A safe harbour from climate change?

Exploring the potential of cold microrefugia in Swedish forests

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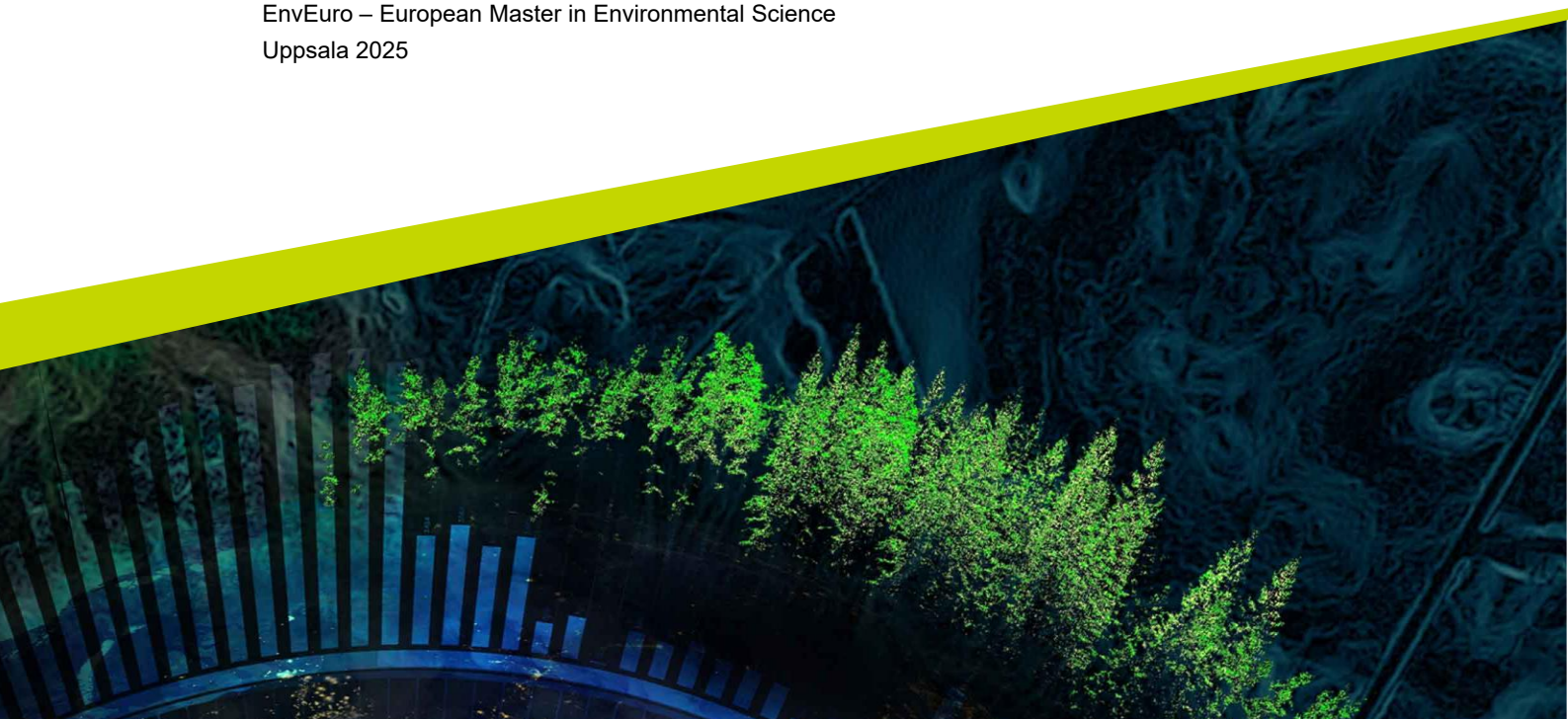

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Abstract

Rising temperatures lead to species range shifts and thermophilisation of communities. Forests buffer temperatures and can provide relatively cool microclimates. These microclimates could act as refugia for cold adapted plant species facing the pressure of climate change. As forest microclimates are dependent on stand characteristics, forest management plays an important role in shaping them. This thesis explores the microrefugia potential on the forest ground in three Swedish regions and asks two main questions: First, where can relatively cold microclimates be found and what factors contribute to the difference in temperature? Second, where are cold communities located, and do they occur in cold microclimates? For analyses multiple linear regression models were used to explore microclimate temperature at 15 cm above ground and its drivers. The relationship between temperature and plant communities on the ground was investigated using correlation tests. Temperature and soil moisture data were obtained from microclimate loggers and plant occurrence from vegetation inventories. Additionally, predicted temperature maps were created based on open-source data on landscape features, microclimate temperature and linear models. Moreover, the microclimate models based on in-situ predictors and models with mapped predictors were compared. The relatively cold microclimates in the research areas were mainly driven by elevation, soil moisture and canopy openness. Cold plant communities were found in cold places, but there was no significant correlation with temperature along microclimate gradients within the individual regions. This could reflect limitations of the CTI (Community temperature index) as measurement for relative cold/warm adaptation of the ground plant communities. Future studies could focus on absence/presence of species close to the warm edge of their range, which may result in stronger correlations. Nevertheless, the study highlights that forest management can facilitate relatively cold places, which could be used for climate change adaption and mitigation strategies in boreal forests. Additionally, the results show that national scale data might be a helpful tool to incorporate microclimates in management and planning

Keywords: Microclimate, Refugia, Boreal Forests, Climate Change, Thermophilisation

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Abbreviations

Abbreviation	Description
STI	Species Temperature Index
CTI	Community Temperature Index
HLI	Heat Load Index
DEM	Digital Elevation Model
SLU	Swedish University of Agricultural Sciences

1. Introduction

Anthropogenic climate change is one of the most pressing current global challenges society and nature are facing. With global trends of temperature rise, weather changes and increase in temperature extremes, climate change impacts ecosystems, their functions and processes (Calvin et al., 2023; Reid et al., 2010). Forest plant communities have been observed to respond slower to macroclimatic change and rise in atmospheric temperature than the increase in temperature would suggest. This climatic lag was connected to the forest canopy and its effect on the climate underneath (Bertrand et al., 2011; De Frenne et al., 2013). Especially for relatively cold adapted plant species, this slower warming rate could conserve suitable habitats (Hylander et al., 2022). Therefore, this thesis will explore the potential of forest microclimates to act as microrefugia for relatively cold adapted species in the face of global climate change.

1.1 Climate Change and Thermophilisation

Two impacts of climate change on plant species and communities are range shifts and thermophilisation (De Frenne et al., 2013; Govaert et al., 2021; Maciejewski et al., 2020; Mäkinen et al., 2025). Thermophilisation or community warming is a change within a communities' composition following an increase in warm-adapted species and a decrease of cold-adapted species (Mäkinen et al., 2025). This results from species range shifts towards higher latitudes and altitudes, facilitated by rise in global temperatures (Govaert et al., 2021; Stevens et al., 2015). Depending on the ecosystem and taxa, this interplay of species distribution and community level change can be expressed differently (Mäkinen et al., 2025). Thermophilisation has been studied with the community temperature index (CTI) across different taxa, for example birds, butterflies, and plants (Devictor et al., 2012; Mäkinen et al., 2025; Richard et al., 2021; Savage & Vellend, 2015). This index is a (weighted) average of the species temperature preferences in a community that allows to compare the relative warm/cold adaptation of different communities or to study community changes over time (Sparrius et al., 2018). A study in French forests showed that the CTIs of understory plant communities do not represent the atmospheric temperature change. Even though thermophilisation did occur in the communities, its rate lagged behind the rate of macroclimatic temperature rise. Moreover, the thermophilisation rate was connected to forest characteristics (Richard et al., 2021). For example, thermophilisation was found to be less pronounced in understory plants underneath a denser forest cover (De Frenne et al., 2013). An explanation for the lower CTIs and thermophilisation rate in forests could be the temperature buffering function of forest canopies, which sustains suitable microclimates. This is supported by a study from Zellweger et

al., where the temperature and its change over time within forests was measured and connected to the thermophilisation rate of understory plant communities. They showed that community change was related to micro- rather than macroclimatic temperatures and changes in forest cover, hence to microclimates (Zellweger et al., 2020).

1.2 Forest Microclimates and Boreal Forests

Microclimates are spatially defined areas with their own climate, that can span a variety of spatial and temporal scales (Bramer et al., 2018; Kemppinen et al., 2024). One of the important functions of forests for providing microclimates is temperature buffering. This means that temperatures within forests differ to atmospheric temperatures. By buffering minimum and maximum temperatures forests create a more stable temperature range compared to open habitats (De Frenne et al., 2019, 2021; De Lombaerde et al., 2022). Forest microclimates are determined by a combination of topographic and forest characteristics that influence the local radiation balance. Some prominent topographic factors influencing microclimate are elevation, slope and aspect, while important forest characteristics are canopy cover, forest density and soil moisture (De Frenne et al., 2021; Greiser et al., 2018; Vanwalleghem & Meentemeyer, 2009).

A simplified description of the radiation balance would be that incoming short-wave solar radiation warms near ground habitats by day, while outgoing longwave radiation leads to cooling the ground at night. How elevation, slope, aspect, canopy cover, forest density and soil moisture modulate this balance to create microclimates has been well studied (De Frenne et al., 2021; Geiger, 1950; Zellweger et al., 2019). In regions with complex terrain, elevation is important in shaping local temperature. Generally the temperature decreases with height within the troposphere, but temperature inversions can also lead to deviations of this relationship (Frey et al., 2016; Vanwalleghem & Meentemeyer, 2009). Also local depressions might influence the relation between elevation and temperature differently. Depressions could accumulate cold air during the night, leading to cooler temperatures at these local low elevations (Dobrowski, 2011; Greiser et al., 2018). Slope influences the exposure to wind and availability of water, while slope and aspect determine solar radiation exposure. As an example, in the northern hemisphere, a south facing slope could be expected to have warmer microclimates than a north facing slope (Dobrowski, 2011; Geiger, 1950; Vanwalleghem & Meentemeyer, 2009). The forest canopy absorbs and reflects some of the incoming radiation by day, while retaining outgoing longwave radiation by night, which leads to cooling or warming effects, respectively, and buffering of extreme temperatures underneath. Forest density influences at what height in the forest layers and how much of the incoming solar radiation is

absorbed and thus modulates microclimate stratification. Studies observed that density and canopy cover strongly influenced the magnitude of buffering minimum and maximum temperatures in the understory (De Frenne et al., 2019, 2021; Greiser et al., 2018; Zellweger et al., 2019). Additional drivers of cooler microclimates are evaporative cooling and soil moisture. Evaporation of water cools the surrounding air through latent heat flux, which has a stronger cooling effect with higher water availability. Thus, temperature buffering is more pronounced in forests with higher soil moisture (Davis et al., 2019; De Frenne et al., 2021; Greiser et al., 2024).

The relative importance of these factors for temperature buffering is forest specific. The forest type, the landscape topography, the surrounding macroclimate and the local hydrological balance lead to varying magnitude of temperature buffering (Davis et al., 2019; De Frenne et al., 2019; De Lombaerde et al., 2022; Zellweger et al., 2019). Local and regional weather and precipitation patterns, distance to water and the forest edge and the biome shape the atmospheric temperature, wind patterns and water availability the forest is exposed to. Especially, the hydrological balance was found to be important for the temperature buffering capacity of forests. Water availability is not only crucial for vegetation growth and through that influences canopy cover and forest density but also impacts evapotranspiration and its cooling effect (Davis et al., 2019; De Frenne et al., 2021). Boreal forests have a strong seasonality in light, precipitation, temperature, and vegetation phenology, which leads to a variety of microclimatic conditions. Moreover, in boreal forests the buffering of minimum temperature is most pronounced in winter, while the buffering of maximum temperature in summer. Especially for buffering summer maximum temperatures the forest density, in terms of canopy cover and basal area, is important in boreal forests (Greiser et al., 2018). These forests are however greatly impacted by climate change and already experience high rates of warming (Bradshaw & Warkentin, 2015). As boreal forests are the second largest biome on earth (Ruckstuhl et al., 2007) and ground vegetation is important for overall forest biodiversity (Gilliam, 2007), studying microclimates on the ground could inform mitigation and adaption strategies.

