

# Ericaceous Vegetation of the Bale Mountains of Ethiopia Will Prevail in the Face of Climate Change.

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## Research Article

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# Abstract

Climate change impacts ecosystem structure, functioning, and spatial distribution. Among others, it will result in a shift in ecosystem boundaries, which will result in the contraction of some vulnerable ecosystems, such as the alpine zone of high mountains. The African tropical high mountain ecosystems, i.e., Afroalpine ecosystems, are spatially extremely isolated and highly vulnerable. The ecosystems dominated by ericaceous woody plants are vital components at the transition between forests and Afroalpine vegetation. Here, we modeled the impact of projected climate change on the current and future distribution of ericaceous vegetation in the Bale Mountains. We hypothesize climate change will result in modified suitability of sites for ericaceous vegetation, leading to the expansion of ericaceous vegetation to higher elevation and contraction in other altitudes. Consequently, the expansion and dominance of ericaceous vegetation could negatively impact Afroalpine ecosystems. We applied and compared four modeling algorithms based on bioclimatic variables as environmental predictors: Generalized Linear Models (GLMs), Bioclim, Domain, and Support Vector Machines (SVM) algorithms. After testing for collinearity, we selected ten historical (current) and future bioclimatic variables. We used two representative concentration pathways (RCPs) of IPCC5 climate projections, namely RCP4.5 and RCP8.5, for future climate projection. The 2050s and 2070s projections resulted in increased ericaceous vegetation cover towards the midaltitude of northwestern and northern parts of the massif and the Sanetti plateau. Close ericaceous vegetation stands at high altitudes are projected to increase while receding from the lower range of the current distribution range across the massif. Moreover, the current ericaceous vegetation distribution is positively related to the temperature and precipitation trends, which reaffirms the critical role of temperature in shaping species distributions along elevational gradients. The results indicate the high likelihood for considerable changes in this biodiversity hotspot in Eastern Africa.

## 1. Introduction

Tropical Africa high mountain top ecosystems, Afroalpine ecosystems, occur in isolated patches restricted to peaks of the high mountains along the Great Rift Valley and Cameron-Nigeria mountain ranges between Tropic of Capricorn and Tropic of Cancer (Hedberg, 1964; Gehrke and Linder, 2014). These spectacular ecosystems are habitats for unique life forms. Afroalpine plants own distinctive traits and are specially adapted to frost and drought. They exhibit specific morphological and functional adaptations to the predominant diurnal climate extreme, i.e., the high thermal fluctuation between day and night. Moreover, the spatial isolation of mountain that ranges over a long-timescale have supported the evolution of many endemics (Steinbauer et al., 2016; Flantua et al., 2020; Testolin et al., 2021). The uniquely adapted species are sensitive to perturbation, and climate change (Vuilleumier and Monasterio, 1986; Nagy and Grabherr, 2009; Buytaert et al., 2011), which is the most pervasive of the various threats to the planet's biodiversity (Malcolm et al., 2006).

The recently observed climate change across tropical regions is significantly higher than the global average. For example, there are observed temperature increases for the tropical rainforest regions at a mean rate of  $0.26 \pm 0.05^\circ\text{C}$  per decade, with an intensification during the El Niño events (Malhi and

Wright, 2004). Climate will continue warming up throughout the coming century in response to changes in radiative forcing arising from anthropogenic emissions of greenhouse gases and aerosols (IPCC 2014).

Climate change will induce thermal isotherm shifts, disrupting the stability of Afroalpine ecosystems and affecting the unique plant diversity, distribution, and species richness, leading to unexpected species and functional groups reorganization and massive endemic extinction (Malcom et al., 2006; Kreyling et al., 2010). Our species distribution modeling (SDM) to test altitudinal gradient/range shift is widely applied to assess the impact of climate change on a few selected plant diversity and distribution. It is a powerful method for testing biota's ecological and evolutionary responses to geophysical influences, such as temperature and moisture changes.

In general, there are two categories of altitude related factors of environmental changes: (i) those physically tied to meters above sea level (m asl), such as atmospheric pressure, temperature, moisture, and clear-sky turbidity; and (ii) those that are not generally altitude specific, such as hours of sunshine, wind, geology, fire, and even human land use (Körner, 2007). Here, we tested the impact of change in temperature related bioclimatic variables on the diversity and distribution of two common *Erica* spp. of the Bale Mountains and their implication for extensive Afroalpine plateau ecosystems.

Mountains show high biodiversity due to elevational gradients, complex surface structures, and disturbance regimes resulting in a broad range of site conditions and ecological niches (Beierkuhnlein, 2007; Körner, 2007; Nagy and Grabherr, 2009). Many mountain plant species have long life cycles reflected in woody structures above- and belowground, longevity, limited dispersal capacity resulting in inertia at the level of ecosystems (Razgour et al., 2020). The rapid spatial shift of ecosystems or local adaptation to novel climatic conditions is unlikely to happen by plants with broad phenotypic plasticity. For these reasons, tropical alpine and montane ecosystems and the immense biodiversity they harbor are particularly sensitive to climate change induced warming (Malcolm et al., 2006; Razgour et al., 2020). Hence, the anticipated thermal isotherm shifts can disrupt the stability of these ecosystems.

The Bale Mountains of south-central Ethiopia form the largest contiguous massif of most extensive plateaus above 3000 m asl in Africa, supporting the most extensive Ericaceous vegetation on the continent (Miehe and Miehe, 1994). *Erica* spp., commonly known as heathers or heaths, belong to the subfamily Ericoidae, comprising acid loving, woody plants (Wesche et al., 2000; McGuire et al., 2005). The ericaceous vegetation is one of the Afroalpine/Fromontane plants with a broader distribution range, with a high thermal tolerance range and adaptation potential that outcompete some Afroalpine plants (Gehrke and Linder, 2014).

