

MODELLING POTENTIAL RANGE SHIFT OF THREATENED OCEANIC LIVERWORT UNDER A CHANGING CLIMATE

The future of *Anastrophyllum donnianum* and
northern hepatic heaths in Scandinavia



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Frontpage figure: *Anastrophyllum donnianum* in Jämtland, Sweden.
Photo by Niklas Lönnell (2023)

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Abstract

The ongoing climate crisis is deeply connected to biodiversity loss, impacting species' survival worldwide. Range shifts are a common adaptation for temperature and moisture-sensitive species tracking their optimal climate northward or to higher elevation. Liverwort species associated with northern hepatic heaths are one such sensitive group. Their European distribution is restricted along the Atlantic coast of Norway, Faroe Islands, and the British Isles thanks to their limited dispersal abilities and high environmental requirements, which makes them vulnerable to climate change. The discovery of an associated species to the liverwort community, *Anastrophyllum donnianum*, in Sweden suggested additional possible suitable habitat for oceanic species in case of a range shift, inspiring this thesis. This study aimed to increase knowledge about the habitat and possible future range shifts of *Anastrophyllum donnianum* in Scandinavia as a response to climate change. A species distribution model was built using Maxent, projecting possible suitable habitat for the species under three emission rate scenarios during a time period between 2071 and 2100. *A. donnianum* was found to prefer a mean summer temperature of 12°C with summer precipitation exceeding 50 mm monthly, consistent with earlier ecological knowledge. Final projections showed large amounts of highly suitable habitat outside of current known distributions, both in the present projection and in all future scenarios. Projections also showed a clear range shift into higher latitudes with a loss of present habitat as summer temperature increased in higher emission scenarios, resulting in further isolated populations. The most limiting climatic variable was deemed to be mean summer temperature, followed by oceanity and summer precipitation. Furthermore, previously known dispersal limitations were considered to be a severe limiting factor regarding the species current distribution, meaning a focus on ex-situ and in-situ conservation could be beneficial for the species future survival to manually establish populations in future suitable habitat.

Keywords: northern hepatic heath, species distribution modelling (SDM), climate change projections, Maxent, range shifts, conservation

1. Introduction

With an imminent threat of a changing climate, characterised by rising temperatures, shifting rainfall patterns, and unpredictable extreme weather leading to frequent natural disasters, a vast number of species are threatened across the globe. Biodiversity as a whole and many existing natural habitats are at risk as the decrease of biodiversity is strongly connected with climate change and habitat loss (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services [IPBES], 2019; Intergovernmental Panel on Climate Change [IPCC], 2023; Shin et al., 2022). Geographic range shifts in species are a common response to this, whether it is expansion or contraction of suitable habitat (Pecl et al., 2017; Lawlor et al., 2024; Manes et al., 2021; Parmesan, 2006). Abiotic factors such as temperature and precipitation define a species' fundamental niche and are strongly affected by a warming climate. However, several other factors define a species' realised niche, such as limitation of dispersal and other biotic variables and interactions. While geographic range shifts can act as a way for species to keep up with climate change, species that are limited by dispersal and habitat availability stand at a higher risk of extinction (Lawlor et al., 2024). This creates a clear advantage for species without specific habitat requirements, favouring generalist species that are adaptable and can easily disperse. Thus, resulting in the risk that generalist species outcompete vulnerable specialists with increased habitat requirements (Clavel et al., 2011; Lawlor et al., 2024; McKinney & Lockwood, 1999; Sweeney & Jarzyna, 2022). Specialist species are often limited in range, dependent on stable climatic conditions and have low dispersal rates (Clavel et al., 2011). Furthermore, conservation efforts of threatened species and habitats are focused on well-known and charismatic flagship species to appeal to and gain support from a wider range of people. Even though the majority of threatened and endangered species might not be included in said conservation effort (Simberloff, 1998). This puts rare and undervalued species at even greater risk, as they continue to be understudied and under pressure from a plethora of threats endangering their often small and fragmented habitats, which are vulnerable to disturbances (Haddad et al., 2015; Hanski, 2011; Laurance, 2008; Pimm et al., 2014). These threatened habitats further highlight the importance of continued research, conservation, and protection, where rare species otherwise face extinction due to anthropogenically induced climate change and habitat loss (IPCC, 2023; Pimm et al., 2014; Staude et al., 2020; Thomas et al., 2004).

1.1 Species distribution models

Successfully modelling how a species' range might come to change due to climate change can be crucial to current conservation efforts of species and threatened habitats (Manes et al., 2021). There are several tools to achieve this, and species distribution models (SDMs) are a popular choice by many. Machine learning tools such as Maxent are readily available and can produce high performance species distribution models without much previous expertise needed (Blair et al., 2022; Valavi et al., 2022). What these models do is to apply associations between species' known occurrence points and environmental variables to create a relationship, identifying environmental conditions suitable for a species' population to survive (Aiello-Lammens et al., 2023; Blair et al., 2022). This established occurrence-environment relationship can then estimate habitat suitability spatially across a study region. New environmental variables can also be applied to the created model which makes it a valuable tool for identifying potential range shifts of communities affected by climate change (Blair et al., 2022). Important to notice, is that SDMs effectively project a species fundamental niche, which only takes climatic and topographic variables into account of whether a species might be found in a space. An SDM does not take factors such as species interactions, spatial constraints, and dispersal limitations, into consideration. Thus, the model does not give the actual distribution of a species, but rather a potential distribution, where locations may or may not contain the actual species (Aiello-Lammens et al., 2023). Nevertheless, SDMs can act as a useful tool for conservation management planning, especially when it comes to climate change scenarios and the threat it imposes on species and their habitat (Blair et al., 2022).

1.2 Northern hepatic heath

The northern hepatic heath, also commonly referred to as the mixed northern hepatic mat community, is a rare habitat characterised by a group of endemic leafy liverwort species growing together with more widespread species of bryophytes in the under-vegetation of mountainous heath (Averis, 1992; Ratcliffe, 1968). The habitat is tied to an oceanic climate, defined by low annual temperature ranges, evenly distributed heavy rainfall through the year, and often overcast with clouds and strong winds (Averis, 1994; Dahl, 1998; McVean & Ratcliffe, 1962). These rare habitats are sparsely found along the northern Atlantic and are confined to the most oceanic parts along the coast, including the north-westernmost part of the British Isles, Ireland, Faroe Islands, and the south-west coast of Norway (Dahl, 1998; Flagmeier et al., 2014; Hodd, 2012). Despite their longitudinal stretch, northern hepatic heaths are nationally and globally scarce, with the most species-rich habitat located in the Scottish Highlands (Averis, 1992). Some 11 species of liverwort have been described as northern Atlantic and associated with the habitat type (Ratcliffe, 1968).

Despite being associated with an oceanic climate regionally, there are several additional factors deciding on a species' presence or absence locally. Many of the species are dependent on topographical factors such as elevation, aspect, and slope creating sheltered and humid microclimates sufficient for the liverworts to survive (Averis, 1992; Hodd & Skeffington, 2011; Ratcliffe, 1968). Thanks to the species' extremely restricted requirements of very specific climatic and topographic conditions, their distribution is very limited, and suitable habitats are highly vulnerable to disturbance and change (Flagmeier et al., 2014). All associated liverworts are dioecious, with male and female sex organs present on different individuals. However, a clear majority of species have never been noted to sexually reproduce by sporophytes, which speaks of a major disadvantage in their dispersal abilities (Averis, 1992, 1994; Damsholt, 2002; Flagmeier et al., 2013). This suggests that the establishment of new individuals and populations occurs through dispersal of fragments from existing liverworts, which in itself is likely to be a slow, unpredictable, and unreliable process of dispersal for the species (Rothero, 2003). However, many of the oceanic liverworts have been discovered to have a disjunct distribution globally, occurring in both Europe, eastern Asia and north-western America, which one could speculate hints at a previous time of a climate favourable enough to support long-distance spore dispersal (Damsholt, 2002; Rothero, 2003; Schofield & Crum, 1972; Wangen et al., 2016).