1.3 Microrefugia Potential in Sweden

The temperature buffering function of forests has the capacity to mitigate macroclimatic changes (De Frenne et al., 2013, 2021; Xu et al., 2022; Zellweger et al., 2020). Microclimates can offer suitable habitats for relatively cold adapted plant species within warmer atmospheric temperatures and thus potentially act as microrefugia (De Frenne et al., 2021; Frey et al., 2016, p. 201). Microclimate refugia have been discussed in climate change adaptation and mitigation

strategies. If aiming to increase resistance to climate change impacts, microclimate refugia can retain relatively cold adapted species and slow the negative effects on biodiversity. These refugia might give species and forest ecosystems time to adapt to the faster atmospheric change on site or to adjust their distribution range by using microclimates as stepstones (Hylander et al., 2022; Morelli et al., 2020). Forest characteristics, like canopy cover and forest density, have been shown to strongly drive microclimate and modulate the thermophilisation rate of understory plants. This emphasises that forest management could have a positive or negative impact on microclimates by influencing forest stand characteristics (De Frenne et al., 2021; Frey et al., 2016; Greiser et al., 2018). For example, clear cutting forests can destroy existing cold microclimates, whereas continuous-cover forestry could incorporate cold microclimates in its planning (Hylander et al., 2022). Therefore, forest management plays a crucial role in upholding cold microclimates and conserving cold-adapted species. Considering microclimates in management practices is especially important in Sweden, as most boreal forests are intensively managed (Gauthier et al., 2015) and clearcutting is the dominant management system (Roberge et al., 2020). Locating microclimates and managing forests to protect or facilitate relatively cold microclimates could be one way of supporting boreal forests in climate change mitigation and adaptation.

This thesis explores how microclimates could act as microrefugia for relatively cold-adapted ground plant communities in three Swedish forests. The first question investigated relatively cold microclimates and was: Where in the three study areas are the relatively cold places and what are the drivers for their microclimate? The second question explored the relationship between microclimate and relatively cold plant communities on the ground and asked: Are relatively cold adapted communities found at relatively cold places? These questions were addressed by creating microclimate temperature maps to locate cold microclimates and multiple linear regression models to investigate the drivers of the temperature at 15 cm above ground with elevation, deciduousness, canopy openness, a heat load index and soil moisture as predictor variables. Furthermore, the relationship between microclimate temperature and plant communities was investigated using correlation tests between the CTI of ground plant communities and the temperature at 15 cm above ground. Additionally, microclimate models based on local, in-situ predictors and models based on large-scale, open-source predictors were compared regarding their ability to explain the variation in microclimate temperature in the study regions. The findings could contribute to understanding the role of microclimates in climate change mitigation and might provide a potential tool to incorporate microclimates in forest management through use of large-scale data.

2. Methods

This thesis built on existing data from different sources. This included microclimate logger data from 2022/23 and plant inventory data of ground plants from 2024 from the ForestBuffer project on climate under forest canopies. Additionally, open-source data on plant species temperature preferences and on landscape characteristics in Sweden were used, namely data on elevation, basal area and soil moisture.

2.1 Study Areas

Within the ForestBuffer project a network of microclimate loggers in three Swedish forest regions was established with the logger model "TOMST TMS4" (Wild et al., 2019). The selection of the study plots in each region was completed between May and July 2022. The three study areas are Asa, Grimsö and Krycklan and were selected from the SITES network (https://www.fieldsites.se/) within Sweden (see figure 1).

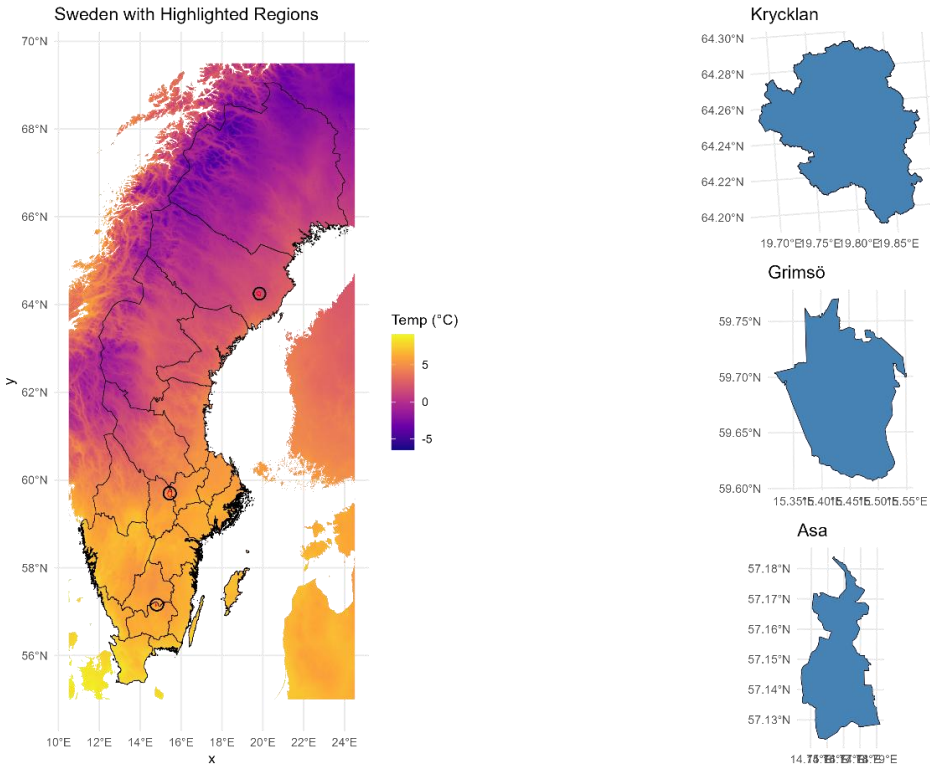

Figure 1: Map of Sweden displaying the annual mean temperature (°C) with the three study locations marked and enlarged on the right side. Climate data is derived from WorldClim v2.1 (Fick & Hijmans, 2017) and boundaries of Sweden from the Global Administrative Areas Database (Hujmans, 2020).

The SITES network is a national network of research stations and infrastructure. Choosing plots within this network allows for greater exchange of information and data, which could potentially be useful for future microclimate research based on logger data. The three study areas lie along a latitudinal gradient within Sweden and are in the hemi-boreal (Asa) or boreal zone (Grimsö, Krycklan). Overall conifer trees are dominant, especially Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), but the forest composition differs between the three regions. Land use in all three areas mainly consists of rotation forestry, leading to a mosaic of clearcuts and relatively even forests of different ages. Nevertheless, also old-growth forest sites without management for prolonged periods are present within the study areas, namely the Krycklan core area and the Helgedomen nature reserve in Grimsö. The logger network for this study was integrated into this existing SITES network of permanent plots. From the permanent plots, the study plots were chosen based on gradients of forest canopy cover (basal area) and soil moisture, a minimum distance from the forest edge and a maximum distance to a road. Over all study plots the mean daily soil moisture ranged from 7 to 56 % and the basal area from 0.00 to 51.52 m^2/ha. Asa and Grimsö contain around 40 plots with a temperature and soil moisture logger on the ground, while Krycklan had additionally 48 logger plots.

2.1.1 Asa

The Asa experimental forest is located in south-central Sweden. The forest is conventionally managed and mainly used for research in forest production and management. The research area spans an area of 1,010 hectares. Of the total area 900 hectares are productive forest, divided into one-half being spruce forests, one-fourth being conifer mixed forest and one-fourth being pine forest with deciduous trees. Climatically Asa belongs to the hemi-boreal zone (*Asa | SITES*, n.d.).

2.1.2 Grimsö

The Grimsö research area is in central Sweden, more precisely in the Bergslagen region. The total area is 13,000 hectares, which mainly consist of managed spruce and pine forests. The climate found in Grimsö can be described as in-between hemi-boreal and boreal. (*Grimsö | SITES*, n.d.).

2.1.3 Krycklan

The study area Krycklan surrounds the Svartberget Research Station and is the most northern study area of the three regions. The Krycklan area is a catchment encompasses a 68 km2 catchment consisting of diverse boreal landscapes like mires, streams, lakes and forests dominated by spruce, but also consisting of pine. The Krycklan area is situated within the boreal zone (Peichl et al., 2023; *Svartberget | SITES*, n.d.).

2.2 Data sources

Two main sources of data were used to investigate the research questions in the three forest regions, namely in-situ data and open sources data. The on-site collected data consists of microclimate variables derived from the loggers, information on forest characteristic and plant occurrence of ground plant species from a plant inventory in the same plots. The open-source data provided information on species temperature preference through the Species temperature index (STI) and information on soil moisture, elevation and basal area mainly based on national wide laser scans.

2.2.1 On-site Data

The logger network in Asa, Krycklan and Grimsö provided data on measured soil moisture and temperature measured by loggers of the model "TOMST TMS4" (Wild et al., 2019). During the fieldwork to retrieve the monitoring data from the loggers in 2022/23 also data on canopy openness and deciduousness for the logger plots were collected. Canopy openness was measured by using hemispheric canopy cover images with a fish-eye lens. These images were analysed with the ImageJ software and the plugin "Hemispherical 2.0" (Beckschäfer, 2015). With this the canopy openness was calculated as the proportion of sky pixels in binarized images. Deciduousness was defined as the proportion of all deciduous trees over all trees at the study plot and was based on local basal area measurements with a standard relascope.

The plant inventory data from 2024 is a species list representing vascular plants, bryophytes and lichens occurring on the ground of each plot. The inventory was conducted within a circular area with a 5 meter radius that had roughly the same centre as the logger plot. After establishing the outlines of the study plots, all species on the ground were noted down and a picture of the plot was taken. For species identification of the ground vegetation in the plots documents of the Swedish National Inventory (NFI) were used. The NFI is an annual sample-based survey covering whole Sweden conducted by the Swedish University of Agricultural Sciences (SLU). Documents on how their fieldwork is conducted, and species lists are available online (https://www.slu.se/en/about-slu/organisation/departments/forest-resource-management/miljoanalys/nfi/about-nfi/field-instructions/). Their protocol for identification of ground vegetation species was used for this study to create a species list showing presence or absence of species at the logger plots in all three regions. Also abundance of species was recorded, however in this thesis only presence-absence data was used.

2.2.2 Open-Source Data

Data on the species temperature index (STI) was provided by the "SpeciesSTI" dataset from Sparrius et al. (2018). The STI reflects species temperature preference and is the long-term average temperature within a species range. This Index is based on presence and absence, rather than abundance. The dataset includes STIs of 7254 taxa of European vascular plants, bryophytes, algae, and ascomycetes including lichens and is itself based on open-source data provided by the Global Biodiversity Information Facility and WorldClim global climate data. To calculate the STI of species Sparrius et al. (2018) used a bootstrapping approach and open-source temperature and occurrence data (Sparrius et al., 2018). The dataset was downloaded on 17 March 2025 from [https://zenodo.org/records/1155850] and is licensed for use as found here: creativecommons.org/licenses/by-nc-nd/3.0/legalcode.

For each region three different open-source raster layers were used, namely maps on basal area, maps on soil moisture and a digital elevation model. An overview of these raster layers and their sources is given in Table 1.

Table 1: An overview of the raster layers, their data, resolution and source that were downloaded and used.