In the Bale Mountains, climate change induced warming and thermal anomalies are expected to generate future environmental conditions that could favor the expansion and dominance of plants with a more comprehensive habitat range, such as Ericaceous vegetation. Kreyling et al. (2010), Wana and Beierkuhnlein (2010), and Kidane et al. (2019) speculated altitudinal range shift and range contraction

because of climate change at the Gughe mountains (Southern Ethiopia) and the Bale Mountains, respectively.

Recent SDMs focus on extinction risks of species or groups rare and under threat of extinction, keystone species, or functional type (Urban 2015). Little is known about the potential range loss among the widespread species such as *Erica*, which is critical as even slight declines in such species can significantly affect ecosystem structure, function, and services (Warren et al., 2013).

To date, the impacts of projected climate change, the extent of the current distribution range and suitable habitat, and the main bioclimatic factors that control *Erica's* expansion and distribution in the Bale Mountains are not well studied. However, the role of fire, land use, and herbivory as central players in *Erica* dynamics are relatively more researched (e.g., Wesche et al., 2000, 2003, 2008; Gizaw et al., 2013; Johansson et al., 2014,2018; Gil-Romera et al., 2019). In general, the role of climate change in determining *Erica* distribution and its implication to associated alpine and subalpine flora is lacking.

Considering the severity of the anticipated climate change, we raised the question, whether the future novel environmental conditions or habitats shift will favor further expansion and dominance of plants with a broader habitat range, such as *Erica*. We hypothesize that climate change will create novel suitable and unsuitable habitats that will be colonized by plant species that are adapted to the new environmental conditions. We further hypothesize that due to its broad phenotypic plasticity, *Erica* will respond to considerable changes and prevail in the location of its potential suitable habitats. Hence, we applied Species Distribution Models (SDMs) and model ensemble to model *Erica's* extent in its current and future distribution range. We projected its future distribution under two RCPs (RCP4.5) average temperature increases 1.4°C (0.9 to 2.0) and RCP8.5 (2070s) with an average temperature increase of 3.7°C (2.6 to 4.8).

Understanding *Erica's* current and future distribution and ecological range in the face of climate change is essential to the science and knowledge basis of *Erica's* ecology and biogeography. It also contributes to the planning and development of sound local management strategies. This research aims to model the current *Erica* distribution range under the current condition and projected climate change. Specifically, 1) to model the current distribution of *Erica*, 2) to identify the main bioclimatic variables that control *Erica's* distribution, and 3) to model the future potential distribution of *Erica* and discuss its implication to the Afroalpine plants.

## 2. Materials And Methods

### 2.1 Study area

#### 2.1.1 Location and geology

The study was carried out in the Bale Mountains of the Southeastern Ethiopian highlands, focusing on the Ericaceous vegetation within an area of geographic extent 39°45'E, 40°00'E and 06°45'S, 07°20'N (Fig.

1). The contiguous massifs are home to the last remaining pristine Afroalpine ecosystems in Africa. The mountains were one of the most extensively glaciated, cooler, and drier during the Pleistocene (the last glaciation), which shaped their recent geomorphology (Bonnefille, 1983). They are fragmented by numerous volcanic plugs, peaks, alpine lakes, and rushing mountain streams that descend into deep rocky gorges. African mountains, especially the Afroalpine proper and Ericaceous zones, were pushed down by ~1000 m and covered larger areas than today during a long period in the Pleistocene (Gottelli et al., 2004). These species assemblages are spatially condensed today.

## 2.1.2 Climate

The Bale Mountains are located at the convergence of the wet East African and dry northeast African mountains of southeast Ethiopia. Rain comes to the mountains from two different sources, the equatorial westerlies (rainfall pattern influenced by the Intertropical Convergence Zone (ITCZ)) and the Indian Ocean Monsoon (Uhlig and Uhlig, 1991). There is pronounced south to north rainfall gradient in the area and the altitude-related temperature gradient. The rainfall is slightly bimodal, with a peak from April to May and a second peak from August to October.

The south and southwest facing slopes are more humid with a subtropical climate, high annual rainfall (up to 1500 mm/year), and the dry season lasting only about two months. The north and northeastern parts experience an annual rainfall from 800 to 1100 mm and a wet season from June to September. Along altitude, precipitation increases up to around 3800 m asl, then decreases towards the summits (Hillman, 1986). The Afroalpine region is often covered with clouds and gains less precipitation than the Afromontane range.

In general, the Afroalpine climate is cold and wet, except in the short dry season, usually lasting from December to January or into March–April during drought years (Miehe and Miehe, 1994). Besides, these ecosystems are characterized by unique climatic conditions of high diurnal temperature fluctuations (warm days alternating with freezing nights) while little seasonal variation in temperature (Hedberg, 1964; Smith and Young, 1987). An extreme diurnal temperature range of about 40°C (-15°C to +26°C) has been recorded during the dry season (Hillmann 1986).

## 2.1.3 The Erica and the Ericaceous Belt

The Bale Mountains exhibit a steep gradient of ecological zones ranging from tropical rainforests to Afroalpine vegetation (Umer et al., 2007; Kidane et al., 2012; 2019). It is divided into distinct habitats such as the Northern Grasslands (Gaysay Valley), Northern Woodlands, Afroalpine Meadows (Sanetti Plateau), Ericaceous belt (*Erica* Moorlands), and the Harena Tropical Rain Forest (Umer et al., 2007).

The area succeeding the upper montane forest, the heathland, is dominated by *Erica arborea* and *Erica trimera*, otherwise known as “the Ericaceous Belt” (Hedberg, 1951; Miehe and Miehe, 1994). The two closely related *Erica* species, *Erica arborea* L. and *Erica trimera* (Engl.) Beentje (henceforth *Erica*) dominates this ecosystem (Hedberg, 1951; Miehe and Miehe, 1994). Both species have similar morphology, distribution, and habitat ecology, making it difficult to distinguish the two species in the field

(Gizaw et al., 2013). *E. arborea* is widely distributed in Africa, the Middle East, and Europe. At the same time, *E. trimera* is endemic to the Afroalpine mountains and occurs in several mountain systems of East Africa and the Ethiopian Highlands (McGuire et al., 2005). *E. trimera* tends to dominate at higher elevations between 3700 m asl to 4150 m asl, while *E. arborea* has a broader distribution range that extends between 3100 m and 4200 m asl (Hedberg, 1986; Miehe and Miehe, 1994), usually in an area that extends 1000 to 1100 m vertical distance.