Anthropogenically-driven environmental changes are the greatest threat to northern hepatic heaths, as with a restricted distribution, and virtually non-existent long-distance dispersal by associated liverworts, any disturbance to existing habitat has a large negative impact on the community. Present threats include overgrazing, burning, and general degradation of habitat through acidification and erosion (Flagmeier et al., 2014; Hodd & Skeffington, 2011; Moore & Crawley, 2015; Ross et al., 2012; Rothero, 2003). However, while the habitat has been described as vulnerable to climate change (Averis, 1992; Ratcliffe, 1968; Rothero, 2003), current conservation strategies rarely take climate change into consideration (Araújo et al., 2011; Hannah et al., 2002). Despite this, many species show signs of potentially shifting their ranges outside protected areas, as the current environment becomes unfavourable with a changing climate (Hodd et al., 2014). There is therefore a lot of uncertainty in the future of hepatic heath communities with limited dispersal abilities along the Atlantic coast, with many of the species already being present on several countries' Red Lists (Hodgetts et al., 2019; Hodgetts & Lockhart, 2025; Høitomt et al., 2021a, 2021b; Sveriges lantbruksuniversitet [SLU] Artdatabanken, 2026). An appearance on the red list should be a cause for concern as the criteria used to assess a species place on the list reliably coincides with the criteria used to assess increased extinction risk because of climate change. This means that all species present on Red Lists have a higher risk of extinction when faced with the effects of climate change (Stanton et al., 2014). Gaining a deeper understanding of how suitable habitat might change in the coming years because of climate change would benefit any efforts for the habitat and its species' conservation.

1.3 *Anastrophyllum donnianum*

Anastrophyllum donnianum is regarded as one of the hardier northern Atlantic species (Ratcliffe 1968). While extremely rare, the liverwort has been observed with sporophytes, making it one of the only species associated with northern hepatic heaths to be so (Averis, 1994). Observations of the species in Europe have been mostly sterile, with sexually differentiated gametophytes being very rare, further limiting its dispersal abilities (Averis, 1994; Damsholt, 2002). Despite this, *A. donnianum* is one of the more widespread typical northern Atlantic species associated with the hepatic community in Norway, together with *Scapania ornithopoides*. The more uncommon *S. nimbosea* and *A. joergensenii* can also be found along the southwestern coast (Averis, 1994; Damsholt, 2002; Jordal & Hassel, 2010). The species are all found in greater abundance at higher elevations in the British Isles, hinting at a preference for prolonged snow coverage (Ratcliffe, 1968). These traits could explain why only some northern Atlantic species are found in northern Europe at higher latitudes with an overall colder climate, and why the British Isles seem to house the highest number of species locally with its mild hyper-oceanic climate more suitable for a wider range of liverworts (Averis, 1992). *Anastrophyllum donnianum* is continuously described as a species that can tolerate a more continental climate, which also flourishes where snow lies late in the season. The species is therefore not as sensitive to drier conditions, as the snow seems to compensate for drier, less humid periods, while protecting it from extreme cold during winters (Ratcliffe, 1968).

In 2023, *A. donnianum* was found in the westernmost part of Jämtland, Sweden. As of 2026, only six locations have been recorded nationally, solely in Jämtland, and none of the other oceanic liverworts highly associated with the habitat has been found so far (SLU Artdatabanken, n.d.). While associated with northern hepatic heaths, the fact that *A. donnianum* is regarded as hardier than many of the other northern Atlantic species could explain its lonesome discovery in Jämtland, Sweden. As the current habitat might not be exemplary for the remaining northern Atlantic species. Nevertheless, it shows that a species associated with hepatic heaths can be found further inland in Scandinavia, which opens up the discussion for potential future habitat and more species of the community being located outside of their current recorded range. Especially when oceanicity along the Atlantic coast is supposed to increase with a warmer and wetter climate (Crawford, 2000; Lind et al., 2023). Therefore, projecting a predicted change in distribution through a species distribution model of a highly associated species like *A. donnianum* would benefit and prioritise conservation efforts, as well as gain insight to how a possible range shift might look like for the affected species in a changing climate.

1.4 Aim

The aim of this study is to increase our knowledge about the ecology and possible future range shifts of species associated with northern hepatic heaths as a response to climate change. This aim will be achieved through projecting the rare liverwort *Anastrophyllum donnianum*'s future fundamental niche and potential habitat in Norway and Sweden under different climate change scenarios through a species distribution model. In doing so, this study will contribute to a better understanding how northern hepatic heath species could respond to climate change and provide knowledge to aid in future conservation efforts.

2. Method

Maxent was chosen as a suitable machine learning model to produce an SDM for *Anastrophyllum donnianum*, as it is readily available with a known high performance (Blair et al., 2022; Valavi et al., 2022). For easier implementation, Maxent was used through the R-based GUI application Wallace (Kass et al., n.d., 2018, 2023). Wallace was created for ecological modelling and focuses on building, evaluating, and visualising species' distributions and niches.

2.1 Occurrence data

European occurrence data for *Anastrophyllum donnianum* was downloaded from the Global Biodiversity Information Facility (GBIF.org, 2026). Records were narrowed down to only include Norwegian and Swedish occurrences and filtered by removing records older than 1970 (Figure 1). Older records were removed because the present environmental data that would be applied most likely differed from when the occurrence was recorded. Duplicate records were removed, as well as a few occurrences missing environmental variables. Heavily clustered records could in some cases represent an observed difference in density of the species but usually occurs due to sampling bias as some locations are easier to reach than others. Thus, noted clustering most likely reflected over-represented areas through sampling effort, which are unlikely to contribute to the representation of the actual distribution of the species, and would reduce model performance (Hughes et al., 2021; Meyer et al., 2016; Phillips et al., 2009). Hence, records that shared the same grid cell were reduced to one per cell, in order to reduce any sampling bias. The final dataset contained 188 occurrences for *A. donnianum* across Norway and Sweden.



Figure 1: Map of filtered occurrence points downloaded from GBIF.org for *Anastrophyllum donnianum* across Norway and Sweden. Note that further filtering occurred within Wallace's interface and is not included in the figure. A total of 1006 occurrences were acquired, with six occurring in Sweden before further filtering was applied, ending up with 188 occurrences total.

2.2 Environmental data

When choosing environmental and topographical variables for a species distribution model (SDM), it is important to select ecologically relevant variables for the chosen species. The complexity of a study needs to be adapted accordingly to avoid under- or overfitting the model, which can be challenging. An underfit model risks not capturing observed occurrence-environment connections properly, which can lead to a misunderstanding of significant factors contributing to a species' distribution and thus over-predict species richness and range (Cao et al., 2013; Merow et al., 2014). Overfitting is another risk when building models, which includes excessive flexibility and an inability to apply training data to test data properly, which inadvertently results in under-predictions

of a species' range (Cao et al., 2013; Farrell et al., 2019; Pothuganti, 2018; Ramampianandra et al., 2023). To reduce the risk of these common mistakes, it is crucial to determine a suitable amount of complexity in an SDM. Underfitting is avoided by choosing a range of different types of environmental variables, both topographical, climatic, and geographical if applicable (Cao et al., 2013). Variables should be ecologically important to the species' distribution to reduce overfitting, which requires good knowledge about the ecological requirements of the study species. High collinearity is also a persistent problem when using SDMs, which risks increasing uncertainty in the model and contributes to overfitting (Dormann et al., 2013; De Marco & Nóbrega, 2018). Although machine learning tools such as Maxent generally handle collinearity better than other SDMs, it is still good practice to keep correlations between variables low. Generally, this is achieved through the Pearson collinearity coefficient (≥ 0.7 ; Farrell et al., 2019; Valavi et al., 2022)

Variables were considered based on existing knowledge about *Anastrophyllum donnianum* and northern hepatic heaths in general (Averis, 1992; Dahl, 1998; Ratcliffe, 1968). Bioclimatic data at a resolution of 1x1 km was sourced from CHELSA V.2.1 (Brun et al., 2022a, 2022b), and a digital elevation model of the same resolution (DEM) was acquired through a downscaled version of the ASTGDEM v3 dataset (Sismanidis, 2025), from which topographical variables could later be derived. Eight climatic- and three topographical variables were chosen as candidates: precipitation seasonality, growing season precipitation, summer precipitation, growing season length, winter temperature, summer temperature, annual precipitation, and oceanity for climatic variables; Elevation, slope, and aspect for topographical variables. These were then reduced to four climatic and two topographic variables that were used in the final model: summer precipitation, growing season length, summer temperature, oceanity, slope, and aspect (Table 1). Additional variables were excluded from the final model as a result of high correlation between the chosen variables according to the Pearson correlation coefficient (≥ 0.7), thus reducing their ecological importance when used together with the remaining variables which would risk overfitting the model. Large portions of northern hepatic heaths located in Scandinavia are covered by snow during the colder winter months, and higher altitudes have heavy snow cover which stays late into the season. Therefore, the snow protects any liverworts from frost penetration, and acts as cover for drier periods (Dahl, 1998; Ratcliffe, 1968). Variables such as temperature become biologically irrelevant during the winter months, hence why only climatic variables that represent the warmer seasons were included in the final model. An exception is oceanity, which uses temperatures spread throughout the year according to the Kerner oceanity index (KOI; Stonevicius et al., 2018).