Dataset	Description	Resolution	Unit	Source
Skogliga grunddata – Grundyta	Basal area	10 m × 10 m	m² per hectare	SLU & Swedish Forest Agency, based on Lantmäteriet LiDAR
SLU Markfuktighet	Annual mean soil moisture (index)	2 m × 2 m	Index 0–100 (dry to wet probability)	SLU, with inputs from Lantmäteriet & field data
Lantmäteriet: Höjddata, Grid 2+ 2019 CLIP (tif) Elevation data	Digital Elevation Model via laser scanning (grid or TIN interpolation)	2 x 2 m	m above sea level	Lantmäteriet

For creating temperature maps, multiple GIS raster datasets from the Swedish Forest Agency were used, all of them in the coordination system EPSG:3006 (SWEREF-99 TM). Soil moisture and basal area were based on airborne laser scanning done between 2009 to 2017. The dataset "Skogligt grunddata - Grundyta" provided information on the basal area in Sweden. The basal area is a measurement in m^2/ha of the forest density and is defined as the cross-sectional area of a trees at breast height. The basal area map was based on laser scanning and sample plots of the National Forest Survey of Sweden from the Swedish University of Agricultural Sciences (SLU) with the resolution being 10 x 10 meter

per raster cell. This dataset was downloaded on the 14 May 2025 from [https://geodpags.skogsstyrelsen.se/geodataport/feeds/SGDGrundyta.xml]. The datasets with information on soil moisture are named “SLU Markfuktighet” of the regions Västerbottens län, Örebro län and Kronobergs län. The soil moisture maps display the average soil moisture on a 2 x 2 meter resolution. The maps provide a continuous gradient on a scale from 0 to 100, where low numbers represent dry soils and high numbers represent wet soils. To create the open-source maps 24 different maps and additional field data from the national forest inventory were reportedly used. The calculations for the gradient are said to be based on artificial intelligence and a mathematical model of water movement and terrain (SLU, 2020). The datasets were downloaded between 15 and 21 May 2025 from [https://geodpags.skogsstyrelsen.se/geodataport/feeds/SLUMarkfuktighet.xml].

The heat load index (HLI) quantifies the amount of heat a location is exposed to through accounting for topographic factors of slope and aspect. Within the R package *spatialEco* a function *hli()* calculates the heat load index for a certain region (Evans & Murphy, 2023). The function follows a method of McCune and Keon (2002) and calculates the HLI by combining slope and aspect in an algorithm that emphasises south-west facing slopes. It considers the hemisphere of the region and gives an output between 0 and 1, with lower numbers reflecting a lower heat load and cooler spots. To use this function a digital elevation model (DEM) of the study regions was needed. The DEM used in this thesis shows the elevation on a 2 x 2 meter grid based on laser data and a triangulated Irregular Network (TIN) for linear interpolation (McCune & Keon, 2002). It was separately cropped to the fit the extent of the study regions. The DEM was derived from the Swedish Land Survey (Lantmäteriet) and named “Lantmäteriet: Höjddata, Grid 2+ 2019 CLIP (tif) Elevation data, Grid 2+”. The DEM used in my analyses was downloaded on 16 of May 2025 from the SLU data base of digital maps and geodata [https://maps.slu.se/get].

2.3 Analysis

The analyses were organized in two parts to explore the cold forest refugia potential and distribution of cold communities within the three different regions respectively. For analysis the temperature derived from the microclimate logger at 15 cm above ground level was aggregated to the monthly average of the daily maximum summer temperatures in the months of June, July or/and August of the seasons 2022 and 2023, which will be shorten in the following to maximum summer temperature.

The first question explored the location of relatively cold places and their drivers. For this I used a multiple linear regression model and the GIS raster

layers to create a predicted temperature map of the maximum summer temperature on ground level. In the model the response variable was the summer maximum temperature, and the explanatory variables were elevation, basal area, soil moisture and heat load index derived from open-source data bases. Here I not only located the relatively cold places in the study regions but also examined how large-scale data can predict local microclimate conditions, in this case the temperature at 15 cm above ground. To explore the drivers of the near ground temperature only on-site data collected in the field studies form 2022/23 was used. I did a multiple regression with the summer maximum temperature as the response variable and canopy openness, deciduousness, elevation, the heat load index and measured soil moisture as the explanatory variables. Furthermore, the models based on in-situ predictors were compared with the models based on mapped predictors.

The second question regarded the relatively cold adaptation of the plant communities and if they also occur in the relative cold microclimates. For this the community temperature index (CTI) for every plot community was calculated. The CTI is defined as the mean of the Species Temperature Indices (STI) of a species assemblage. The CTI allowed to compare the relative cold preferences of the plant communities at plot level. The CTI and measured maximum summer temperature was tested for correlation. Their relation was first investigated within each region and then over all regions taken together. The questions were applied to the three regions respectively.

2.3.1 Data Compilation and R Use

Data preparation and analysis were done in R (R Core Team, 2024). First, I prepared the logger data and its metadata information on the logger sites to create a data frame fitting to the research questions. For this I created a script in R filtering, sub-setting and combining information on the logger sites from different files and adapted it separately to all three regions. This data frame was used for the multiple regression model to identify drivers of cold microclimate. Work with raster layers for analysis and mapping was mainly done using the *terra* package (Hijmans, 2025), which provided functions to use GIS layers and spatial predictions. The *predict()* function in terra was used to create continues temperature maps by applying a linear model based on logger measurements to raster variables. The *hli()* function from the *spatialEco* package (Evans & Murphy, 2023) was used to calculated the heat load index (HLI).

2.3.2 Mapping microclimate

To create predicted temperature maps, I combined the 15 cm above ground temperature data from the logger plots with open sources GIS raster data, which

are described above in more detail. The raster layers contained information on elevation, the HLI, basal area and modelled soil moisture. The *terra* (Hijmans, 2025) package in R was used for working with the raster data and resampling the basal area map to match the resolution of the other raster layers. With the *extract()* function I extracted values from the raster layers at the logger plot locations, which were then used as predictors in the linear model. To model the temperature, I fitted a linear regression model with the *lm()* function using the extracted predictor variables as explanatory variables and the measured maximum summer temperature as the response variable. Finally, I used the *predict()* function to generate predicted temperature values over the whole spatial extent of the study side based on the fitted model and plotted it for a predicted temperature map.

2.3.3 Cold Adaption of Plant Communities

To explore the relationship between relatively cold plots and cold-adapted communities a CTI was calculated for each logger plot. For this I cleaned the plant inventory data and combined it with a dataset of STIs (Sparrius et al., 2018). With the function *match()* in R I matched the ground plant species that occurred on the logger plots with STI values from the open-source dataset. From this I then calculated the mean of all STIs present at a plot, which is the CTI of that community. Generally, the CTI is a relative, dimensionless index. However, in this dataset species temperature preferences are derived from mean annual temperatures (in °C), thus the CTI values can also be interpreted in degrees Celsius. Next, to examine potential correlation between the CTI and the maximum summer temperature, I performed a Pearson or Spearman rank correlation test, depending on the distribution of the data. The Pearson correlation was used in Asa and Krycklan as the CTI, and temperature were both normally distributed. For Grimsö and when analysing all regions together one of the variables was not normality distributed, thus the Spearman rank correlation was applied instead. For determining which test to use, the Shapiro-Wilk test was used first to check the normality of the data. The correlation tests were conducted within the individual study regions and across all regions combined.

2.3.4 Overview of Variables

Table 2 provides an overview of variables that were described above and used during the analyses with short definitions and their sources. It describes the microclimate temperature, elevation, the heat load index, measured and mapped soil moisture, canopy openness, basal area, deciduousness and the community temperature index.

Table 2: Overview of variables used in this thesis including a short description, units and the data source.

Variable	Description	Units	Source
Temperature	Monthly average of daily maximum temperature (June, July and/or August) at 15 cm above ground	°C	In-situ loggers
Elevation	Meters above sea level	m	Lantmäteriet DEM ©
Heat Load Index (HLI)	Terrain-derived index accounting for slope and aspect to estimate site heat exposure	Index from 0-1, lower numbers equal lower heat load	Calculated based on lantmäteriet DEM ©
Measured Soil Moisture	Volumetric soil moisture, volume of water in the soil as a percentage of the total volume	% or decimal	In-situ loggers
Mapped Soil Moisture	Water content in soil	Index from 0-100 representing dry to wet probability	SLU, with inputs from Lantmäteriet & field data
Canopy Openness	Proportion of sky that is not covered by vegetation when viewed from a single point Calculated as proportion of sky pixels in binarized images	% or decimal	In-situ hemispherical photography of canopy
Basal Area	Cross-sectional area at breast height, indicator of forest density	m^2 per hectare	SLU & Swedish Forest Agency, based on Lantmäteriet LiDAR
Deciduousness	Proportion of all deciduous trees over all trees at the plot	% or decimal	In-situ inventory with relascope
Community Temperature Index (CTI)	Community mean of species' temperature preferences, which indicates relative adaptation to warm/cold conditions (Sparrius et al., 2018)	°C, Index derived from mean annual temperatures	Calculated based on STI from Sparrius et al. (2018)

2.3.5 Data covered in the Regions

Due to variations in data availability, not all analyses for each region covered both summers of 2022 and 2023. For the microclimate temperature driver analysis, Asa's data covered all three months, June, July, and August, of both 2022 and 2023. Grimsö's analysis included all three months of 2022, and June and July of 2023. Krycklan's analysis spanned only July and August of 2022. In the models for the predicted temperature maps, Asa's data again covered all three summer months of 2022 and 2023. Grimsö's model included data for all three months of 2022, and June and July of 2023, while Krycklan's model was based on data from July and August of 2022 and all three summer months of 2023. Possible limitations of this will be discussed.

3. Results

3.1 Asa

The monthly average of daily maximum temperature in the summer months in Asa ranged from 16.33°C to 32.17°C with the mean of 21.99 ° and a standard deviation of 3.14. This was also seen in the temperature map of Asa, where most areas are coloured in a light green representing temperatures between 22° to 24°. Colder (dark blue) and warmer (yellow) areas were also present, but less spread (see figure 2).

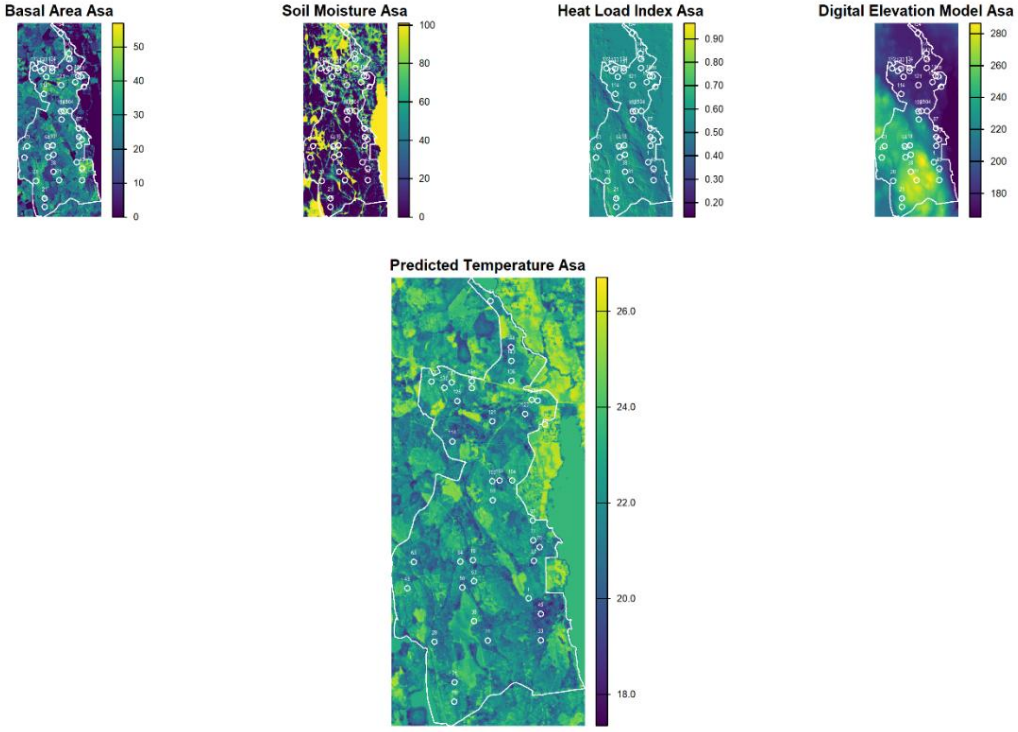

Figure 2: Five maps of Asa with the study regions outline and plot IDs, showing the basal area (m^2/ha), mapped soil moisture, heat load index, digital elevation (m) and the predicted temperature (°C) map. A linear model and the four smaller maps were the base for predicting the temperatures in the fifth map.

