Hyper-oceanic liverwort species of conservation concern: Evidence for dispersal limitation and identification of suitable uncolonised regions

Kristin Wangen*, James D. M. Speed**, Kristian Hassel

NTNU University Museum, Norwegian University of Science and Technology, Trondheim NO-7491, Norway.

*Present address: Gunnars veg 10, 6630 Tingvoll, Norway.

**Correspondence E-mail: james.speed@ntnu.no Phone: +47 73592251

Wangen, K., Speed, J.D.M. & Hassel, K. (2016) Hyper-oceanic liverwort species of conservation concern: evidence for dispersal limitation and identification of suitable uncolonised regions. *Biodiversity and Conservation* 25: 1053-1071.

Postprint 10.1007/s10531-016-1105-y

Abstract

In order to successfully manage and conserve species and plant communities, it is important to have a good understanding of their ecology and distributions. The three liverwort species *Anastrophyllum donnianum*, *Scapania ornithopodioides* and *Scapania nimbosa*, are restricted to the mixed northern hepatic mat community found in the most oceanic parts of north-western Europe. These species are of conservation concern because they are globally rare with strict environmental requirements and a limited dispersal potential, which makes them vulnerable to disturbance and climate change. In this study we used species distribution modelling to (1) predict their potential distribution in Norway, (2) to assess whether they are limited by dispersal or suitable climate, (3) identify which climatic factors are most important in determining their distribution and (4) suggest regions for further field based surveys. Maximum entropy (MaxEnt) models were developed for each species using target-group background data, and five environmental coverage layers. Our results indicate that all three species are limited by dispersal rather than the availability of suitable areas in Norway. In particular, *A. donnianum* seems to be limited from reaching uncolonised highly suitable areas in northern Norway due to a barrier unsuitable region with insufficient summer rain. *S. ornithopodioides* is absent from northern Norway despite the presence of highly suitable regions scattered along the coast. The models locate highly suitable areas where conservation measures should be focused when they overlap with known populations. Areas of interest for targeting searches for potentially undiscovered populations are indicated.

Keywords: Mixed northern hepatic mat, limiting factors, climate change, threatened species, species distribution modelling.

Introduction

Conservation efforts and research often focus on desirable, charismatic and flagship species (Simberloff 1998). However, the majority of the worlds' species do not fall into this category. Undervalued and under studied species may be at greater risk due to the lack of concern for them. In the hyper-oceanic mountainous areas along the western coast of Norway, the European fringe populations of species belonging to the rare mixed northern hepatic mat community are 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).

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 the community also occurs elsewhere in the British Isles (including Ireland), the Faeroe Islands and in south-western Norway (Ratcliffe 1968; Paton 1999; Damsholt 2002). Two of the more common species of the northern hepatic mat in Norway are *Anastrophyllum donnianum* (Hook.) Steph. and *Scapania ornithopodioides* (With.) Waddell, while *Herbertus hutchinsiae* (Gottsche & Rabenh.) A. Evans is a common species of the northern hepatic mat in Britain and Ireland has a restricted distribution in Norway, mainly limited to Rogaland County in the southwestern part of the coast. The same restricted distribution is also found for other typical northern hepatic mat species like *Anastrophyllum joergensenii* Schiffn. and *Scapania nimbosa* Taylor. Many of the characteristic mixed northern hepatic mat species have disjunct world distributions with populations in north-western North America, eastern Himalayas and western Asia (Schofield and Crum 1972). The community has a north-western distribution in Europe, where it is confined to areas with an oceanic climate. In Norway, the mixed northern hepatic mat species have a south-western distribution (Figure 1). The association with highly oceanic regions reflects their 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 rarity in dioicous bryophytes is due to dispersal limitation, as production of spores is rare and asexual propagules have limited dispersal distances (Laaka-Lindberg et al. 2000; Söderström and During 2005; Flagmeier et al. 2013).However, Laenen et al. (2015) found no correlation between reproduction by spores or asexual produced gemmae and the geographical distribution range of the species. The species characteristic of the mixed northern hepatic mat community have never (with few exceptions) been observed with sporophytes, and only a few produce gemmae (asexual propagules). This implies that dispersal of fragments for instance spread by animals or wind is the most important means for dispersal and for maintaining local populations today (Flagmeier 2013).

A low dispersal potential may lead to a reduced actual distribution if climate change leads to a shift in suitable habitats. In the face of climate change, Norway is likely to still have large, climatically suitable areas, some which may even become more suitable than today (Hanssen-Bauer et al. 2003). This underlines the international conservation responsibility Norway has for this community. In many areas, the community is under threat from anthropogenic activities such as husbandry (Holyoak 2006; Long 2010), burning (Rothero 2003) and direct human activities such as mining (Jordal and Hassel 2010). In order to conserve and manage the community, it is important to understand its distribution and climatic requirements. Consequently, many of the northern hepatic mat species are on the Norwegian red list, i.e. *Anastrophyllum donnianum* NT, *A. joergensenii* EN, *Herbertus hutchinsiae* NT and *Scapania nimbosa* EN (Hassel et al. 2015) The mixed northern hepatic mat community has been described by several authors, who have related their distribution to macro-climatic variables (Ratcliffe 1968; Störmer 1969; Dahl 1998; Hill and Preston 1998). However, few attempts have been made to explicitly model the distributions of the constituent species (Hodd et al. 2014). Over the last decade there has been an enormous development in species distribution modelling (SDM) techniques and an increased availability of environmental coverage data (Hijmans et al. 2005; Franklin 2010).

This allows 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 field surveys to improve search success (Bourg et al. 2005), as well as supporting conservation decisions (Guisan and Thuiller 2005; Hodd et al. 2014). The aims of this study are (1) to estimate climate suitability for the mixed northern hepatic mat species *Anastrophyllum donnianum*, *Scapania ornithopodioides* and *S. nimbosa* (Paton 1999; Damsholt 2002) along the Norwegian coast through species distribution modelling (SDM). (2) To assess whether the distributions of these three species are constrained by suitable climate or dispersal in Norway. (3) Identify the species' climate requirements and which environmental variables are the most important in predicting their potential distribution. (4) Suggest new areas for surveys with the aim of finding potentially undiscovered populations and areas suitable for conservation translocation attempts.