Northern hepatic heaths are directly tied to an oceanic climate, with associated species requiring a mild and humid environment, hence why Kerner oceanity index (KOI) was chosen to be included in the final model as a climatic variable. KOI was calculated by dividing the mean monthly air temperature difference between October and April, with the difference between mean monthly temperature of the coldest and warmest months. High values (11 - 50) indicate oceanic conditions, while low or negative values (-10 - 10) signal continental conditions (Stonevicius et al., 2018). Liverworts endemic to oceanic climates usually follows distribution patterns defined by factors such as precipitation amount, humidity, and precipitation frequency rather than winter temperatures (Dahl, 1998; Ratcliffe, 1968). Therefore, to indicate the wetness of the climate, precipitation was deemed suitable to include as a variable. Precipitation during winter, however, was considered of little biological importance as liverworts are dormant and protected underneath an isolating snow cover (Dahl, 1998; Ratcliffe, 1968), which is why summer precipitation was deemed as a more suitable variable to include in the model. With moisture being a key variable in the suitability of habitat for oceanic species, it is important to take note of the interaction between moisture and temperature. More specifically, the way higher temperatures increase evaporation, especially in combination with vegetation exposed to high amounts of solar radiation (Dahl, 1998; Wangen et al., 2016). Given by the species' distributional patterns, it is suggested that many northern Atlantic species are limited by an intolerance to high temperatures (Ratcliffe, 1968) Hence why summer temperature was chosen as a relevant variable. *Anastrophyllum donnianum* is noted

to be more adapted to thrive where snow lies late (Ratcliffe, 1968). A variable representing growing season length should therefore reflect areas with late snow cover, and at the same time cover the amount of time the species would be vulnerable to temperature and humidity while not protected by snow. Topographical factors play a big role in forming suitable habitat for northern hepatic heath species on a local scale (Dahl, 1998). It is noted that associated species such as *A. donnianum* are scarce or absent on sun-exposed aspects, while more abundant and thriving on rocky north-facing, steep slopes sheltered in dark hollows where snow lies late (Damsholt, 2002; Ratcliffe, 1968). It is not unusual for the species to be limited by the absence of suitable topographical habitats rather than unsuitable climate. However, the two are strongly connected, as local climate is formed by topography, so a clear separation of the factors can be difficult (Ratcliffe, 1968). Nevertheless, elevation was deemed to have too high of a correlation with temperature and was excluded. With a resolution of 1 x 1 km, the variable slope was inevitably affected by slope reduction as the slope overall becomes flatter at a coarser resolution (Qinke et al., 2008). This will be further discussed later.

Table 1: Final climatic and topographic variables included in the model with description, range, and mean. Climatic variables sourced from CHELSA V.2.1 were transformed using the recommended scaling factors and offsets described by Karger (2022) to convert raw values into mm and °C for easier implementation into the model.

Variable name	Description	Unit	Min value	Max value	Mean	Time period	Resolution
MTWQ	Mean temperature of the warmest quarter (summer temperature)	°C	1.15	17.95	12.40	1981 - 2010	30 arcsec (~1km ²)
PWQ	Precipitation warmest quarter (summer precipitation)	mm	13.75	122.30	33.29	1981 - 2010	30 arcsec (~1km ²)
GSL	Growing season length	days	0	365	142.81	1981 - 2010	30 arcsec (~1km ²)
Oceanity	Oceanity according to the Kerner oceanic index (KOI)	KOI	-1.19	35.0	6.49	1981 - 2010	30 arcsec (~1km ²)
Slope	Inclination of slope	degrees	0	30.64	2.92	2000 - 2013	1km ²
Aspect	360° divided into northness and eastness	[-1, 1]	-1	1	-	2000 - 2013	1km ²

2.3 Model settings

With most of the collected observations for species being presence-only data, machine learning models have been designed to be able to work around the lack of absence points usually needed for more traditional SDMs. By creating theoretical absence points by using a set of randomly selected background points from the study area, a machine learning model can contrast available environmental conditions with requirements at known occurrence points (Baker et al., 2024; Valavi et al., 2022). Mapping a study region is an important step in determining the spatial extent for the model, including setting the range and combinations of environmental conditions associated with the species. This allows the model, if transferred to another region or time, to identify suitable or unsuitable habitat for the study species as the environment changes (Williams & Jackson, 2007). Important when transferring the model to different regions or times, is that the selected study region should not include geographic areas that the species are absent from due to dispersal barriers, such as mountain ranges or large masses of water. Inclusion of these areas would create false negative signals, which would create a strong bias, affecting the results and any conclusions drawn from the model (Anderson, 2015). With this known, a suitable study region was mapped out including all

188 occurrences with a study region buffer distance of 0.2 (~22 km), from which then 10 000 background points could be sampled from the total amount of points (~192 000). To further reduce any suspected sample bias, a spatial block-partition ($k = 4$) was applied to the remaining occurrences. This is especially advantageous when the model will be transferred to new environments and times, as the spatial partitioning mimics the degree of environmental extrapolation that will be necessary for the transferred model (Muscarella et al., 2013). No categorical variables were used, and the variable aspect was converted into “northness” and “eastness”, to avoid any problems with radially distributed variables (Pearson et al., 2007). When using Maxent to build an SDM, several models can be built to assess the best alternatives among the many options available to Wallace users. It can be especially tricky to evaluate the best fitting model without absence data, but with a combination of a low AIC (Akaike Information Criterion) of 3777.92 with a delta.AICc of 0, and a high (0.91) AUC (Area Under the Curve), it was decided that Maxent would be allowed to use all four available feature classes: linear, quadratic, hinge, and product (LQHP). With a model smoothing (rm) of 0.5 for optimal performance. Response curves were created for each variable, to assess habitat preference and suitability of the species according to the model. Finally, the model was transferred outside of the selected study region and extrapolated to include the whole of Norway and Sweden. The default logistic output was used to describe habitat suitability, depicted as a range of values between 0 - 1 where 0.5 represented “typical” habitat at the study sites. Thus, areas with suitability ≥ 0.5 could be considered favourable for *A. donnianum*. ArcGIS Pro was then used to finalise the maps (ESRI, 2025).

2.4 Climate projections

Future climatic variables were sourced from CHELSA V.2.1 (Brun et al., 2022b), with the same resolution of 1 x 1 km to successfully transfer the model to visualise suitable habitat under different climate change scenarios. A period between 2071 - 2100 was deemed suitable to ensure clear differences between the chosen scenarios. Three CMIP6 climate scenarios were available for download with different shared socio-economic pathways (SSP) which included varying projected emission rates: SSP 126, 370, and 585, which represent low, moderate and high emission rates respectively (Brun et al., 2022b). Each CMIP6 scenario projection was available by five different climate models, four were downloaded according to ISIMIP3 given priority list (Karger et al., 2022). A mean was calculated between these four models, which could then be applied to the SDM and visualised. To evaluate each model, a multivariate environmental similarity surface (MESS) analysis was performed for each scenario for an overview of dissimilarity between the training data and projected environment. This can be useful when extrapolating data in environmental space, as the novel environment usually has high levels of uncertainty and should be interpreted with caution. MESS analyses identify these areas, which get negative values. The larger the negative value, the more dissimilar the environment is when compared to the environment of the study region (Wangen et al., 2016). This was done together with an MoD analysis to show which variable had the most effect on the species absence and dissimilarity of the environment.

3. Results

3.1 Model response curves and present projection

The produced model variable response curves (Figure 2) indicate that the study species *Anastrophyllum donnianum* prefers an average monthly mean summer temperature around 12°C, with suitability decreasing drastically with mean summer temperatures exceeding 14 °C. Average summer precipitation amounts exceeding 50 mm monthly were deemed suitable for the species. Habitat suitability peaks around 15 - 20 KOI when coming to oceanity, and a growing season lasting at least 80 days is necessary. A clear preference for north-facing habitat is insinuated, including northwest and northeast. Finally, *A. donnianum* is absent from flat habitat, and suitable habitat is likely to be found by steep north-facing slopes. The visualised projection for the present model indicates that there is highly suitable habitat (≥ 0.5) well outside the recorded geographical

range for *A. donnianum* (Figure 3). Two large areas were deemed suitable along the western coast of Norway, with a gap between the two areas with unsuitable habitat. Instead, specks of suitable habitat surround the area further inlands, near the Swedish border.

