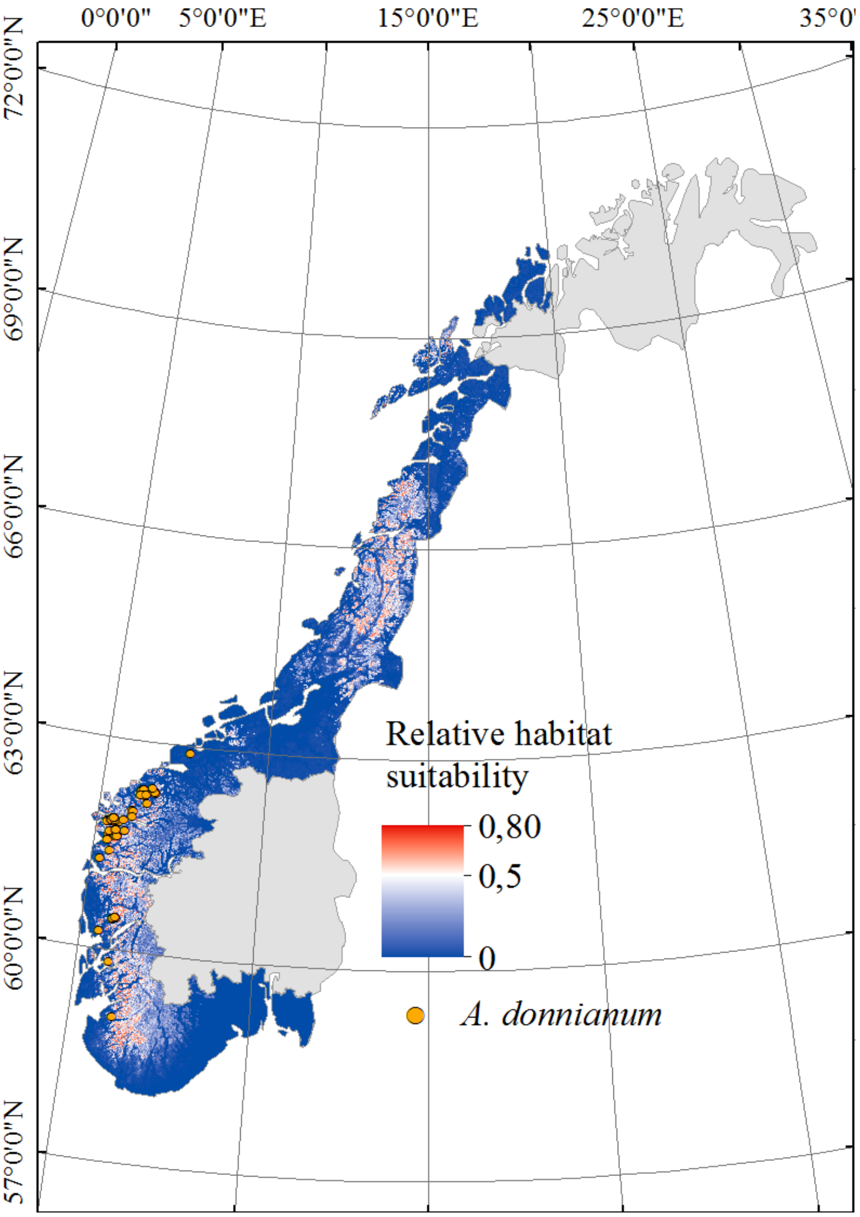


Figure 4: Predicted habitat suitability for *A. donnianum* from the TGB-model. The habitat suitability can be interpreted as more or less suitable than the typical environment at the presence sites (0.5).

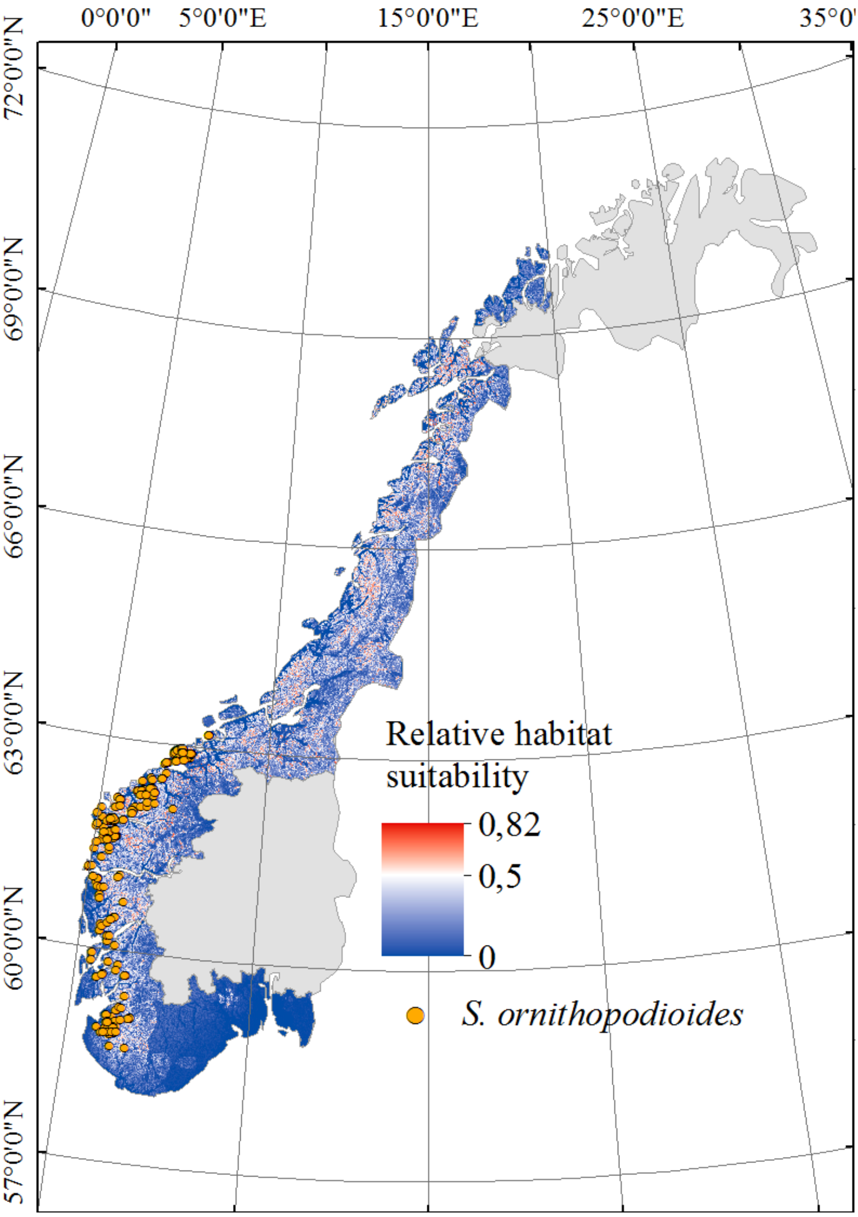


Figure 5: Predicted habitat suitability for *S. ornithopodioides* from the TGB-model. The habitat suitability can be interpreted as more or less suitable than the typical environment at the presence sites (0.5).

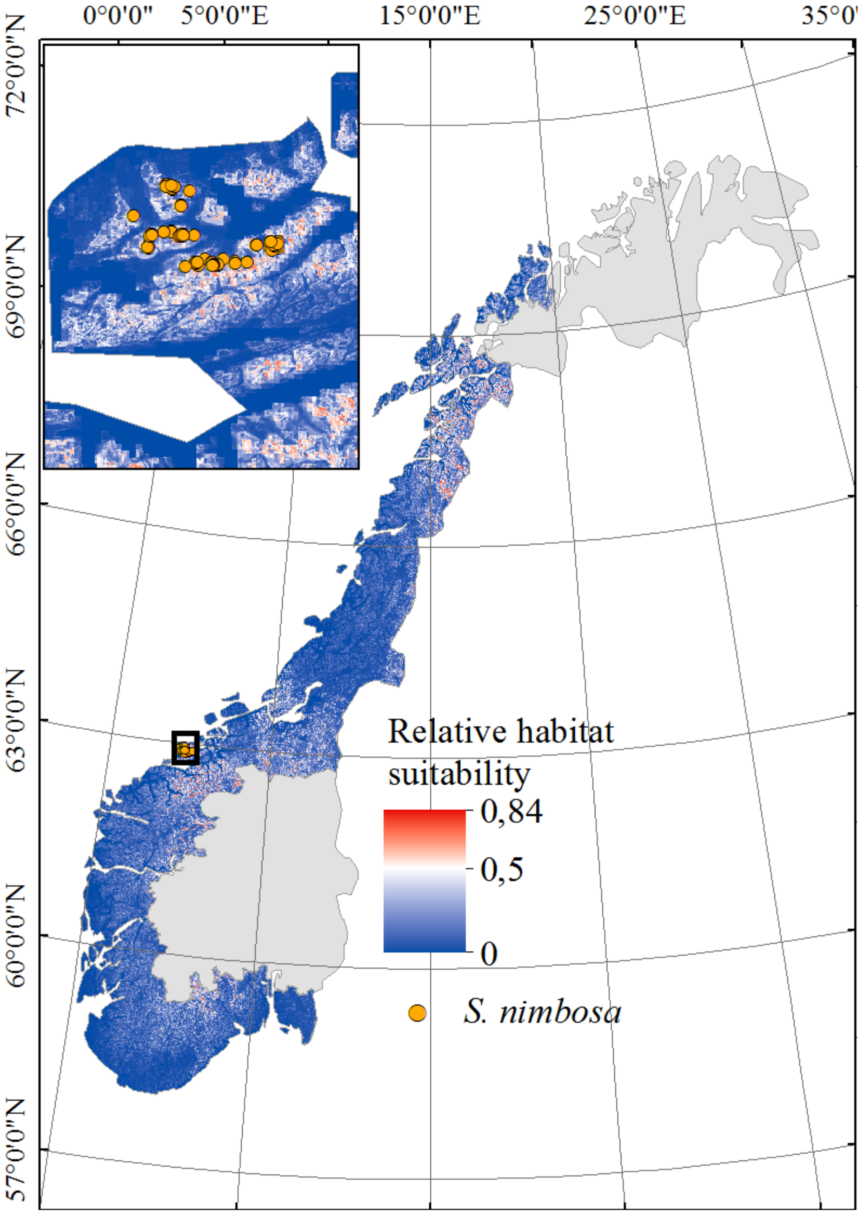


Figure 6: Predicted habitat suitability for *S. nimbosa* from the TGB-model. The habitat suitability can be interpreted as more or less suitable than the typical environment at the presence sites (0.5). The inset map in top left corner is zoomed in on the geographical range of *S. nimbosa*.