Method

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 (Jordal and Hassel 2010). 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 is within the highly (O3) and markedly (O2) oceanic sections as described by Moen (1999) (Figure 1), which typically experience mild winters, cools summers and high humidity through high and frequent rainfall and high cloudiness (Crawford 2000).

The known distribution of the study species within Norway is presented in Figure 1. We suspect that suitable climate exists more widely 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 (Figure 1).

<Figure 1 here, 1 column width>

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 a machine learning method particularly suitable for presence only data (Phillips et al. 2004; Phillips et al. 2006). 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. 2012).

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 attempt to identify them. As the aim of this study was to predict the current habitat suitability, records from 1950 or older were excluded from the analysis. The data was cleaned by removing duplicates, controlling the locations with their description, and by correction of sample bias. The final datasets for *A. donnianum*, *S. ornithopodioides* and *S. nimbosa* had 173, 611 and 165 presence records respectively.

Background data.

MaxEnt is designed for modelling species distribution based on presence-only 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 from which the random background data is generated. 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 expect that our study species are not at equilibrium with the environment, and since we are investigating whether the species are dispersal limited we 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* were defined 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* were defined as those municipalities with occurrences, and one municipality in buffer around (Figure 1).

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 data is to use target-group background (TGB) data. This can be 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 correcting 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, models were made using TGB data, which included the occurrence records (both observations and museum collections) from the taxon Marchantiophyta from Norwegian Biodiversity Information Centre (2015). The TGB data were cleaned in the same way as the presence data. 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* (see Online Resource 1). This dataset also included the presence records, since MaxEnt uses background data (which includes presence points, Mateo et al. 2010). The Marchantiophyta (liverworts) were considered a good representation for the TGB data because anyone collecting or recording liverworts would presumably also locate the study species (although this assumes that the recording of liverworts is not spatially biased, which may not be the case given the relative inaccessibility of the hepatic mat community habitat). One consequence of this choice was that areas that are generally unsuitable to liverworts were under-represented in the model.

The use of random background data gave similar findings for *S. ornithopodioides* and *A. donnianum*, but the output differed for *S. nimbosa* (described in Wangen 2015).

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 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).

Environmental coverage data

When building SDMs it is important to use existing knowledge and theory to select variables that are ecologically relevant and at appropriate spatial temporal scales for the modelled species (Mac Nally 2000). Variables that directly affect a species' distribution (proximal variables) should as far as possible be used, since the correlation of these to variables that indirectly affect distribution (distal variables) may vary in space or time (Austin 2002). 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 reasonably well (Merow et al. 2013). The Pearson correlation coefficients between the variables are presented in Online Resource 1. Selection between correlated variables (Pearson correlation coefficient ≥ 0.6) was based on knowledge of the species' ecological requirements. In addition, a jackknife test based on a 10-fold cross-validation 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 were based on existing knowledge of the mixed northern hepatic mat community (Ratcliffe 1968; Dahl 1998; Hodd and Sheehy Skeffington

2011). 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. Mean January temperature and elevation were excluded from the candidate set due to high correlation to other variables. The ecological relevance of the remaining variables is explained in Table 1. The rain frequency variable was defined based on of the requirement for a parameter which reflects the wetness of the climate during the period that the liverworts are most susceptible to dry out, which is the period when they are not protected by the snow. All variables were projected onto a UTM grid (zone 33N) and cropped to the study regions shown in Fig. 1. Maps of the climatic and topographic layers are presented in Figure A1.

<Table 1 here, 2 column width>

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 (regularization parameter) based on the method applied by Elith et al. (2010) and recommended by Merow et al. (2013). Many different beta-multiplier values were tested, varying by 0.5 and starting at 2.5, and the effect visually assessed by looking at the smoothness of the response curves (Figure 5). A beta-multiplier that removed locally complex patterns was chosen for each species: 2 for *A. donnianum* and *S. ornithopodioides*; 1.5 for *S. nimbosa*.

Variable importance and climate preference.

To assess and rank the importance of the variables in each model, a jackknife test was conducted on the test data set. The variable that yields the highest model gain when used in isolation contains the most useful information by itself. This measure from the mean of a 10-fold cross-validation 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 predicted climate 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. Maps of the limiting factors were made according to the instructions in the supported materials of Elith et al. (2010), which generates the maps in the following way: in each site in the study area, the value of each variable one at the time is changed from the value at that site to the mean value across the presence points. The variable that increases the habitat suitability the most when this is done is considered as the limiting factor in that site.

To assess climate-habitat preference, or the response of the predicted habitat suitability to the variables used in the models, response curves were built. The aspect variable was defined as categorical with nine levels (see Table 1). Otherwise, MaxEnt was allowed to select automatically among all feature classes which it offers (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 can 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 ≥ 0.5 were considered highly suitable. The actual number is not comparable between models (Phillips and Dudík 2008; Elith et al. 2011; Bombosch et al. 2014). Other variables that are not accounted for in our study also affect liverwort habitat suitability, for example edaphic factors. Therefore, our use of the term habitat suitability here can be interpreted as climatic and topographical suitability.

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

remaining 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 were then used 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. 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). However, it cannot be used to compare the performance of different models, due to different occurrence data sets (Elith et al. 2011).

In this study, predictions were made outside the geographical range of the training data into environments that 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 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 sampled locations. The MESS maps were used to identify areas with novel environments in which the predictions were considered as unreliable (Elith et al. 2010).

