

MODELLING SUITABLE HABITAT FOR ANASTROPHYLLUM DONNIANUM IN JÄMTLAND, SWEDEN

Using the species distribution model Maxent



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Abstract

Anastrophyllum donnianum, a liverwort species associated with the mixed northern liverwort heaths was recently (2023) found in Sweden for the first time. In order to conserve and manage the species and its habitat, knowledge about *A. donnianum*'s current distribution and ecology is necessary. Species distribution modelling (SDM) is a valuable tool to find suitable habitats and understand the ecological requirements for the habitats to exist. The aim of this study was to identify the environmental conditions for the suitable habitat of *A. donnianum* in the province of Jämtland, Sweden and to evaluate whether the species is dispersal or habitat limited in Jämtland. This was achieved by constructing a SDM with the Maxent model from Wallace, including both Sweden and Norway's occurrence points from GBIF and five non-correlated environmental layers created by weather station data and digital elevation models. The results indicate that the most important factor for suitable habitat is humidity and rain frequency, where the suitability of habitat increases with higher moisture availability. It shows that the suitable habitat for the species exists in mountainous north-facing areas with wet conditions and low sun exposure. The results also show that there are uninhabited highly suitable habitats (HSH) in Jämtland, with two hotspots south of the current known locations of *A. donnianum*. Additionally, the known Swedish occurrences were mainly found in a suboptimal habitat rather than HSH. The most important factors limiting the species is difficult to conclude only from the SDM, but the availability of suitable habitats suggests that dispersal is likely an important limitation. If the hotspots were to be visited in search of undiscovered populations, areas close to lake Anjan, Storrensjön or Storlien are recommended. Overall, the findings improve understanding of the ecological requirements and potential distribution of suitable habitat for *A. donnianum* in Sweden.

Keywords: Mixed northern liverwort heaths, Species distribution model, Maxent, Jämtland, suitable habitat, conservation.

1. Introduction

1.1 Bryophytes

Bryophytes evolved over 700 mya, making them one of the most primitive land plants (Hedges, 2002). Consisting of three different groups, mosses, liverworts and hornworts, they are a fundamental component of the world's terrestrial ecosystems, contributing disproportionately to numerous ecosystem functions. Despite their small individual sizes (Eldridge et al, 2023), their biomass can be more than 50% of the total above-ground biomass in some environments, such as tundra (Huemmerich et al., 2010; Wielgolaski, 1972). Bryophytes have a major ecological importance, being involved in biogeochemical cycling, soil climate, carbon and nitrogen cycling due to their efficient low use of nitrogen and promotion of nitrogen fixation (Cornelissen et al., 2007; Lett et al., 2021; Turetsky et al. 2010, 2012). The low use of nitrogen also seems to affect the decomposition rate of bryophytes, which alter peat properties (Turetsky et al., 2012). Water retention is likewise a major contribution to bryophytes' ecological importance since water absorption and retention are mechanisms that improve species richness and productivity (Rixen & Mulder, 2005). Bryophytes are also ideal as indicators of environmental change as they have not evolved vascular tissues, thus they directly absorb all the substances around them into their cells (Crandal-Stotler & Stotler, 2000). This characteristic makes their reaction to air pollutants and water contamination fast and absolute. As a result, they have been used as indicators of sulphur-dioxide pollution (Gilbert, 1968; Wielgolaski, 1975) and of climate change over centuries (Zechmeister et al., 2018). Although bryophytes share many physiological characteristics, substantial variation exists among their major groups, particularly in morphology and reproduction.

1.2 Liverworts

Liverworts have two subdivisions, leafy liverworts (Jungermannioids) and complex thalloid liverworts (marchantioids). Almost 85% of all liverwort species are leafy liverworts, including *Anastrophyllum donnianum*. Like other bryophytes, these groups have alternation of generations with different life stages. The gametophyte stage is the most dominant in the life cycle, it's where photosynthesis occurs and the reproductive organs are created. Fertilization needs free water for the sperm to reach the egg, after which a sporophyte is created. The sporophyte starts producing spores that will be dispersed and give rise to new gametophytes (Crandal-Stotler & Stotler, 2000). Unlike all other liverworts of the liverwort heath community, *A. donnianum* is the only species that have been recorded producing spores, on one instance in 1922 in Britain (Paton, 1999) it proves that free water is necessary for spore creation. The spores then disperse long distances with the help of wind connectivity or from endozoochory of transequatorial migrant birds (Lewis et al., 2014; Muñoz et al., 2004). Over short distances in places with low wind connectivity, the spores can disperse through zoochory, where the spores get stuck in the fur or feathers of animals (Heinken et al., 2001). Like all liverworts, *A. donnianum*'s asexual reproduction can be from both fragmentation and vegetative propagules, where both seem to be for local dispersal (Crandal-Stotler & Stotler, 2000; Vanderpoort & Goffinet, 2009). However, some later studies have shown that vegetative propagules can be linked to long distance dispersal. One European moss species, *Sphagnum subnitens*, was found to have contributed 100% of the gene pool in northwest North America, most likely from the event of a vegetative propagation (Karlin et al., 2011). However, like the other dioecious British liverworts in liverwort heaths, *A. donnianum* has never been

recorded to produce asexual propagules (Hill et al., 1991; Paton, 1999). This can indicate that the species use fragmentation as a way of dispersal and therefore zoochory become even more important in the northern environments (Flagmeier et al., 2013).

1.3 Distribution

Liverworts exist almost all over the world (Konrat et al., 2008) where the distribution pattern depends on the latitude with a more concentrated distribution around mountains (Wang et al., 2025). Even though it prefers mountainous areas, the distribution of *A. donnianum* is not as extensive as it only coexists with a few liverworts, the liverworts of the liverwort heaths (Flagmeier et al., 2013), also be called mixed northern hepatic mats (Hodd & Skeffington, 2011) or oceanic montane liverwort-rich heath (Flagmeier et al., 2013). The distribution of the liverwort heaths are more limited than other liverworts due to their restriction to the oceanic regions in Europe (Hodd & Skeffington, 2011). In Europe, the distribution of liverwort heaths is mostly restricted to the north/northwest in the countries of Scotland, Ireland, Norway and Faeroe Islands (Damsholt, 2002; Ratcliffe, 1968). Outside of Europe some of the species found in liverwort heaths can be found in the northwestern North America, Nepal and China (Damsholt, 2002; Flagmeier et al., 2020). Even though the northern liverwort heaths are species-poor in terms of large leafy liverworts compared to the British Isles, they consist of the same vegetation, leafy liverworts, mosses and dwarf shrubs where mosses and dwarf shrubs dominate. They are one of the most vulnerable vegetation types, mostly because of their limited environmental requirements. In Scotland the cover of graminoids, forbs and pteridophytes in the liverwort heaths have increased in the last 50 years (Flagmeier et al., 2013; Hodd & Skeffington, 2011).