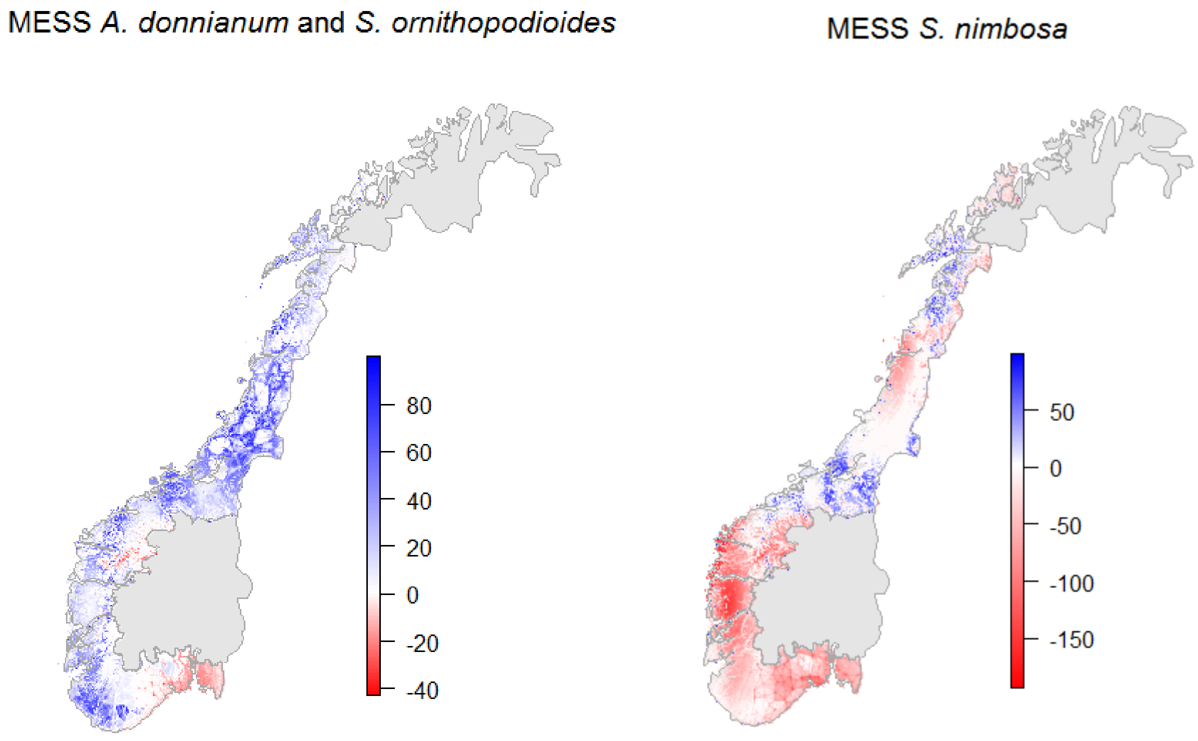


Figure 7: MESS-maps (Multivariate Environmental Similarity Surfaces) warning against prediction uncertainty in red areas. Red areas indicate ”novel” environments compared to the environment at the sampled sites. The larger the positive value, the more similar the environment is compared to the environment at the presence locations. A location get negative values if at least one variable has a value which is outside the range of the environmental range of the sampled points (Elith *et al.*, 2010).

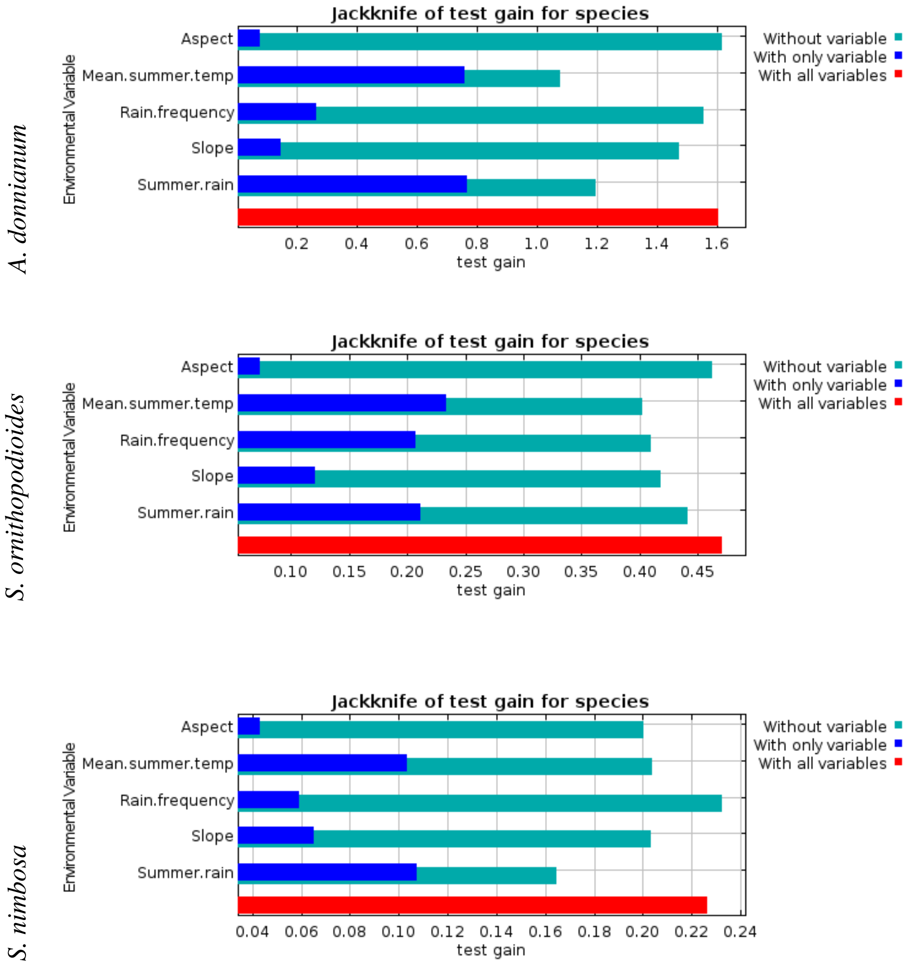


Figure 8: Jackknife test for the TGB-model of each species showing the effect of removing variables from the model (light blue), and using variables in isolation (dark blue), compared with the full model (red bar) on the model gain using the test data. The higher test gain the single variable models have, the more information the respective variable contain in itself. This measure was used to rank the importance of the variables to the models (Table 3). The jackknife test is the mean from a 10-fold cross-validation. For description of variables, see Table 2.

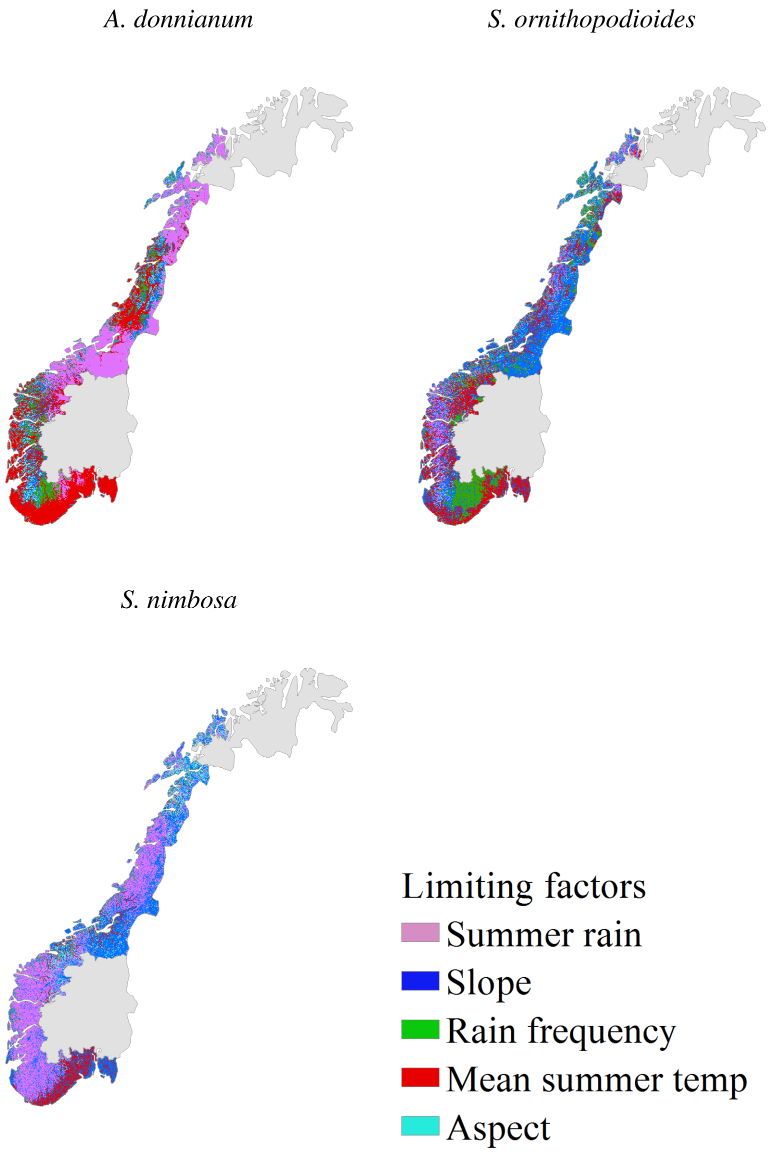
reason for low habitat suitability in central and northern parts of the study area. Too high summer temperatures seems to be the case also for *S. ornithopodioides* in the south and south-eastern parts of the study area, in addition to too low rain frequency. Too low summer temperatures seems to be the case in some of the montane inland areas in the central part of the study area. Slope stand out as the limiting factor in large parts of the areas with high habitat suitability, but intermixed with summer rain along the south-western parts of the coast. For *S. nimbosa*, summer rain is the limiting factor in most part of the areas with low habitat suitability, apart from a small area in the south, where too high summer temperatures is the most limiting factor. Also here, slope is the dominating limiting factor in areas with high habitat suitability.

3.3 Habitat preference

Habitat preference is interpreted from the response of the predicted habitat suitability to a marginal change in each variable, all other variables set to their average value. Values giving a high habitat suitability ($\geq$0.5) can be considered as preferable for the species. The response curves are presented in Figure 10 for the TGB-models. The response to summer rain varies between species. *Anastrophyllum donnianum* responds abruptly from low to high habitat suitability as summer rain increases past approximately 270 mm in the warmest quarter, while *S. ornithopodioides* responds with a stable habitat suitability at 0.5 after a small peak at approximately 250 mm. *Scapania nimbosa* has a humped shape response, with a peak at approximately 245 mm. Both *A. donnianum* and *S. ornithopodioides* has a humped-shaped response to mean summer temperature, with highest habitat suitability at intermediate mean temperatures peaking at approximately 10 $^\circ C$. *Scapania nimbosa* has highest habitat suitability at approximately 8 $^\circ C$, which decrease with increasing mean temperatures up to 13 $^\circ C$. As the frequency of rain days during the growth season increase, the habitat suitability increases steadily with a small hump around 0.7 for *A. donnianum*, and with an abrupt increase in habitat suitability after a small peak at approximately 0.65 for *S. ornithopodioides*, but decreases steadily for *S. nimbosa*. The response to slope is similar for both *S. ornithopodioides* and *S. nimbosa*, with low habitat suitability in flat areas, then stable, and relative high habitat suitability at slopes between approximately 12-64°. *Anastrophyllum donnianum* responds with a peak habitat suitability at approximately 15°, which then decrease strongly towards 64° and more weakly towards flat ground. There is no strong response to aspect, but a small decrease in habitat suitability towards north-west to west for *A. donnianum*, in south-east to south-west facing slopes for *S. ornithopodioides* and towards the north and south for *S. nimbosa*.

3.4 Model evaluation

Since predictions were made into new geographical areas, MESS-maps were made to assess the reliability of the predictions. Red areas in the map indicate areas where the environment fall outside the range of the sampled sites. These areas are predicted based on



A. donnianum

S. ornithopodioides

S. nimbosa

Figure 9: Maps showing which variable is the limiting factor across the study area based on the TGB-model for all three study species. The limiting factor is the variable which increases the habitat suitability the most when the value in that site is changed to the mean value of that variable across the presence points.