Results

Prediction maps

Predicted climate-habitat suitability for the three species across the study area is presented in Figure 2. The prediction maps illustrate habitat suitability relative to the suitable habitat for all liverworts. For all three species, the models predict suitable habitats outside the current geographical range. At a regional scale, the predicted suitable habitat for *A. donnianum* seems 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 for *S. nimbosa* shows the same general pattern, although areas with habitat suitability ≥0.5 is much more sparse than for *A. donnianum*. The model for *S. ornithopodioides* predicts suitable habitats more evenly spread out throughout the whole study area. Even though the areas with habitat suitability ≥0.5 seem quite continuous within the two suitable areas for *A. donnianum* and for *S. ornithopodioides* at a regional scale, at a local scale they do have a patchy distribution. For *S. nimbosa*, areas with habitat suitability ≥0.5 are even rarer and more spread out.

<Figure 2 here, 2 column width>

<Figure 3 here, 1.5 column width>

Variable importance

The ranked importance of the variables to the models is presented in Table 2 and is based on the jackknife test presented in Online Resource 1. 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.

<Table 2 here, 2 column width>

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 3. 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 (Online Resource 1). 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. Little summer rain is the main reason for low habitat suitability in

central and northern parts of the study area. High summer temperatures also limit the habitat suitability for *S. ornithopodioides* in the south and south-eastern parts of the study area, as does low rain frequency. Low summer temperatures limit habitat suitability 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.

<Figure 4 here, 2 column width>

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 (≥0.5) can be considered as preferable for the species, although they may also be found in areas with lower habitat suitability. The response curves are presented in Figure 4. The response to summer rain varies between species. *Anastrophyllum donnianum* shows a threshold increase 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 around 0.5 after a small peak at approximately 250 mm in the warmest quarter. *Scapania nimbosa* has a humped shape response, with a peak at approximately 245 mm in the warmest quarter. Both *A. donnianum* and *S. ornithopodioides* have a humped-shaped response to mean summer temperature, with highest habitat suitability at intermediate mean temperatures peaking at approximately 10°C. *Scapania nimbosa* has highest habitat suitability at approximately 8°C, which decreases with increasing mean temperatures up to 13°C. As the frequency of rain days during the growth season increases, the habitat suitability increases steadily with a small hump around 0.7 for *A. donnianum*, shows 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 decreases 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*.

<Figure 5 here, 2 column width>

Model evaluation

Since predictions were made within new geographical areas, MESS-maps were made to assess the reliability of the predictions. Red areas in the map indicate areas where the environment falls outside the range of the sampled sites (Figure 3). Predictions within these areas are thus based on extrapolation and are hence associated with uncertainty. 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 (these species have the same MESS map since they use the same TGB data points). The MESS-map for *S. nimbosa* warns against prediction uncertainty in large part of the study area, especially south of the current geographical range of the species, and some parts in northern Norway.

Discussion

The mixed northern hepatic mat community is globally rare and of high conservation interest (ECCB 1995; Hassel et al. 2010), yet is undervalued and under-studied. The community is characterised by liverwort species with strict ecological requirements found in only a few parts of the world, and highly scattered in the landscape. Their strict ecological requirements and low dispersal capacity makes them vulnerable to disturbance and climate change. In order to successfully manage and conserve the constituent species, it is important to understand their distribution and ecological requirements. The results presented here show that large areas of highly suitable habitats (in terms of climate) are available outside the known geographical range of the study species, indicating that they are dispersal limited rather than climate limited in Norway. The results locate highly suitable areas that may sustain

populations in the face of climate change. These areas are of special conservation interest when they overlap with actual populations.

Predicted habitat suitability and known distribution.

For both *A. donnianum* and *S. ornithopodioides*, high habitat suitability (≥0.5) is predicted in new areas both outside and inside the currently known geographical rage. This result indicates that these two species are not constrained by the availability of suitable climate in Norway. Dispersal limitation is a more likely constraining factor; this coincides with findings from studies of epiphytic, saxicolous, and desert bryophytes (Snäll et al. 2004; Löbel et al. 2006; Virtanen and Oksanen 2007, Devos et al. 2011; Smith and Stark 2014). However, at larger scales (Macaronesian Islands) climate has also been shown to be an important factor for explaining species distribution in liverworts (Aranda et al. 2014). At a regional scale, the highly suitable habitats for *A. donnianum* are split in two large areas (Figure 2). 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 4). 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. None of the study species are known to produce sporophytes, and *S. ornithopodioides* has only been found with gemmae a few times in Norway (Jørgensen 1934; 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 thought to be the main factors determining the degree of habitat limitation (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*. Due to the high uncertainty in the model for *S. nimbosa*, the predictions and results of this model will not be discussed further.

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 that has shrunk in response to changing climate across the time of history. The dispersal hypothesis suggests that the species with such disjunct distribution have arrived in Europe more recently through long distance dispersal of 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 (Heinrichs et al. 2009). This is supported by several studies that 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 suggests that it has reproduced sexually after it came to Scotland (Flagmeier 2013). The large difference in known geographical range for the three study species in Norway despite large, seemingly unoccupied areas with suitable habitats for all suggests that *S. ornithopodioides* arrived in 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 Norwegian coast may be because of wind-based dispersal sourced from the British Isles (Hurrell et al. 2003), where the three study species are more common (Blockeel et al. 2014).

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 1998; Moen 1999). This explains the pattern illustrated in

the maps of the limiting factors (Figure 3), 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 rain, 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 (Ratcliffe 1968; Hodd and Sheehy Skeffington 2011). 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 correlation 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 (Online Resource 1).

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 that add uncertainty to the predictions. These have to be kept in mind when interpreting the results. Although one should be careful to compare different models, it is evident that areas with habitat suitability ≥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).

Climate change

Climate change is projected to increase the amount of precipitation during the winter, and possibly also during the summer along the south-western coast of Norway by 2030-2049 (Hanssen-Bauer et al. 2003). 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 (~64°N) 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 high summer temperature is already 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 overall changed climate 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 (McGrath et al. 2008). This is similar (excepting the decrease in summer precipitation) 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 potential restricted mainly to the spread and regeneration of plant fragments, a shift in actual distribution in face of a change in potential distribution 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*.