*Erica* displays different phenotypes across elevational gradients (Fig. 2), mainly driven by environmental factors such as temperature and moisture (Gil-Romera et al., 2019). It appears as evergreen dwarf shrubs of a few centimeters high to trees up to 12 m (Miehe and Miehe 1994; Gizaw et al., 2013). This older *Erica* forest has dense multi-stem trees covered with prominent epiphytes such as mosses and ferns. Above the old growth is the mid-altitude of *Erica* distribution, the dense shrubland covered with shrubs of approximately 0.5 m to 4 m. Here, in between the after fire resprouting *Erica* shrubs are distinct species of grasses and herbs growing. Finally, it occurs as few centimeter-high shrubs at a higher elevation.

## 2.1.4 The Afroalpine Ecosystem

One-third of the species in the Afroalpine flora are exclusively alpine, while many species can have a broader range of distribution that extends to the lower vegetation belts (Chala et al., 2017; Kidane et al., 2019). On the Senetti plateau above the treeline are the Afroalpine plant communities, composed of a mixture of low-growing, perennial life forms and giant rosettes (*Dendrosenecio* and *Lobelia*). Plants such as *Eriocaulon schimperi*, *Carex monostachya*, *Helichrysum* (*H. citrispinum*, *H. cymosum*, *H. gofense*, and *H. Splendidum*), *Alchemilla* (*A. abyssinica*, *A. rothii*, and *A. Cyclophylla*), and *Artemisia afra* are typical plants of this habitat.

## 2.2. Data collection

### 2.2.1 Ground controlling points collection and data preparation

Landsat TM + 8 remote sensing images 30 m x 30 m resolution from March 8, 2017, paths 167 and 168, and raw 55 and 56 were acquired from the United States Geological Survey homepage (USGS, 2018). The images were classified based on the known eight major Afroalpine and Afromontane vegetation classes of the area (Kidane et al., 2019).

The vegetation cover classes were identified and cross-checked using ground controlling points acquired from vegetation sampling plots and GPS ground control points collected across the Bale massif. The plot ground controlling points were taken from floristic inventory transects established across the Goba-Rira-Dolo Mena road North-South-Southeast transect across the massif. During the image classification, GoogleEarth images and pictures were used to cross-check any recent vegetation cover change. The altitude and coordinates of each sampling plot were recorded using Garmin GPS 3.1. The data preparation steps and modeling are described in Fig. 3.

## 2.2.2 Image classification and occurrence data collection

We applied the QGIS Semi-Automatic Classification image processing approach. The object based supervised maximum likelihood algorithm was used to classify the images. In such an approach, the analyst defines areas where the land cover is known, predefines the LULC types and the number of classes based on selected parameters (Foody, 2002; Wegmann et al., 2016). This approach enhances the delineation objectivity, interpretation repeatability, and processing efficiency (Duveiller et al., 2008). Classification accuracy was evaluated using the kappa coefficient, a widely used technique for image classification accuracy assessment. We achieved a Kappa coefficient and overall accuracy of 93%. Usually, the image classification Kappa coefficient and overall accuracy above 73% are acceptable and required (Foody, 2002).

Georeferencing, image classification, occurrence points extraction, and coordinates cross check were carried out using QGIS 3.4 (QGIS Development Team 2018). After classification, the other landcover classes, other than *Erica*, were masked. The upper and lower occurrence range of *Erica* in the Bale Mountains, between 3100 and 4200 m asl, were delineated. Species occurrence points were extracted from the *Erica* class of the classified images. More than 3220 *Erica* occurrence points were extracted from the modeled *Erica* occurrence points.

The modeling, including further data preparation, cleaning, and calibration were carried out following the SDMs steps described in Hijmans and Elith (2017). 45 *Erica* occurrence duplicate points were removed from the database during the modeling proceedings. Error-free and adequately representing occurrence points were compiled and used for modeling.

## 3.2 Predictor variables selection and preparation

Model outputs are primarily driven by choice of predictor variables fitted into the models and the type and level of adjustment between the response and predictor variables (Araujo and Guisan, 2006; Naimi and Araújo, 2016). We used the bioclimatic variables provided by WorldClim as our main environmental predictors. The historical (current) climate data for 1970–2000 and future 2050s (projected climate data for 2046–2065) and 2070s (projected climate data for 2081–2100) of 19 bioclimatic predictor variables at 30arc sec ( $\sim 1 \text{ km}^2$ ) spatial resolution were downloaded from WorldClim version 1.4 (Hijmans et al., 2005).

We used the bioclimatic variables (environmental change factors strictly tied to altitude or factors physically linked to m asl) for our modeling purpose. We selected two representative CMIP5 (Coupled Model Inter-comparison Project Phase 5) concentration pathways (RCPs) of IPCC5 climate projections (IPCC 2014). We used RCP4.5 for the 2050s with a lower radiative forcing temperature increase average of  $1.4^\circ\text{C}$  (0.9 to 2.0) and RCP8.5 (2070s) with a higher radiative forcing temperature increase of  $3.7^\circ\text{C}$  (2.6 to 4.8). RCP4.5 is described by the IPCC 2014 as an intermediate scenario or likelihood that climate change will be constrained to  $2^\circ\text{C}$  above pre-industrial levels and RCP8.5 as a worst-case scenario because it assumes emissions continue to rise throughout the 21st century.