Overall, the linear model used for creating the maps of Asa explains 19.0 % of the microclimate temperature variation in Asa. It indicated that the higher the basal area and soil moisture, the colder the temperature. The HLI and elevation were not significant (see table 3). The inverse relation of temperature with soil moisture and basal area was also visualized in the map (see figure 2). Areas with higher values on the soil moisture and basal area map, matched with relatively colder areas on the temperature map.

Table 3: Output of the linear model that is used to predict the temperature map. The response variable is the monthly mean of the daily maximum temperature at 15 cm above ground (°C), and the predictors are elevation (m), basal area (m^2/ha), mapped soil moisture and the heat load index (HLI).

	Temperature				
Predictors	*Estimates*	*std. Beta*	*CI*	*standardized CI*	*p*
(Intercept)	25.290	0.000	21.333 – 29.247	-0.118 – 0.118	**<0.001**
Elevation	-0.010	-0.096	-0.023 – 0.004	-0.234 – 0.042	0.172
HLI	4.166	0.097	-1.175 – 9.507	-0.027 – 0.221	0.126
Basal area	-0.122	-0.396	-0.160 – -0.085	-0.518 – -0.274	**<0.001**
Soilmoisture map	-0.024	-0.218	-0.039 – -0.009	-0.357 – -0.080	**0.002**
Observations	226				
R^2 / R^2 adjusted	0.205 / 0.190				

The second model, which was based on local monitoring data explains 35,7 % of variation in microclimate temperature with the key driving factors being soil moisture, canopy openness and the HLI. The model associated colder temperatures with higher soil moisture, more canopy cover, higher elevation and lower heat load. Only deciduousness did not show a significant impact (see table 4).

Table 4: Output of the linear model based on logger data from summers of 2022/23. The response variable is the monthly mean of the daily maximum temperature at 15 cm above ground (°C), and the explanatory variables are measured soil moisture, elevation (m), canopy openness and the heat load index (HLI).

	Temperature				
Predictors	*Estimates*	*std. Beta*	*CI*	*standardized CI*	*p*
(Intercept)	22.107	-0.000	18.961 – 25.253	-0.107 – 0.107	**<0.001**
Soil moisture	-15.069	-0.462	-18.734 – -11.404	-0.575 – -0.350	**<0.001**
Elevation	-0.011	-0.113	-0.022 – -0.000	-0.224 – -0.002	**0.047**
Canopy openness	0.134	0.319	0.086 – 0.182	0.205 – 0.432	**<0.001**
Deciduousness	-0.004	-0.021	-0.023 – 0.016	-0.128 – 0.087	0.706
HLI	7.328	0.186	2.896 – 11.761	0.073 – 0.298	**0.001**
Observations	220				
R^2 / R^2 adjusted	0.372 / 0.357				

The calculated community temperature index (CTI) in Asa ranged from 5.457°C to 6.627°C with the mean of 5.941°. As illustrated in figure 3 species composition of the different plots was quite similar, with a few species occurring at nearly every plot, like the mosses *Pleurozium schreberi* and *Hylocomium splendens*.

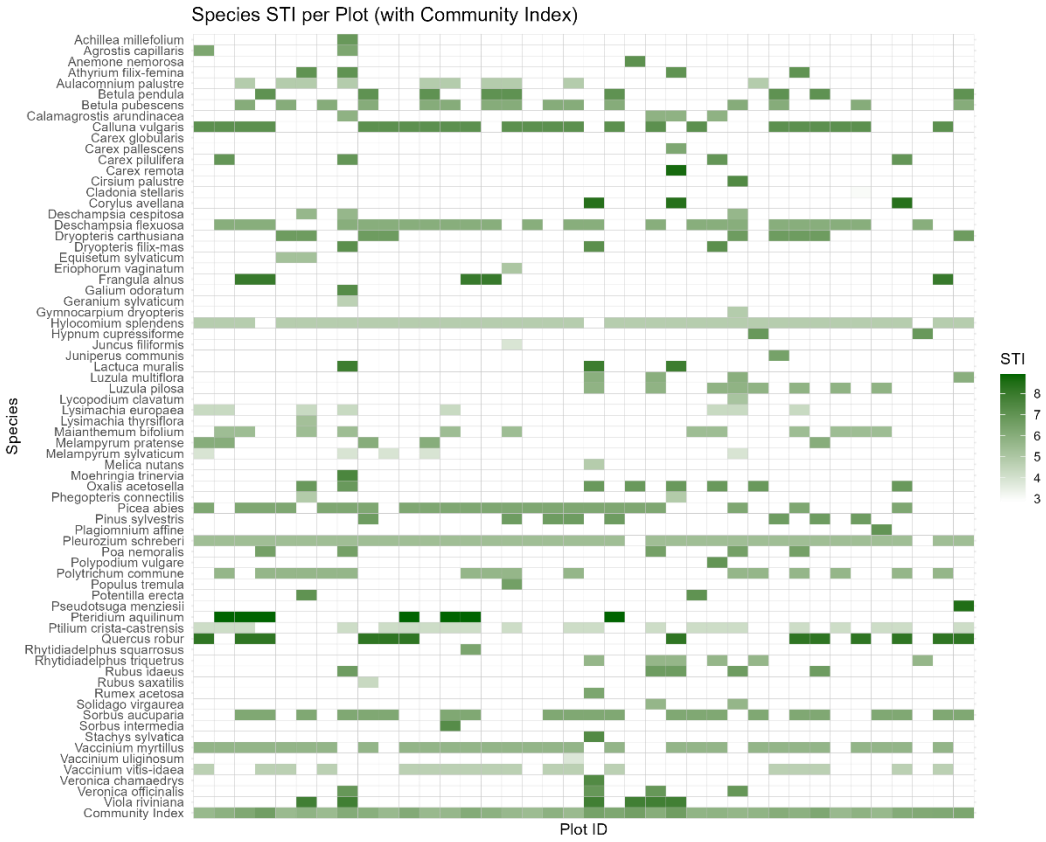

Figure 3: Species occurring at plot level in Asa with colour coded STIs. The bottom line represents the mean of all STIs at one plot, therefore representing the CTI of this plot.

The CTI showed a slight positive, but not significant correlation to microclimate temperature within Asa (Pearson's r = 0.06, p = 0.72).

3.2 Grimsö

The monthly average of daily maximum Temperature in the summer months in Grimsö ranged from 17.22°C to 33.99°C with the mean of 23.01 ° and a standard deviation of 3.24. Thus, having a slightly warmer range than Asa, even though Grimsö is located a bit further north. The temperature map of Grimsö reflected this, as light green to yellow areas, representing temperatures between 23° to 25°, dominated. In the southern part of Grimsö also a few darker blue areas were visible, indicating temperatures under 20°C. Whereas the norther part showed lighter colouring, reflecting temperatures even around 26°C (see figure 4).

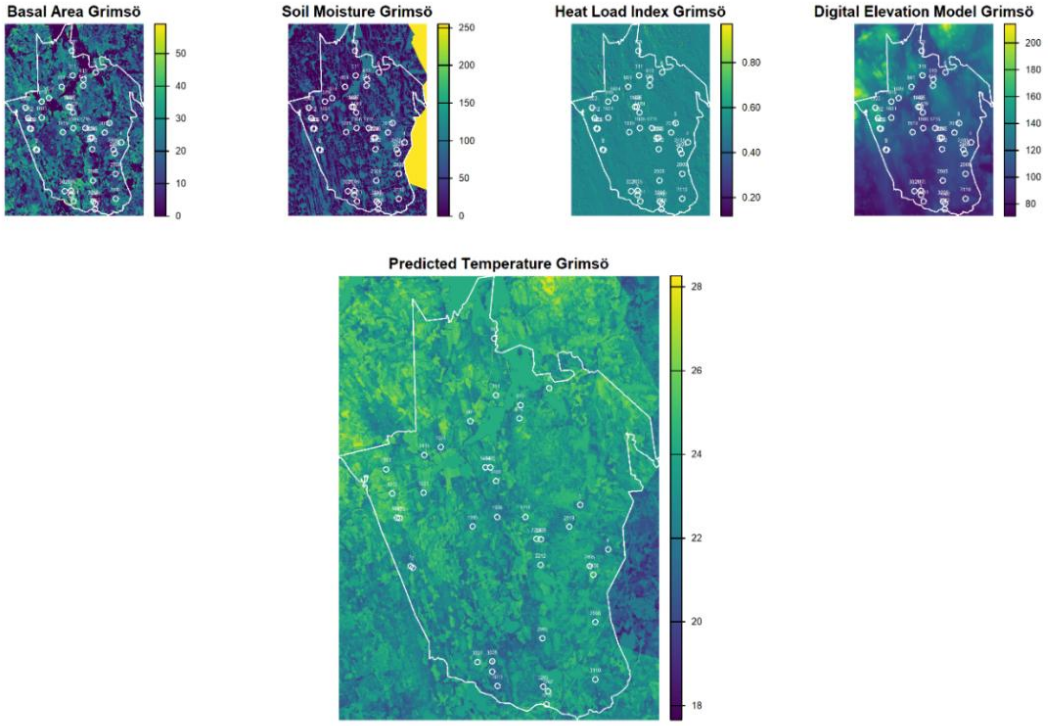

Figure 4: Five maps of Grimsö with the areas outline and plot IDs, showing the basal area (m^2/ha), mapped soil moisture, heat load index, digital elevation (m) and the predicted temperature (°C) map. A linear model and the four smaller maps were the base for predicting the temperatures in the fifth map.

Overall, the linear model used for creating the maps of Grimsö only explained 8.8 % of the temperature variation within the research area (see table 5). Just the basal area showed significance as predictor variable for microclimate temperature. The negative relation indicated that a higher basal area, therefore more tree cover, lead to lower temperatures. However, elevation, HLI and soil moisture did not have a significant impact on temperature in this model.

Table 5: Output of the linear model that is used to predict the temperature map. The response variable is the monthly mean of the daily maximum temperature at 15 cm above ground (°C), and the predictors are elevation (m), basal area (m^2/ha), mapped soil moisture and the heat load index (HLI).

	Temperature				
Predictors	*Estimates*	*std. Beta*	*CI*	*standardized CI*	*p*
(Intercept)	21.559	0.000	15.139 – 27.979	-0.143 – 0.143	**<0.001**
Elevation	0.028	0.127	-0.004 – 0.060	-0.017 – 0.270	0.084
HLI	1.415	0.021	-8.393 – 11.223	-0.123 – 0.164	0.776
Basal area	-0.084	-0.268	-0.130 – -0.038	-0.414 – -0.122	**<0.001**
Soilmoisture map	-0.010	-0.085	-0.026 – 0.007	-0.231 – 0.061	0.253
Observations	174				
R^2 / R^2 adjusted	0.109 / 0.088				

In contrast, the explanatory power of the model based on local monitoring data was nearly five times higher and explained 40.9% of the variation in Grimsö's microclimate temperature (see table 6). This model reflected the same trends seen already in Asa, namely that plots with higher soil moisture and more canopy cover had relatively colder temperatures also in Grimsö. The explanatory variables with significant influence were soil moisture and canopy openness. Elevation, deciduousness and HLI did not have a significant impact.