1.4 Ecology

The most important factors for liverwort heaths to thrive are foremost humidity, summer precipitation frequency and low summer temperatures (Dahl, 1998; Damsholt, 2002; Ratcliffe, 1968). It is also believed that the frequency of precipitation is more important than the amount, where liverworts need a more wet climate, thereby the importance of humidity and precipitation frequency (Hodd & Skeffington, 2011; Ratcliffe, 1968). An example of this is in Lake District and North Wales where it rains up to 100 inches annually, but the liverworts flourish more in western Ireland and western Highlands where the accumulated rain only reaches 70–80 inches annually. Due to it being more spread out during the whole year (Ratcliffe, 1968). Not only do the climate conditions need to be fulfilled for the liverworts to grow, the topographic elements are also important to create the microclimates needed for these communities to exist (Hodd & Skeffington 2011). Since they want a humid environment, low sun exposure from the terrain orientation is needed to keep the soil moist but they also prefer slopes where the water drains well (Ratcliffe, 1968). Elevation is also believed to be a major contribution to the survival of liverworts, but primarily due to the effect of elevation on other climatic factors. Higher elevation is associated with lower temperatures and increased humidity due to fog formation (Schemenauer et al., 1995). Elevation may also contribute to prolonged snow cover which protects the species from frost events during cold winters (Jordal & Hassel, 2010).

1.5 Ecology of *Anastrophyllum donnianum*

Since *Anastrophyllum donnianum* rarely exists as single plants and mostly exists in the liverwort heath community, their ecology is very similar to the rest of the species of the liverwort heath

community. However, there are some differences, it prefer moist acidic soil with minimum sun exposure, therefore north or west facing slopes, on top of boulders or near the edge of flat rocks (Damsholt, 2002). The elevation range for *A. donnianum* is moderate, it is rarely reported lower than 300 m a.s.l and are most abundant around 610 m, but in some cases, it occurs over 1000 m (Averis, 1994; Damsholt, 2002; Ratcliffe, 1968). One major difference is the number of rain days (days with at least 1 mm of rain), where *A. donnianum* requires between 180–200 days. The same as *Anastrophyllum joergensenii* and *Scapania ornithopodioides*, whereas the rarer *S. nimbosa* needs over 200 rain days (Ratcliffe, 1968).

1.6 Conservation

The distribution of *A. donnianum* is like that of the liverwort heaths, it is most dominant in Ireland, Scotland and Norway but it has also been found in Sweden for the first time in 2023 with five different localities (Ratcliffe, 1968; SLU Artdatabanken, 2026a; Figure 4). Due to the limited distribution, *A. donnianum* was listed as vulnerable (VU) on the Swedish red list 2025 (SLU Artdatabanken, 2026b). On Norway's red list, the category for the species is also vulnerable (VU) due to the small population size, even though Norway has over 1000 occurrences (Artsdatabanken, 2016; Høitomt et al., 2021). For the 2017 IUCN red list *A. donnianum* is placed in the near threatened category (NT) due to it being assessed as non-decreasing in population size (Hallingbäck, 2019).

Action programs for bryophytes have been in action in Sweden for many years, including the programs for three different leafy liverworts of the *Scapania* spp. or *Dicranum viride*, where successful transplantation was used to increase the localities (Norkvist, 2020). Flagmeier et al. (2014) also transplanted the leafy liverwort *Herbertus hutchinsiae* that is part of the liverwort heath community, this was also successful where all sites showed an increase in biomass weight. It has also been proven successful that *A. donnianum* can regenerate ex situ from fragments which would benefit future action programs if needed (Flagmeier et al., 2013).

1.7 Threats

1.7.1 Anthropogenic threats

The threats to the liverwort heath community are mostly anthropogenic, even though there are some natural causes as well. The most critical threat in Scotland and Ireland is overgrazing by sheep (Hodd & Skeffington, 2011). Up until the early 1990s the destruction of habitat in the hills by sheep was widespread, which affected the structure of the vegetation for the whole of Ireland (McAdam, 2024). This caused bryophytes of the hepatic mat community to disappear from previously known locations (Holyoak, 2006). The best known example of this is the *Adelanthus lindenbergianus* in the mountains of the Twelve Bens of Connemara where it was first discovered in 1962 in large heaths and in later times it was only found in a small patch after multiple visits (Long, 2010). Overgrazing is also the reason for the increased grazing-tolerant graminoids that are taking over the liverwort heaths (Flagmeier et al., 2014). The natural threats are mostly erosion since liverwort heaths prefer well drained slopes (Hodd & Skeffington, 2011). Since the population is small and concentrated in Sweden it has a higher risk for stochastic events that could cause extinction (Menges, 1992). At the same time, it has been shown that *A. donnianum* has good regeneration capabilities from fragments (Flagmeier et al., 2014), therefore total extinction is unlikely. Disturbance from humans can also be a threat where construction of road,

water pipes and hydroelectrical projects is a potential threat for the *Scapania nimbosa* (Jordal & Hassel 2010).

1.7.2 Climate change

It is to no surprise that the climate is changing where the locations for *A. donnianum* exist, Scotland, Norway and Sweden (Barnett et al., 2006; Lind et al., 2023). For the Scandes the precipitation will increase during the whole year, and the specific humidity will increase, making the climate wetter and moister. Interestingly, the increased temperatures will be greater at higher elevations, such as the Scandes (Lind et al., 2023). Also, the summer temperatures are the most limiting factor in the south of Norway (Wangen et al., 2016). The warmer climate will not only make the summers hotter, making the environment too dry for liverworts, it also minimizes the snow cover during the winter which is essential for the species to not experience frost events (Lind et al., 2023; Ratcliffe, 1968). It has been shown that the liverwort vegetation in Scotland over the last 50 years has had a decrease in species needing more precipitation and an increase in species needing warmer winter and summer temperatures (Flagmeier et al., 2013). Since the required climate will move north, the liverwort heaths species need to move with the climate to survive long term. Due to the limited dispersal possibilities for the liverworts, they will unlikely reach their designated climate in time (Hodd et al., 2014).

1.8 Species distribution models

Species distribution modeling (SDM) is a popular process in species ecology and conservation with an increase of over 4500 articles published since February 2019 when searching “species distribution modeling MaxEnt” on Web of Science and comparing with Lissovsky & Dudov (2021) search results. The distribution modeling is based on presence only data where the model extract variable data from the known occurrence points from the environment layers to gather the required conditions for the species. The model then projects these relationships onto areas with similar environmental characteristics to estimate habitat suitability, either in absence or presence or probability (Pearson, 2010). Because presence only models such as Maxent only uses occurrence points to find possible habitats it should not be used to predict the fundamental or realized niche since it only represents the niche that is represented by the observed points. Limiting factors such as dispersal or competition are not taken into consideration. However, SDMs remain valuable tools for identifying potential localities that meet the environmental requirements of rare species. (Pearson, 2010).