Species occurrence data and the types of environments in which species prevail are important because SDMs are sensitive to sample size and biases in data distribution (Araujo and Guisan, 2006). We tested the 19 bioclimatic variables for collinearity using Variance Inflation Factor (VIF) VIFcor functions in R within the USDM package (Naimi et al., 2014). VIF measures the severity of multicollinearity in regression analysis and is a pairwise correlation that excludes the highly correlated variables stepwise. We applied the default threshold of 0.9. Variables above the threshold were excluded. Consequently, ten predictor variables were identified as suitable predictors for the *Erica* SDM Table 1.

Table 1  
The identified ten suitable bioclimatic variables which were used to generate the *Erica* distribution models.

No	Environmental predictor variable	Code
1	Mean Diurnal Range (Mean of monthly (max temp - min temp))	Bio2
2	Mean Temperature of Wettest Quarter	Bio8
3	Mean Temperature of Driest Quarter	Bio9
4	Mean Temperature of Warmest Quarter	Bio10
5	Mean Temperature of Coldest Quarter	Bio11
6	Precipitation of Wettest Month	Bio13
7	Precipitation of Driest Month	Bio14
8	Precipitation Seasonality (Coefficient of Variation)	Bio15
9	Precipitation of Warmest Quarter	Bio18
10	Precipitation of Coldest Quarter	Bio19

## 3.3 Data analysis

### 3.3.1 Modeling approach

All the predictor variables were of the same spatial extent, resolution, origin, projection, and organized as raster ".tif" data. They were layer stacked (Fig. 4a). The dependent (predicted values) and independent variables (bioclimatic predictors and *Erica* presence values) were identified, then the models were fitted. Cross-validation was carried out by creating a training and testing data set through random sampling and modeling with the data set of known occurrences (Fig. 4b).

The *Erica* occurrence database, together with ten current and future bioclimatic predictors, were preprocessed with R version 3.6.0, focusing on the packages "dismo" (Elith et al., 2009) and "raster" (Hijmans and van Etten, 2011). Subsampling within the range of our study area was run to reduce sampling bias and produce more balanced samples for model calibration. The modeling data sets were



created through random sampling from a single data set. For model evaluation, 1572 (75%) training and 487 (25%) test values were sampled. Model performance was assessed by calculating area Under the Curve (AUC).

AUC is a measure of rank-correlation commonly used in SDM studies because it is insensitive to species prevalence and does not require a threshold value to convert probabilities to presence-absence (Hijmans and Elith 2017). Our model AUC values range between 0.81 and 0.86. In unbiased data, a high AUC indicates sites with high predicted suitability (areas of known presence), while AUC below zero indicates species absence. Elith et al. (2006), in their model comparison, found the best SDM models for each of their species distribution prediction had an AUC value of  $> 0.75$ .

### **3.3.2 Modeling methods**

SDMs comprise significant spatial and temporal data and advanced modeling methods that are object-oriented and reproducible platforms (Peterson et al., 2011; Naimi and Araújo, 2016). They are critical to fundamental and applied research in biogeography (Araújo and Guisan, 2006). They are especially suited to assess species and ecosystem status over wide, remote, and inaccessible areas such as mountain ecosystems (Kreyling et al., 2010).

SDMs use individual species and community-based approaches to project potential species distributions in space and time (Naimi and Araújo, 2016). They enable us to build a basic understanding of vascular plants' distribution and diversity patterns in the face of climate change. Hence, we selected four widely used correlative modeling methods because of their wide use and strong predictive performance: the profile methods (Bioclim and Domain), regression (Generalized Linear Methods (GLMs)), and machine learning (Support Vector Machines (SVMs)). These algorithms have proven to perform well for species distribution modeling that uses species occurrence data and bioclimatic variables (Elith et al., 2006). They all compute habitat similarity by comparing the values of bioclimatic variables to a percentile distribution of known species occurrence locations.

Finally, we ensembled the models by applying model averaging to produce a more reliable prediction. Model ensembles are fitted and evaluated to project potential species distributions in space and time (Naimi and Araújo, 2016). The use of many models and applying model averaging to reduce reliance on a single model is suggested by many as a sound approach for better predictions (e.g., Naimi and Araújo, 2016; Hijmans and Elith, 2017). Hence, the four individual model predictions were ensembled based on their AUC values, and the mean predicted values were calculated. Furthermore, we run a change matrix between the averaged models of the different time steps, i.e., between current and the 2050s and current and 2070s.

The modeling, including data preparation, cleaning, and calibration, was carried out following the SDMs steps and r-scrip presented in Hijmans and Elith (2017).

## **4. Results**

## 4.1 Bioclim

The Bioclim model predicted *Erica's* current and future occurrence ranges (Fig. 5) with AUC values ranging between 0.82 and 0.84. For all time steps, the model values go from 0 to 0.7. The values above 0 are environmental conditions that allow *Erica* to satisfy its minimum requirements to flourish and occupy its optimal niche. The niche where *Erica's* establishment rate is equal to or greater than its death rate (e.g., Chase and Leibold 2003). The future models 2050s (Fig. 5b) and 2070s (Fig. 5c) predicted *Erica* persists within the current range while gaining stronghold and expanding towards midaltitude of southwestern and western parts of the mountains. The future models also predicted *Erica's* consolidation within the current range while shrinking from its lower and upper distribution ranges.

## 4.2 Domain

The Domain model predicted *Erica's* occurrence (Fig. 6) with model AUC values ranging between 0.81 and 0.83. Unlike Bioclim, Domain predicted the Afroalpine habitat to be suitable for *Erica*. For all time steps, the model values range from 0 to 0.8. The future predictions of the 2050s (Fig. 6b) and the 2070s (Fig. 6c) indicated *Erica's* persistence within the current distribution range while expanding throughout its current range. The future models further predicted successive consolidation of *Erica* within the current range, on the Afroalpine range, and west and northwards expansion with time while retracting from all its lower ranges.