Conservation application

Norway is likely to be the main habitat for the mixed northern hepatic mat community under future climatic change, it is therefore 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 populations may be found, or new populations could establish. Considering ongoing climate change, conservation measures threatened species through translocation of turfs or fragments

may be a possibility (Flagmeier et al. 2013). Due to the specific topographic requirements it is also important to combine this with a good ecological understanding at a local scale. Another conservation measure is to sustain already solid populations safely within the climatically suitable areas, by buffering effects of climate change, such as rise in the tree line, through measures such as maintaining low levels of livestock grazing (Speed et al. 2010). This should however be done with care, since too high intensities of grazing is a threat to the mixed northern hepatic mat community (Holyoak 2006, Long 2010), and some currently occupied areas already have high abundances of red deer (*Cervus elaphus*, Austrheim et al. 2008). Other conservation measures include the avoidance of disturbance by direct human activity, such as mining and road building (Jordal and Hassel 2010). Such conservation measures should be focussed on populations safely within climatically suitable areas; the prediction maps from this study will be useful to locate such areas. Areas predicted to be highly suitable are likely also to sustain populations even though the climate becomes somewhat less suitable in the face of climate change.

Areas suggested for new surveys

Many areas in Norway are still poorly surveyed by bryologists. Thus, undiscovered populations of the study species may exist outside the currently known geographical range. The areas indicated as highly suitable for *A. donnianum* between latitudes 64-67°N (mainly in Nordland county in northern Norway) would be potential regions for undiscovered populations. This region is also predicted as suitable for *S. ornithopodioides*. Other areas of interest include the Fosen Peninsula 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 to consist of suitable habitat. The same areas are predicted as suitable for *S. ornithopodioides*.

Conclusion

Our study demonstrates the application of ecological research based upon publically available data to further the conservation of an undervalued set of species. It identifies suitable habitat outside the current range of three mixed northern hepatic mat species *A. donnianum*, *S. ornithopodioides* and *S.*

nimbosa. This suggests that these species are limited by dispersal rather than the availability of suitable habitats in Norway. In the face of climate change, these species are at risk of a reduction of actual distribution due to a low dispersal capacity and specific environmental requirements only found scattered in the landscape. This underlines the importance of the conservation of existing populations, especially when they are located in highly suitable areas.

Acknowledgements

We thank the Norwegian Environment Agency for funding through the Nature Index project. We also want to thank staff at the NTNU University Museum, Marc Daverdin, Even Hauge Juberg and Narjes Yousefi for helping with technical challenges. We thank the Norwegian Water Resources and Energy Directorate (NVE) and the Norwegian Meteorological Institute for providing us with environmental data for the rain frequency variable. Finally, we are grateful to two anonymous reviewers for constructive comments provided on a previous version of this work.

References

Aranda, S. C., Gabriel, R., Borges, P. A. V., Santos, A. M. C., de Azevedo, E. B., Patiño, J., Hortal, J., Lobo, J. M. 2014. (2014) Geographical, Temporal and Environmental Determinants of Bryophyte Species Richness in the Macaronesian Islands PLoS One 9: e101786

Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling Ecol Model 157:101-118

Austrheim G, Solberg EJ, Mysterud A, Daverdin M, Andersen R (2008) Hjortedyr og husdyr på beite i norsk utmark i perioden 1949–1999. NTNU (Norwegian University of Science and Technology), Trondheim, Norway

Blockeel T, Bosanquet S, Hill M, Preston C (2014) Atlas of British & Irish bryophytes vol 1. Pisces Publications, Newbury, UK

Bombosch A, Zitterbart DP, Van Opzeeland I, Frickenhaus S, Burkhardt E, Wisz MS, Boebel O (2014) Predictive habitat modelling of humpback (Megaptera novaeangliae) and Antarctic

minke (Balaenoptera bonaerensis) whales in the Southern Ocean as a planning tool for seismic surveys Deep Sea Research Part I: Oceanographic Research Papers 91:101-114

Bourg NA, McShea WJ, Gill DE (2005) Putting a CART before the search: successful habitat prediction for a rare forest herb Ecology 86:2793-2804

Crawford RMM (2000) Ecological hazards of oceanic environments New Phytol 147:257-281

Dahl E (1998) The phytogeography of northern Europe: British Isles, Fennoscandia, and adjacent areas. Cambridge University Press, New York, USA

Damsholt K (2002) Illustrated flora of Nordic liverworts and hornworts. Nordic Bryological Society, Lund, Sweden

Devos, N., Renner, M. A. M., Gradstein, R., Shaw, A. J., Laenen, B., Vanderpoorten, A. (2011) Evolution of sexual systems, dispersal strategies and habitat selection in the liverwort genus Radula New Phytol 192: 225-236.

ECCB (1995) Red data book of European bryophytes. European Committee for Conservation of Bryophytes, Trondheim, Norway

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species Methods in Ecology and Evolution 1:330-342

Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time Annu Rev Ecol Evol S 40:677

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists Divers Distrib 17:43-57

Flagmeier M (2013) Scottish liverwort heath: response to a changing environment and prospects for the future. PhD, University of Aberdeen

Flagmeier M, Long DG, Genney DR, Hollingsworth PM, Woodin SJ (2013) Regeneration capacity of oceanic-montane liverworts: implications for community distribution and conservation J Bryol 35:12-19

Franklin J (2010) Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge, UK

Furness S, Grime J (1982) Growth rate and temperature responses in bryophytes: II. A comparative study of species of contrasted ecology J Ecol 70:525-536

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models Ecol Lett 8:993-1009

Hanssen-Bauer I, Førland EJ, Haugen JE, Tveito OE (2003) Temperature and precipitation scenarios for Norway: comparison of results from dynamical and empirical donwscaling. Oslo, Norway

Hassel K, Blom HH, Flatberg KI, Halvorsen R, Johansen JI (2010) Moser: Anthocerophyta, Marchantiophyta, Bryophyta. In: Kålås J, Viken Å, Henriksen S, Skjelseth S (eds) The 2010 Norwegian red list for species. Norwegian Biodiversity Information Centre, Norway, pp 139-153

Hassel, K., Halvorsen, R., Blom, H.H., Høitomt, T. (2015) Moser Anthocerotophyta, Marchantiophyta, Bryophyta. In: Henriksen S., Hilmo O. (eds.) 2015 Norsk rødliste for arter 2015. Artsdatabanken, Norge.