Table 6: Output of linear model based on the logger data from 2022/23. The response variable is the monthly mean of the daily maximum temperature at 15 cm above ground (°C), and the explanatory variables are measured soil moisture, elevation (m), canopy openness, deciduousness and heat load index (HLI).

	Temperature				
Predictors	*Estimates*	*std. Beta*	*CI*	*standardized CI*	*p*
(Intercept)	20.561	-0.000	14.396 – 26.725	-0.117 – 0.117	**<0.001**
Soil moisture	-10.213	-0.278	-14.655 – -5.771	-0.399 – -0.157	**<0.001**
Elevation	-0.009	-0.041	-0.035 – 0.017	-0.163 – 0.080	0.503
Canopy openness	0.247	0.616	0.198 – 0.296	0.494 – 0.738	**<0.001**
Deciduousness	0.007	0.021	-0.035 – 0.050	-0.101 – 0.144	0.731
HLI	3.890	0.057	-4.432 – 12.212	-0.065 – 0.178	0.357
Observations	169				
R^2 / R^2 adjusted	0.426 / 0.409				

The calculated community temperature index (CTI) in Grimsö ranged from 4.377°C to 6.259°C and a mean of 5.670°. Also in Grimsö a few species occured in a majority of plots, for example *Deschampsia flexuosa, Hylocomium splendens, Pleurozium schreberi* and *Vaccinium uliginosum* (see figure 5).

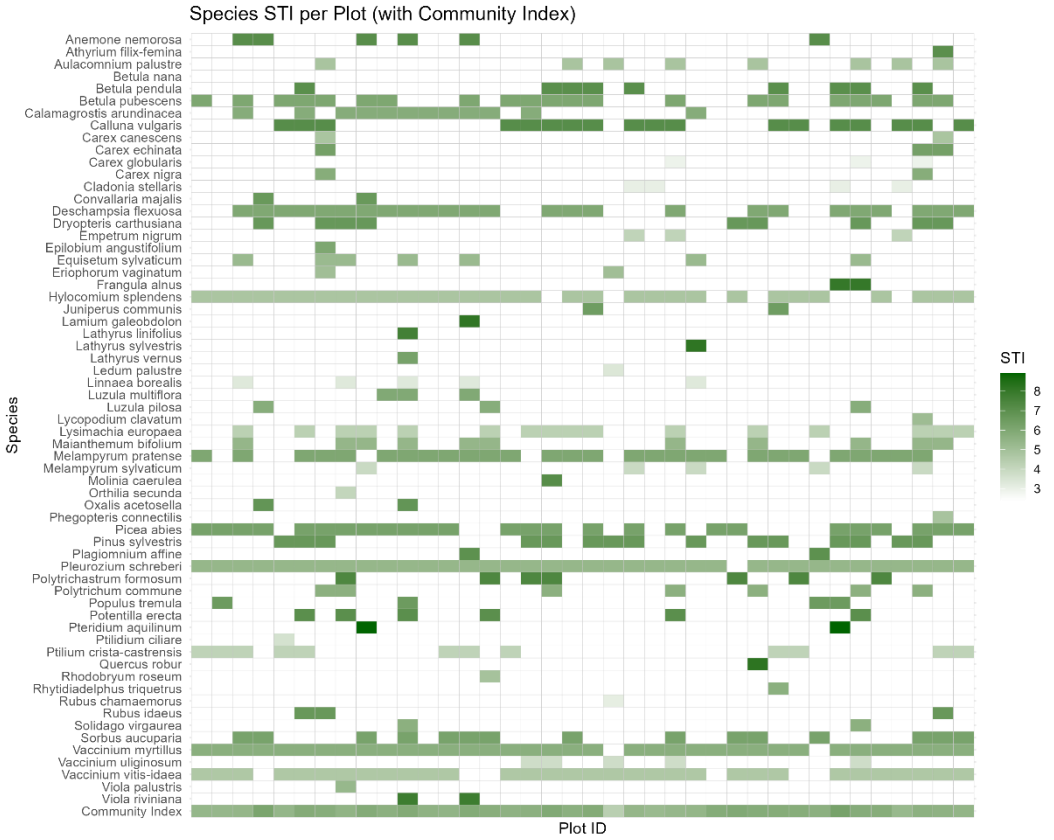

Figure 5: Species occurring at plot level in Grimsö with colour coded STIs. The bottom line represents the mean of all STIs at one plot, therefore representing the CTI of this plot.

In contrast to Asa and the expected relationship, the trend in Grimsö between CTI and temperature was found to be negative, but also not significant (Spearman's $\rho = -0.34$, $p = 0.052$).

3.3 Krycklan

The monthly average of daily maximum Temperature in the summer month in Krycklan ranged from 16.55°C to 30.23°C with the mean of 20.77 ° and a standard deviation of 2.78. Thus, Krycklan had a slightly colder range than both Asa and Grimsö. In the temperature map of Krycklan stronger contrasts were observed. In the northern part dark blue dominated, reflecting colder Temperatures under 21°C. Whereas the southern part showed lighter green and yellow areas, indicating relatively warmer temperatures over 26°C (see figure 6).

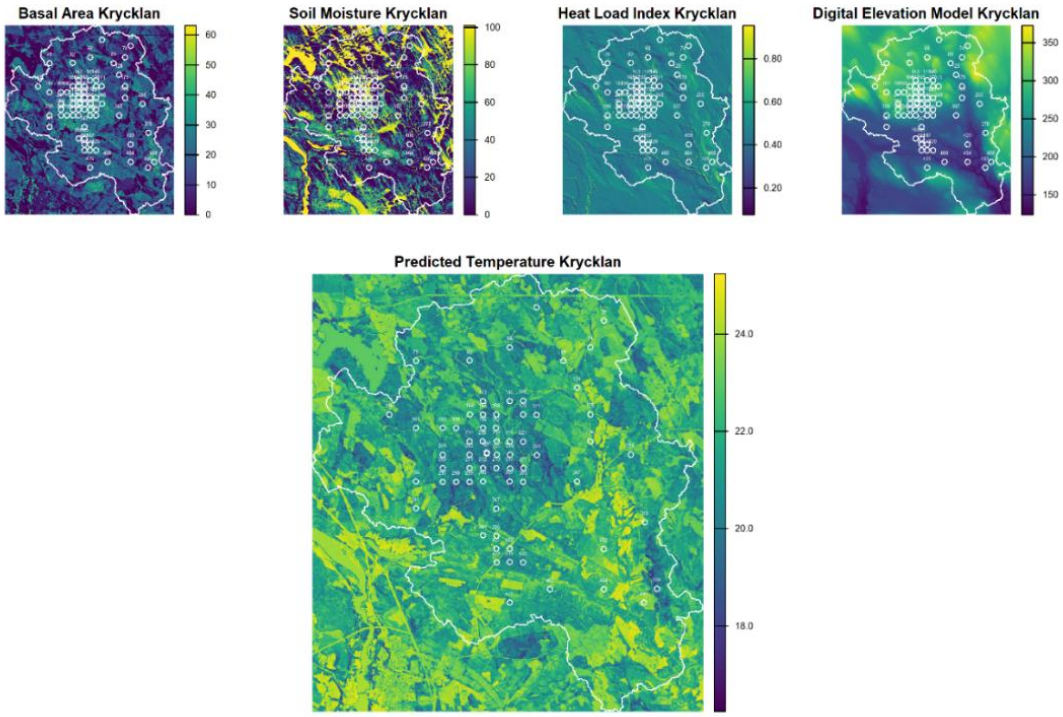

Figure 6: Five maps of Krycklan with the areas outline and plot IDs, showing the basal area (m^2/ha), mapped soil moisture, heat load index, digital elevation (m) and the predicted temperature (°C) map. A linear model and the four smaller maps were the base for predicting the temperatures in the fifth map.

The linear model for predicting temperatures on the maps of Krycklan explained 16,6% of the microclimatic temperature variation. The model indicated that areas with higher soil moister, more tree cover and at higher elevations, showed colder temperatures, as all three had a significant, negative impact on temperature. While the HLI was not significant (see table 7). This was also reflected in Krycklans temperature map, where areas with colder temperature matched areas with higher numbers on the maps of the basal area, soil moisture and elevation (see figure 6).

Table 7: Output of the linear model that is used to predict the temperature map. The response variable is the monthly mean of the daily maximum temperature at 15 cm above ground and the predictors are elevation (m), basal area (m^2/ha), mapped soil moisture and the heat load index (HLI).

	Temperature				
Predictors	*Estimates*	*std. Beta*	*CI*	*standardized CI*	*p*
(Intercept)	25.745	0.000	22.522 – 28.968	-0.098 – 0.098	**<0.001**
Elevation	-0.008	-0.115	-0.015 – -0.001	-0.218 – -0.011	**0.030**
HLI	0.847	0.016	-4.535 – 6.229	-0.085 – 0.117	0.757
Basal area	-0.130	-0.388	-0.163 – -0.097	-0.486 – -0.289	**<0.001**
Soilmoisture map	-0.010	-0.115	-0.019 – -0.001	-0.220 – -0.010	**0.032**
Observations	334				
R^2 / R^2 adjusted	0.176 / 0.166				

Elevation and canopy openness were also significant predictors in the model based on logger data from the summer months in 2022 (see table 8). The model explained 65.0% of the variation found in the microclimate temperature and indicated that in Krycklans ground temperatures were significantly colder at higher elevations and in areas with higher canopy cover. Neither soil moisture nor deciduousness and the HLI had a significant impact.

Table 8: Output of linear model based on the logger data from Sommer months of 2022. The response variable is the monthly mean of the daily maximum temperature at 15 cm above ground (°C), and the explanatory variables are measured soil moisture, elevation (m), canopy openness, deciduousness and heat load index (HLI).

	Temperature				
Predictors	*Estimates*	*std. Beta*	*CI*	*standardized CI*	*p*
(Intercept)	16.119	0.000	13.711 – 18.527	-0.102 – 0.102	**<0.001**
Soil moisture	0.501	0.021	-2.112 – 3.114	-0.090 – 0.132	0.705
Elevation	-0.007	-0.176	-0.011 – -0.003	-0.280 – -0.073	**0.001**
Canopy openness	0.153	0.747	0.132 – 0.174	0.642 – 0.851	**<0.001**
Deciduousness	-0.021	-0.110	-0.042 – 0.001	-0.222 – 0.003	0.056
HLI	3.721	0.098	-0.241 – 7.683	-0.006 – 0.202	0.065
Observations	132				
R^2 / R^2 adjusted	0.663 / 0.650				

The CTI in Krycklan ranged from 4.519°C to 6.010°C with the mean of 5.319°. As in the other regions, some species were found in the majority of plots, like *Vaccinium myrtillius, Plerozium schreberi, Picea abies and Betulla pubescens* (see figure 7).