3.2 Future projections

Results from the calculated mean of climatic scenario models indicate an increase of mean summer temperature across Scandinavia across all three scenarios (Table 2). Together with a slight increase in precipitation amount. Warmer temperatures result in a longer growing season overall, which the model suggests, with a mean length of 260 days during high emission (SSP585). Oceanity increases vastly in the moderate emission scenario (SSP370), with a mean of 20.17 KOI, but reduces in the high emission scenario. The modelled projections indicate that a clear expansion of present suitable habitat will occur within all projected scenarios, with the low emission scenario (SSP 126), showing the clearest range expansion northward along the coast of Norway and in the Swedish mountains (Figure 4). Large amounts of Jämtland, Sweden show high suitability (≥ 0.5) for *A. donnianum* in a low emission scenario, while this suitability decreases slightly in higher emission scenarios (Figures 5-6). Instead, the moderate and high emission scenario indicate a loss of present habitat, and a range shift towards higher altitudes in Norway and Sweden, while also shifting further north towards higher latitudes. In all three scenarios the gap between the northern and southern suitable area persists, leaving two separated areas of highly suitable habitat, albeit with a smaller gap in a low emission scenario (Figure 4).

Table 2: Values and means of bioclimatic variables between 2071 to 2100, sourced from CHELSA V.2.1 (Brun et al., 2022b). Variables for each climatic scenario was calculated from an ensemble mean of four climatic CMIP6 models. Multi-model ensembles reduce individual biases of single models and generally perform better as a consensus projection.

Variable	Unit	Scenario								
		SSP126			SSP370			SSP585		
		Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
MTWQ	C°	3.53	19.83	14.53	6.10	22.33	17.18	6.93	23.18	18.06
PWQ	mm	14.69	128.47	35.48	13.09	123.78	34.60	13.32	123.14	34.86
GSL	days	0.00	365.00	187.70	10.50	365.00	241.52	19.75	365.00	260.10
Oceanity	KOI	1.12	38.46	9.35	9.32	55.85	20.17	3.69	41.70	12.05

3.3 MESS- and MoD analysis

With the model being extrapolated outside the training area and time period, the MESS (Multivariate Environmental Similarity Surfaces) analysis performed for each projection showed differing amounts of dissimilarity of the environment (Figure 7). The present extrapolation showed no certain uncertainty of the environment, whereas the different climate scenarios showed strong uncertainty and dissimilarity of the environment along the eastern coast and the south of Sweden. The MoD analysis done for each projection produced similar results for the three future climate projections, where summer temperature seemed to have the most effect on the species absence (Figure 8). For the present projection, summer temperature, slope, and oceanity seemed to be contributing factors to why the environment was deemed dissimilar for the species preferences. Along the present known distribution of *A. donnianum* habitat in Norway, a dissimilarity of growing season length indicates a possible barrier for the species to migrate to higher altitudes further inland.

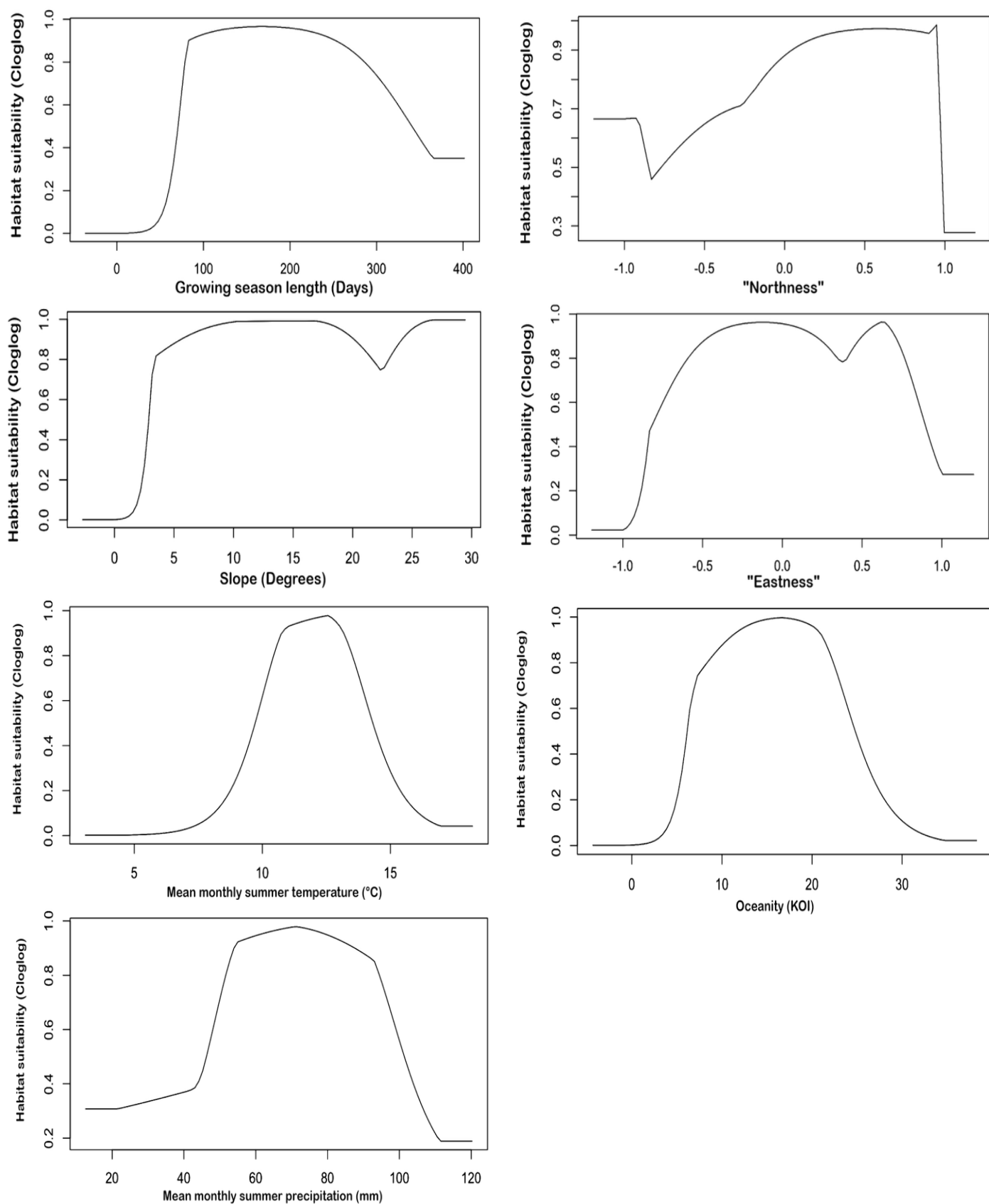


Figure 2: Model response curves of the included climatic and topographical variables; growing season length, northness, slope, eastness, mean monthly summer temperature, oceanity, and mean monthly summer precipitation as predictors of habitat suitability (Cloglog) for *Anastrophyllum donnianum*.