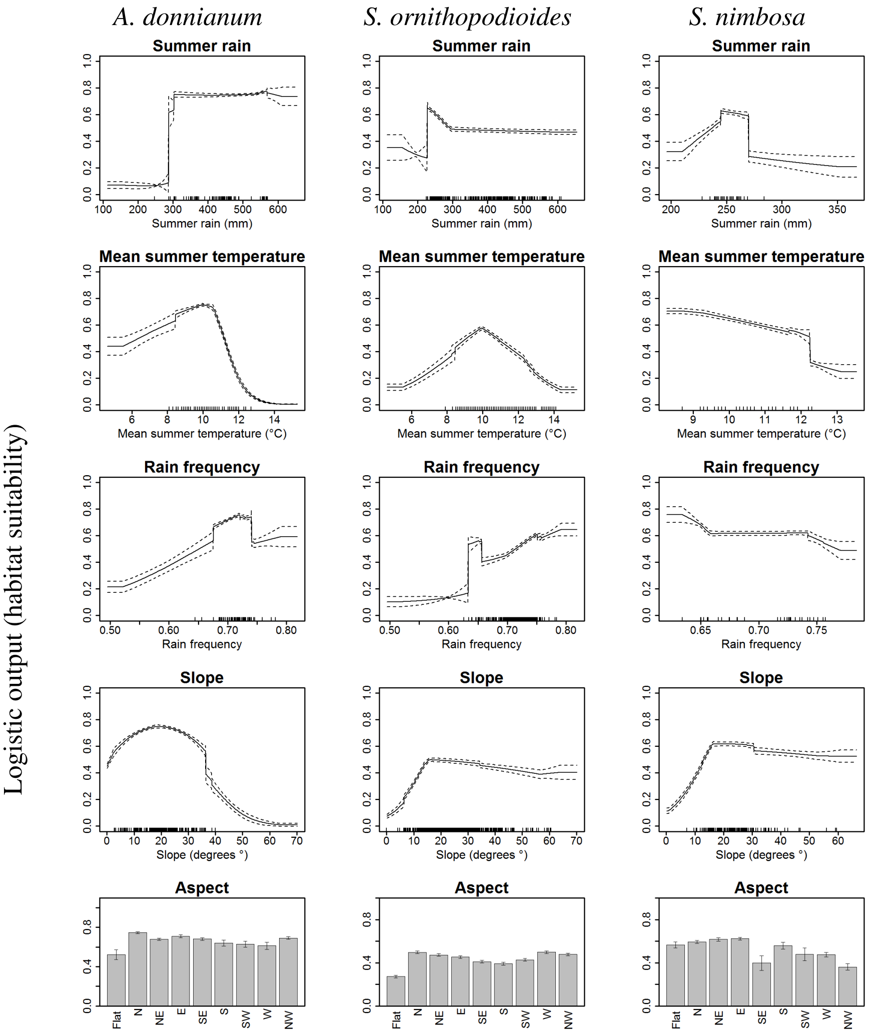


Figure 10: Response curves from TGB-model of *A. donnianum* (left column), *S. ornithopodioides* (centre) and *S. nimbosa* (right column). The curves show how the habitat suitability vary with a marginal change of each variable (solid line) with standard deviation (stippled line), all other variables set to their average value. The curves are based on a 10-fold cross-validation. The presence records are marked with tick marks on inside of x-axis. The response curves reflect the habitat preference for each species.

extrapolation, which is associated with uncertainty. The MESS map of the TGB-models is presented in Figure 7. Two areas are associated with uncertainty for *A. donnianum* and *S. ornithopodioides*: one in the south-west of the study area, and one in the central, inland areas. The MESS-map for *S. nimbosa* warn against uncertainty in large part of the study area, especially south of the current geographical range of the species, and some parts in northern Norway.

The AUC-values for *A. donnianum* (0.926) is higher than for *S. ornithopodioides* (0.769), which again is higher than for *S. nimbosa* (0.689) (Table 3).

4. Discussion

Highly suitable habitat is predicted both inside and outside the known geographical range of the study species, indicating that they are dispersal limited, rather than habitat limited in Norway. *Anastrophyllum donnianum* seem to be limited from reaching the highly suitable areas in northern Norway due to insufficient summer rain in the area in between. *Scapania ornithopodioides* is absent from northern Norway despite frequent but fragmented occurrence of suitable areas throughout the study area. The predicted habitat preference for *A. donnianum* and *S. ornithopodioides* agree with the established view that mixed northern hepatic mat species are confined to areas with wet climate, and are limited by high summer temperatures (Ratcliffe, 1968). Due to the high uncertainty in the model for *S. nimbosa*, the predictions and results of this model will not be discussed further.

4.1 Predicted habitat suitability and known distribution.

For both *A. donnianum* and *S. ornithopodioides*, habitat suitability ≥ 0.5 is predicted in new areas both outside and inside the currently known geographical rage. This study thus indicate that these two species are constrained by dispersal rather than suitable habitats in Norway. At a regional scale, the highly suitable habitats for *A. donnianum* seem to be split in two large areas (Figure 4). This suggests that *A. donnianum* is constrained from reaching the suitable areas in the north by a dispersal barrier consisting of unsuitable habitats mainly due to insufficient summer rain (Figure 9). A distinct dispersal barrier like this does not seem to be the case for *S. ornithopodioides*, which has highly suitable areas predicted more evenly throughout the study area (Figure 5). None of the study species are known to produce sporophytes, and *S. ornithopodioides* is only rarely found with gemmae in Norway (Damsholt, 2002). Thus they most likely disperse through plant fragments (Flagmeier, 2013), which makes it challenging to spread even relatively short distances within or between mountains. The highly suitable areas seem to be fragmented at a local scale, and are even more fragmented at a micro-scale, since they depend on specific topographic combinations, only found scattered in the landscape (Ratcliffe, 1968).

Distance between suitable habitats and dispersal ability are though to be the main factors determining the degree of habitat limitations (Herben and Söderström, 1992). Thus, the fragmented suitable habitats and the relatively poor dispersal ability of these two species may explain why their actual range is much smaller than their potential range, and why the density of *A. donnianum* seems to be very low especially in some areas. The fact that *S. ornithopodioides* sometimes does produce gemmae might be a reason why it is more common and widespread than *A. donnianum* (Hassel *et al.*, 2010).

Historical factors also affect distribution patterns. There are two main hypothesis about how the disjunct worldwide distributions of the study species has occurred. The 'vicariance hypothesis' suggests that the European populations are remains of a more widespread, continuous distribution which has shrunk in response to changing climate across the time of history. The 'dispersal hypothesis' suggests that the species with such disjunct distribution has arrived Europe more recently through long distance dispersal by wind-borne spores (Schofield and Crum, 1972; Schuster, 1983). Although both hypothesis may play a role together in explaining the global disjunction, the distribution hypothesis seems to be the most likely for the characteristic mixed northern hepatic mat species (Hodd and Skeffington, 2011). The big difference in known geographical range for these three species in Norway despite large, seemingly unoccupied areas with suitable habitats suggests that *S. ornithopodioides* arrived Norway before *A. donnianum*, which again arrived before *S. nimbosa*. Another explanation may be that they have colonized Norway through several, few and one colonization event, respectively. The reason for the centred distribution for all three species in the north-western part of the coast may be because the winds here often have swept the British Isles, where the three study species are more common (Blockeel *et al.*, 2014), before arriving the Norwegian coast. Thus, the south-western coast of Norway stands out as a natural landing place for anything arriving with the winds (Hurrell *et al.*, 2003).

4.2 Variable importance and habitat preference

The climatic variables are the most important in predicting the distribution both for *A. donnianum* and *S. ornithopodioides*. This is consistent with the general view that distributions at regional scale are mainly shaped by climate, while topographic and edaphic factors tune this into a complex, heterogeneous pattern at a local scale (Dahl, 2007; Moen, 1999). This explains the pattern illustrated in the maps of the limiting factors (Figure 9), where climatic variables are the main limiting factors in areas with low habitat suitability, and topographic variables in areas with high habitat suitability.

Both *A. donnianum* and *S. ornithopodioides* have similar habitat preferences. They prefer high amount of summer precipitation, high rain frequency during the growth season, and medium summer temperatures with a peak at approximately 10 $°C$. This is consistent with the established view that mixed northern hepatic mat species are restricted to wet climates and are limited by high summer temperatures (Hodd and Skeffington, 2011; Ratcliffe, 1968). Low summer temperatures are probably not directly problematic for the mixed northern hepatic mat species since bryophytes generally grow well even at low temperatures (Furness and Grime, 1982). The low preference to low summer temperatures may thus be related to a high positive correlated to mean January temperature (Pearson correlation coefficient of 0.65), which may reflect a limitation to severe winter frost (Ratcliffe, 1968). Since the study species are almost exclusively found in north-west to east facing slopes it was surprising that aspect had almost no impact on any of the models. One reason for this may be that the distribution of the TGB data along the aspect variable was similar to that of the presence data (not presented). Another explanation may be that the scale used for the aspect variable have prevented the model from catching this relationship. The variable used in the model had a resolution of 25×25 m. Both 100×100 m and 250×250 m were also tested (not presented), but this had no significant effect on the models.

4.3 Reliability of model predictions

The SDMs represent a qualified guess about how the habitat suitability for each species is distributed in space. They do however have several weaknesses which add uncertainty to the predictions (Section 2). These have to be kept in mind when interpreting the results.

The model for *A. donnianum* has a higher AUC than the model for *S. ornithopodioides*. Although one should be careful to compare different models, it is evident that areas with habitat suitability $\geq$0.5 is more evenly distributed within the study area for *S. ornithopodioides* than for *A. donnianum*. Together this may indicate that *S. ornithopodioides* has less strict habitat preferences than *A. donnianum* (Lobo *et al.*, 2008).

4.4 Climate change

Climate change within 2030-2049 is projected to increase the amount of precipitation during the winter, and possibly also during the summer along the south-western coast of Norway. An increased temperature of 1-2.5 $°C$ is projected depending on the location in Norway, with less increase in temperature along the coast than further inland. Reduced snow-cover during the winter may be one of the consequences (Hanssen-Bauer *et al.*, 2003). The predicted habitat preference for *A. donnianum* and *S. ornithopodioides* suggest that an increase in precipitation will likely be favourable, possibly increasing the habitat suitability in central Norway where summer rain is currently the limiting factor for *A. donnianum*. An increase in temperature will likely be unfavourable, possibly reducing the potential distribution both for *A. donnianum* and *S. ornithopodioides* in the southern parts of the study area, where too high summer temperatures already is the limiting factor. A reduced snow cover may lead to loss of protection from winter frost, which is considered important especially for the more montane mixed northern hepatic mat species such as *A. donnianum* and *S. nimbosa* (Ratcliffe, 1968). How the sum of the climate change will affect the potential and actual distribution of the mixed northern hepatic mat species is uncertain. A study from Ireland projects that this community will mainly show a northward shift in potential distribution in response to climate change in Ireland, but the cause of this shift is unclear (Hodd *et al.*, 2014). In Ireland, climate change is projected to lead to higher annual temperatures, increased winter precipitation and decreased summer precipitation (Dunne *et al.*, 2008). Apart from a decrease in summer precipitation, this is similar to the changes that are projected to occur in Norway. Thus a northward shift in potential distribution may also be the case in Norway. Due to limited dispersal mainly in form of plant fragments, a shift in actual distribution in face of climate change may be challenging, possibly leading to a reduction in actual distribution. Thus, conservation actions may be appropriate, especially for the more rare mixed northern hepatic mat species such as *S. nimbosa*.

4.5 Conservation application

In order to manage the mixed northern hepatic mat community in Norway, it is important to have knowledge about the current distribution and the ecological requirement of the constituent species. This study improves our understanding of the ecology at a regional scale, and provides prediction maps of the habitat suitability of three mixed northern hepatic mat species. The prediction maps can be useful to locate areas where new yet undiscovered population may be found, or new populations could establish. Considering the ongoing climate change, conservation actions of threatened species through translocation of turfs or fragments may be a possibility (Flagmeier *et al.*, 2013). Due to the specific topographic requirements it is however also important with a good ecological understanding at a local scale. The study in Manuscript II (Wangen, Unpublished) suggests that we understand the ecology of *S. nimbosa* quite well.