Hastie T, Tibshirani R, Friedman J (2009) The elements of statistical learning, 2nd edn. Springer

Heinrichs J, Hentschel J, Feldberg K, Bombosch A, Schneider H (2009) Phylogenetic biogeography and taxonomy of disjunctly distributed bryophytes J Syst Evol 47:497-508

Herben T, Söderström L (1992) Which habitat parameters are most important for the persistence of a bryophyte species on patchy, temporary substrates? Biol Conserv 59:121-126

Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods Ecography 29:773-785

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas Int J Climatol 25:1965-1978

Hijmans RJ, Phillips S, Leathwick J, Elith J (2012) dismo: species distribution modeling.

Hill MO, Preston CD (1998) The geographical relationships of British and Irish bryophytes J Bryol 20:127-226

Hodd RL, Bourke D, Sheehy Skeffington M (2014) Projected range contractions of European protected oceanic montane plant communities: focus on climate change impacts is essential for their future conservation PloS one 9:e95147

Hodd RL, Sheehy Skeffington M (2011) Mixed northern hepatic mat: a threatened and unique bryophyte community Field Bryology 104:2-11

Holyoak D (2006) Progress towards a species inventory for conservation of bryophytes in Ireland. In: Biology & Environment: Proceedings of the Royal Irish Academy pp 225-236

Hurrell JW, Kushnir Y, Ottersen G, Visbeck M (2003) An overview of the North Atlantic Oscillation. In: Hurrell JW, Kushnir Y, Ottersen G, Visbeck M (eds) The North Atlantic Oscilliation: climate significance and environmental impact, vol 134. American Geophysical Union, Washington DC, USA, pp 1-36

Jordal JB, Hassel K (2010) The rare liverwort *Scapania nimbosa* - new knowledge about distribution and ecology in Norway Lindbergia 33:81-91

Jørgensen EH (1934) Norges levermoser Bergen Museum Skrifter 16:1-343

Laaka-Lindberg, S., Hedderson, T. A., Longton, R. E. (2000) Rarity and reproductive characters in the British hepatic flora. Lindbergia 25: 78-84

Laenen, B., Machac, A., Gradstein, S. R., Shaw, B., Patiño, J., Désamoré, A., Goffinet, B., Cox, C. J., Shaw, J., Vanderpoorten, A. (2016) Geographical range in liverworts: does sex really matter? J Biogeogr 43: 627-635.

Lobo JM, Jiménez-Valverde A, Real R (2008) AUC: a misleading measure of the performance of predictive distribution models Global Ecol Biogeogr 17:145-151

Löbel, S., Snäll, T., Rydin, H. (2006) Metapopulation processes in epiphytes inferred from patterns of regional distribution and local abundance in fragmented forest landscapes J Ecol 94: 856-868.

Long D (2010) The tragedy of the Twelve Bens of Connemara: is there a future for *Adelanthus lindenbergianus* Field Bryology 100:2-8

Mac Nally R (2000) Regression and model-building in conservation biology, biogeography and ecology: the distinction between–and reconciliation of–‘predictive’and ‘explanatory’models Biodivers Conserv 9:655-671

Mateo RG, Croat TB, Felicísimo ÁM, Munoz J (2010) Profile or group discriminative techniques? Generating reliable species distribution models using pseudo-absences and target-group absences from natural history collections Divers Distrib 16:84-94

McGrath R et al. (2008) Ireland in a warmer world; scientific predictions of the Irish climate in the twenty-first century. Met Éireann, Dublin, Ireland

Merow C, Smith MJ, Silander JA (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter Ecography 36:1058-1069

Moen A (1999) National atlas of Norway: vegetation. Norwegian Mapping Authority, Hønefoss, Norway

Muñoz J, Felicísimo ÁM, Cabezas F, Burgaz AR, Martínez I (2004) Wind as a long-distance dispersal vehicle in the Southern Hemisphere Science 304:1144-1147

Norwegian Biodiversity Information Centre (2015) Artskart 1.6 - Search: Marchantiophyta http://artskart.artsdatabanken.no/FaneKart.aspx? Accessed 28.01 2015

Norwegian Mapping Authority (2001) DTM Digital terrengmodell.

Norwegian Meteorological Institute and NVE (2014a) Daily precipitation. http://senorge.no/.

Norwegian Meteorological Institute and NVE (2014b) Snowdepth in mm. http://senorge.no/.

Paton JA (1999) The liverwort flora of the British Isles. Harley Books, Colchester, UK

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions Ecol Model 190:231-259

Phillips SJ, Dudík M (2008) Modeling of species distributions with MaxEnt: new extensions and a comprehensive evaluation Ecography 31:161-175

Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data Ecol Appl 19:181-197

Phillips SJ, Dudík M, Schapire RE (2004) A maximum entropy approach to species distribution modeling. In: Proceedings of the Twenty-First International Conference on Machine Learning, Alberta, Canada. ACM, pp 655-662

Ponder WF, Carter GA, Flemons P, Chapman RR (2001) Evaluation of museum collection data for use in biodiversity assessment Conserv Biol 15:648-657

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Ratcliffe D (1968) An ecological account of Atlantic bryophytes in the British Isles New Phytol 67:365-439

Rothero G (2003) Bryophyte conservation in Scotland Transactions and Proceedings of the Botanical Society of Edinburgh and Botanical Society of Edinburgh Transactions 55:17-26

Schofield W, Crum H (1972) Disjunctions in bryophytes Ann Mo Bot Gard 59:174-202

Schuster R (1983) Phytogeography of the Bryophyta. In: New manual of bryology, vol 1. The Hattori Botanical Laboratory, Nichinan, Miyazaki, Japan, p 626

Simberloff D (1998) Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biol Conserv 83:247-257

Smith, R. J., Stark, L. R. (2014) Habitat vs. dispersal constraint's on bryophyte diversity in the Mojave Desert, USA J Arid Environ 102: 76-81.