1.9 Knowledge gap

There is much we don't know about why *Anastrophyllum donnianum* exists in Sweden since it has only been found in highly clustered occurrences in the northwest of Jämtland. This makes it difficult to identify the full extent of the suitable habitat. Consequently, the fine-scale spatial distribution of climatically and topographically suitable areas remains largely unknown.

Although the ecology of the species has been studied more thoroughly in Norway and the British Isles (Damsholt, 2002; Ratcliffe, 1968), the importance of these climatic and topographic variables has not been quantitatively assessed in relation to the Swedish occurrences. Although there have been SDMs made for *A. donnianum* by Wangen et al. (2016) and Zanatta (2018), none have been made for the province of Jämtland and even further, none have been made at high resolution.

2. Aim

The aim of this study is to get a better understanding into why the red-listed *Anastrophyllum donnianum* exists in Jämtland, Sweden and how it can exist here despite the lack of the oceanic climate it is typically associated with. In particular I aim to better understand the environmental conditions in which *A. donnianum* can occur, and to identify suitable habitats for the species in the province of Jämtland. Specifically, I ask:

- What environmental conditions best predict the suitable habitats for *A. donnianum*?
- Are there any more suitable habitats for this species in Jämtland?
- Does *A. donnianum* appear to be limited more by dispersal or by environmentally suitable conditions within Sweden?

3. Method

3.1 Study area

The study area, Jämtland, is characterized by a mountainous environment with the Scandinavian mountains in the west stretching over 1700m above the sea level. The mountain range divides into valleys far-reaching to the Norwegian sea (Rafstedt, 1984). Due to a limited and clustered number of occurrences in Sweden, Norway's occurrences were included to provide sufficient data for a confident SDM. The environmental variable layers extent was determined by delineating a bounding box which contained most of the Norwegian occurrences and all of Jämtland (Figure 1). The training extent for the model was acquired from a minimum convex polygon of the occurrences. This included all the Norwegian occurrences within the environmental layers and the only occurrences from Sweden (Figure 1). The study area for Jämtland also included adjacent areas of Norway as the areas with high suitability were close to the border (Figure 3).

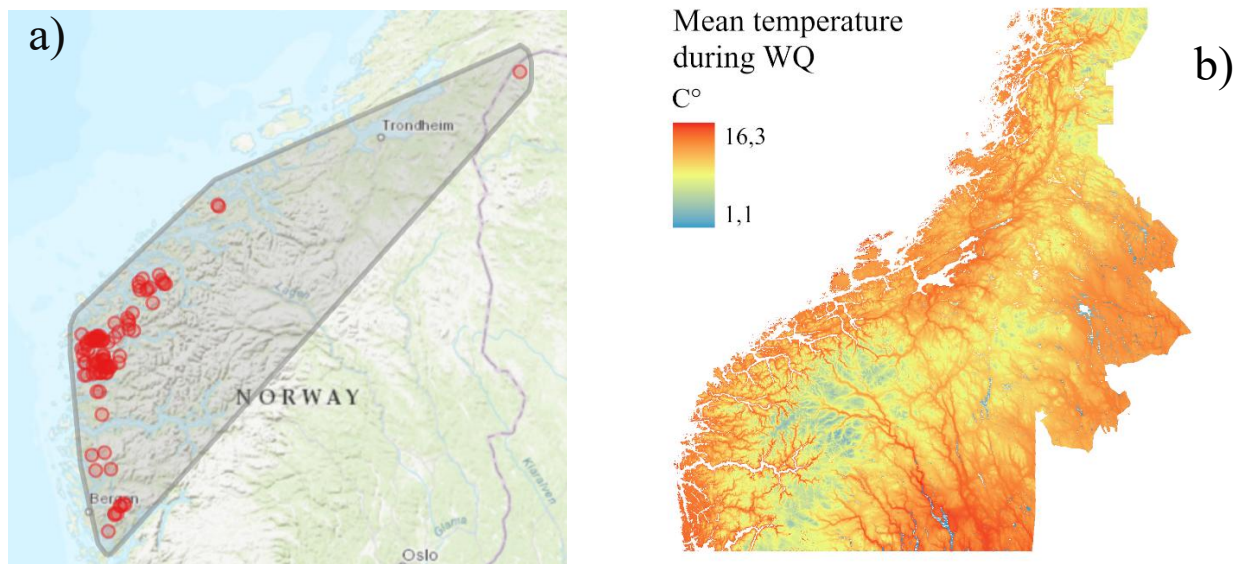


Figure 1. a) Map of the training extent used for the model. b) Map of the temperature raster used for the final model. See Table 1 for description.

3.2 Environmental variables

Taking into consideration that *Anastrophyllum donnianum* thrive in wet mountainous climate with high oceanity (Dahl, 1998; Jordal & Hassel, 2010) the variables that initially were going to be tested in the model was three topographic and seven climatic variables: Elevation, slope aspect, mean temperature during warmest quarter, total precipitation during warmest quarter, total number of rain days during the year, number of days with zero snow cover during the year, relative humidity during warmest quarter, rain fraction during warmest quarter and oceanity.

Firstly, the Swedish elevation data was downloaded from Lantmäteriet (2025) in a resolution of 50x50m cells covering the entirety of Jämtland. Kartverket (2020) was used to obtain the digital elevation model for Norway with the same resolution. The elevation layers was later used to create the aspect and slope layers with the same resolution using the spatial analyst tool in ArcGIS pro (Esri Inc, 2025). All topographic layers were transformed into the coordinate system WGS84 (EPSG:4326), the standard coordinate system for Wallace (Kass et al., 2023). The aspect layer was transformed to degrees 0°–360° while the slope was in degrees from 0.01°–90°. The slope layer was altered to remove any body of water as a possible habitat. Removing all slope cells with <0.01 degrees removed almost all bodies of water while keeping suitable land. The slope layer was also used to mask all other layers to match spatial extent, resolution and alignment across all environmental layers.