4.6 Areas suggested for new surveys

Many areas are still not well surveyed by bryologists. Thus, there might still be undiscovered populations of the study species outside the currently known geographical range. Especially the area indicated as highly suitable for *A. donnianum* between latitudes 64-67°N mainly in Nordland county in northern Norway would be interesting to survey since it is large, and has been relatively poorly surveyed for liverworts earlier. While Nordland county (38,481 km^2) has 2698 observations and herbarium collects of liverworts (Marchantiophyta), the geographically much smaller counties Møre og Romsdal (15,100 km^2) and Sogn og Fjordane (17,619 km^2) has 6917 and 3476 observations and herbarium collects respectively (Norwegian Biodiversity Information Centre, 2015). The main know distribution of *A. donnianum* is found in the transition between these two counties. The area in Nordland also comprises areas indicated as suitable for *S. ornithopodioides*. Other areas of interest are the Fosen Peninsula at the coast at approximately 64°N and the Lofoten Islands between 68-69°N. These areas are environmentally similar to that of the sampled sites for *S. nimbosa* and are also predicted as suitable. The same areas are predicted as suitable for *S. ornithopodioides*, but only the Lofoten Islands are also predicted as suitable for *A. donnianum*.

4.7 Further study

The study species seem to be at non-equilibrium in Norway, thus it would be interesting to make a model including the British Isles and the Faeroe Islands in order to get more data on their distribution in environmental space. This would probably improve the accuracy of the models, especially for *S. nimbosa* which probably only is found within a small part of its environmental range in Norway (Jordal and Hassel, 2010). To be able to more precisely answer the question of whether the study species are at equilibrium with the suitable environment in Norway, it would be useful to also model the actual distribution for comparison. In such a model, variables of dispersal constraint should be included.

5. Conclusion

This study provides predicted habitat suitability maps for the three mixed northern hepatic mat species *A. donnianum*, *S. ornithopodioides* and *S. nimbosa*. The results indicate that none of the species are limited by suitable habitats in Norway although the model for *S. nimbosa* is uncertain. Both *A. donnianum* and *S. ornithopodioides* prefer high rain frequency and summer rain, and medium mean summer temperatures at approximately 10 $^{\circ}C$. This agrees with the known ecology of these species (Ratcliffe, 1968). Two highly suitable areas for *A. donnianum* seems to be split by unsuitable areas due to insufficient summer rain. This area may become more suitable if climate change leads to increased summer precipitation. Both species seem to be limited by too high summer temperatures in southern Norway. If climate change leads to increased temperatures, their range may be contracted in the southern parts. Areas of special interest for new field surveys with the aim at finding potentially undiscovered populations include the Fosen Peninsula, the Lofoten Islands and the areas indicated as highly suitable for *A. donnianum* in northern Norway.

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A. Appendix

Table A1: Pearson correlation matrix with correlation coefficient for all pairs of variables in the candidate set. Values higher than 0.50 are highlighted in bold. A correlation value of 0.6 was selected as the threshold for accepted correlation between variables in the models. Selection between correlated variables was based on knowledge of the species' ecological requirements.

Variables	Mean summer temp	Summer rain	Rain frequency	Mean Jan temp	Slope	Aspect	Elevation
Mean summer temp	1						
Summer rain	0.18	1					
Rain frequency	0.46	0.48	1				
Mean Jan temp	**0.65**	0.31	0.05	1			
Slope	0.22	0.17	0.13	0.0034	1		
Aspect	0.12	0.06	0.43	0.088	0.48	1	
Elevation	**0.55**	0.43	0.096	**0.54**	0.35	0.38	1

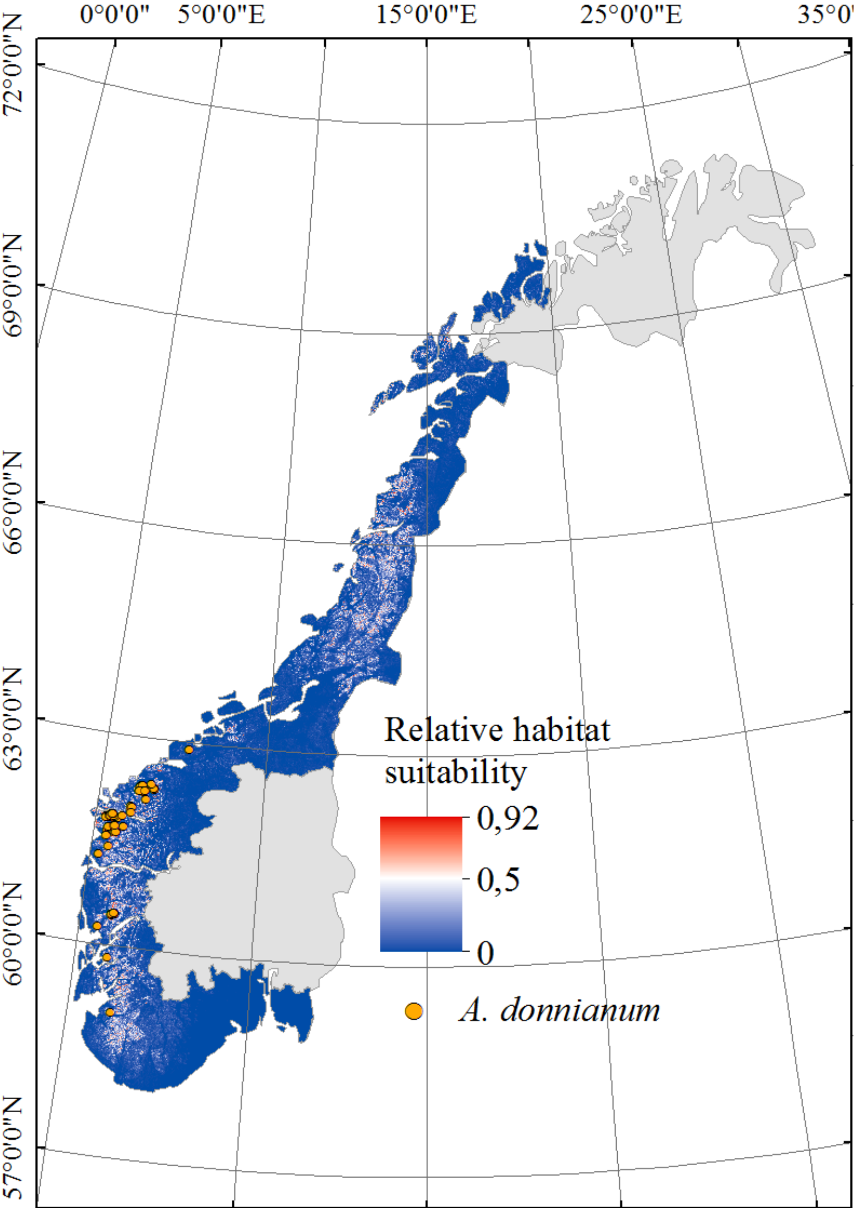

Figure A1: Predicted habitat suitability for *A. donnianum* from the BG-model. The habitat suitability can be interpreted as better or worse than the typical environment at the presence sites (0.5).

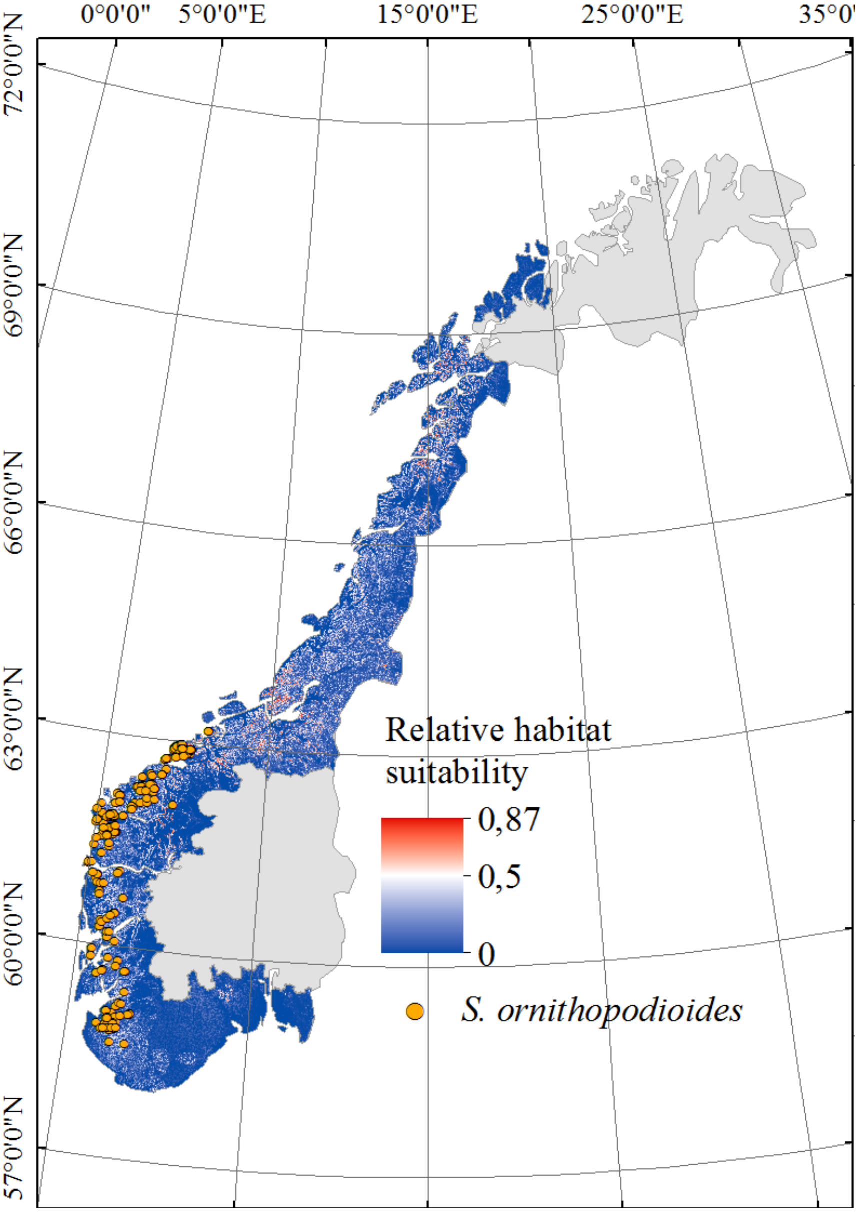

Figure A2: Predicted habitat suitability for *S. ornithopodioides* from the BG-model. The habitat suitability can be interpreted as better or worse than the typical environment at the presence sites (0.5).

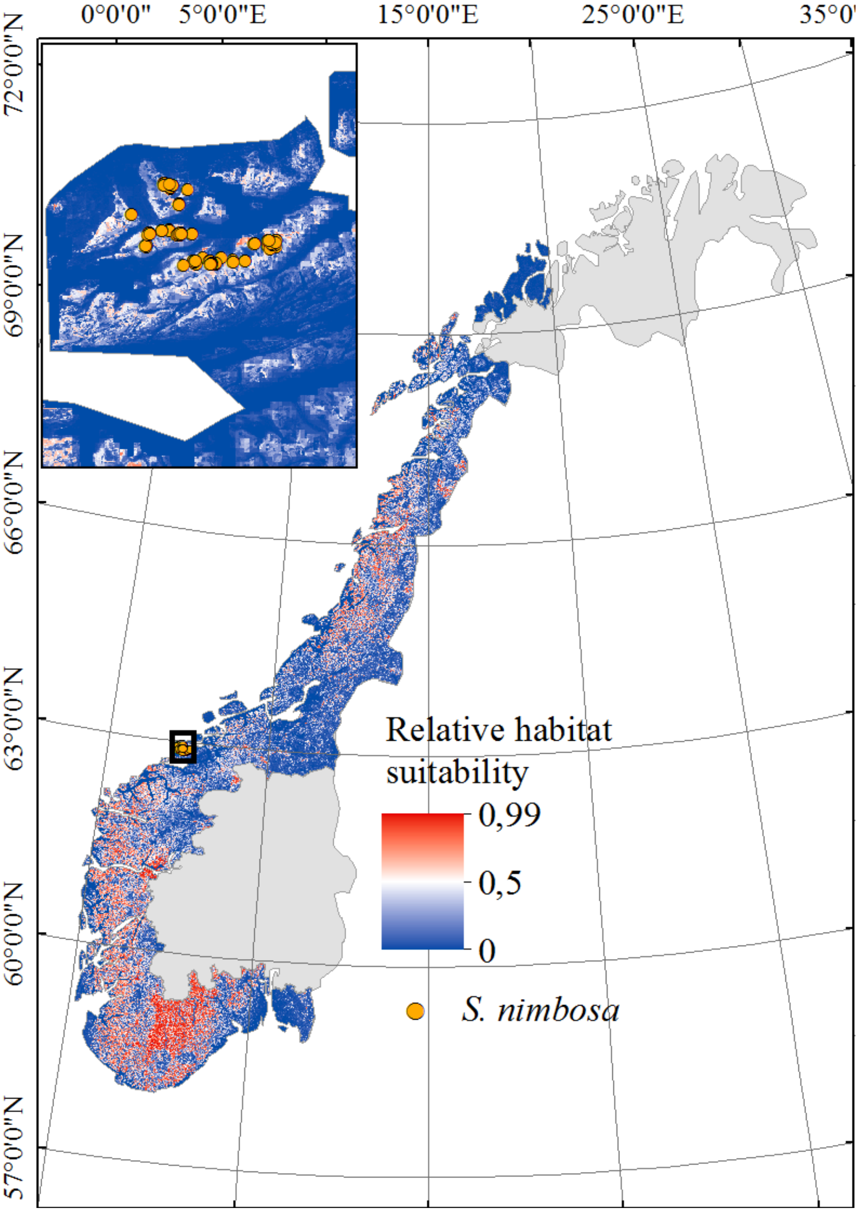

Figure A3: Predicted habitat suitability for *S. nimbosa* from the BG-model. The habitat suitability can be interpreted as better or worse than the typical environment at the presence sites (0.5). The inset map in top left corner is zoomed in on the geographical range of *S. nimbosa*.