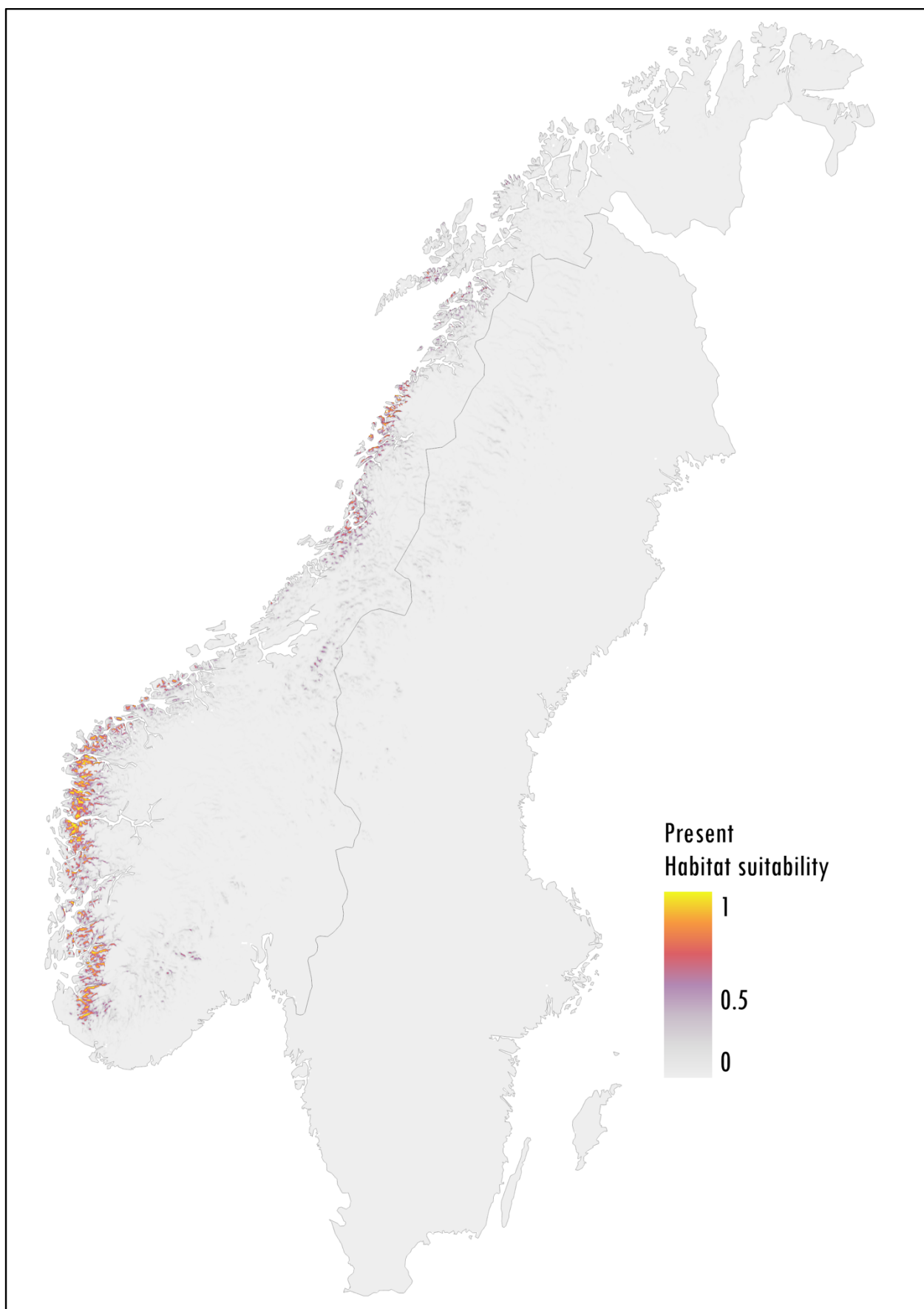


Figure 3: Present projection of suitable habitat for *Anastrophyllum donnianum* across Norway and Sweden. A habitat suitability of 0.5 is considered typical for the species at current occurrences, and anything above indicates highly suitable habitat (≥ 0.5).

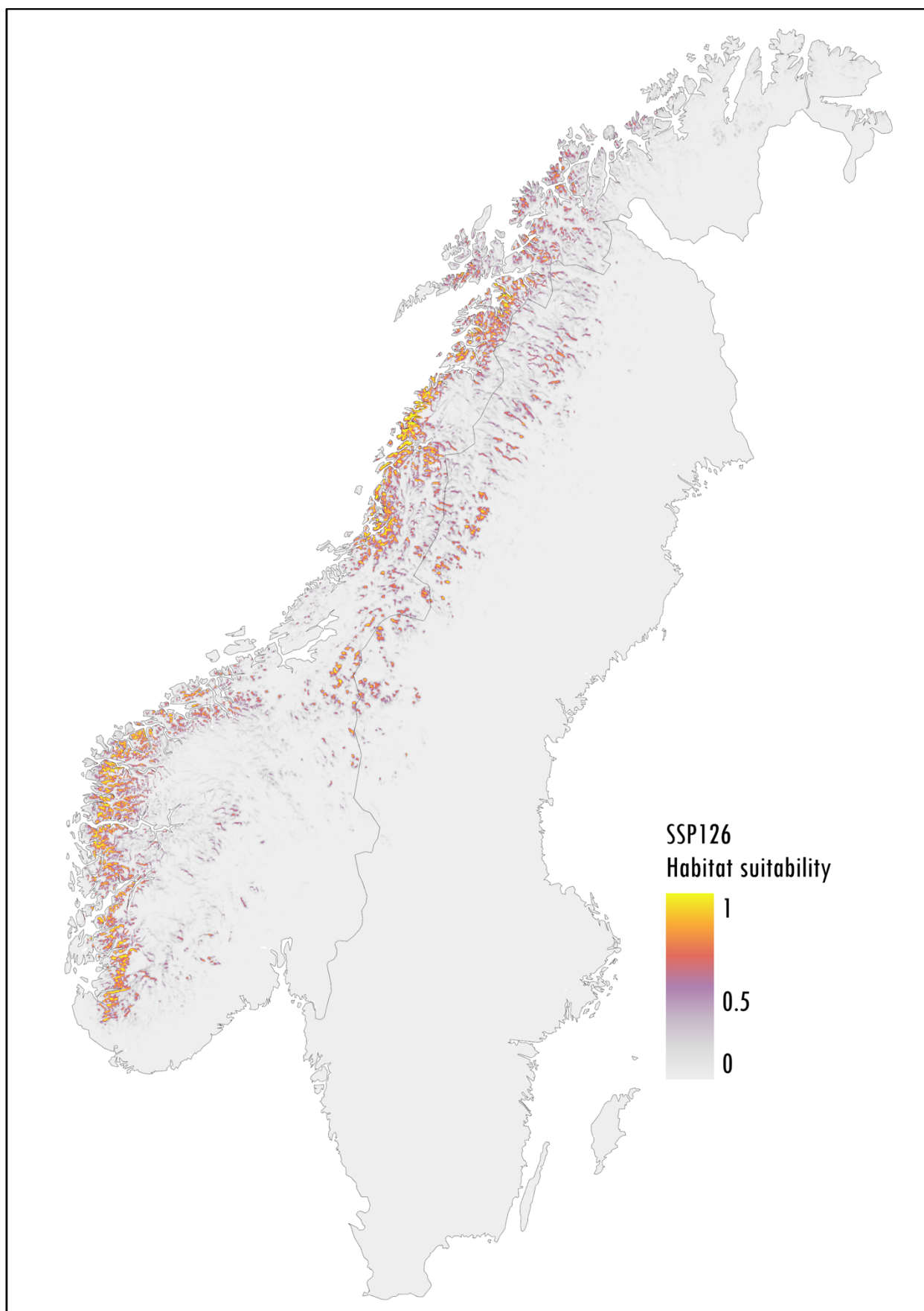


Figure 4: SSP126 (low emission) climate scenario projection of suitable habitat for *Anastrophyllum donnianum* across Norway and Sweden. A habitat suitability of 0.5 is considered typical for the species at current occurrences, and anything above indicates highly suitable habitat (≥ 0.5).