All environment layers were created by downloading weather station data from SMHI (2025a, 2025b, 2025c) and The Norwegian meteorological institute (2025a, 2025b, 2025c) through their API using R (Team, R., 2025). Only data after 1980 was used as the World Meteorological Organization (2007) states that the climatological standard normals range from 1980–2010 or 1990–2020 and the availability of data before 1980 was poor. Because some years were partially missing data, to minimize missing data, only data during the warmest quarter were used. The warmest quarter was calculated by proceeding with the 90-day period with the highest mean temperature for Sweden during the entire year. This revealed to be from 1st of June to the 30th of august. This period was also applied to Norway. Acquiring a mean for every weather station was achieved by filtering out any station that did not have a minimum ten years of daily data during the warmest quarter for all the variables. Then calculating the mean for every warmest quarter for every year, next, determining the mean for all the years for all the variables and station. Rain fraction was calculated by dividing the number of days with >0mm precipitation by the number of days in the warmest quarter, which in this case was 90. The oceanity was calculated using the Kerner oceanity index:

$$KOI = \frac{100(T_{oct} - T_{apr})}{T_{max} - T_{min}}$$

Where T_{oct} and T_{apr} (°C) is the mean temperature of October and April, T_{max} is the mean temperature of the warmest month of the year and T_{min} is the mean temperature of the coldest month of the year (Stonevicius et al., 2018). This created points with one mean for every variable for both Sweden and Norway. The points were then imported into ArcGIS pro (Esri Inc, 2025) where the class Bayesian kriging was used to interpolate the points into all environmental layers, since it is more complex (Samanta et al., 2012). Elevation was used as an explanatory variable in Bayesian kriging when interpolating mean temperature (Figure 1). However, elevation was not

used as an explanatory variable in any other variable because of high correlation to temperature and the variables not being affected by elevation. The final output resolution for all the layers was a cell size of 50x50m using the coordinate system WGS84 (EPSG:4326). When all layers were completed a Pearson correlation check was performed to see which layers had <0.7 in correlation, and only layers with less than the said number were used. This resulted in using the variables: slope, aspect, mean temperature, total precipitation, rain fraction, relative humidity and oceanity.

After adjusting the model to minimize AIC and maximizing AUC, oceanity and total precipitation were excluded from the model because of interpolation uncertainty and weak kriging output. This made the model have significantly improved evaluation metrics. The model was proceeded with the remaining five variables, two topographic and three climatic that can be seen in Table 1.

Table 1. Description of the environmental layers used for the final model and the ecological importance. The year represent the time frame used for the data to create the raster.

Variables	Description	Ecological importance	Resolution	Range	Year	References
Humidity	Mean relative humidity in the warmest quarter	High humidity reduces desiccation risk (Ratcliffe 1968).	50x50 m	69.63–85.07%	1980–2025	(SMHI, 2025a; The Norwegian Meteorological Institute, 2025a)
Rain fraction	Number of days with >0mm precipitation in warmest quarter divided by number of days during warmest quarter	Frequent precipitation maintains humid microclimatic conditions (Ratcliffe, 1968).	50x50 m	0.46–0.75	1980–2025	(SMHI, 2025b; The Norwegian Meteorological Institute, 2025b)
Temperature	Mean temperature during warmest quarter	Cool summer temperatures reduce drying and maintain suitable microclimatic conditions (Ratcliffe, 1968).	50 x 50 m	1.10–16.34°C	1980–2025	(SMHI, 2025c; The Norwegian Meteorological Institute, 2025c)
Slope	Steepness of the terrain in degrees	Steep slopes provide well-drained yet moist habitats (Damsholt, 2002).	50 x 50 m	0.01–78.57°	(2025, SWE; 2020, NO)	Developed from (Lantmäteriet, 2025; Kartverket (Norwegian Mapping Authority), 2020)
Aspect	Direction a slope faces in degrees	North-facing slopes reduce sun exposure and maintain cooler, moister conditions (Damsholt, 2002).	50 x 50 m	0–360°	(2025, SWE; 2020, NO)	Developed from (Lantmäteriet, 2025; Kartverket (Norwegian Mapping Authority), 2020)

3.3 Modeling algorithm

The species distribution modelling (SDM) was performed using a maximum entropy algorithm (Maxent) which is implemented within the Wallace v2.2.0 package in R. Wallace promotes reproducible and transparent modelling workflow by integrating different systems into one structured framework, while the model itself is Maxent (Kass et al., 2023; Philips et al, 2006). Although different alternatives such as the package maxnet are available in Wallace, the java implementation of Maxent (maxent.jar) was used to build the model in this study. This is due to its widespread use and strong performance of presence only modelling. Wallace includes all the different configurations for a SDM (Kass et al., 2018, 2023). The configuration used in this study can be seen below.

Maxent uses presence only data, thus the occurrences for *Anastrophyllum donnianum* for both Sweden and Norway were imported from the global biodiversity information center, (GBIF, 2026) were only records having coordinates and uncertainty under 1.0 km were used. For the time range, all records from 1950–2026 were included to maximize possible different habitats. Older occurrences were removed since they might not remain, as a consequence of climate change. The occurrences were inserted into Wallace which totaled 943 records after the duplicates and records outside my environmental layers were removed. Due to the majority of the Norwegian records occurring in cluster, spatial thinning in Wallace was used to minimize spatial sample bias and ensuring the clusters did not over influence model predictions (Steen, 2021). After thinning species 1.0 km from each other only 95 records were remaining.

Since the model needs to be trained on the total areas available for *Anastrophyllum donnianum*, a study extent was chosen as a minimum convex polygon around the occurrence points with a buffer of 0.2 degrees. Not including the 0.2 degrees buffer around the polygon created errors, which is why it was used (Figure 1). The polygon is where the model will draw its background points from. For the model fitting the default number of background points is 10 000, but sometimes only 90% of the background points were sampled as some points fell within cells with no data value. Therefore 11 000 background points were randomly sampled from the study extent to ensure at least 10 000 background points were used. The occurrences were later spatially partitioned with the “block” method using 4-fold for cross validation since it was proven to improve accuracy (Koldasbayeva, 2025). The blocks method draws one latitudinal and one longitudinal line to separate the area with the occurrences into four boxes with different environments (Kass et al, 2023).

When creating the actual model in Wallace, the default settings were used except for the following. The java implementation of maxent (maxent.jar) was used. Model tuning was performed by testing multiple combinations of the settings. The tuning was performed on all settings, testing all different feature classes, and the regularization multiplier was adjusted from 0.5–4.5. The final model used the feature class “LQH”, linear, quadratic and hinge since this provided the response curves with more flexibility while avoiding overly complex models. The best regularization multiplier was 2.5, as this reduced overfitting and improved model generalization. The selection for the final model was assessed on the combination of the model with the lowest corrected Akaike Information Criterion (AICc) and highest area under the curve (AUC) since they are acceptable as a way of selecting models (Elith et al., 2006; Katz & Zellmer, 2018). The evaluation metrics are calculated by Wallace when creating the model (Figure 5).

After the final model was chosen, a model prediction map was generated by carrying out a prediction for the training extent using a binary, suitable or unsuitable map. With a threshold based on the 10th percentile of training presence values. This model prediction was required for the model to be transferred to another extent. Therefore, after the model prediction, the model was projected upon the target study extent, the province of Jämtland. The “cloglog” transformation was used to convert the raw output from Maxent (relative occurrence rate) to a logistic model of 0–1 which represents the approximately probability of presence for the species. This created a continuous prediction map that can be seen in Figure 3.