## 4.3 Generalized Linear Model (GLM)

The GLM model predicted *Erica's* occurrence (Fig. 7) with model AUC values ranging between 0.81 and 0.86. The model values go from -1 to 1. The future models predicted *Erica's* substantial upward expansion while losing ground in all the lower ranges (Fig. 7b and Fig. 7c). The GLM prediction is similar to Domain model predictions. All predicted substantial loss of lower distribution range with time while expanding upwards to the upper ends of the Afroalpine plateau. Both future projections indicate a solid midaltitude hold of *Erica* within its current range and the Afroalpine range while retreating upwards in all lower ranges.

## 4.4 Support Vector Machine (SVM)

The SVM model predicted *Erica's* occurrence (Fig. 8) with model AUC values ranging between 0.82 and 0.86. For all time steps, the model values go from -0.5 to 1. SVM predicted a substantial consolidation of *Erica* within its current range, slight expansion towards the Afroalpine range, and pronounced loss on all mountains' lower ranges. The SVM predictions are like the other three model predictions. Both future projections indicate *Erica's* stronghold on its current range and westward expansion into the current dispersed *Erica* habitat and light upward expansion towards the Afroalpine habitat while losing from its lower ranges.

All four models predicted loss of suitable habitat at lower ranges, especially at the southwestern range, while the substantial gain on the western, northern, and eastern parts of the mountain.

## 4.5 Ensemble model predictions

The averaged model values (Fig. 9: **a-c**) projected habitat loss on all the lower range of the current *Erica* distribution range in the future. The models further predicting substantial consolidation of *Erica* on most of its current range, substantial expansion towards the western, northern, and eastern part of the massif, and the Afroalpine range. For all time steps, the model values range from - 1 to 1. The values above 0 are environmental conditions that satisfy *Erica's* minimum requirements to flourish and occupy its optimal niche, while values below 0 are unsuitable habitats.

## 4.6 Change comparison between the different time steps.

The difference between the current and 2050s (Fig. 10: **1a & 1b**) shows *Erica* is projected to expand towards the western and northwestern parts of the mountains while maintaining its current range. The difference between the current and 2070s (Fig. 10: **2a & 2b**) shows *Erica* is projected to continue expanding towards the western and northern parts of the mountains while maintaining a stronghold of its current range. However, towards the turn of the century, *Erica* will retreat from all lower ranges of its current distribution.

## 5. Discussion

The SDMs and the ensemble models projected future *Erica* distribution and provided insight into *Erica's* future habitat such as the area of habitat gain (expansion) - western, northern, and eastern flanks of the massif and Afroalpine top; persistence and dominance - most of the midaltitude and its current range; and loss (reduction/ contraction) - most of the lower ranges of current distribution. It provided information about *Erica's* bioclimatic requirements and its current distribution range, including remote and inaccessible areas free of human habitation. The models projected *Erica* distribution with a reliable model AUC value, 0.81 to 0.86, for all time steps.

Tropical alpine and montane ecosystems and the immense biodiversity they harbor are susceptible to climate change induced warming (Malcolm et al., 2006; Buytaert et al., 2011; IPCC, 2014). It is likely that species with a wider thermal range, such as *Erica*, will track the novel niche and dominate the suitable habitat while receding from the unsuitable habitats. Across tropical mountains with a constant lapse rate of about 0.6–0.7°C per 100 m (Sarmiento, 1986), the current temperature projections indicate that present temperature regimes will shift upward between about 140 and 800 m (Buytaert et al., 2011).

*Erica's* response to climate change will not be different from what has been observed in other places. Malcolm et al. (2006) projected an increase in temperature could induce a similar upward shift of altitudinal ecotone succession, leading to a loss of biodiversity at the ecosystem level. Peterson et al. (2011) and Gentili et al. (2015) indicated that mountain species would respond to climate change by migrating toward higher elevations and summits, in situ resilience of communities and species within microrefugia, adaptation and evolution through genetic differentiation and/or extinction. Warren et al. (2013), in their global analysis of the impacts of climatic change on the range of common species,

indicated that even without mitigation, on average  $57 \pm 7\%$  of plants are likely to lose  $\geq 50\%$  of their current climatic range by the 2080s.

The predicted *Erica* expansion towards the Afroalpine habitat in response to climatic change and the possible effect of these responses on the structure and function of Afroalpine ecosystems is essential. Climate change is expected to play a significant role in shaping plant communities and displacing ecosystem boundaries along the Bale mountains massif. As indicated by Steinbauer et al. (2018) in their global assessment, it will result in losses of natural habitats, which will lead to a rapid loss and extinction of species with their adaptations both at lower elevations and mountain top. Furthermore, it will strongly reduce the Afroalpine habitat's total area, endangering the many Afroalpine habitat specialists and distinctively adapted endemics.

The Bale Mountain Afroalpine plants will be outcompeted by *Erica* and other similar species under climate change. Due to its phenotypic plasticity, genetic adaptation to a wide variety of habitats, and broader temperature tolerance range, *Erica* will force many Afroalpine endemics that have restricted habitat ranges. The movement towards a new climatic niche is a long evolutionary process for most Afroalpine specialists. In addition, the unique topography of the plateau does not allow an upward shift because of the smaller area of the few mountain summits. Therefore, the alpine plants are likely to face an ecological dead-end (Kidane et al., 2019).

Under both future climate change scenarios (RCP45 and RCP85), many Afroalpine plants will decline and suffer local extinction. Global extinction risks increase from 2.8% at present to 5.2% at the international policy target of a 2°C (RCP45) post-industrial rise, which most experts believe is no longer achievable. If the Earth warms by 3°C, the extinction risk will rise to 8.5%. One of the current business as usual trajectory RCP 8.5 (up to  $\sim 4.3^\circ\text{C}$  rise), climate change threatens one in six species (16%) of global species (Urban, 2015). In the Bale massif, where about one-third of the plant species are exclusively alpine, a 2°C increase can cause potential local extinction of 8.7% of all endemic species. In contrast, 3°C or 4°C predicted about 36% of 41 endemic species extinction (Kidane et al., 2019).