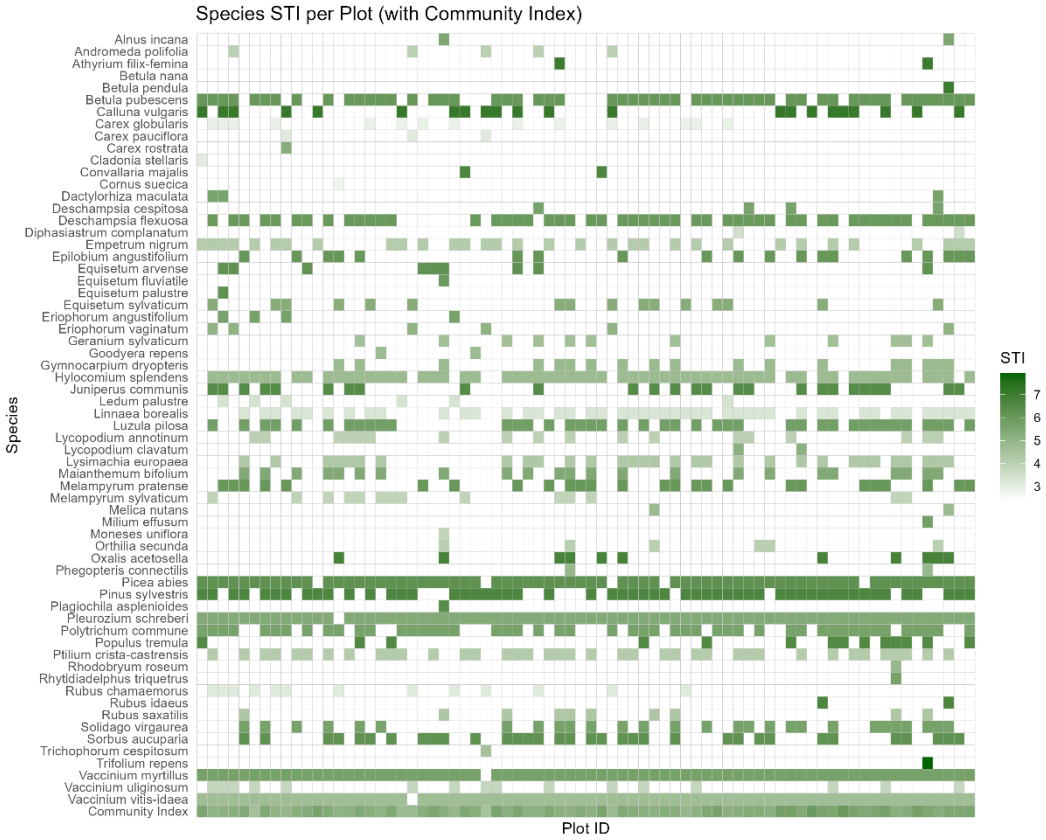

Figure 7: Species occurring at plot level in Krycklan with colour coded STIs. The bottom line represents the mean of all STIs at one plot, therefore representing the CTI of this plot.

Similar to Asa the trend observed between the CTI and temperature in Krycklan was positive. However, also this correlation was not found to be significant (Pearson's r = 0.19, p = 0.14).

3.4 CTI over All Regions

As described above, the correlation between temperature and CTI on a regional level showed a positive trend in two regions, but it was not significant. However, if considering all three regions, a significant, slightly positive correlation between microclimatic temperature and CTI was observed (Spearman's $\rho = 0.255$, $p = 0.004$). This is visualized in figure 8.

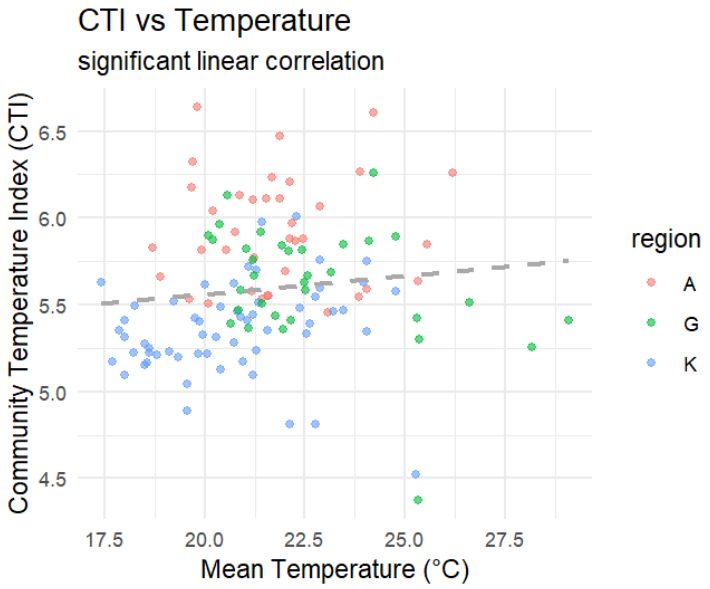

Figure 8: Correlation plot between the summer maximum temperature and CTI at plot level over all three regions Asa, Grimsö and Krycklan.

Therefore, a lower CTI, representing relatively cold adapted communities, occurred in places of colder ground temperatures. Furthermore, the differences in CTI between the regions showed the expected pattern of a lower CTI in higher latitudes, with colder temperatures (see figure 9).

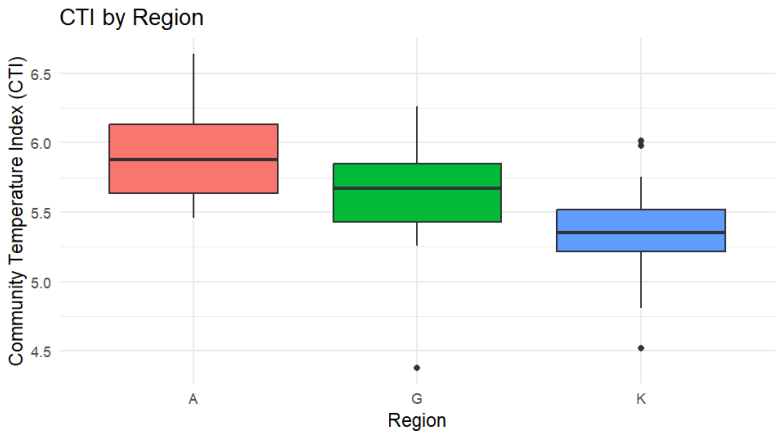

Figure 9: Boxplots of the CTI of the regions Asa (A), Grimsö (G) and Krycklan (K).

This pattern was also visible in the species occurring in the regions, represented by their STIs. A higher number of relatively cold adapted species with a lower STI was found in Krycklan compared to both other regions. While Asa had more relatively warm adapted species and Grimsö a mix of both (see figure 10).

However, the correlation of the CTI to temperature spanning over all regions reflected the macroclimatic gradient between the latitudes rather than microclimate effects.

Figure 10: Species occurring at plot level in Asa (A), Grimsö (G) and Krycklan (K) with colour coded STIs. The bottom line represents the mean of all STIs at one plot, therefore representing the CTI of this plot.

4. Discussion

The aim of this thesis was to explore relatively cold microclimates in three Swedish forests, their drivers, relation to cold adapted understory plant communities and the role of large-scale data to locate them.
The study showed that microclimatic temperature can be modelled and predicted with the help of large-scale geographic data. With larger amount of local temperature data and improved models, the accuracy of the predictions could be increased. Similarly to findings of other studies (Davis et al., 2019; De Frenne et al., 2019; Greiser et al., 2018) two of the key drivers of microclimatic temperature in the three regions were forest characteristic, namely soil moisture and canopy cover. These characteristics are shaped by forest management, which highlights its importance for microclimatic conditions also within boreal forests (De Lombaerde et al., 2022; Hylander et al., 2022). Furthermore, this study tentatively connected the temperature preferences of local plant composition on the ground, through the CTI, to microclimate temperature. The significant correlation of the CTI and temperature over all three regions suggested that relatively cold adapted communities were found in relatively cold locations. However, this reflected the macroclimatic gradient of the regions rather than the microclimate differences.

4.1 Microclimate Drivers and Mapping

Cold places were found in areas with denser canopy cover, high soil moisture and at higher elevations. This supports findings of other papers, where forest microclimate was connected to these characteristics (De Frenne et al., 2021; Greiser et al., 2018, 2024; Vanwalleghem & Meentemeyer, 2009). Thus, the importance of forest characteristic for microclimate and temperature buffering is emphasized. Elevation was also found to be a key driver of microclimate temperature and reflected the influence of the atmospheric lapse rate during the day. Therefore, higher elevations showed lower temperatures. Moreover, with the predicted temperature maps relatively cold places could be located visually.

The explanatory power of the large-scale models for the maps was limited, with their R^2 ranging from 8.8% to 19%. This was likely due to possible time lags, the input data's resolution and ecological complexity of forest microclimates. The laser scans for the open-source data on soil moisture and basal area in Sweden that were used for mapping were done between 2009 to 2017. As forests and their management are dynamic, there is probably a discrepancy between the older map data and the more recent microclimate data. Due to this time lag the older data could be limited in representing current forest structures and microclimate conditions. Furthermore, microclimate drivers can vary on a small local scale,

which is why coarse resolution potentially does not capture their effects appropriately (Haesen et al., 2021; Lenoir et al., 2017). The resolution of the map data for elevation and soil moisture was originally 2 x 2 meters, while the basal area had a resolution of 10 x 10 meters and had to be resampled to match the resolution the other map layers. Thus, especially the resolution of the basal area could be improved to better predict the fine-scale heterogeneity of microclimate on the forest ground. Additionally, microclimates are dependent on more factors than what was explored in this study. Unaccounted variables, such distance to the water bodies (lakes, streams) or to forest edge, could therefore lead to higher R^2 (Bramer et al., 2018; Vanwalleghem & Meentemeyer, 2009). Especially in boreal and temporal forests seasonal and daily changes in environmental conditions and light availability are important factors to consider (Greiser et al., 2018; Zellweger et al., 2019). In contrast, the models based on logger data performed better with R^2 between 35.7% to 65%, which highlights the value of local and on-site measurements to complement large scale data. Therefore, the large-scale datasets are a useful tool for mapping microclimate, but their accuracy can be improved with higher resolution forest data, more recent scans and adding further variables or seasonal dynamics into the model.

4.2 CTI and Correlation

The Community Temperature Index (CTI) was used to explore the relationship between ground plant communities and microclimate temperature. Across all three forest regions, the CTI followed the latitudinal pattern and showed lower values, indicating colder-adapted communities, in the northern region (Krycklan) and higher values, representing warmer-adapted communities, in the southern region (Asa). This correlation over all regions between CTI and temperature was statistically significant, but it reflects the large-scale climate gradient between regions rather than local microclimatic effects. When looking at each region individually, the relationship between CTI and microclimate temperature was not statistically significant. Two regions showed weak positive trends. This could hint that colder communities may occur in cooler forest plots. Possible explanations for the lack of correlation on the landscape scale are the choice of measurement and its resolution, the homogeneity of species, limits in data and time lags.

Firstly, the CTI as an index might be limited in reflecting the local variation in the quite homogeneous forest patches of the three regions. Species temperature preferences, and through that the CTI, covary with other species attributes like habitat preferences. Thus, the CTI is affected by other environmental factors, not only temperature. This means that spatial and temporal differences in CTI can have multiple drivers (Bowler & Böhning-Gaese, 2017). Additionally, there might be a mismatch between the resolution of the CTI and microclimate temperature.

The species plot inventories had a radius of 5 meters, while the microclimate temperature was modelled at 2 meters. Therefore, the logger data might only reflect very local conditions on the ground. Furthermore, species response take time before communities reflect environmental conditions (such as microclimate), therefore the CTI could lag behind temperature changes (Block et al., 2022; Chen et al., 2023). Additionally, the species present in the regions are relatively homogeneous and some species have large distributions across Sweden, which might have further limited finding a stronger correlation (Esseen et al., 1997). Lastly, the microclimate data used only covers summer months and maximum temperatures, therefore seasonal changes in species composition and temperature are not covered (Greiser et al., 2018; Zellweger et al., 2019). The CTI is nevertheless a useful measurement to consider when studying environmental change impacts. A study by Christiansen et al. (2022), for example, used the CTI to explore forest management and its impact in boreal forests on plant species distribution over 10 years. It showed that especially forest density shapes plant distribution and the CTI, rather than macroclimate change. This not only supports the findings of this thesis, but also the use of the CTI (Christiansen et al., 2022). Moreover, considering these limitations it is interesting to even find trends between the CTI and local microclimate temperature, which should be investigated further. Future studies could consider including a temporal element or focus on absence/presence of species close to the warm edge of their range, which may result in stronger signals.