3.4 Assessing dispersal or habitat limitation

To determine if the distribution of *A. donnianum* is more strongly limited by habitat suitability or dispersal, the predicted suitability of habitats was compared with the currently known distribution. If suitable habitat was restricted to areas where the species is already known to occur, this would suggest that habitat availability is the most limiting factor. Contrarily, if suitable habitat was predicted beyond the known distribution, this would indicate that dispersal limitation might contribute to the species' restricted range.

4. Results

4.1 Predicted habitat suitability

The Maxent model predicted habitat suitability for *A. donnianum* covering two areas, one for the study area and one for the transferred area of Jämtland, which can be seen in Figure 2–4. The Swedish suitable habitat showed spatially restricted distribution to the western Jämtland. The predicted suitability of habitats ≥ 0.6 (highly suitable habitats, HSH) was found close to the Norwegian border in discontinued patches, on north-northeast facing slopes in mountainous terrain with high humidity. On a regional scale the suitable habitat seem quite continuous, but on a local scale the HSH are fragmented with no continuous corridors where the HSH are separated by unsuitable terrain. Two larger hotspots of more concentrated suitable habitat were found foremost around lake Anjan and to the west of Storlien, south of the known occurrences. Most of the Norwegian occurrences overlap the HSH in Norway while the Swedish occurrences occur in more moderate suitability, outside of the HSH.

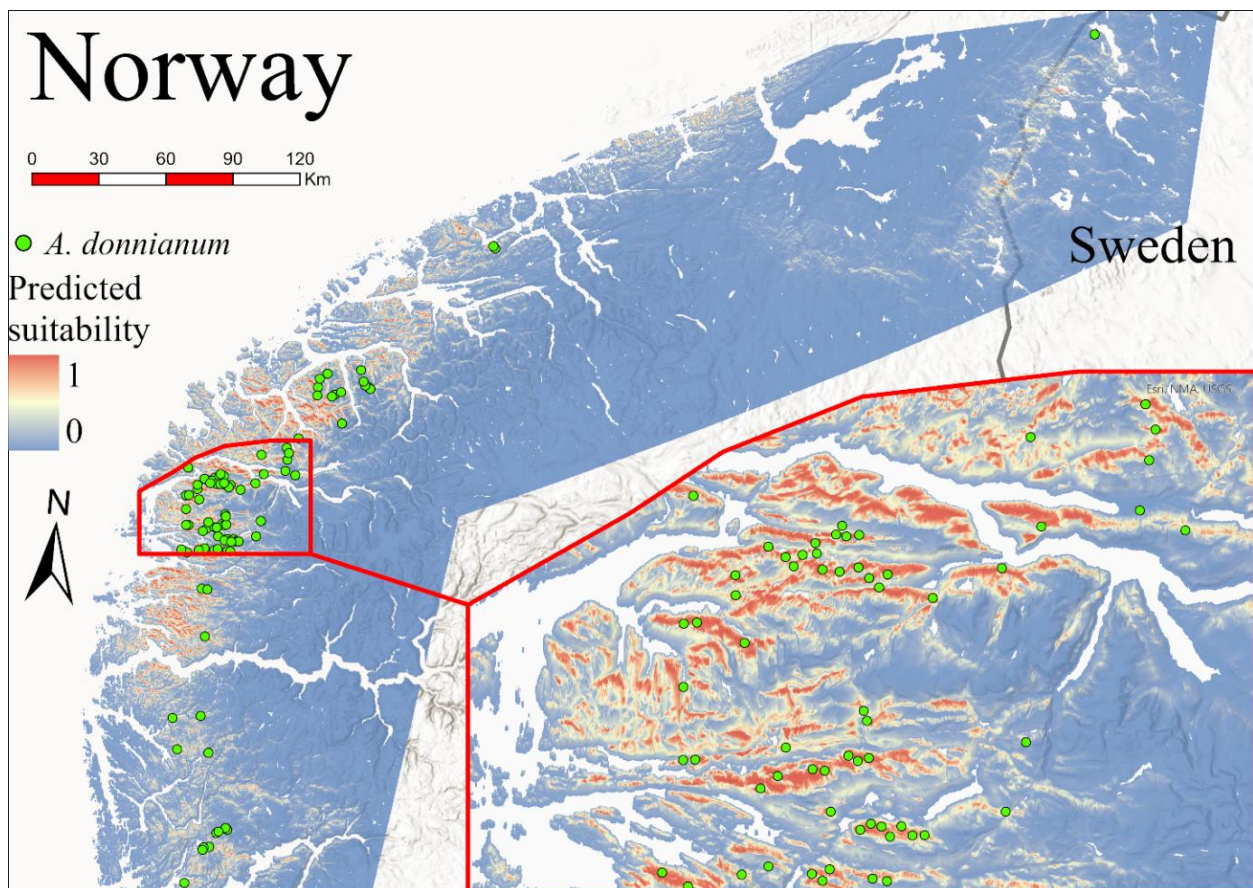


Figure 2. The predicted suitability of *A. donnianum* from the Maxent model with the filtered occurrences of *A. donnianum* for Norway and Sweden.