In the Ethiopian mountains, the alpine and subalpine vegetation have been oscillating in response to the changing climate (Bonnefille et al. 1990; Gottelli et al., 2004; Ossendorf et al., 2019) and has been shaped by the change in temperature-related bioclimatic variables. Gottelli et al. (2004), Chala et al. (2017), Ossendorf et al. (2019) indicated that the Afroalpine vegetation was expanded towards the lower altitudes during the glaciation periods. McGuire et al. (2005) suggested that the Ericaceous belt existing today as refugia on high mountains in East Africa would have been more typical of tropical Africa than the present lowland vegetation when the European and African continents came into contact 17 Ma in the mid-Miocene, and the area suitable for exploitation by *Erica* species along the recently uplifted areas would have been more significant than it is today.

*Erica* expansion might lead to considerable species replacement, local extinction, and a significant decrease in species richness, especially those endemics across the massif. However, the topography of the steeper slopes may cause small-scale climatic heterogeneity allowing the coexistence of species with

differing environmental tolerances in smaller areas compared to the relatively flat plateau (Winkler et al., 2016). Such adaptation to a warming climate and dominance across the landscape will further be aided by gene flow from populations in already warmer areas of the species range (Buytaert et al., 2011) and the different microrefugia across the mountain range (e.g., Gentili et al., 2015).

Besides climate change, species are likely to respond to no temperature related multiple environmental factors with varying degrees of influence, significantly as the environmental conditions change with increasing altitude. Environmental change factors such as geographic barriers that limit dispersal, topography, microrefugia, aspect, and local relief can blur the bioclimatic factors. Therefore, species may not occupy all suitable sites in the future (e.g., Gentili et al., 2015; Winkler et al., 2016). Besides, the effects of orography related precipitation and resource diversity may influence species distribution patterns. Other environmental factors such as atmospheric pressure, CO<sub>2</sub> concentration, length of the vegetation period, nutrient availability, and soil quality decreased with altitude. The frequency of cold and frosty nights and solar radiation that increase with altitude might restrict *Erica's* expansion towards the Afroalpine plateau.

The ensembled models built with different techniques are promising for modeling species assemblages (Naimi and Araújo, 2016; Elith et al., 2017). Our model ensemble had high AUC values (0.84). Elith et al. (2006), in their model comparison, found the best SDM models for each of their species distribution prediction had an AUC value of > 0.75. Overall, our modeling results reveal that the application of SDM to model single species spatial and temporal pattern at the landscape level is promising and easily replicable to other similar species and ecosystems.

## 6. Conclusions

The Bale Mountains' Ericaceous vegetation will persist as the massif's critical ecosystem even under changing climate. Our models and ensembled model projected areas of potential suitable climate space of *Erica* at 1 km resolution and provided *Erica's* possible future distribution range within the Bale massif. We believe our findings will contribute to the science and understanding of the potential impacts of climate change on *Erica* or other species with high phenotypic plasticity and environmental range. Furthermore, our research that comprises different data sources and models shows how such concerns could be addressed to improve and support local conservation efforts and set management priorities.

Climate change is likely to disrupt and alter the current spatial arrangement, diversity, and distribution of many endemic and non-endemic species of the Afroalpine range. In the Bale mountains, both the upper and lower margins of distributions of *Erica* are highly likely to be affected. Hence, our modeling provided insight into *Erica's* future habitat such as the area of habitat gain (expansion) - western, northern, and eastern flanks of the massif and Afroalpine top; persistence and dominance - most of the midaltitude and its current range; and loss (reduction/ contraction) - most of the lower ranges of current distribution. However, *Erica's* future expansion will lead to considerable species replacement, local extinction, and a significant decrease in the species richness of those endemics on the Afroalpine plateau.

Conservation and adaptation measures such as expanding the park's territory, creating a buffer zone, limiting human activities, and accessing the Afroalpine region are recommended. Overall, there is a need for strict implementation of the existing biodiversity management strategies such as monitoring and periodic assessments of ecosystem status and limiting human access to the Afroalpine plateau.

## 7. Biosketches

Yohannes Kidane Ogubamichael is interested in the characterization and protection of biodiversity in tropical landscapes and mountain ecosystems, global change issues, and ecosystems' response to climate change.

Samuel Hoffmann is a postdoctoral researcher at the Biogeography Department, University of Bayreuth. His research covers biogeography and macroecology, with a special interest in species diversity, climate change, remote sensing, and protected areas.

Mirela Beloiu is fascinated by forest dynamics and spatial patterns of tree species. The protection of tree species is necessary for the conservation of their genetic diversity.

Anja Jaeschke is a postdoctoral researcher at the University of Bayreuth within the Department of Biogeography. Her research focuses on the application and methodological advancement of species distribution models to assess climate change impacts related to nature conservation and vector-borne diseases.

Carl Beierkuhnlein focuses, among other topics, on the role of biodiversity for ecosystem functioning, on the explanation of spatial patterns of biodiversity, and biogeography in the face of global change.

## Declarations

Author contributions: Y.K. and C.B. conceived the ideas; Y.K. collected the data; Y.K. led the writing and analyzed the data; SH, MB, and AJ participated in writing and evaluating the results.

## References

1. Araújo, M.B., and Guisan, A., 2006. Five (or so) challenges for species distribution modeling. *Journal of Biogeography*. 33(10), 1677-1688. doi.org/10.1111/j.1365-2699.2006.01584.x
2. Beierkuhnlein, C., 2007. *Biogeografie. Die räumliche Organisation des Lebens in einer sich verändernden Welt*. Eugen Ulmer Verlag, Stuttgart. 400 pp.
3. Bonnefille, R., 1983. Evidence for a cooler and drier climate in the Ethiopian uplands towards 2.5 Myr ago. *Nature* 303, 487–491. doi.org/10.1038/303487a0
4. Bonnefille, R., Roeland, J.C., Guiot, J. 1990. Temperature and rainfall estimates for the past 40,000 years in equatorial Africa. *Nature* 346. 347–349.