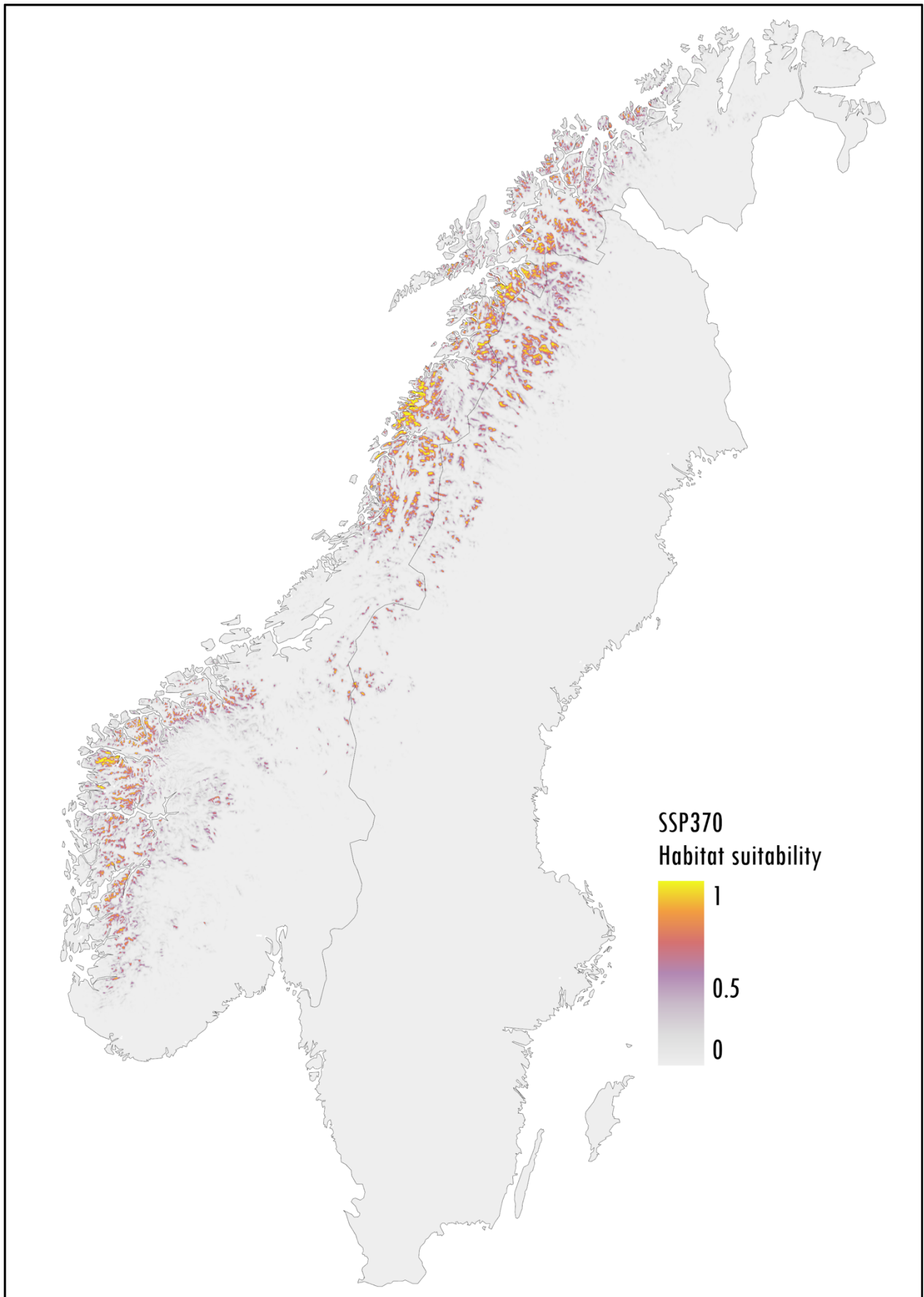


Figure 5: SSP370 (moderate emission) climate scenario projection of suitable habitat for *Anastrophyllum donnianum* across Norway and Sweden. A habitat suitability of 0.5 is considered typical for the species at current occurrences, and anything above indicates highly suitable habitat (≥ 0.5).

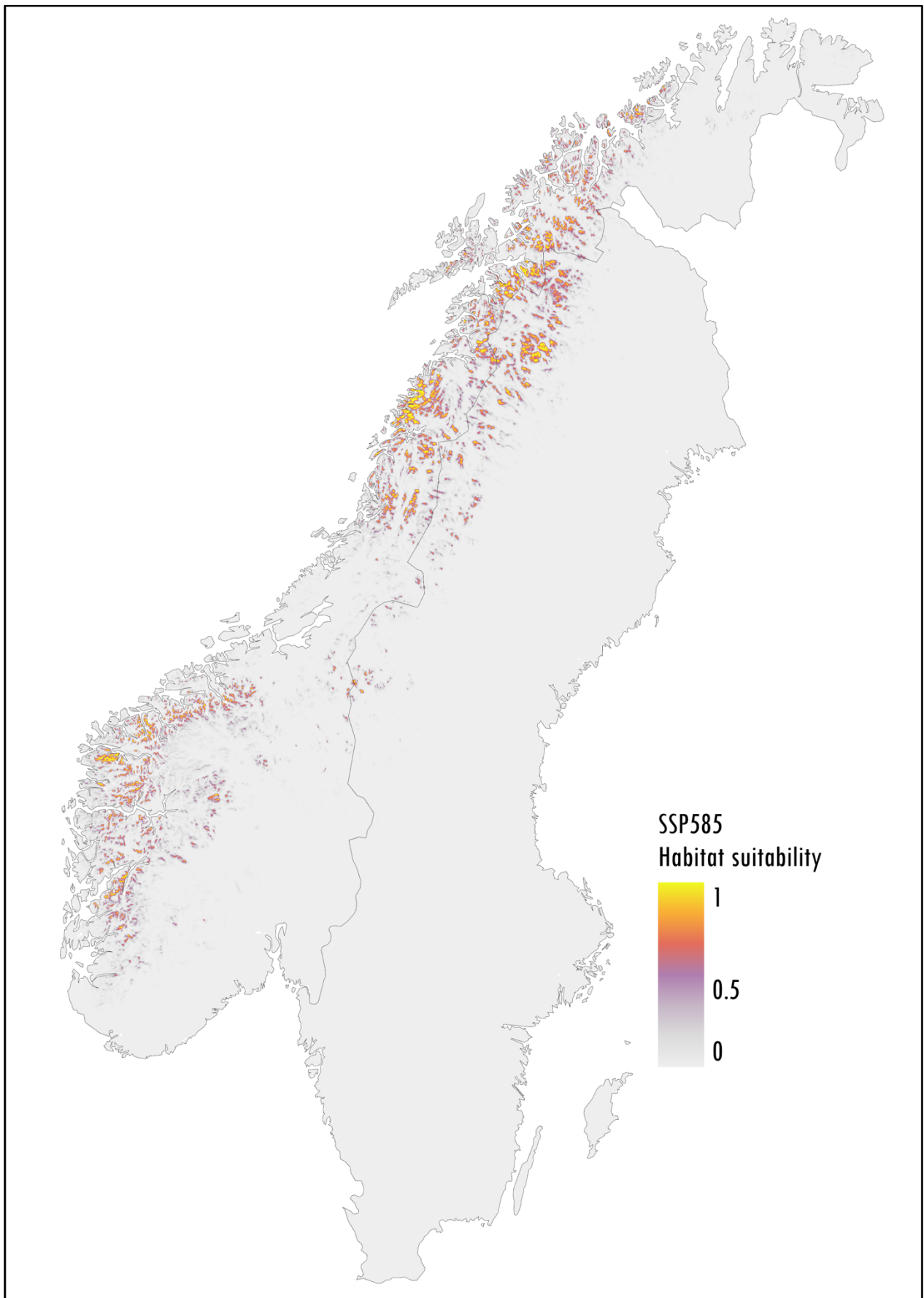


Figure 6: SSP585 (high emission) climate scenario projection of suitable habitat for *Anastrophyllum donnianum* across Norway and Sweden. A habitat suitability of 0.5 is considered typical for the species at current occurrences, and anything above indicates highly suitable habitat (≥ 0.5).