Snäll, T., Hagstrom, A., Rudolphi, J., Rydin, H. (2004) Distribution pattern of the epiphyte Neckera pennata on three spatial scales - importance of past landscape structure, connectivity and local conditions Ecography 27: 757-766

Speed JDM, Austrheim G, Hester AJ, Mysterud A (2010) Experimental evidence for herbivore limitation of the treeline Ecology 91:3414-3420

Störmer P (1969) Mosses with a western and southern distribution in Norway. Universitetsforlaget, Oslo, Norway

Sundberg S (2013) Spore rain in relation to regional sources and beyond Ecography 36:364-373

Söderström L, During HJ (2005) Bryophyte rarity viewed from the perspectives of life history strategy and metapopulation dynamics J Bryol 27:261-268

Vanderpoorten A, Goffinet B (2009) Introduction to bryophytes. Cambridge University Press, Cambridge, UK

Virtanen, R., Oksanen, J. (2007) The effects of habitat connectivity on cryptogam richness in boulder metacommunity Biol Conserv 135: 415-422.

Wangen, K. (2015) 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. Master Thesis. Norwegian University of Science and Technology, Trondheim Norway pp.74

Tables

Table 1 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 1. *Growth season was defined as 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}*.	Rain frequency is linked to the stability of humid conditions, one of the most characteristic features of the oceanic climate.	1 km^2	0.40–1.88	1990-2014	Derived (Norwegian Meteorological Institute and NVE 2014b, a)
Summer rain	Precipitation (mm) in warmest quarter.	Summer rain contributes to high humidity as required by the species of the hepatic mat community.	30 seconds (~1 km^2)	14.5–64.3 mm	1950-2000	(Hijmans et al. 2005)
Mean summer temperature	Mean temperature in warmest quarter (°C).	Liverworts of the western element are believed to be limited by high summer temperatures (Ratcliffe 1968).	30 seconds (~1 km^2)	2.0–16.3°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 (Ratcliffe 1968).	25×25 m	0° to 85°	2001	Derived (Norwegian Mapping Authority 2001)
Aspect	360° divided into cardinal and intercardinal directions.	Hepatic mat species are almost exclusively found in NW to E facing slopes (Ratcliffe 1968).	25×25 m	Flat and eight cardinal directions	2001	

Table 2 Ranked importance (1-5) of variables to each 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

Figures

Fig. 1 (a) The study area shown for each species (red line). This 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). (b) 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 were collected from.

Fig. 2 Predicted habitat suitability for *A. donnianum* (top left), *S. ornithopodioides* (top right) and *S. nimbosa* (bottom left). 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 in the map of *S. nimbosa* is zoomed in on its geographical range.

Fig. 3 Maps showing which variable is the limiting factor across the study area based on the models 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.

Fig. 4 Response curves from the models 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.

Fig. 5 Multivariate Environmental Similarity Surfaces (MESS) 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 sampled 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).

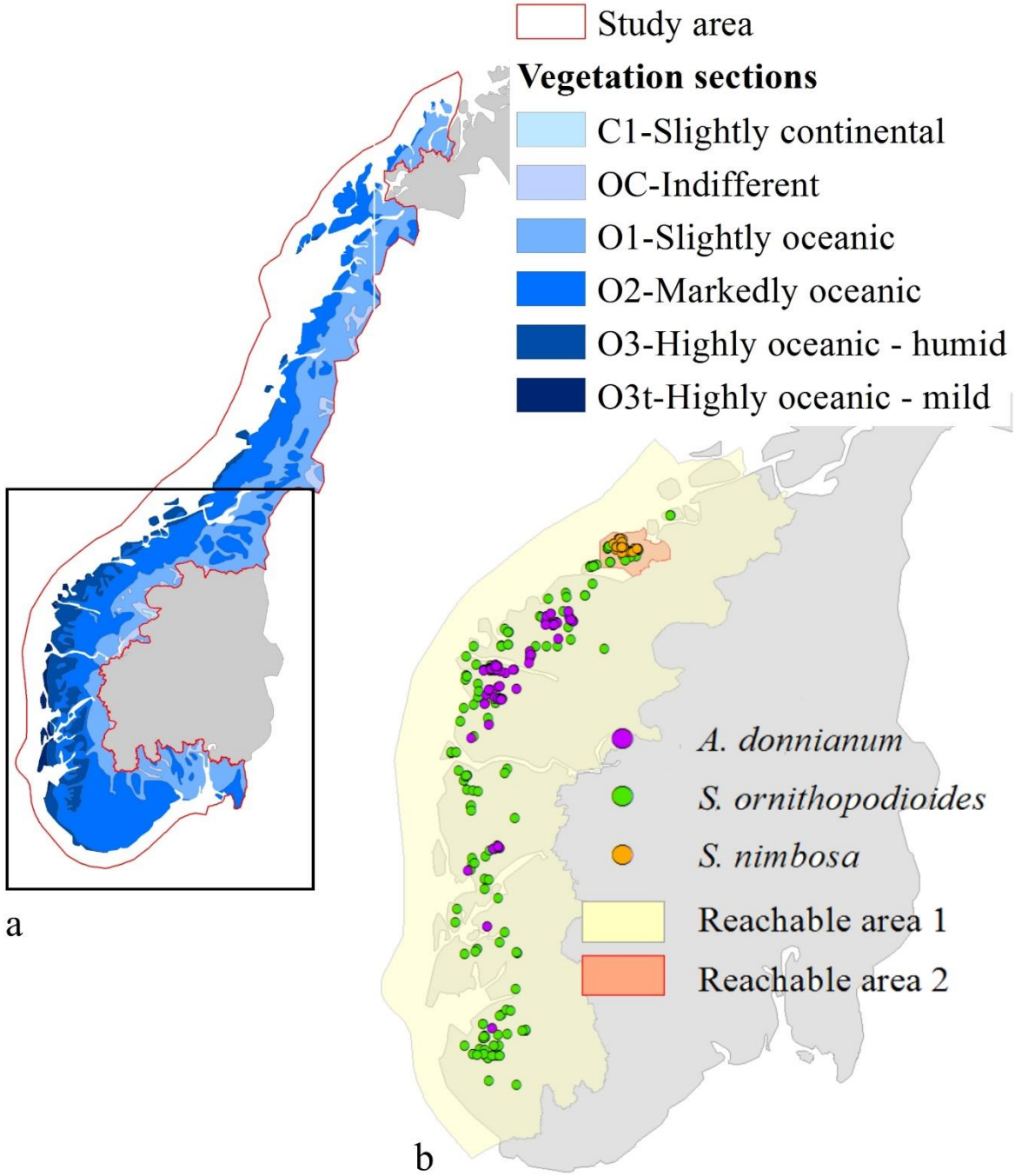
Study area
Vegetation sections
C1-Slightly continental
OC-Indifferent
O1-Slightly oceanic
O2-Markedly oceanic
O3-Highly oceanic - humid
O3t-Highly oceanic - mild
a
A. donnianum
S. ornithopodioides
S. nimbosa
Reachable area 1
Reachable area 2
b