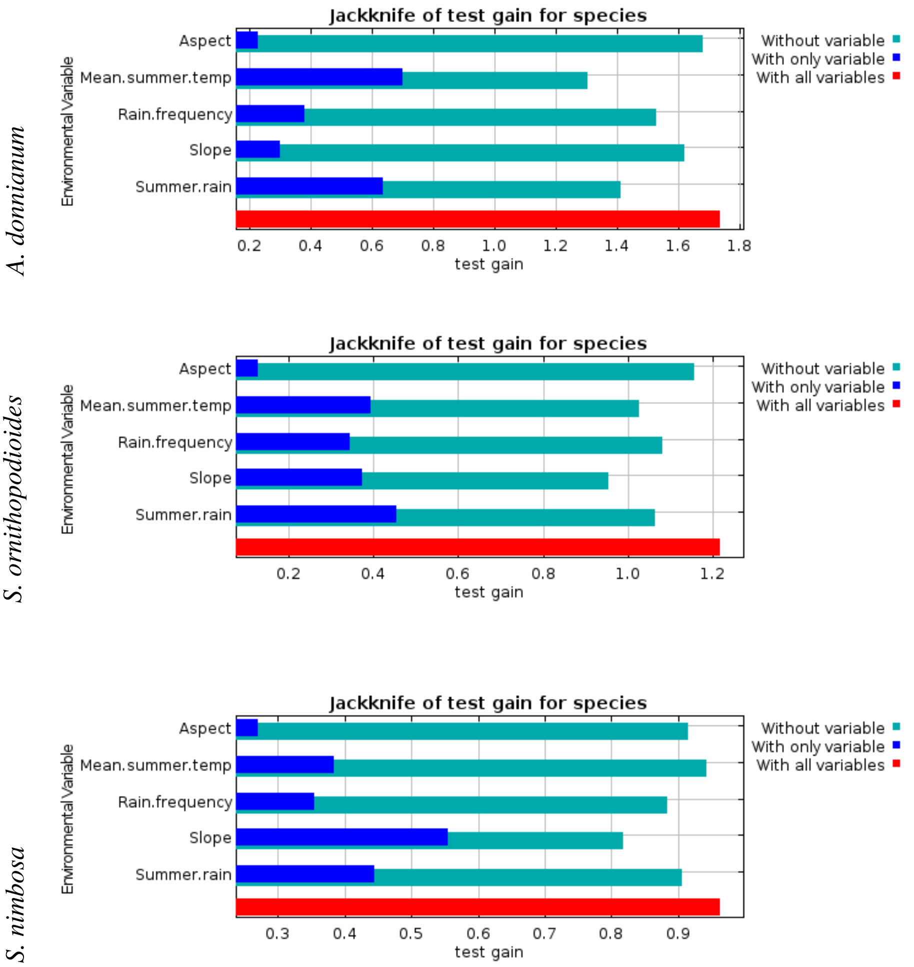

Figure A4: Jackknife test for the BG-models showing the effect of removing variables from the model (light blue), and using single variables in isolation (dark blue), compared with the full model (red bar) on the model gain using the test data. The higher test gain the single variable models have, the more information the respective variable contain in itself. This measure is used to rank the importance of the variables to the models (Table A2). The jackknife test is the mean from a 10-fold cross-validation. Top row: *A. donnianum*; middle row: *S. ornithopodioides*; bottom row: *S. nimbosa*. For description of variables, see Table 2.

Table A2: Ranked importance (1-5) of variables to each BG-model based on the mean test gain obtained from a jackknife analysis when that variable is used in isolation; and mean AUC (bottom line) from a 10-fold cross-validation.

		Ordered variable importance.		
		A. donnianum	*S. ornithopodioides*	*S. nimbosa*
Variables	Summer rain	2	1	2
	Mean summer temp	1	2	3
	Rain frequency	3	4	4
	Slope	4	3	1
	Aspect	5	5	5
Mean AUC±SD		0.928±0.036	0.891±0.012	0.847±0.026

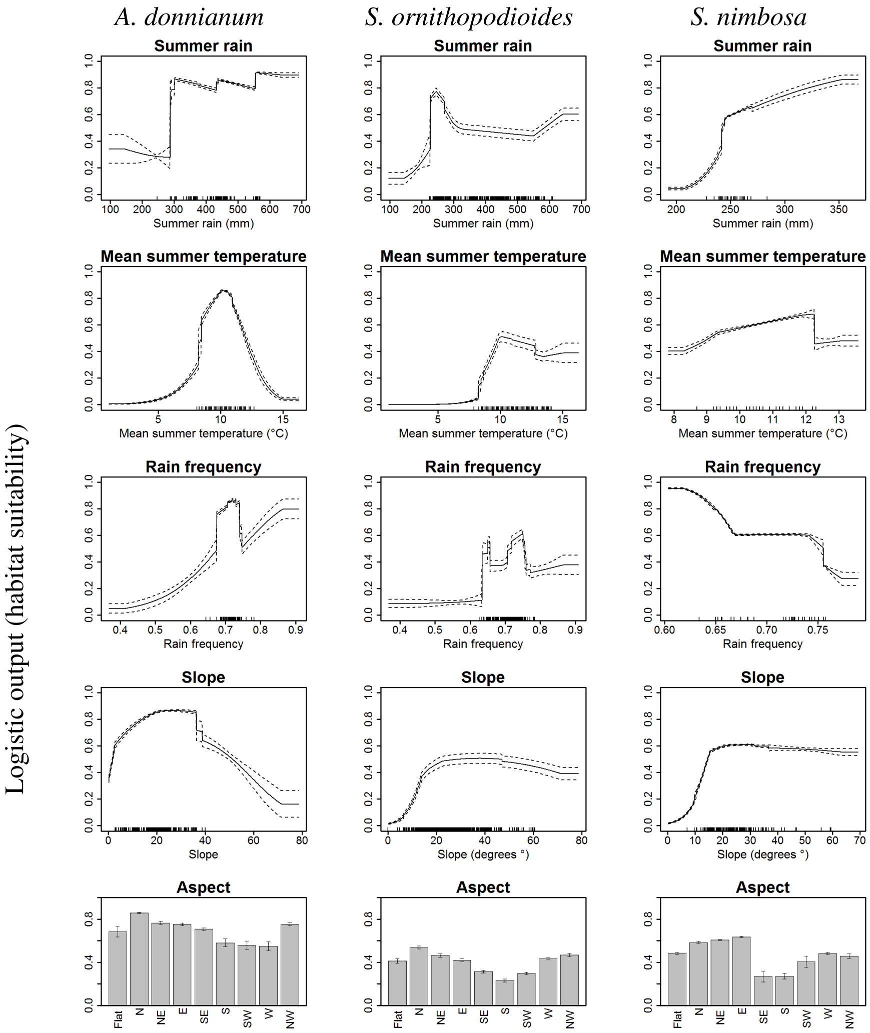

Figure A5: Response curves from TGB-model of *A. donnianum* (left column), *S. ornithopodioides* (centre) and *S. nimbosa* (right column). The curves show how the habitat suitability vary with a marginal change of each variable (solid line) with standard deviation (stippled line), all other variables set to their average value. The curves are based on a 10-fold cross-validation. The presence records are marked with tick marks on inside of x-axis. The response curves reflect the habitat preference for each species.

Growth of the mixed northern hepatic mat species *Scapania nimbosa*

Kristin Wangen

15th May 2015

Abstract

The distribution of species is determined by many factors. Among others climatic and topographic factors determining their potential distribution. Dispersal mode further affect their actual distribution through the ability to disperse and establish in suitable habitats. Liverworts may reproduce both sexually through spores, or asexually through specialized propagules or through regeneration of plant fragments. The characteristic mixed northern hepatic mat species, which are restricted to the most oceanic parts of north-western Europe, seem mainly to rely on plant fragments to disperse and maintain local populations. Their limited distribution potential seems to be the reason for the rarity of many of the mixed northern hepatic mat species rather than the availability of suitable habitats, since many seem to be absent from seemingly suitable areas. Understanding a species' means for population maintenance and dispersal potential is important for a successful management. This study aims at increasing our knowledge of the local scale ecology and growth of *Scapania nimbosa* Taylor through measuring its growth *in situ* in Norway, and to see whether there is a difference in micro-climate between presence sites and seemingly suitable absence sites. The results suggest that *S. nimbosa* grows approximately 4.68±2.25 mm during one growth season, but there is a large variation between shoots. No difference in micro-climate was found between the presence and absence sites, suggesting that *S. nimbosa* is limited by dispersal, not by suitable habitats. Available habitats, and the ability to identify these, opens up the possibility to expand its range through transplantation of plan fragments, which has been successful for other species from the same community (*Herbertus hutchinsiae* (Gottsche) A.Evans in Scotland). This is especially relevant for *S. nimbosa*, since its known distribution is geographically small and it has a limited dispersal potential, which makes it vulnerable to climate change.

Keywords: Mixed northern hepatic mat, *Scapania nimbosa*, *in situ* growth measurements, micro-climate, dispersal limitation, conservation.