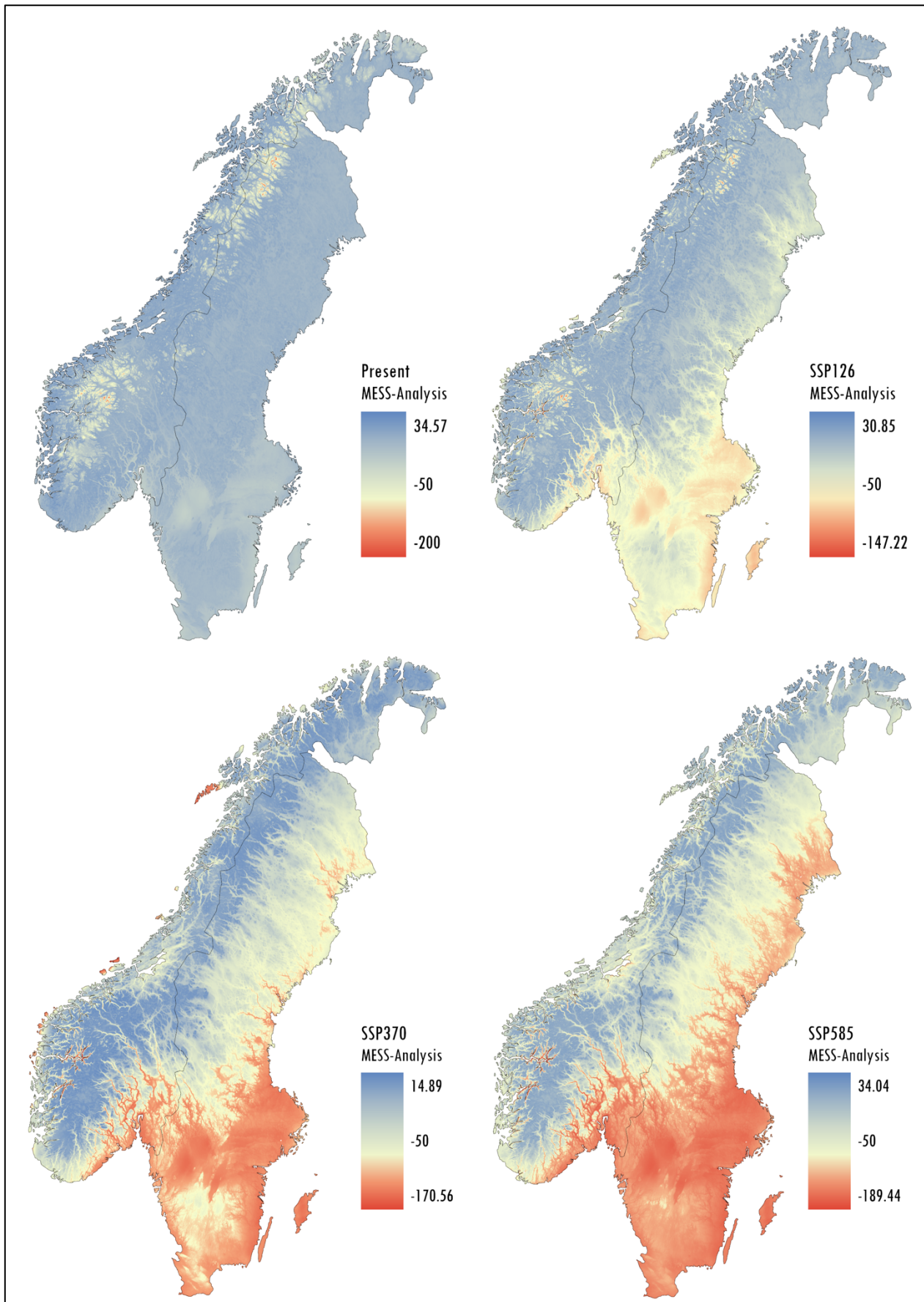


Figure 7: MESS-analyses (Multivariate Environmental Similarity Surfaces) of all projections and climatic scenarios. Indicating environmental dissimilarity compared to the study area of current occurrences. Negative values indicate an environmental dissimilarity strong enough to the point of a novel climate compared to the study area. Positive values indicate environmental values similar to that of the study area containing *Anastrophyllum donnianum*.

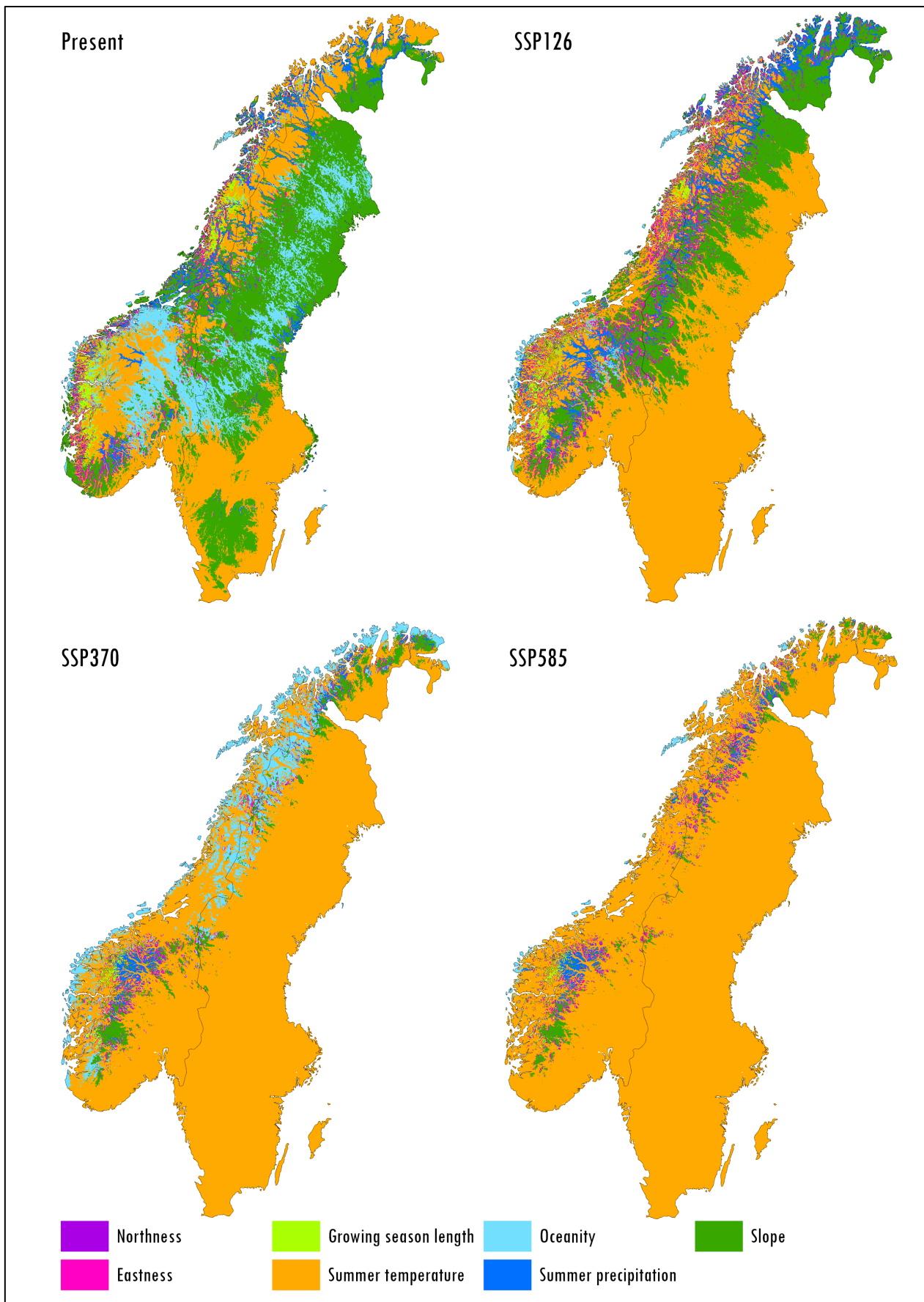


Figure 8: MoD-analyses of all projections and climatic scenarios, visualising the variable most dissimilar to the environmental range of current occurrences of *Anastrophylum donnianum*.

4. Discussion

The result of this study shows that the area of habitat suitable for *A. donnianum* is expected to change drastically in response to future climate change in all applied scenarios. The current southwestern Norwegian habitat will move inland, likely to higher elevation as summer temperature rises (Table 2), and much of the Swedish mountain range will have higher suitability for the species than present projections. Climate change will undoubtedly force species to adapt as their suitable ranges shift. Hence, why species with low dispersal rates stand before the greatest challenge as their habitat changes (IPBES, 2019; IPCC, 2023). The future projections show a clear range expansion in all scenarios. While the low emission scenario (Figure 4) projects quite a large range expansion, it might be overly optimistic with such a low emission rate given the current trajectory. Likewise, the high emission (Figure 6) may be overly pessimistic of a scenario (IPCC, 2023; Hausfather & Peters, 2020).

The response curves indicate habitat preferences of *A. donnianum* that seem to agree with earlier knowledge of the species preferences. With earlier records suggesting that high temperatures are detrimental to *A. donnianum* (Ratcliffe, 1968), all MoD maps seem to reinforce that theory as a strong majority of the most dissimilar variable is summer temperature (Figure 8), followed by oceanity and summer precipitation. However, with the clear increase of suitable habitat it is also suggested that an increased oceanity is predicted to expand further inland as the climate becomes somewhat wetter and warmer depending on the scenario (Table 2; Crawford, 2000). The importance of slope as a predictor of habitat suitability was likely affected by slope reduction and should not be taken into consideration unless paired with strong uncertainty, as Sweden would be considered flat in comparison to Norway where the study area was selected. The MESS analysis indicates a dissimilar environment along the eastern coast and to the south of Sweden, and while these projections are uncertain, they also show a clear dissimilarity of environmental values as climate change shifts values outside the current range that the model was trained upon.