5. Buytaert, W., Cuesta-Camacho, F., and Tobon, C., 2011. Potential impacts of climate change on the environmental services of humid tropical alpine regions. *Global Ecology and Biogeography* 20, 19-33. doi.org/10.1111/j.1466-8238.2010.00585.x
6. Chala, D., Niklaus, E., Zimmermann, E.Z., Brochmann, C., and Bakkestuen, V., 2017 Migration corridors for alpine plants among the "sky islands" of eastern Africa: do they, or did they exist? *Alp Botany*. 127, 133–144. DOI 10.1007/s00035-017-0184-z
7. Chase, J.M., and Leibold, M.A., 2003. *Ecological niches: Linking classical and contemporary approaches*. The University of Chicago Press, Chicago.
8. Duveiller, G., Defourny, P., Descle'e, B., and Mayaux, P., 2008. Deforestation in Central Africa: Estimates at regional, national, and landscape levels by advanced processing of systematically distributed Landsat extracts. *Remote Sensing of Environment*. 112 (5), 1969-1981. doi:10.1016/j.rse.2007.07.026.
9. Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, A., Jacob, Mc.C., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, M.S., and Zimmermann, N.E., 2006. Novel methods improve prediction of 'species' distributions from occurrence data. *Ecography*. 29, 129-151.
10. Elith, J., Leathwick, J.R., and Hastie, T., 2009. A working guide to boosted regression trees. *Journal of Animal Ecology*. 77, 802-81.
11. Flantua, S.G.A., Payne, D., Borregaard, M.K., Beierkuhnlein, C., Steinbauer, M.J., Dullinger, S., Ess, F., Irl, S.D.H., Kienle, D., Kreft, H., Lenzner, B., Norder, S.J., Rijdsdijk, K.F., Rumpf, S.B., Weigelt, P., and Field, R., 2020. Snapshot isolation and isolation history challenge the analogy between mountains and islands used to understand endemism. *Global Ecology Biogeography*. 29:1651–1673. DOI: 10.1111/geb.13155
12. Foody, G.M., 2002. Status of land cover classification accuracy assessment. *Remote Sensing of Environment*. 80 (1), 185-201. doi:10.1016/S0034-4257(01)00295-4.
13. Gehrke, B., and Linder, H.P., 2014. Species richness, endemism, and species composition in the tropical Afroalpine flora. *Alpine Botany*. 124,165 – 177.
14. Gentili, R., Baroni, C., Caccianiga, M., Armiraglio, S., Ghiani, A., and Citterio, S., 2015. Review: Potential warm stage microrefugia for alpine plants: Feedback between geomorphological and biological processes. *Ecological Complexity*. 21, 87–99. DOI.org/10.1016/j.ecocom.2014.11.006.
15. Gil-Romera, G., Adolf, C., Benito, B.M., Bittner, L., Johansson, M.U., Grady, D.A., Lamb, H.F., Lemma, B., Fekadu, M., Glaser, B., Mekonnen, B., Callejo, M.S., Zech, M., Zech, W., and Mieke, G., 2019. Long-term fire resilience of the Ericaceous Belt, Bale Mountains, Ethiopia. *Biol. Lett.* 15, 20190357. http://dx.doi.org/10.1098/rsbl.2019.0357
16. Gizaw, A., Kebede, M., Nemomissa, S., Ehrich, D., Bekele, B., et al., 2013. Phylogeography of the heathers *Erica arborea* and *E. trimera* in the afro-alpine 'sky islands' inferred from AFLPs and plastid DNA sequences, *Flora*. 208, 453-463.

17. Gottelli, D., Marino, J., Sillero-Zubiri, C., Funk, S.M., 2004. The effect of the last glacial age on speciation and population genetic structure of the endangered Ethiopian wolf (*Canis simensis*). *Mol. Ecol.* 13, 2275–2286.
18. Hedberg, O., 1951. Vegetation belts of the East African mountains. *Sven. Bot. Tidskr.* 45, 140 - 202.
19. Hedberg, O. 1964. Features of Afroalpine Plant Ecology. *Acta Phytogeographica Suecica.* 49, 1-144. Uppsala, Sweden.
20. Hedberg, O., 1986. Origins of the Afroalpine Flora. In *High Mountains Tropical Biogeography*. Eds. Vuilleumier F and Monasterio M. Published by Oxford University Press and the American Museum of Natural History. Oxford University Press. New York.
21. Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A., 2005. Very high-resolution interpolated climate surfaces for global land areas. *International Journal of Climatology.* 25, 1965-1978.
22. Hijmans, R.J., van Etten, J., 2011. raster: Geographic Analysis and Modeling with Raster Data. R package version 1.8-39, URL <http://CRAN.R-project.org/package=raster> (accessed July 2018).
23. Hijmans, R.J., and Elith, J., 2017. Species distribution modeling with R. <https://cran.r-project.org/web/packages/dismo/vignettes/sdm.pdf> (accessed July 2018).
24. Hillman, J.C., 1986. Conservation in Ethiopia's Bale Mountains. *Endangered Species* 3: 1-4.
25. IPCC, 2014. In Pachauri, R.K., Meyer, L.A. (Eds.), *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II, and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change Core Writing Team*. IPCC, Geneva, Switzerland, p. 151.
26. Johansson, M.U., and Granström, A., 2014. Fuel, fire, and cattle in African highlands: traditional management maintains a mosaic heathland landscape. *Journal of Applied Ecology.* 51, 1396-1405. DOI: 10.1111/1365-2664.12291
27. Johansson, M.U., Frisk, C.A., Nemomissa, S., and Hylander, K., 2018. Disturbance from traditional fire management in subalpine heathlands increases Afro-alpine plant resilience to climate change. *Global Change Biology.* 24 (7), 2952-2964. DOI: 10.1111/gcb.14121.
28. Kidane, Y.O., Stahlman, R., and Beierkuhnlein, C., 2012. Vegetation dynamics, and land use and land cover change in the Bale Mountains, Ethiopia. *Environmental Monitoring Assessment.* 184 (12), 7473 - 7489. doi.org/10.1007/s10661-011-2514-8.
29. Kidane, Y.O., Steinbauer, M.J., and Beierkuhnlein, C., 2019. Dead end for endemic plant species? A biodiversity hotspot under pressure. *Global Ecology and Conservation.* 19, 1-12. doi.org/10.1016/j.gecco. 2019.e00670
30. Körner, C., 2007. The use of 'altitude' for ecological research. *Trends in Ecology and Evolution.* 22 (11), 569-574. doi.org/10.1016/j.tree.2007.09.006.
31. Kreyling, J., Wana, D., Beierkuhnlein, C., 2010. Climate warming and tropical plant species – consequence of the potential upslope shift of isotherms in southern Ethiopia. *Diversity and Distribution.* 16, 593-605. doi.org/10.1111/j.1472-4642.2010.00675.x.