1. Introduction

The distribution of species is determined by many factors, among others historical factors such as continental drift and ice ages (Schuster, 1983), and climatic and topographic factors determining the potential distribution (Dahl, 2007). Life history traits affect the species' ability to disperse and establish in suitable habitats (During, 1979, 1992; Flagmeier *et al.*, 2013; Laaka-Lindberg *et al.*, 2000; Longton, 1992). Reproduction in liverworts can be sexual through spore production, or asexual through production of specialized propagules (e.g. gemmae, bulbils, or tubers) or simply trough regeneration or small plant fragments (Vanderpoorten and Goffinet, 2009). The mixed northern hepatic mat community is characterized by a group of large leafy liverworts, in addition to some more widespread species (Ratcliffe, 1968). All the characteristic species of this community are dioicous, have almost never been recorded producing sporophytes in Europe, and only a few, such as *Scapania ornithopodioides* (With.) Waddell and *S. nimbosa* Taylor do rarely or very rarely produce specialized asexual propagules such as gemmae (Damsholt, 2002; Paton, 1999). Thus, these species seem to mainly rely on fragmentation to maintain populations and to disperse today (Flagmeier, 2013). The mixed northern hepatic mat community has a northern Atlantic distribution in Europe (Ratcliffe, 1968), where it is found in the most oceanic parts of the British Isles and Ireland, the Faeroe Islands and in south-western Norway (Damsholt, 2002; Paton, 1999). Many of the species characteristic of this community have disjunct populations in north-western North America, eastern Himalayas and eastern Asia (Schofield and Crum, 1972). The characteristic species of the mixed northern hepatic mat community are mostly considered rare or scarce in the UK (Preston, 2006, 2010), which is likely to be the case also in Norway. Rarity may be due to few available habitats, or due to dispersal limitation. The degree of habitat limitation can be thought of as the proportion of the suitable habitat that are colonized, and seems to mainly depend on the distance between suitable habitat patches and dispersal ability (Herben and Söderström, 1992). Dispersal limitation seems to be true for at least some species of this community which are absent from sites where their climatic requirements seem to be fulfilled (Flagmeier *et al.*, 2013; Jordal and Hassel, 2010; Wangen, Unpublished). Some studies have tested the regeneration capacity of mixed northern hepatic mat species from fragments and from whole shoots, both *in situ* and *ex situ* (Flagmeier *et al.*, 2013; Løe and Söderström, 2001). Such studies are important in order to understand the means of population maintenance and dispersal potential. The experience from such studies also provide a tool for the introduction of rare mixed northern hepatic mat species into new sites as a conservation strategy, since many are threatened (ECCB, 1995; Hassel *et al.*, 2010), and may decrease in range in the face of climate change (Hodd *et al.*, 2014; Hodd and Skeffington, 2011). This study aims at increasing our knowledge of the ecology and the growth of *S. nimbosa*, in Norway. The study aims to:

1. Estimate how much *S. nimbosa* grows during one growth season across the study area.
2. Find which environmental factors that affect the habitat quality of *S. nimbosa*, represented by the growth rate.
3. Finally we want to discuss if *S. nimbosa* is habitat limited or dispersal limited in Norway, and relate this to future conservation of the species.

2. Method

2.1 Study area.

The study area comprises the known geographical range of *S. nimbosa* in Norway, which is located on the north-western coast of Møre and Romsdal county. Here it is restricted to a small area covering about 20×12 km in the municipalities Eide, Gjemnes and Fræna (Figure 1; Norwegian Biodiversity Information Centre, 2015). Today there are more than 30 known localities occurring 5-20 km from the coast, and ranging from approximately 200-550 m a.s.l., with mean altitude increasing with the distance from the coast. All localities are in north-east to north-west facing slopes, typically on moist, peaty soil, at or above the tree line. The study area is characterized by a rough topography with steep mountains rising up from the fjords. While some mountains have a clear alpine structure with elevation up to 1000 m a.s.l., others are lower, more rounded hills (Jordal and Hassel, 2010). The climate in the study area is characterized as highly oceanic (Moen, 1999), with mild winters, cool summers, and approximately 220-250 days with precipitation >0.1 mm a year. The yearly precipitation is relatively high (1400-2300 mm per year), although this vary a lot locally due to the mountains, with less precipitation in the lowland and at the outer coast. The lower altitudes are covered by forest (mainly birch *Betula pubescens* and pine *Pinus sylvestris*, and some planted spruce *Picea abies* and *P sitchensis*), mires and coastal *Calluna* heath, apart from those areas used for agriculture and settlements. Above the tree line, moist heath, mires, scree areas with ferns, grasses or tall herb vegetation dominates (Jordal and Hassel, 2010).

2.2 Data collection

Micro-climatic temperature and humidity data and growth data were collected from several localities spread throughout the known geographical range of *S. nimbosa*. Figure 1 gives an overview of the set-up of the growth measurements. It included localities where only micro-climatic data was collected (blue triangles), where both micro-climatic data

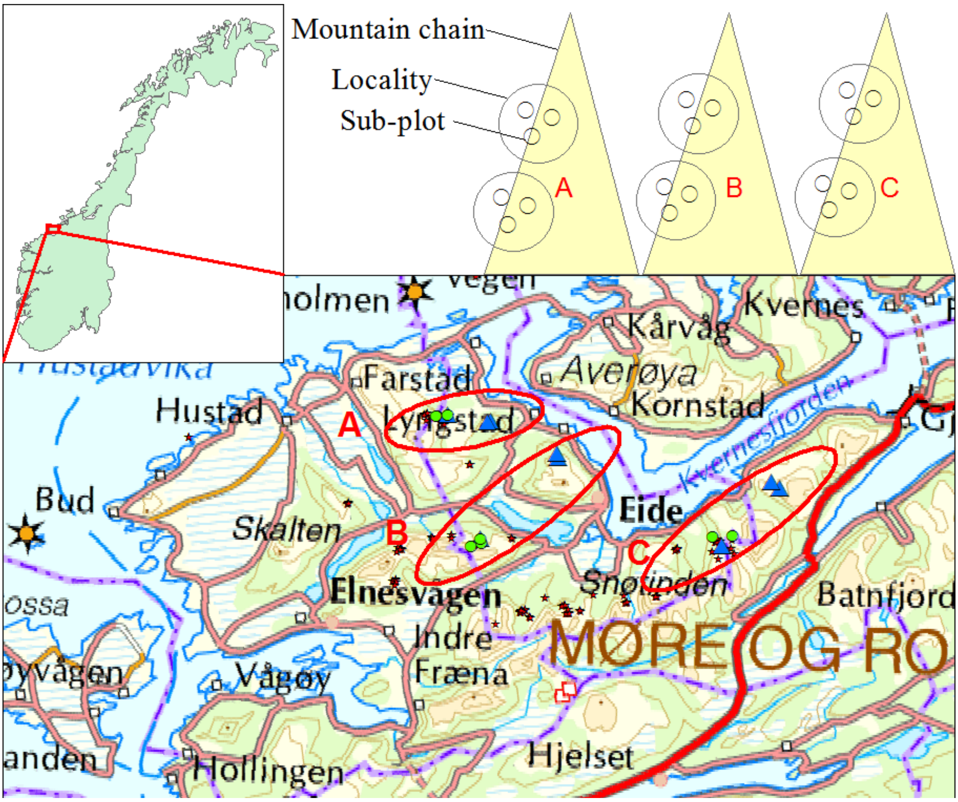

Figure 1: Set up of the growth and micro-climatic measurements. Loggers were placed out in both green and blue dots. Blue triangles show absence localities, and green circles show presence localities where growth measurements were made. The three mountain chains (A, B and C) are marked in red circles. The known geographical range of *S. nimbosa* is shown as red stars. The illustration above the map shows how the growth measurements were set up: in upper and lower range in each mountain, a locality with three sub-plots was set up, 10 shoots were measured in each sub-plot. This sum up to 180 shoots measured.

and growth data were collected (green circles), and the occurrences of *S. nimbosa* from Norwegian Biodiversity Information Centre (2015).

2.2.1 Micro-climatic data.

Micro-climatic data were collected between the summer of 2012 and fall 2014, using three types of loggers (Alpha Mach Inc., 2011; Lascar Electornics, 2012; MadgeTech, 2011) that measured temperature and in some places humidity once every hour. The main set-up of the loggers is illustrated in Figure 1. Three mountain chains are situated along the coast with increasing distance to the ocean. Two mountains were selected from each mountain chain. Micro-climatic data was collected from one mountain where *S. nimbosa* was found, and another mountain where it was not known to occur, but where conditions seemed suitable, and many of its associated species were found. To capture the width of the environmental range in which the species currently grows, the loggers were placed at the upper and lower range for the species in each mountain. This added up to 12 localities spread out on six different mountains along three mountain chains, which covered most of the current range of *S. nimbosa* in Norway. In addition, a few absence sites were set up on the presence mountains to find out whether these sites actually did differ from the presence sites.

2.2.2 Growth measurements.

The growth data of *S. nimbosa* was collected during the summer 2013 and 2014. The cranked wire method used in 2013 (mostly used for measuring *Sphagnum* growth; Clymo, 1970) did not work for *S. nimbosa*. For more details on how this was carried out, see the Appendix. During the summer 2014, a novel ”thread method” was used. Threads were tied around the shoots, between 2-7 mm below the apex, which was assumed to be the area of elongation. The thread had to be tight enough to avoid sliding off, and loose enough to avoid affecting the shoot negatively. The distance between the thread and the apex was measured with a calliper, as shown in Figure 2. The shoots were identified through the colour of the threads (5 colours) and the ID of the wire that the threads were tied to (wire nr 1 and 2) within each sub-plot (see description below). After the summer, the distance between the thread and the apex were measured again. The growth in mm could thus be derived from the difference in distance between the thread and apex before and after the summer. Growth measurements were made for 30 shoots divided between three sub-plots in each of the localities, summing up to 180 shoots measured. Each shoot was measured three times to reduce the measurement error. According to the power of test executed before going to field, this set-up would allow to detect a true difference in mean growth of 0.3 mm during the measurement period between sub-plots with a significance level of 0.05, given a measurement error of 0.4 mm and a power of 0.8. The first growth measurements were done as soon as the snow had disappeared: 5th to 7th of May for the localities where the snow melted first, and 11th and 12th of June for the rest of the localities. The second measurement were made September 15th to 19th. This corresponds to a length of the measurement periods between 131-137 days in the localities where the

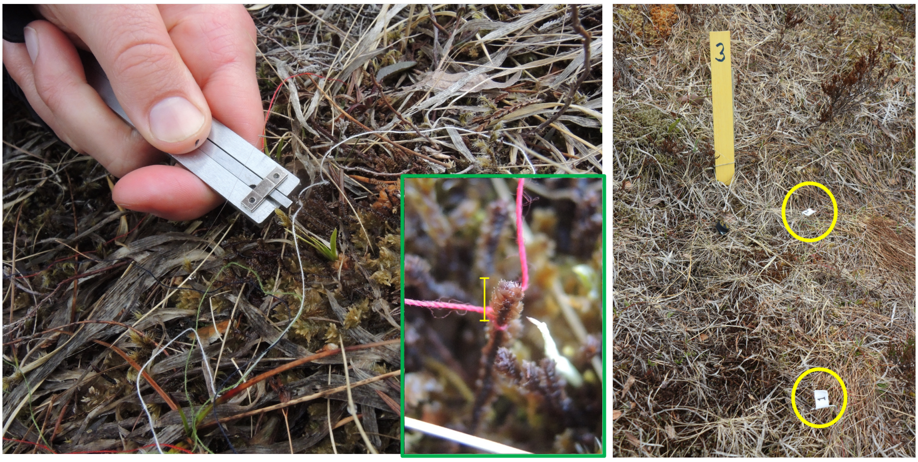

Figure 2: Method for measuring *S. nimbosa*. Left: Measuring of *S. nimbosa* in the field using a calliper. The area marked with yellow in the right bottom corner was measured in the beginning and the end of the growth season. Right: A sub-plot indicated by the numbered yellow stick, where five threads were attached to two numbered wires, indicated by the yellow circles in the picture.

snow disappeared the first, and 95-100 days in the localities where the snow disappeared the last in the spring. We did the first measurements in two rounds, because the snow had not disappeared from all sites the first time. Because of this, there was a difference of 1 month between the shortest and longest measurement period. The growth rate is likely to vary somewhat within the growth season (Martínez-Abaigar *et al.*, 1994), which has to be taken into consideration when interpreting the results.

Using the increase in shoot length as a measurement for growth is quite straight forward because *S. nimbosa* has a low degree of branching. By using this as a measure of growth, it is also assumed that there was relatively low variation among shoots in other costly traits such as leaf size, shoot diameter and distance between leaves. Growth rate was calculated as the total growth divided by the number of days that the growth was measured. This was used as a measure of habitat quality. Growth during the growth season was calculated as the growth rate multiplied by the number of days in the growth season, as estimated by the logger data (see below).