4.1 Dispersal limitations

The present projection (Figure 3) shows that there is further highly suitable habitat (>0.5) outside of the current range of *A. donnianum* along the western coast of Norway, which suggests that it is currently dispersal that limits the species. The MoD-analysis (Figure 8) indicates that it is a mixture between oceanity and insufficient summer rain that prevents the species from reaching further suitable areas up north. This is acknowledged in additional studies regarding the distribution of *A. donnianum* in Norway as well, which have found similar results (Wangen et al., 2016). With this known, it should be considered that the known limited dispersal capability of the species will likely impact its ability to move across the mentioned area which is below typical suitability in all three climate scenarios. This drastically decreases any future suitable habitat reachable for the species. Without access to the higher latitudes, moderate (Figure 5) and high emission (Figure 6) projections show that areas of suitable habitat become more isolated from one another, which should be a cause of concern when populations that become fragmented and isolated results in decreased dispersal abilities (Jager & Soons, 2023). Furthermore, the increased risk of extinction caused by stochastic events that comes with small and isolated populations should not be overlooked (Lande, 1993). As a result of a warming climate, higher temperatures will likely force lower altitude species to migrate to higher altitudes as current habitat become unsuitable, which in turn increases competition among montane species at higher altitudes, further hindering any attempts of dispersal and successful establishment of new populations (Hodd et al., 2014).

4.2 Model improvements

Species distribution models are suitable tools for ecologists and conservationists in order to visualise species' distributions and niches, especially in the light of the challenges that come with a changing climate. However, SDMs such as Maxent assume that the study species are in total equilibrium with the environment, meaning that no biotic drives such as dispersal ability are

considered. Therefore, any modelled results must not be taken as the actual distribution of the species, but merely a projection of potential habitat if the species would reach it, which risks easily being misinterpreted. This is especially true when it comes to models that will be transferred to different time periods and geographical or environmental spaces (Charney et al., 2021). The achieved projections could act as a guide for future conservation among the species but should not be trusted blindly and caution should be taken when learning about a species' response to climate change which might influence future management (Ramampandra et al., 2023). Machine learning models are constantly improving to more accurately reflect the real world but ultimately does not achieve the same level of complexity and stochasticity found in nature. Furthermore, SDMs are controlled by a number of environmental factors at different spatial scales and have difficulty projecting local microclimates when modelled at a larger scale across countries (Hodd et al., 2014). The final model shows an adequate performance with the variables provided. However, the topographical variable slope was affected by slope reduction, and the performance of the model would undoubtedly improve should this be prevented by re-scaling slope to more accurately represent the actual values (Qinke et al., 2008). Furthermore, a more suitable choice of variables would certainly also give a fuller picture of the ecological needs of *A. donnianum*. One such variable might be snow cover, as with a warmer climate, a heavy snow cover during winter might not be as common as today and would make *A. donnianum* more vulnerable to drought and low temperatures during winter if absent (Lind et al., 2023). This snow protection is described as one of the reasons why the species can tolerate harsher fluctuations of temperature and oceanicity compared to other liverwort community species (Ratcliffe, 1968). The inclusion of such a variable would therefore surely affect the distribution of suitable habitat under different climate scenarios.

4.3 Future conservation efforts

With different climate scenarios projected, a more complete picture of *A. donnianum*'s future possible distribution can be pieced together, and in turn the future of northern hepatic heaths in Scandinavia. With several of the associated species present on red lists (Høitomt et al., 2021a, 2021b; Hodgetts et al., 2019; Hodgetts & Lockhart, 2025; SLU Artdatabanken, n.d., 2026), northern hepatic heaths and any associated species' conservation should be discussed. With limited dispersal, and a particular vulnerability to disturbances, the protection of present hepatic heaths is very much important. What these projections suggest is that a future range shift for a species associated with the habitat (*A. donnianum*) is likely to occur, no matter what climate scenario comes to resemble the actual future trajectory. Furthermore, with associated species in Norway and Sweden seemingly limited by dispersal, any attempted natural range shift is sure to be slow and unreliable, and without improved conservation would surely see a decrease in distribution of northern hepatic heaths and any associated species in Scandinavia (Rothero, 2003; Wangen et al., 2016). Hepatic heaths located in Scotland and along the surrounding Atlantic coast note the same results, as temperatures have been noted to increase, together with decreased summer precipitation and a suspected distinct range shift northward as a consequence of climate change. As a result, the community has become less distinct and is threatened to become homogenised with the loss of many liverwort species (Flagmeier et al., 2014; Hodd et al., 2014).

The specific protection of these liverwort communities is currently lacking across their distribution in Europe, and few conservation efforts include prevention of threats such as range shift as a result of climate change (Araújo et al., 2011; Hannah et al., 2002; Littlefield et al., 2019). With a projected northward range shift both in Scandinavia and the remaining European locations, the responsibility of conservation needs to fall on several countries, both where the habitat is present today and where possible future suitable habitat might appear or expand as a result of a changing climate (Harrison et al., 2006; Hodd et al., 2014). Sweden falls into the latter, and the habitat is not officially recognised within EU as a nature type with its sparse distribution in Jämtland and lack of further associated species. Instead, it is nestled within subtypes of more extensive habitats included in the EUNIS habitat classification, Annex I habitat types, more

specifically under European dry heaths (4030, S42) or Northern Atlantic wet heaths (4010, S41; European Environment Agency [EEA], 2021; Chytrý et al., 2020). This makes the habitat vulnerable as it holds no specific legal protection within the EEA, and many conservation efforts suitable for dry heaths, like burning, is detrimental to a majority of the northern Atlantic liverwort species (Flagmeier et al., 2014; Hodd, 2012). As a result, there is no major conservation plans for the threatened liverwort community across its distribution in Europe, save for specific regional conservation priorities (Bosanquet et al., 2018; Lindgaard & Henriksen, 2011). With southern European habitats notably decreasing in range (Flagmeier et al., 2014; Hodd et al., 2014), future possible new habitats at higher latitudes should be regarded as an opportunity for the conservation of Atlantic liverwort species and associated vegetation and should be in each country's best interest to pursue in order to preserve the rare community. Hence, increasing public awareness of the existence of these niche habitats could prove to be beneficial to their conservation.

It is suggested that the European populations of oceanic liverworts may be at their climatic range limit, explaining the lack of sexual reproduction among the species. While cloning by fragmentation may be sufficient for current relict populations to remain, it is uncertain whether this method would suffice to establish new populations in case of a suggested northward range shift (Flagmeier et al., 2020). Liverworts can in general disperse further by sexual means, while vegetative propagules are more likely to support local populations. The limited distribution of the community in Europe is thought to be due to this limited long-distance dispersal rather than any local regeneration issues (Flagmeier et al., 2013; Wangen et al., 2016). In order to assist the establishment of new populations, especially in the case of a northward range shift as a result of climate change, both ex-situ and in-situ conservation of species should be considered. As projected presently (Figure 3), there are suitable habitats further north in Norway where an associated northern Atlantic species is able to persist and thrive should a population manage to establish, this is also shown in all future climate scenarios (Figures 4–6). Furthermore, a number of species alongside *A. donnianum* have been shown to be able to successfully regenerate from fragments and grow both in situ and ex situ with favourable conditions (Flagmeier et al., 2013). Which suggests that in the light of a range shift and loss of present habitat as a result of climate change, there is potential for manual conservation management to assist with dispersal and expand their future distribution across Scandinavia.

5. Conclusion

This study has given insight to how habitat suitable to *Anastrophyllum donnianum*, a species associated with northern hepatic heaths, could shift in Scandinavia under three different future climate scenarios between 2071 and 2100. The results indicate that while highly suitable habitat will expand both in Norway and Sweden as the climate turns more humid and warmer, a possible range shift northward or towards higher elevation will likely displace current populations as a result of range contraction caused by increased temperatures in the south. Across all projections, suitable habitat in Norway was separated into two large areas with a gap of unsuitable habitat between, possibly thanks to present insufficient summer precipitation and oceanicity, and future increased summer temperature. This gap likely acts as an ecological barrier for the species which are known for having limited dispersal abilities. Legal protection of *A. donnianum* and any species associated with northern hepatic heaths is currently lacking, and a range shift induced by a changing climate would likely be harmful to the species' survival. Any future efforts aside from protection of current habitat should preferably be focused around assisted ex-situ and in-situ conservation for the affected species to ensure the species' survival by manual distribution to circumvent any dispersal limitations and possible ecological barriers. Increasing public awareness could also generally benefit the conservation of these oceanic species, as knowledge about the existence of northern hepatic heaths in Scandinavia is currently rare.

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