Fig. 1

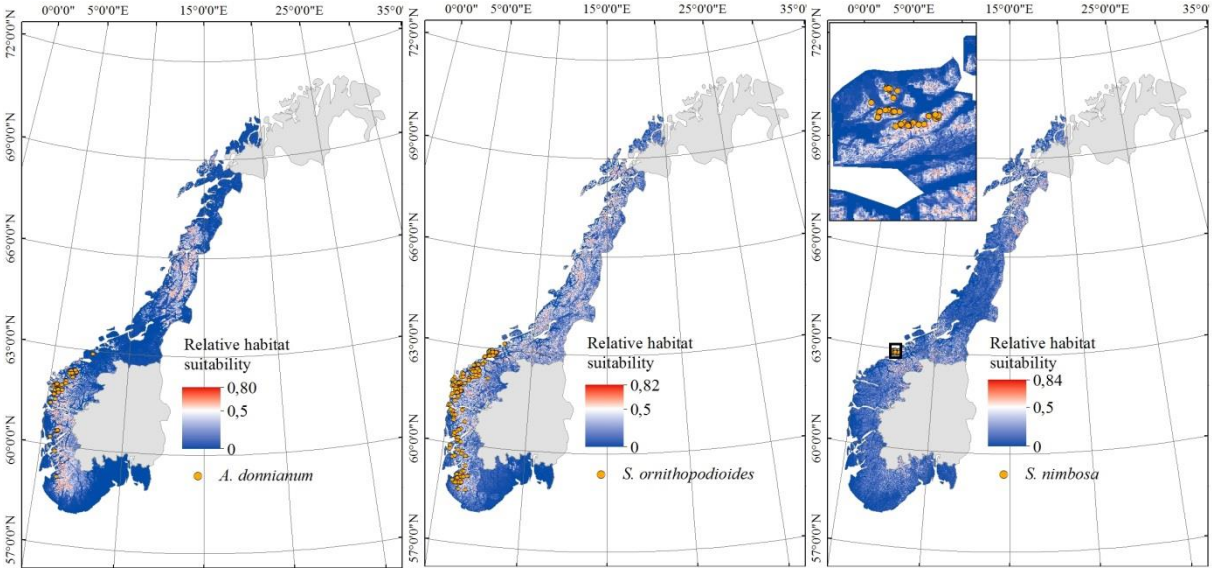
0°0'0"
5°0'0"E
15°0'0"E
25°0'0"E
35°0'
72°0'0"N
69°0'0"N
66°0'0"N
63°0'0"N
60°0'0"N
57°0'0"N
Relative habitat suitability
0,80
0,5
0
A. donnianum
0,82
S. ornithopodioides
0,84
S. nimbosa

Fig. 2

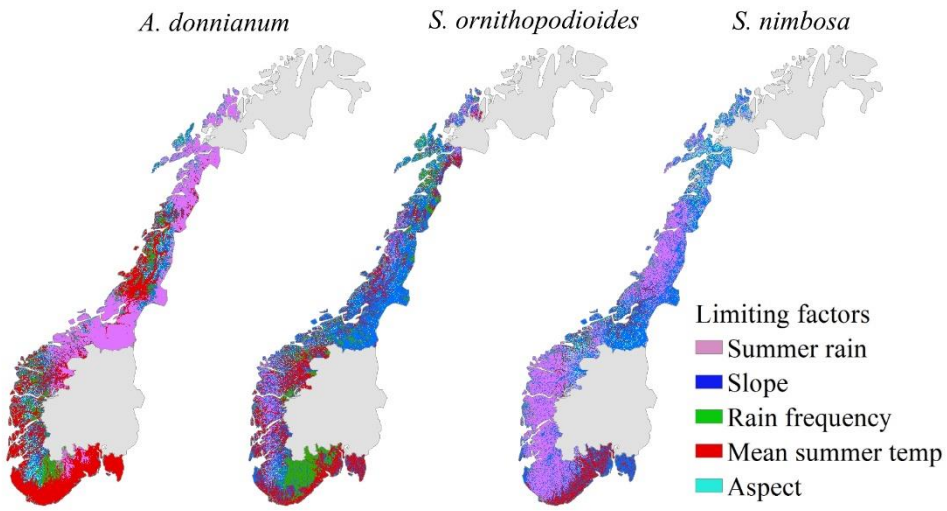
A. donnianum
S. ornithopodioides
S. nimbosa
Limiting factors
Summer rain
Slope
Rain frequency
Mean summer temp
Aspect