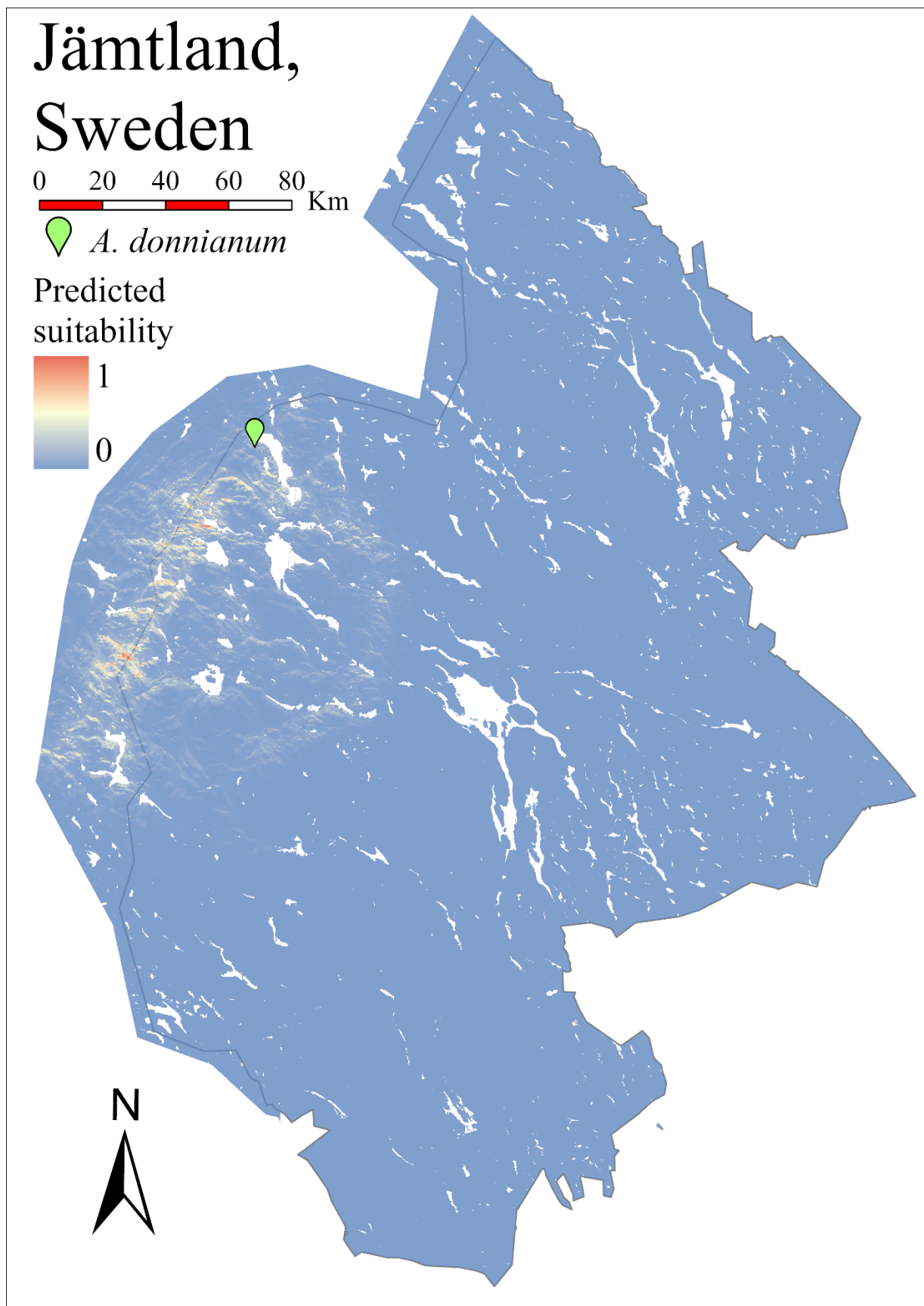


Figure 3. The predicted suitability of Jämtland, Sweden from the Maxent Model with some hotspots diverging over the border to Norway and the Swedish occurrences of *A. donnianum*.

West Jämtland

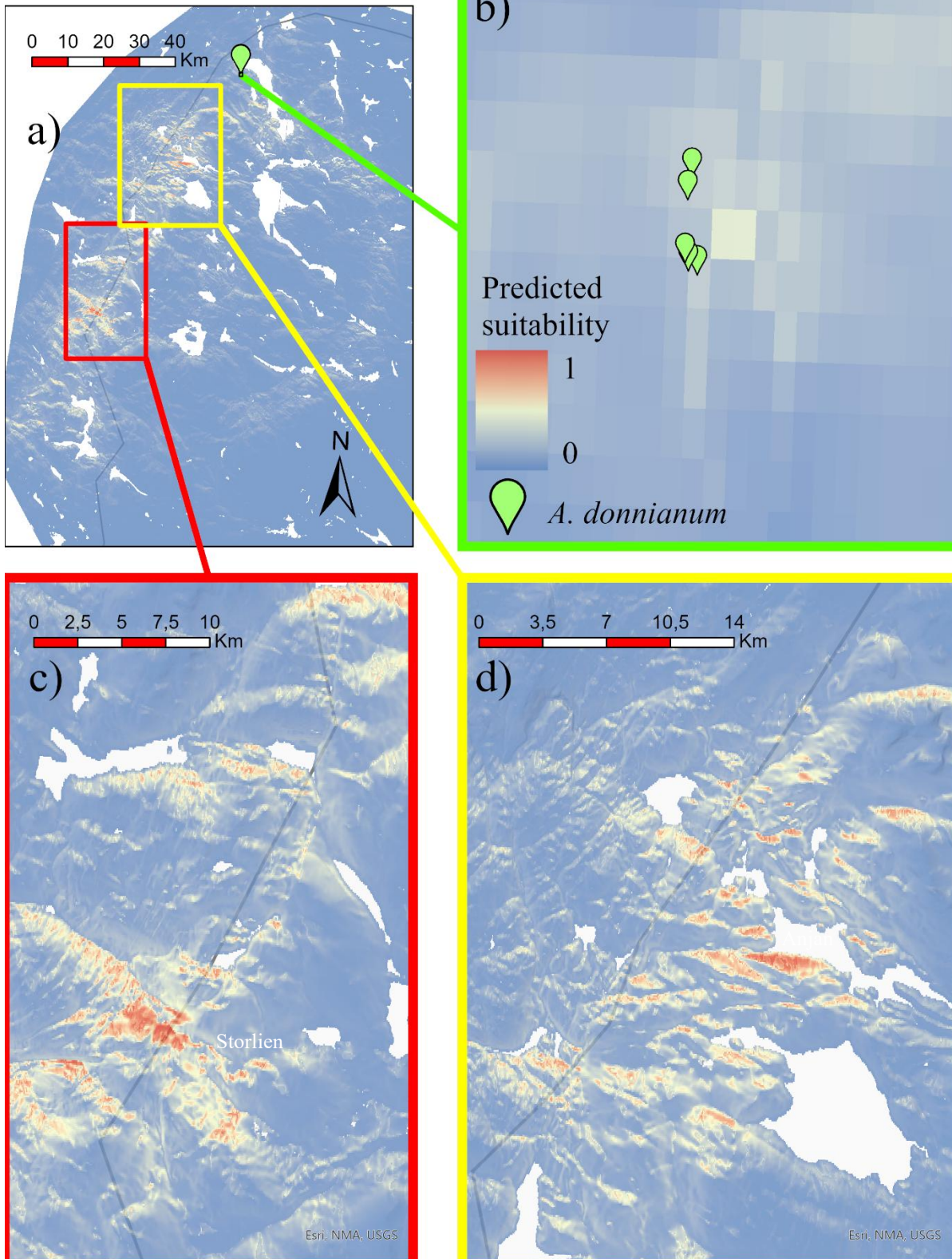


Figure 4. a) Zoom in over western Jämtland. b) The Swedish occurrences of *A. donnianum*. c) Concentrated spot of suitable habitats for *A. donnianum* west of the city Storlien. d) Another concentrated spot of more suitable habitats for *A. donnianum* around lake Anjan.