4.3 Implications for Forest Management and Conservation

Combining these insights shows that managing forests to preserve and support cold microclimates could be a sensible strategy to mitigate the impact of macroclimatic change on relatively cold adapted species and boreal forests. The potential that microrefugia offer for conservation and climate change mitigation is highlighted by other studies (De Lombaerde et al., 2022; Greiser et al., 2020; Suggitt et al., 2018). One describes them as “slow-lanes” for resident biodiversity and ecosystem functions to adapt to faster global change (Morelli et al., 2020). Another study argues that the inclusion of microrefugia in management strategies can enhance the ecosystems resistance (Hylander et al., 2022). This thesis demonstrates that local monitoring data combined with large scale databases, can be useful tools for investigation, management and planning with respect to microclimate and through that species. A study by Greiser et al. (2020) also highlights this and identifies that microrefugia for boreal forest understory species are found in areas with lower summer and autumn maximum temperatures, high forest basal area, and reduced solar radiation (Greiser et al., 2020). Especially, in planning forest management this could be used to actively support colder

microclimates and through that uphold refugia for relatively cold adapted species. Actions to enhance colder microclimates could be measures to enhance soil moisture or canopy closure. Both are influenced by harvesting regime and species selection in managed forests, thus actions could be to reduce clear-cutting and preserving moist soils through reduction of drainage and support of the water holding capacity (Greiser et al., 2024; Hylander et al., 2022). It is important to note that there are more factors influencing microclimates, biodiversity and forest ecosystem adaptiveness, thus cold microclimates could be seen as a part within promoting landscape heterogeneity and other adaptive measures (Gauthier et al., 2014). Nevertheless, potential benefits of supporting cold forest refugia, is not only conservation of biodiversity in itself, but also giving ecosystems and species time to adapt to global climate change and through that supporting ecosystem functions (Hylander et al., 2022; Morelli et al., 2016). Integrating microclimate considerations into forest planning could thus be a valuable strategy for climate adaptation and conservation.

4.4 Limitations, Outlook and Summary

The study should be viewed as an exploration of microclimates as cold refugia in three Swedish forests, that could guide further research and management. The study was based on existing data and open-source datasets rather than my own field-collected data. The existing temperature logger and plant inventory data were good quality, but some data gaps were found during the analysis. Because of missing data for some summer months in certain regions, the data availability was different across the regions. This limited direct comparison of Asa, Grimsö and Krycklan. Furthermore, being aware of data gaps is important as smaller datasets can reduce statistical power and might not detect certain ecological patterns. At the same time limited data increases the risk of overfitting and producing exaggerated findings. Asa covered data of the entire two summer season, but Grimsö and Krycklan had some data gaps. Furthermore, Krycklan had twice as many logger sites, which could explain the more robust outcome of the model for microclimate drivers, even though it covered less time. Nevertheless, the findings open questions and provide a foundation for future research on microclimates and their potential as refugia in a globally changing climate.

Further expansion of temperature monitoring loggers across regions would allow for higher quality predictions and conclusions on drivers and patterns regarding microclimate, climate change and species distribution (De Frenne et al., 2021). Additionally, the models for predicting and mapping microclimates could be improved by adapting them to land use and management options. This could provide a more accessible way to integrate cold refugia in management plans. Furthermore, using a different statistical model could account better for ecological

complexity, an example would be linear mixed models (Harrison et al., 2018). Another topic worth exploring would be the importance of forest buffering in other seasons than summer. Snow cover dynamics, differing forest structure and seasonal water balance impact ground-level temperature and their connected microclimates (De Frenne et al., 2021; Greiser et al., 2018, 2024; Zellweger et al., 2020). Previous studies have discussed the microclimate drivers over different seasons. In winter the minimum temperature offset is influenced by the snow cover, which can act as an insulating layer and even decouple the microclimate from macroclimate. This effect could however be reduced by forest canopy, as denser canopies might decrease the snow layer (De Frenne et al., 2021). Changes in canopy cover through seasons impact light availability and warming through solar radiation. In mixed forests for example leaf-off seasons might increase solar radiation that reaches the ground (De Frenne et al., 2021; Greiser et al., 2024). Finally, this study only investigated a simple correlation between microclimate and species. Therefore, more in-depth studies focused on species and community characteristics, like survival and reproduction, connected to cold microclimate could be insightful to better understand biological patterns. It could be expected that cold-adapted plant species perform better in cold microclimates, where their competitiveness is higher (Borderieux et al., 2025). These are just a few possible ways to further understand the potential role of forest buffering and microclimates for species and forest ecosystems under climate change.

To summarize, with predicted temperature maps relatively cold and warm places in all three regions were located. All models were significant, which shows that larger, national scale data could be used to map local microclimates. Nevertheless, the explanatory power of the models varies between regions and is rather low, showing limitations and potential for improvement. Furthermore, through multiple linear regressions the main drivers for microclimatic temperature were found to be soil moisture, canopy openness and elevation. Canopy openness was significant in all three regions, while soil moisture and elevation were significant in two regions respectively. Therefore, relatively cold places were found to be plots with higher canopy cover, higher soil moisture and at higher elevations. The significance of canopy cover and soil moisture in facilitating colder temperatures highlights the importance of forest characteristics for shaping microclimate. Lastly, a connection between relatively cold plant communities and cold plots was observed. The analysis of the CTI and ground temperature over all regions had a positive, significant correlation, meaning that relatively cold communities were found in relatively cold plots. However, this likely reflects the macroclimatic gradient between the three regions, rather than the influence of microclimates on ground plant communities. Within the individual regions the correlation between CTI and ground temperature was not significant.

References

Asa | SITES. (n.d.). Retrieved 23 May 2025, from https://meta.fieldsites.se/resources/stations/Asa

Beckschäfer, P. (2015). *Hemispherical_2.0 – Batch processing hemispherical and canopy photographs with ImageJ – User Manual*. Chair of Forest Inventory and Remote Sensing, Georg-August-Universität Göttingen, Germany. https://doi.org/10.13140/RG.2.1.3059.4088

Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.-C., & Gégout, J.-C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, *479*(7374), 517–520. https://doi.org/10.1038/nature10548

Block, S., Maechler, M.-J., Levine, J. I., Alexander, J. M., Pellissier, L., & Levine, J. M. (2022). Ecological lags govern the pace and outcome of plant community responses to 21st-century climate change. *Ecology Letters*, *25*(10), 2156–2166. https://doi.org/10.1111/ele.14087

Borderieux, J., De Lombaerde, E., De Pauw, K., Sanczuk, P., Vangansbeke, P., Vanneste, T., De Frenne, P., Gégout, J.-C., & Serra-Diaz, J. (2025). Cool topoclimates promote cold-adapted plant diversity in temperate mountain forests. *Peer Community Journal*, *5*. https://doi.org/10.24072/pcjournal.519

Bowler, D., & Böhning-Gaese, K. (2017). Improving the community-temperature index as a climate change indicator. *PLOS ONE*, *12*(9), e0184275. https://doi.org/10.1371/journal.pone.0184275

Bradshaw, C. J. A., & Warkentin, I. G. (2015). Global estimates of boreal forest carbon stocks and flux. *Global and Planetary Change*, *128*, 24–30. https://doi.org/10.1016/j.gloplacha.2015.02.004

Bramer, I., Anderson, B. J., Bennie, J., Bladon, A. J., De Frenne, P., Hemming, D., Hill, R. A., Kearney, M. R., Körner, C., Korstjens, A. H., Lenoir, J., Maclean, I. M. D., Marsh, C. D., Morecroft, M. D., Ohlemüller, R., Slater, H. D., Suggitt, A. J., Zellweger, F., & Gillingham, P. K. (2018). Chapter Three—Advances in Monitoring and Modelling Climate at Ecologically Relevant Scales. In D. A. Bohan, A. J. Dumbrell, G. Woodward, & M. Jackson (Eds.), *Advances in Ecological Research* (Vol. 58, pp. 101–161). Academic Press. https://doi.org/10.1016/bs.aecr.2017.12.005

Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P. W., Trisos, C., Romero, J., Aldunce, P., Barrett, K., Blanco, G., Cheung, W. W. L., Connors, S., Denton, F., Diongue-Niang, A., Dodman, D., Garschagen, M., Geden, O., Hayward, B., Jones, C., … Péan, C. (2023). *IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland.* (First). Intergovernmental Panel on Climate Change (IPCC). https://doi.org/10.59327/IPCC/AR6-9789291691647

Chen, X., Wang, Q., Cui, B., Chen, G., Xie, T., & Yang, W. (2023). Ecological time lags in biodiversity response to habitat changes. *Journal of Environmental Management*, *346*, 118965. https://doi.org/10.1016/j.jenvman.2023.118965

Christiansen, D. M., Iversen, L. L., Ehrlén, J., & Hylander, K. (2022). Changes in forest structure drive temperature preferences of boreal understorey plant communities. *Journal of Ecology*, *110*(3), 631–643. https://doi.org/10.1111/1365-2745.13825

Davis, K. T., Dobrowski, S. Z., Holden, Z. A., Higuera, P. E., & Abatzoglou, J. T. (2019). Microclimatic buffering in forests of the future: The role of local water balance. *Ecography*, *42*(1), 1–11. https://doi.org/10.1111/ecog.03836

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D. M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klinges, D. H., Koelemeijer, I. A., Lembrechts, J. J., Marrec, R., … Hylander, K. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, *27*(11), 2279–2297. https://doi.org/10.1111/gcb.15569

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C. D., Brunet, J., Cornelis, J., Decocq, G. M., Dierschke, H., Eriksson, O., Gilliam, F. S., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M. A., … Verheyen, K. (2013). Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences*, *110*(46), 18561–18565. https://doi.org/10.1073/pnas.1311190110

De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, *3*(5), 744–749. https://doi.org/10.1038/s41559-019-0842-1

De Lombaerde, E., Vangansbeke, P., Lenoir, J., Van Meerbeek, K., Lembrechts, J., Rodríguez-Sánchez, F., Luoto, M., Scheffers, B., Haesen, S., Aalto, J., Christiansen, D. M., De Pauw, K., Depauw, L., Govaert, S., Greiser, C., Hampe, A., Hylander, K., Klinges, D., Koelemeijer, I., … De Frenne, P. (2022). Maintaining forest cover to enhance temperature buffering under future climate change. *Science of The Total Environment*, *810*, 151338. https://doi.org/10.1016/j.scitotenv.2021.151338

Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D. B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., … Jiguet, F. (2012). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, *2*(2), 121–124. https://doi.org/10.1038/nclimate1347

Dobrowski, S. Z. (2011). A climatic basis for microrefugia: The influence of terrain on climate. *Global Change Biology*, *17*(2), 1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x

Esseen, P.-A., Ehnström, B., Ericson, L., & Sjöberg, K. (1997). Boreal Forests. *Ecological Bulletins*, *46*, 16–47.