Of the 180 shoots measured before the summer, 44 shoots were missing by the end of the summer. Another 29 shoots were discarded for various reasons: some shoots had been pulled out from the ground; some had a too loose thread; some had negative growth, probably because the thread had moved outwards during the summer; and some were misidentified (*S. ornithopodioides*). This left 107 shoots for the analysis. Temperature was logged in each sub-plots, but relative humidity was only available from one sub-plot within each locality. Thus there were only 28 growth measurements with corresponding relative humidity data.

2.3 Data analysis

Micro-climatic variables. The choice of micro-climatic variables for the analysis was based on current knowledge about the ecology of *S. nimbosa* (Table 1; Jordal and Hassel, 2010; Ratcliffe, 1968). This species is, like the other hepatic mat species, thought to be limited by severe frost during winter, which is thought to be the reason why it is associated with prolonged snow-cover as it protects from severe winter cold (Jordal and Hassel, 2010; Ratcliffe, 1968). For this reason, the number of snow days, frost days and frost events were considered as possibly important variables. The frost and the snow variables reflect two sides of the same factor, namely the exposure to or protection from severe winter frost. While the number of frost days reflects the total exposure to frost, the number of frost events is assumed to be stressful for the plant due to the repeated freeze-thaw events. This has been shown to be associated to leakage of macro-nutrients in mosses in Antarctic environments, which may influence the survivability of living plants (Seppelt, 2011). Mild periods during the winter may be associated with poor protection from snow, and thus low survivability. The length of the growth season reflects the time the plant will have for growth. However, photosynthesis and metabolism stops when liverworts become dry and they thus depend on staying moist in order to grow (Vanderpoorten and Goffinet, 2009). A high amount of rain, frequent rainfall and high humidity seems to be the main controlling factor in the distribution of mixed northern hepatic mats species (Ratcliffe, 1968), thus relative humidity was included in the analysis. Mixed northern hepatic mat species are also considered limited by high summer temperature (Ratcliffe, 1968). Metabolic rate generally increases with increasing temperatures before decreasing again (humped-shaped) (Vanderpoorten and Goffinet, 2009), but the risk of desiccation also increases with increasing temperatures. Thus, mean summer temperature was included in the analysis. The final variables deduced from the logger data for use in the hypothesis testing included: the number of snow days, frost days, frost events and mild days during the winter; the length of the growth season; and the mean relative humidity and mean temperature during the summer (Table 1). All the variables were considered likely to differ between the selected presence and absence sites if the absence sites had unsuitable micro-climate. Mean summer temperature and mean summer humidity were also thought to affect the growth rate, but here measurements from the growth measurement period was used instead (correlation coefficient of 0.7). Periods with snow could be detected from the logged temperature data as periods with stable temperatures in contrast to the fluctuating temperatures when there was no snow. Frost periods were defined as days without snow and with temperatures at or below -1 $^{\circ}C$ for 4 hours in a 6 hour period. Mild periods were defined the same way: as periods without snow, and with temperatures at or above 1 $^{\circ}C$ for 4 out of 6 hour in a row. Start and end of the growth season was based on the last and first period of snow. Sometimes, a short period of snow in early May was not defined as part of the winter, as there was a long mild period between this snowfall and the snowfall before. The growth season in the lower part of Herskedalen is approximated based on the date in which the snow disappeared from the other localities at the same mountain, and elevation. Frost events was the number of times when the temperature went from positive to negative. Correlation between variables was calculated in R (Table A2 in the Appendix) (R Core Team, 2014).

Table 1: Description of the variables used to test the difference in micro-climate between the selected presence and absence sites, their ecological significance, and the time period from which the variables derives.

Variable	Description	Ecological significance	Time period
Snow days	Days with snow during the winter.	S. nimbosa is associated with fairly prolonged snow cover...	Oct. 2012 to May 2013
Frost days	Days with no snow and frost during the winter.	...which is thought protect it from severe winter frost (Ratcliffe, 1968).	Oct. 2012 to May 2013
Frost events	Frost periods during the winter.	Repeated freeze-thaw events may reduce survivability of the plant since it is associated with loss of macro-nutrients in other bryophytes (Seppelt, 2011).	Oct. 2012 to May 2013
Mild days	Days with no snow and positive temperatures during the winter.	Mild periods during the winter may be associated with poor protection from snow, and thus low survivability.	Oct. 2012 to May 2013
Length growth season	Period between last and first snow period.	The length of the growth season may reflect the plant will have for growth...	2013
Mean % RH	Mean relative humidity from the logger data during the summer.	...although it depend on staying moist to sustain metabolism and photosynthesis (Vanderpoorten and Goffinet, 2009, chap. 8)	13th June to 15th Sep. 2013
Mean temperature	Mean temperature from the logger data during the summer.	*S. nimbosa* is considered limited by high summer temperatures (Ratcliffe, 1968).	13th June to 15th Sep. 2013
Habitat suitability	Habitat suitability as predicted in Manuscript I (Wangen, Unpublished).		

Hypothesis testing The effect of mean relative humidity and mean summer temperature on the growth rate was tested with an analysis of variance (ANOVA), where the intercept model was compared with each single-variable model. To take into consideration the dependency between the growth measurements within sub-plots, linear mixed models (lme; Pinheiro *et al.*, 2014) were made, with sub-plot ID set to random factor. Although the set-up of the experiment makes the localities nested within mountain chain, this is considered negligible. A potential non-linear response was not expected to be revealed within the small range of the mean temperature and relative humidity that was measured.

To test whether there was a significant difference in micro-climate between the selected presence and absence sites, two-sided t-tests were made for each variable. The difference in habitat suitability as predicted in Manuscript I (Wangen, Unpublished) was also tested, but the absence localities in Mælen and Hældalen were removed from this T-test. This was because they were very close to presence sites, and the model was constructed to distinguish habitat suitability at a smaller scale.

3. Results

Growth in growth season The mean, minimum and maximum growth throughout the estimated growth season across all localities was 4.68 mm, 0.16 mm and 12.45 mm, with a standard deviation of 2.52 mm. The growth is nearly normally distributed, but somewhat skewed towards the lower range, as illustrated in Figure 3.

Habitat quality The habitat quality is expected to be reflected by the growth rate, which is used as a predictor for this. The mean, minimum and maximum growth rate across all localities is 0.024 $\mathrm{mm}\times\mathrm{day}^{-1}$, 0.001 $\mathrm{mm}\times\mathrm{day}^{-1}$ and 0.060 $\mathrm{mm}\times\mathrm{day}^{-1}$ respectively, with a standard deviation of 0.013 $\mathrm{mm}\times\mathrm{day}^{-1}$. The distribution of the growth rate across all the localities is normally distributed, but somewhat skewed towards the lower range, as shown in Figure 4. The results from the hypothesis testing is presented in Table 3. There was a significant negative effect of relative humidity during the measurement period on the growth rate (p=0.02), but this is considered unreliable due to a low sample size and a high uncertainty in the measurements of % RH. Mean summer temperature had no significant effect on the growth rate.

Table 2: Result from the ANOVA testing the effect of mean summer temperature and relative humidity on the growth rate.

Model	Estimate	Std. Error	F-stat.	p-value	n
Growth rate $\sim$ mean temp	0.002	0.003	0.52	0.47	107
Growth rate $\sim$ % RH	-0.002	0.0007	5.68	**0.02**	28

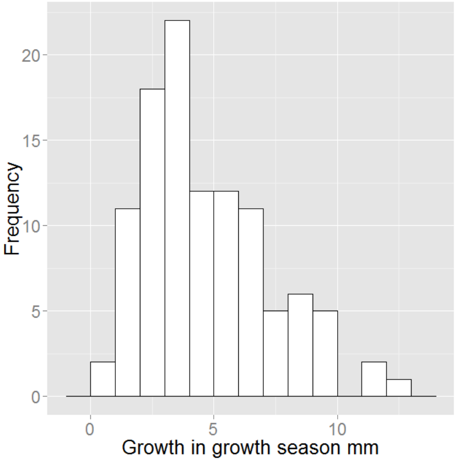

Figure 3: Histogram of the estimated growth during the growth season as estimated by the logger data. Mean, minimum and maximum growth equals 4.68 mm, 0.16 mm and 12.45 mm respectively. n=107.

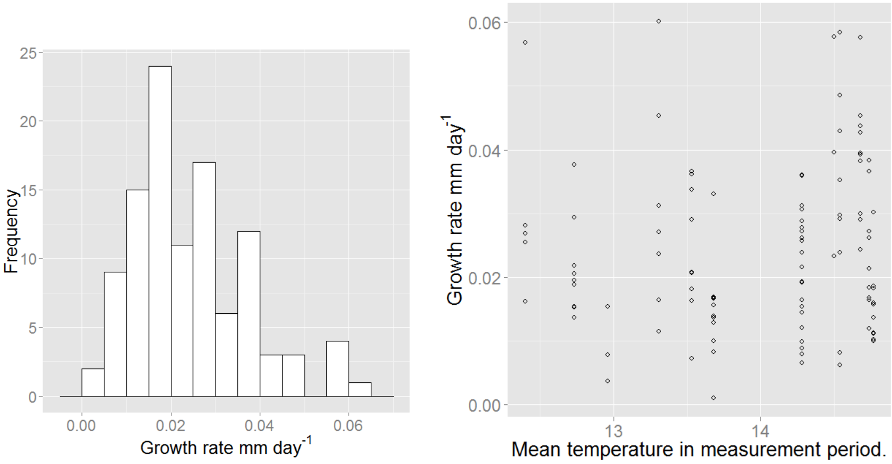

Figure 4: Results for habitat quality, represented by growth rate. Left: The distribution of estimated growth rate across all localities. Right: Growth rate plotted against temperature during the growth rate. n=107.

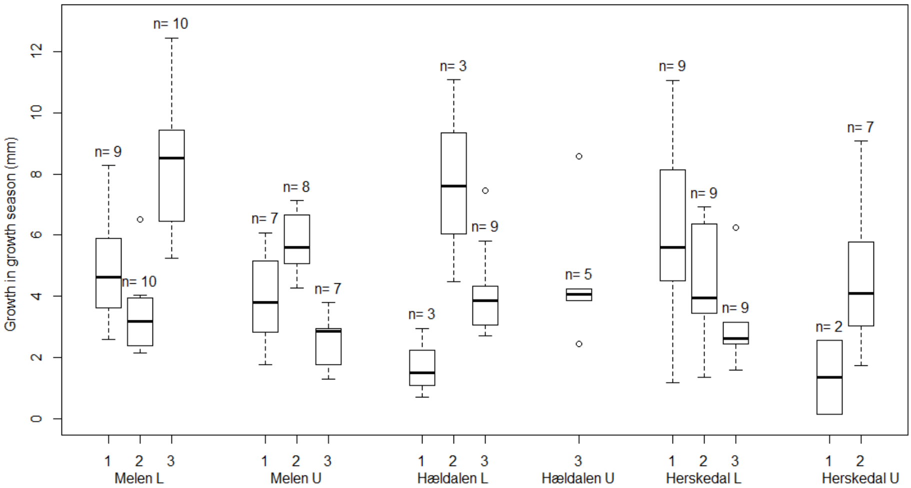

Figure 5: The estimated growth during the growth season in sub-plots 1 to 3 in the lower (L) and upper (U) part of the three mountains Mælen, Hældalen and Herskedal (mountain chain A, B and C respectively). Number of shoots in each sub-plot and outliers are indicated.

Table 3: Results from testing the difference in micro-climatic variables between presence and absence sites using a two-sided t-test. The mean value of each variable in the presence and absence sites is presented along with the test statistic, the p-value and total number of presence and absence sites.

Variable	Mean presence	Mean absence	T-stat.	p-value	n
Snow days	152	134	0.766	0.46	14
Frost days	29	35	-0.574	0.58	14
Frost events	2.3	3.1	-0.672	0.51	14
Mild days	17	21	-0.628	0.54	14
Mean % RH	90	87	0.858	0.42	11
Mean temperature	12.82	12.15	1.245	0.24	14
Length gs.	185	195	-0.839	0.42	13
Habitat suitability	0.49	0.35	1.380	0.20	13

Micro-climate in presence and absence sites. It was not possible to detect a difference in micro-climate or in predicted habitat suitability (from Manuscript I (Wangen, Unpublished)) between presence and absence sites (Table 3). The result from the analysis of the logger data, which was the basis for the hypothesis testing, is presented in Table A1 in the Appendix.