4.2 Environmental predictors of habitat suitability

The response curves (Figure 5) illustrate the relationship between each variable and the predicted suitability of habitat (y-axis) and the range of the variable. The most influential variable is the relative humidity, followed by rain fraction, aspect, mean temperature, and slope. Predicted suitability sharply increased when relative humidity increased above 78%, peaking at approximately 79% before declining slightly. The predicted suitability increased continuously with increasing rain fraction, where the highest point of rain fractions shows the highest predicted suitability. Aspect shows that predicted suitability increased towards the northern degrees with the lowest predicted suitability occurring at south-facing slopes. The range of mean summer temperatures had the highest predicted suitability between 11–13°C, peaking around 12°C. Slope showed the broadest range variable with predicted suitability sharply increases around 0° while peaking around 20° and then decrease steadily towards 65°.

Response curves for *Anastrophyllum donnianum*

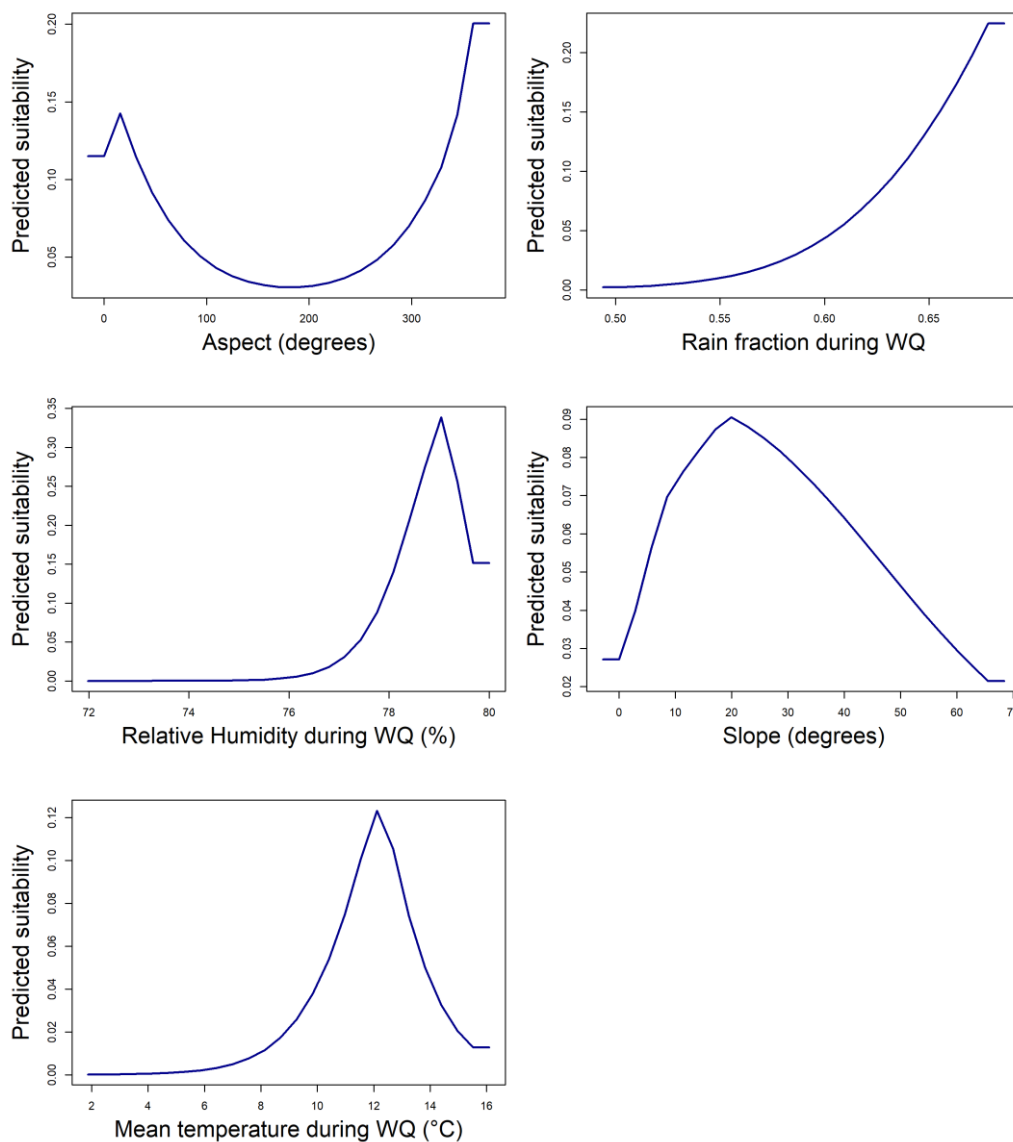


Figure 5. Response curves from Maxent for *Anastrophyllum donnianum* for all the variables used in the Maxent model. They show how the predicted suitability changes based on the value of the variable. The response of a single variable is shown while all other variables are held at their mean values.

5. Discussion

The aim of the study was to better understand the environmental requirements of the liverwort heath species, *Anastrophyllum donnianum*, as well as to identify additional suitable habitats in Jämtland, Sweden. The model predicted that there should be more suitable habitats in Jämtland, where the key predictors were the relative humidity and the rain fraction, which contribute to the same key point, that the species need a wet climate.

5.1 Importance of environmental predictors

The climatic factors are the most important influence in determining the suitable habitats for *A. donnianum*, as shown from the modeled response curves. Humidity and rain fraction were found to contribute most to the prediction of suitable habitat, suggesting that the species needs a wet climate to flourish. As these species lack vascular tissue and depend on atmospheric humidity to not dry out, a wet climate is necessary for photosynthesis to be as effective as possible. Water absorption and retention also increase the species richness, and since it has been recorded that *A. donnianum* can create sporophytes, free water is necessary. Therefore, humidity and rain fraction is very important for both growth and reproduction. The rain fraction response curve showed a unidirectional increase in habitat suitability with increasing rain fraction, suggesting that the more often it rains the more suitable the habitat is, which mirrors what we already know about the species. Surprisingly, aspect had a relatively large influence on the suitability of habitat, which contradicts Wangen et al. (2016) results, where aspect had almost no impact on the model. The reason behind this might be because Wangen et al. used aspect as a categorical variable where this model had aspect as a continuous variable. This model found the species preferring north-facing slopes, which also confirms the known ecology. Likely to achieve the right microclimate needed to keep the sun exposure low and soil moisture high, which is why the HSH locations are so fragmented, since it can only survive on one side of a mountain. The slope adds to this even further where it makes the side shadier and the soil moister with more water retention, which the results suggest as it favors slopes between 10–40°. One reason why the slope has such a small impact on the model could be caused by an interaction between aspect and the elevation model in the temperature variable. Since suitable habitats are concentrated in north-facing mountainous terrain, steep slopes are already characteristic of these environments, thereby reducing the independent contribution of slope to the model. The response curves also suggest that *A. donnianum* prefers low summer temperatures between 11–13°C, peaking at 12°C, suggesting that it lowers the risk of desiccation during the summer. It also shows a high correlation with elevation (Pearson correlation index of 0.98) likely due in part to cooler temperatures at higher elevations. These results suggest that suitable habitat occurs at higher elevation both for the summer, but also during the winter when the species will be covered by snow therefore being protected from frost events. This increases the confidence that the model captures ecological meaningful habitats because of the prediction and what is already known.