Fig. 3

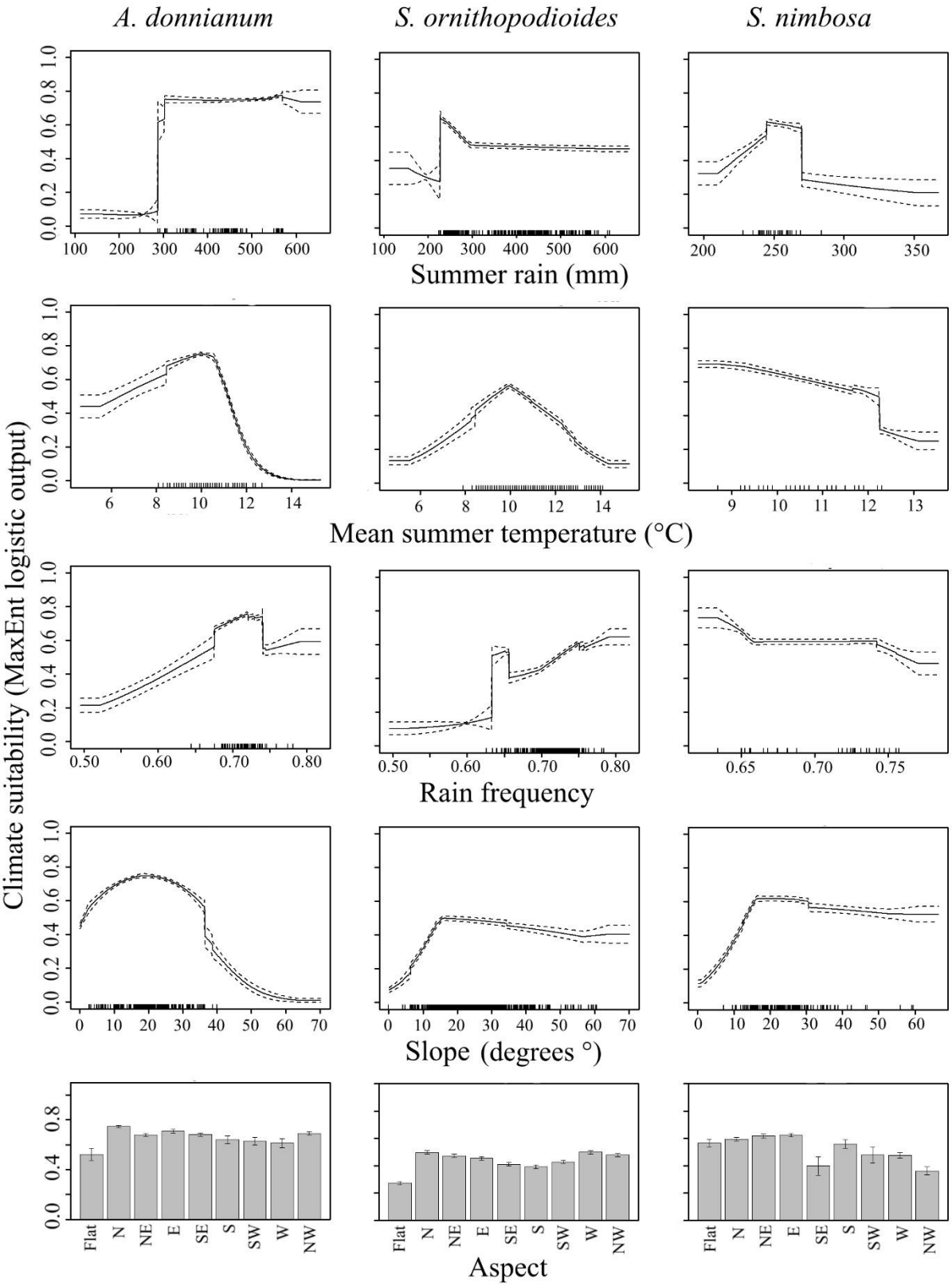
A. donnianum
S. ornithopodioides
S. nimbosa
Climate suitability (MaxEnt logistic output)
Summer rain (mm)
Mean summer temperature (°C)
Rain frequency
Slope (degrees °)
Aspect
Flat
N
NE
E
SE
S
SW
W
NW

Fig. 4

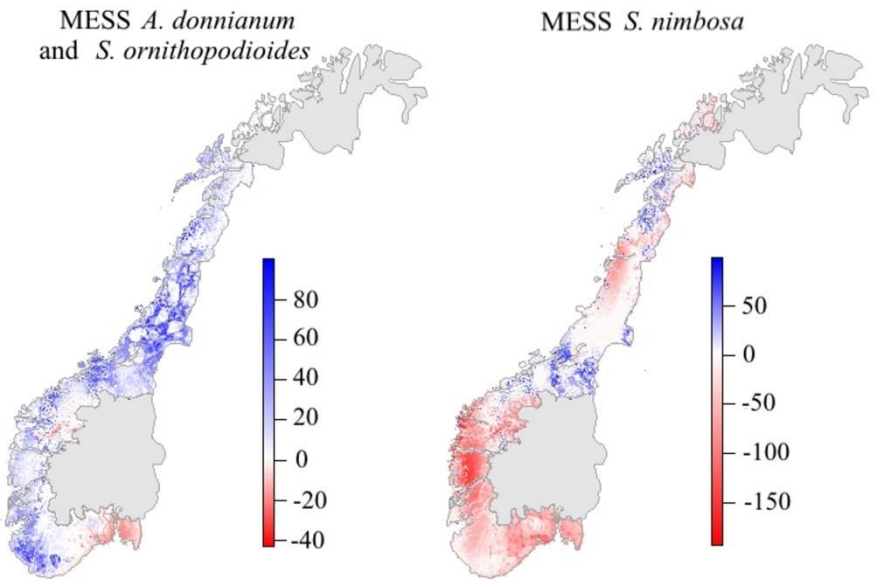
MESS *A. donnianum* and *S. ornithopodioides*
80
60
40
20
0
-20
-40
MESS *S. nimbosa*
50
0
-50
-100
-150

Fig. 5