Evans, J. S., & Murphy, M. A. (2023). *spatialEco* (Version R package version 2.0-2) [Dataset]. https://github.com/jeffreyevans/spatialEco

Frey, S. J. K., Hadley, A. S., Johnson, S. L., Schulze, M., Jones, J. A., & Betts, M. G. (2016). Spatial models reveal the microclimatic buffering capacity of old-growth forests. *Science Advances*, *2*(4), e1501392. https://doi.org/10.1126/sciadv.1501392

Gauthier, S., Bernier, P., Burton, P. J., Edwards, J., Isaac, K., Isabel, N., Jayen, K., Le Goff, H., & Nelson, E. A. (2014). Climate change vulnerability and adaptation in the managed Canadian boreal forest. *Environmental Reviews*, *22*(3), 256–285. https://doi.org/10.1139/er-2013-0064

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z., & Schepaschenko, D. G. (2015). Boreal forest health and global change. *Science*, *349*(6250), 819–822. https://doi.org/10.1126/science.aaa9092

Geiger, R. (1950). *The Climate Near The Ground* (2nd ed.). Harvard University Press.

Gilliam, F. S. (2007). The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems. *BioScience*, *57*(10), 845–858. https://doi.org/10.1641/B571007

Govaert, S., Vangansbeke, P., Blondeel, H., Steppe, K., Verheyen, K., & De Frenne, P. (2021). Rapid thermophilization of understorey plant communities in a 9 year-long temperate forest experiment. *Journal of Ecology*, *109*(6), 2434–2447. https://doi.org/10.1111/1365-2745.13653

Greiser, C., Ehrlén, J., Meineri, E., & Hylander, K. (2020). Hiding from the climate: Characterizing microrefugia for boreal forest understory species. *Global Change Biology*, *26*(2), 471–483. https://doi.org/10.1111/gcb.14874

Greiser, C., Hederová, L., Vico, G., Wild, J., Macek, M., & Kopecký, M. (2024). Higher soil moisture increases microclimate temperature buffering in temperate broadleaf forests. *Agricultural and Forest Meteorology*, *345*, 109828. https://doi.org/10.1016/j.agrformet.2023.109828

Greiser, C., Meineri, E., Luoto, M., Ehrlén, J., & Hylander, K. (2018). Monthly microclimate models in a managed boreal forest landscape. *Agricultural and Forest Meteorology*, *250–251*, 147–158. https://doi.org/10.1016/j.agrformet.2017.12.252

Grimsö | SITES. (n.d.). Retrieved 23 May 2025, from https://meta.fieldsites.se/resources/stations/Grimso

Haesen, S., Lembrechts, J. J., De Frenne, P., Lenoir, J., Aalto, J., Ashcroft, M. B., Kopecký, M., Luoto, M., Maclean, I., Nijs, I., Niittynen, P., Van Den Hoogen, J., Arriga, N., Brůna, J., Buchmann, N., Čiliak, M., Collalti, A., De Lombaerde, E., Descombes, P., … Van Meerbeek, K. (2021). ForestTemp – Sub-canopy microclimate temperatures of European forests. *Global Change Biology*, *27*(23), 6307–6319. https://doi.org/10.1111/gcb.15892

Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., Robinson, B. S., Hodgson, D. J., & Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, *6*, e4794. https://doi.org/10.7717/peerj.4794

Hijmans, R. (2025). *terra: Spatial Data Analysis* (Version R package version 1.8-42) [Dataset]. https://CRAN.R-project.org/package=terra?utm_source=chatgpt.com

Hylander, K., Greiser, C., Christiansen, D. M., & Koelemeijer, I. A. (2022). Climate adaptation of biodiversity conservation in managed forest landscapes. *Conservation Biology*, *36*(3), e13847. https://doi.org/10.1111/cobi.13847

Kemppinen, J., Lembrechts, J. J., Van Meerbeek, K., Carnicer, J., Chardon, N. I., Kardol, P., Lenoir, J., Liu, D., Maclean, I., Pergl, J., Saccone, P., Senior, R. A., Shen, T., Słowińska, S., Vandvik, V., von Oppen, J., Aalto, J., Ayalew, B., Bates, O., …

De Frenne, P. (2024). Microclimate, an important part of ecology and biogeography. *Global Ecology and Biogeography*, *33*(6), e13834. https://doi.org/10.1111/geb.13834

Lenoir, J., Hattab, T., & Pierre, G. (2017). Climatic microrefugia under anthropogenic climate change: Implications for species redistribution. *Ecography*, *40*(2), 253–266. https://doi.org/10.1111/ecog.02788

Maciejewski, L., Kuhn, E., Gégout-Petit, A., & Gégout, J.-C. (2020). Natura 2000 forest habitats: Climatic debt in lowlands and thermophilization in highlands. *Biodiversity and Conservation*, *29*(13), 3689–3701. https://doi.org/10.1007/s10531-020-02044-z

Mäkinen, J., Ellis, E. E., Antão, L. H., Davrinche, A., Laine, A.-L., Saastamoinen, M., Conenna, I., Hällfors, M., Santangeli, A., Kaarlejärvi, E., Heliölä, J., Huikkonen, I.-M., Kuussaari, M., Leinonen, R., Lehikoinen, A., Pöyry, J., Suuronen, A., Salemaa, M., Tonteri, T., … Roslin, T. (2025). Thermal homogenization of boreal communities in response to climate warming. *Proceedings of the National Academy of Sciences*, *122*(17), e2415260122. https://doi.org/10.1073/pnas.2415260122

McCune, B., & Keon, D. (2002). Equations for potential annual direct incident radiation and heat load index. *Journal of Vegetation Science*.

Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T. D., Ebersole, J. L., Krawchuk, M. A., Letcher, B. H., Mahalovich, M. F., Meigs, G. W., Michalak, J. L., Millar, C. I., Quiñones, R. M., Stralberg, D., & Thorne, J. H. (2020). Climate-change refugia: Biodiversity in the slow lane. *Frontiers in Ecology and the Environment*, *18*(5), 228–234. https://doi.org/10.1002/fee.2189

Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., Lundquist, J. D., Millar, C. I., Maher, S. P., Monahan, W. B., Nydick, K. R., Redmond, K. T., Sawyer, S. C., Stock, S., & Beissinger, S. R. (2016). Managing Climate Change Refugia for Climate Adaptation. *PLOS ONE*, *11*(8), e0159909. https://doi.org/10.1371/journal.pone.0159909

Peichl, M., Martínez-García, E., Fransson, J. E. S., Wallerman, J., Laudon, H., Lundmark, T., & Nilsson, M. B. (2023). Landscape-variability of the carbon balance across managed boreal forests. *Global Change Biology*, *29*(4), 1119–1132. https://doi.org/10.1111/gcb.16534

R Core Team. (2024). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Reid, W. V., Chen, D., Goldfarb, L., Hackmann, H., Lee, Y. T., Mokhele, K., Ostrom, E., Raivio, K., Rockström, J., Schellnhuber, H. J., & Whyte, A. (2010). Earth System Science for Global Sustainability: Grand Challenges. *Science*, *330*(6006), 916–917. https://doi.org/10.1126/science.1196263

Richard, B., Dupouey, J., Corcket, E., Alard, D., Archaux, F., Aubert, M., Boulanger, V., Gillet, F., Langlois, E., Macé, S., Montpied, P., Beaufils, T., Begeot, C., Behr, P., Boissier, J., Camaret, S., Chevalier, R., Decocq, G., Dumas, Y., … Lenoir, J. (2021). The climatic debt is growing in the understorey of temperate forests: Stand characteristics matter. *Global Ecology and Biogeography*, *30*(7), 1474–1487. https://doi.org/10.1111/geb.13312

Roberge, J.-M., Fries, C., Normark, E., Mårald, E., Sténs, A., Sandström, C., Sonesson, J., Appelqvist, C., & Lundmark, T. (2020). *Forest Management In Sweden—Current practice and historical background*.

Ruckstuhl, K. e, Johnson, E. a, & Miyanishi, K. (2007). Introduction. The boreal forest and global change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1501), 2243–2247. https://doi.org/10.1098/rstb.2007.2196

Savage, J., & Vellend, M. (2015). Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. *Ecography*, *38*(6), 546–555. https://doi.org/10.1111/ecog.01131

SLU. (2020, October 16). *Produktbeskrivning: SLU Markfuktighetskarta version 1.0 – markfuktighetsskattningar från laserdata*.

Sparrius, L. B., van den Top, G. G., & van Swaay, C. A. M. (2018). *An approach to calculate a Species Temperature Index for flora based on open data*.

Stevens, J. T., Safford, H. D., Harrison, S., & Latimer, A. M. (2015). Forest disturbance accelerates thermophilization of understory plant communities. *Journal of Ecology*, *103*(5), 1253–1263. https://doi.org/10.1111/1365-2745.12426

Suggitt, A. J., Wilson, R. J., Isaac, N. J. B., Beale, C. M., Auffret, A. G., August, T., Bennie, J. J., Crick, H. Q. P., Duffield, S., Fox, R., Hopkins, J. J., Macgregor, N. A., Morecroft, M. D., Walker, K. J., & Maclean, I. M. D. (2018). Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change*, *8*(8), 713–717. https://doi.org/10.1038/s41558-018-0231-9

Svartberget | SITES. (n.d.). Retrieved 23 May 2025, from https://meta.fieldsites.se/resources/stations/Svartberget

Vanwalleghem, T., & Meentemeyer, R. K. (2009). Predicting Forest Microclimate in Heterogeneous Landscapes. *Ecosystems*, *12*(7), 1158–1172. https://doi.org/10.1007/s10021-009-9281-1

Wild, J., Kopecký, M., Macek, M., Šanda, M., Jankovec, J., & Haase, T. (2019). Climate at ecologically relevant scales: A new temperature and soil moisture logger for long-term microclimate measurement. *Agricultural and Forest Meteorology*, *268*, 40–47. https://doi.org/10.1016/j.agrformet.2018.12.018

Xu, X., Huang, A., Belle, E., De Frenne, P., & Jia, G. (2022). Protected areas provide thermal buffer against climate change. *Science Advances*, *8*(44), eabo0119. https://doi.org/10.1126/sciadv.abo0119

Zellweger, F., Coomes, D., Lenoir, J., Depauw, L., Maes, S. L., Wulf, M., Kirby, K. J., Brunet, J., Kopecký, M., Máliš, F., Schmidt, W., Heinrichs, S., den Ouden, J., Jaroszewicz, B., Buyse, G., Spicher, F., Verheyen, K., & De Frenne, P. (2019). Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. *Global Ecology and Biogeography*, *28*(12), 1774–1786. https://doi.org/10.1111/geb.12991

Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., Van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecký, M., Máliš, F., … Coomes, D. (2020). Forest microclimate dynamics drive plant responses to warming. *Science*, *368*(6492), 772–775. https://doi.org/10.1126/science.aba6880

Popular science summary

Can forests help cold-adapted plants against climate change?

Climate change is warming the planet, and it has far reaching impacts on nature. Especially plants, that are less mobile than animals, cannot just move away from unsuitable climate conditions. Some plant species are adapted to cold temperatures, which means they grow and survive in northern latitudes or high elevations, where other plants could not exist. As temperature rises these cold adapted plants are losing suitable habitats. However, forests may offer a safe harbour for cold adapted understory plants from climate change. Under dense forest canopies temperatures on the forest floor are often cooler and more stable than in the surrounding area. These microclimates are created by many different factors, but some important ones are the canopy that shades and shelters the ground from sun and soil moisture that additionally cools.

In my master thesis I studied these cold microclimates on the ground in three Swedish forest regions, namely Asa, Grimsö and Krycklan. The aim was to locate of the colder places in these forests and see if cold-adapted understory plants also occur there. The results showed that cooler microclimates were found in areas with dense canopies, high soil moisture and at higher elevations. Cold adapted plant species did occur in colder place, but the relationship in the individual regions was not significant and would need to be studied further. Still, the results suggest that forests and forest management have a potential to protect cold microclimates, which could support boreal forests adapt and mitigate to impacts of climate change.

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