5.2 Suitable habitats in Jämtland

The HSH found by the model are foremost located close to the Norwegian border in north facing slopes in mountainous terrain. This pattern matches the topography of the known occurrences of *A. donnianum*, making the habitat a possibility if the species were to disperse. On a regional scale the HSH are concentrated to the west of Jämtland, since this is the only part of Jämtland that has a very wet climate with high elevation. On a local scale the HSH are very fragmented with many small patches where the topography requirements are met. This fragmentation will reduce the likelihood of colonization between patches.

The HSH do not contain any Swedish occurrences of the species. This could be due to lack of detection: either due to under-sampling, since the terrain is quite hard to access, or because the species is difficult to spot, since *A. donnianum* grows in heaths with other mosses and shrubs. In

contrast, these could be true absences, if the species has not successfully dispersed and established in these areas. The known occurrences in Norway mostly fall within the HSH suggesting that the predicted suitable habitats are good enough for the species to live in. Even though the known occurrences in Sweden live in a suboptimal suitable habitat outside the HSH, this only indicates the potential of the species to thrive in Sweden as well. Alternatively, this result could indicate that the model does not capture the full habitat, or that local characteristics outside of the variables included in this study have a bigger influence on the species.

5.3 Dispersal or habitat limitations

The HSH identified in this study fall outside the currently known distribution of *A. donnianum* in Sweden. The presence of suitable but unoccupied habitats suggests that the species is dispersal limited, although environmental conditions still limit where suitable habitats can occur in Jämtland. Thus, environmental factors appear to determine the spatial extent of potential habitat, while dispersal influences whether these habitats become occupied. Establishment can also contribute to the low number of known occurrences in Sweden. Although *A. donnianum* has demonstrated the ability to regenerate from fragments *ex situ*, this does not necessarily mean that successful establishment will occur under natural conditions. Establishment is likely influenced by additional ecological factors, including competition with other bryophytes within liverwort heath communities and the availability of suitable microhabitats, such as rock and boulder structures, which were not included in the present model. Furthermore, stochastic processes can possibly affect establishment success, where survival is not guaranteed and annual variation in precipitation could have an influence. The scattered distribution of HSH will also limit the expansion of *A. donnianum*, as suitable habitats are isolated and separated by unsuitable terrain, which likely will reduce connectivity between habitats and make it difficult for gradual colonization. Since spores are extremely rare and vegetative propagules are not produced, fragmentation represents the primary mode of dispersal, but because fragmentation is primarily used for local expansion this can hinder colonization of distant HSH. Under these circumstances, zoochory and endozoochory become particularly important for dispersal, as fragments could potentially attach to animal fur or be transported by birds to otherwise isolated habitats. The fragmented nature of suitable habitats should also result in isolated populations with reduced gene flow, potentially increasing vulnerability to stochastic events and local extinction. Consequently, while the results suggest that dispersal limitation contributes to the current Swedish distribution of *A. donnianum*, nothing can be concluded about the greatest limitation in Sweden from the species distribution model alone. More models would be needed to further evaluate the question, such as model evaluation- and MESS-maps. However, to get a final answer, translocation of the species to the HSH would be needed.

5.4 Climate change

Because of the projected climate change and the vulnerability of the liverwort heaths, it is rather predictable that they are at risk of disappearing, since they are already being reduced in Scotland. However, since the precipitation and humidity seem to increase in future simulations, climate change might benefit suitable habitats since the model prefer high rain frequency and more humid conditions. Assuming that the increased temperature does not make it drier despite increased precipitation. Even though Scotland has already seen a decrease in species in need of high precipitation, it might not be the same for the northern liverwort heaths since the climatic conditions differ substantially. In the future climate, the regional temperatures will increase causing warmer summers, this also means warmer winters, which lead to less snow protecting the species from frost events. The variables protecting the species from the hot summers, north-facing slopes could therefore become even more important in the future to create the microhabitat needed. The increased warmth might still be the most affecting element, because of the narrow window of preferred temperatures for suitable habitat. If the oceanic climate slowly moves north,

the species could move with it, but because of their low dispersal ability and the relative fast-moving climate, it limits the species capacity to track shifting climate conditions.

5.5 Conservation

The results of this study help better understand the oceanic environment located in the western Jämtland and manage the only known Swedish occurrences of *A. donnianum*. Predicted suitability maps are valuable to protect the areas of conservation interest and to prevent further deterioration of the species red-list status. Knowledge of the ecological requirements are useful to better know how the areas should be managed for conservation purposes. If the species' conservation status were to worsen, an action program could be a viable option. The species demonstrated ability to regenerate ex situ show that translocation of fragments or single plants may be a conservation option, therefore a map of suitable habitats are necessary. Future field studies should prioritize areas with HSH, recommendations such as, south of Anjan or southwest of Storlien should be considered.

5.6 Study limitations

The biggest limitation for this study is that the predicted suitable habitat hasn't been investigated in field. Field validation could help assess the accuracy of the model predictions and identify areas where the model may over- or underpredict habitat suitability. Furthermore, because the species relies highly on microhabitat created by rocks, boulders and acidic soil. The lack of raster's of the microtopography and the soil of the terrain limits the model at a micro-scale. Therefore, a combination of even smaller scale used for all raster's with more vegetation and soil variables would certainly improve the model, despite the enormous data sizes. Additionally, the environmental layers could be improved with better knowledge about interpolation settings. For example, different settings produced different looking climate layers which could have an effect on the final model. Lastly, the warmest quarter period derived for Sweden was also applied to the Norwegian data. While the difference in warmest quarter timing between regions was relatively small (approximately two weeks), this still introduces a degree of temporal mismatch. A more robust approach would estimate station-specific warmest quarter periods for calculating mean temperature.

5.7 Conclusion

In conclusion, the strongest predictors for habitat suitability for the species *Anastrophyllum donnianum* are humidity, rain frequency and aspect while mean summer temperatures and slope showed lower contribution. The model predicted that fragmented patches exist of unoccupied HSH south of the current known populations. This study cannot conclude that the species is dispersal or habitat limited, since both environmental- and dispersal limitations likely explain the distribution of the Swedish occurrences. The results can guide further field studies by mapping unoccupied HSH that may contain undiscovered populations.

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