Method evaluation Each shoot was measured three times, and the mean standard deviation of all the shoot measurements was 0.185 mm. The length from the thread to the apex did not significantly affect the standard deviation (p=0.85). This was tested with a linear model for all lengths measured and the corresponding standard deviation.

4. Discussion

This study indicates that *S. nimbosa* has a mean growth of 4.68±2.25 mm throughout one growth season, although there seems to be a large variation within its geographical range. There was no difference in micro-climate between presence sites and seemingly suitable absence sites, which indicates that the species is dispersal limited rather than habitat limited in Norway, and that we have a reasonably good understanding if its ecology. Thus conservation measures such as transplanting turfs of plant fragments may be a possibility for *S. nimbosa*.

4.1 Growth and habitat quality.

The mean growth during the estimated growth season was 4.68±2.25 mm, with the minimum and maximum extremes of 0.16 mm and 12.45 mm respectively. The extreme values might partially be due to measurement error or other sources of error. The extreme values within the 95 % confidence interval was 2.17 mm and 8.06 mm (12.5 % and 87.5 % quantiles respectively). Considering the relatively small measurement error (sd=0.185 mm for all measurements), this indicates a very large variation among the shoots. The mean growth corresponded to a growth rate of 0.73 $\text{mm}\times\text{month}^{-1}$. Flagmeier *et al.* (2013) found the *ex situ* mean growth rate of *S. nimbosa* in growth chambers to be 1.44 $\text{mm}\times\text{month}^{-1}$ in the main stem. The reason why they found better growth may be because they grew the shoots in growth chambers with stable and good conditions, while our shoots were measured *in situ* and during the summer, which is the part of the growth season when shoots are most likely to dry out. Bryophytes species likely to dry out during the summer have shown to decrease in chlorophyll content during the summer compared to early spring and late fall (Martínez-Abaigar *et al.*, 1994). Thus, our measurement is probably done during the more unsuitable period during the growth season, which may have led to an underestimate. In addition, our measurements were done at the limit of the upper and lower elevational range within the study area, where there might be less growth than in the intermediate ranges.

The relative humidity varied between 82.24 % RH and 92.25 % RH in the measurement period (not presented). The % RH had a significant effect on the growth rate, although not the expected way. Growth rate decreased rather than increased with increasing relative humidity. This does not agree with the general recognition of high humidity as one of the main factors driving the distribution of hepatic mat species at regional scale (Ratcliffe, 1968). Due to the low sample size and the uncertainty in the measurement of humidity (Section 4.3) this result is considered as unreliable.

The mean summer temperature among the sub-plots varied between 12.40 °C and 14.77 °C, but there was no significant effect on the growth rate. One possible reason for this might be that the environmental range within the currently known geographical range of *S. nimbosa* is too small to see any difference in the growth rate. Some bryophytes have shown to have a weak response in growth rate to temperature (Furness and Grime, 1982). If this is true also for *S. nimbosa*, then growth would have to be measured over a much larger range, or the sample size would have to be bigger in order to see any response. It is likely that *S. nimbosa* has a much broader potential environmental range than that exhibited in Norway, since it in the British Isles covers almost the same geographical range as *S. ornithopodioides* (Blockeel *et al.*, 2014). Another possibility is that the response to temperature is hidden due to the effect of other, possibly more important variables such as relative humidity. Since liverworts are poikilohydric, their metabolism and photosynthesis will stop when they dry out, and water availability thus has a major impact on their growth (Vanderpoorten and Goffinet, 2009). Thus, it is likely that there is an interaction effect between temperature and wetness factors on the growth rate. Confounding effects could have been ruled out by doing such measurements in the laboratory. The box-plot in Figure 4 shows that there is a large variation in growth rate especially within some of the sub-plots. This indicates that there are variables at even larger scale at play affecting the growth rate, which is expected. This could be due to the actual neighbour with its competing or facilitating effect, or due to edaphic factors or soil moisture at that specific site (Hanslin, 1999).

4.2 Habitat limitation and conservation.

The absence of *S. nimbosa* in the seemingly suitable absence sites is either because it has not been able to arrive and establish there, or because the site is actually unsuitable. We were not able to detect a significant difference in micro-climate between the selected presence and absence sites, and there was no significant difference in estimated habitat suitability based on the species distribution model from Manuscript I (Wangen, Unpublished), although this model is associated with uncertainty. This indicates that *S. nimbosa* is limited by dispersal rather than by suitable habitats, and that there is a possibility for the species to spread to new sites. It also indicate that we have a reasonably good understanding of the ecology of this species. This is useful in a conservation perspective. A possible conservation measure is to expand their distribution by translocating turfs or plant fragments to suitable absence sites, in which case it is important to choose sites that are actually suitable. The study by Flagmeier *et al.* (2013) shows that regeneration in the field from plant fragments is possible for the mixed northern hepatic mat species *Herbertus hutchinsiae* (Gottsche) A.Evans. Their study also suggest that other species belonging to this community will be able to establish from fragments in the field. Such conservation measures are especially relevant for *S. nimbosa* in Norway, since it has a geographically small distribution and limited dispersal potential, which makes it vulnerable to climate change (Jordal and Hassel, 2010).

4.3 Evaluation of growth measurement method.

Generally, the thread method used in this study gave a small standard deviation, thus the results are relatively reliable if other sources of error can be eliminated. The method is also likely to work for other species with similar growth forms to *S. nimbosa*, as long as the species is large enough to allow the thread to be placed between the leaves without tying the thread too tight. That includes species which have a low degree of branching and low variation in traits such as leaf size, distance between leaves and shoot diameter, which will allow growth of shoot length to work as a good measure of energy spent on growth. The biggest source of error is probably the possibility of the thread to move out along the shoot during the summer if the thread is tied too loose. Outwards movement of the thread would lead to a measured growth lower than the actual growth. Another possible source of error is the effect of the treatment on the shoots. Slightly pulling the shoot out of the ground when tying the thread or by animals passing by during the summer is presumably the most harmful effect, since this would make them more vulnerable to desiccation. Such sources of error and the disturbance by animals during the summer was the biggest source of sample size reduction in this study.

Suggestions for improvements. Some suggestions for improvement of the method, sorted by importance, includes: (1) Avoiding disturbance from animals by covering the plots with a fence (e.g. chicken wire); (2) do the field work in good enough weather. Especially when it was raining, condensation formed on the hand lens, and the chance of measuring the wrong species increases. It was also a harder to do high precision work such as tying threads around the shoots in wet and cold conditions; (3) be sure to tie the thread tight enough to avoid that it will move, but not too tight. Bring plenty of extra threads to the field in order to allow for some unsuccessful attempts; (4) it was easier to measure short than long distances and it did not affect the measurement error. Tying the thread approximately 2-3 mm below the apex was perfect in my opinion.

4.4 Further study

This study was not able to find an effect of temperature or humidity on the growth rate. This would be easier to test under controlled experiments for example in growth chambers.

Measuring the growth rate and survival of shoots under different temperature and humidity condition can be useful for understanding its environmental range, and to identify the optimal climatic conditions and interaction effects between variables. This can be useful for identifying sites with optimal climate in which the species can be introduced for conservation purposes.

5. Conclusion

The estimated mean growth of *S. nimbosa* during one growth season was 4.68±2.25 mm, but this is likely an underestimate, and the variation in growth was large within its geographical range. It was not possible to find an effect of temperature or humidity on the growth rate in this study. The presence sites did not differ from the absence sites in microclimate, which suggests that *S. nimbosa* is dispersal limited in Norway. The availability of suitable habitats and the ability to identify them opens up the possibility to expand it's range and abundance with conservation measures such as translocating of turfs or plant fragments. Such conservation measures are especially relevant for *S. nimbosa*, since it is restricted to a small geographical area in Norway and has limited dispersal potential, which makes it vulnerable to climate change.

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A. Appendix

A.1 Cranked wire method

During the summer 2013, the growth of *S. nimbosa* was measured based on the cranked wire method, which has been used for measuring growth in *Sphagnum* (Clymo, 1970). The method is illustrated in Figure A1. Cranked wires of stainless steel shaped like an L were placed upside down into the ground. The horizontal part of the wire was aligned with the tip of the shoot, and the location of the shoot along the wire was marked with permanent marker. At the end of the summer, the part of the shoot that had passed above the wire was measured as the growth.

This method did not work well for *S. nimbosa*. The main reason was that the position of the shoot above the ground differed, thus only one to four shoots could be measured by one wire. Thus it was difficult to identify which shoot was measured at the end of the summer. In addition, the wire seemed to negatively affect some of the shoots that had been touching the wire, since they had changed colour, and had not been growing anything at all.

Figure A1: Illustration of the cranked wire method. The picture is from the beginning of the growth season. The tip of the shoots that were measured were aligned with horizontal part of the wire, and the position along the shoot indicated by a black mark on the wire to avoid measuring the wrong shoots at the end of the growth season. Identifying the shoots that were measured was the main challenge with this method.

A.2 Micro-climatic variables

Table A1: Results from the analysis of the logger data. All variables are from 2013. Abbreviations: MC = mountain chain; gs=growth season estimated for 2013. The habitat suitability is base on the predictions from the TGB-model in Manuscript I (Wangen, Unpublished). Mean temperature and mean % RH was measured for the period 13.6-15.9 2013. See Table 1 and Section 2.3 for variable description.

Locality	Presence	MC	Snow days	Frost days	Mild days	Frost events	Length gs.*	Mean temp	Mean % RH	Habitat suitability
Melen U (1)	1	A	148	33	13	2	198	12.86	89.6	0.58
Melen L (2)	1	A	116	33	27	4	216	13.89	-	0.57
Melen L (3)	0	A	88	51	43	8	211	11.94	-	0.54
Lyngstadfj U (4)	0	A	97	67	31	6	-	12.90	79.66	0.16
Lyngstadfj L (5)	0	A	105	44	24	3	-	13.06	91.12	0.12
Hældal L (13)	1	B	136	50	14	3	192	11.76	93.67	0.58
Hældal U (15)	1	B	208	0	0	0	151	11.43	92.64	0.60
Høldal L (16)	0	B	133	34	25	2	200	12.98	88.86	0.51
Hældal L (17)	1	B	119	38	36	4	198	-	-	0.53
Silsetfj U (11)	0	B	215	0	3	0	174	10.39	-	0.33
Silsetfj L (12)	0	B	76	49	20	4	217	12.46	92.39	0.39
Herskedal U (6)	1	C	182	17	9	1	151	13.02	84.81	0.53
Herskedal M (7)	0	C	177	17	10	1	187	12.02	94.67	0.37
Herskedal L (8)	1	C	-	-	-	-	189	13.97	90.39	0.47
Bjørndal U (9)	0	C	131	17.5	44.5	3	180	12.18	75.915	0.71

Table A2: Pearson correlation matrix with correlation coefficient for all pairs of the variables used to test the difference in micro climate between presence and absence sites. Abbreviations: gs=growth season estimated for 2013. H. suitability=habitat suitability. Mean temperature and % RH was calculated for the period 13.6-15.9 2013. See Table 1 and Section 2.3 for variable description.

Variables	Snow days	Frost days	Frost events	Mild days	Length gs.	Mean temp	Mean % RH	H. suitability
Snow days	1							
Frost days	0.92	1						
Frost events	0.87	0.85	1					
Mild days	0.85	0.77	0.91	1				
Length gs.	0.87	0.79	0.74	0.74	1			
Mean temp	0.58	0.50	0.37	0.51	0.36	1		
Mean % RH	0.0091	0.10	0.22	0.27	0.26	0.029	1	
H. suitability	0.027	0.046	0.013	0.064	0.38	0.004	0.21	1