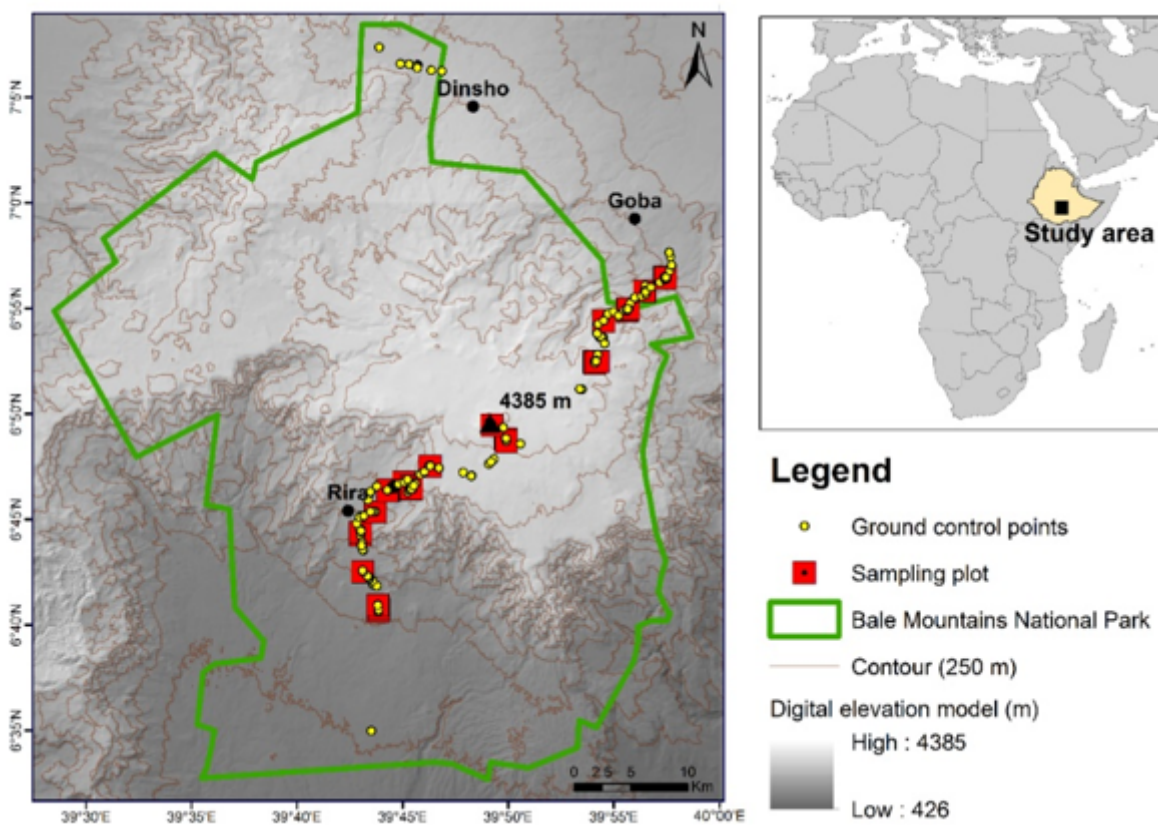


32. Malhi, Y., and Wright, J., 2004. Spatial patterns and recent trends in the climate of tropical rainforest regions. *Trans. R. Soc. Lond. B.* 359, 311-329. doi: 10.1098/rstb.2003.1433 Phil.
33. Malcolm, J.R., Liu, C., Neilson, R.O., Hansen, A., and Hannah, L., 2006. Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biol.* 20 (2), 538-548. <https://doi.org/10.1111/j.1523-1739.2006.00364.x>
34. McGuire, A.F., Kathleen, A., Kron, K.A., 2005. Phylogenetic Relationships of European and African Ericas, *International Journal of Plant Sciences*, 162 (2): 311-318. <https://doi.org/10.1086/427478>
35. Miehe, S., and Miehe, G., 1994. Ericaceous forests and heathlands in the Bale Mountains of South Ethiopia. *Ecology and man's impact. Stiftung Walderhaltung in Africa, Hamburg.*
36. Nagy, L., and Grabherr, G., 2009. *The Biology of Alpine Habitats.* Oxford University Press, Oxford.
37. Naimi, B., and Araújo, M.B., 2016. SDM: a reproducible and extensible R platform for species distribution modeling. *Ecography.* 39, 368–375. DOI: 10.1111/ecog.01881.
38. Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K., and Toxopeus, A.G., 2014. Where is positional uncertainty a problem for species distribution modeling? *Ecography.* 37 (2), 191-203.
39. Ossendorf, G., Groos, A.R., Bromm, T., Tekelemariam, M.G., Glaser, B., Lesur, J., Schmidt, J., Akçar, N., Bekele, T., Beldados, A., Demissew, S., Kahsay, T.H., Nash, B.P., Nauss, T., Negash, A., Nemomissa, S., Veit, H., Vogelsang, R., Woldu, Z., Zech, W., Opgenoorth, L., and Miehe, G., 2019. Middle Stone Age foragers resided in high elevations of the glaciated Bale Mountains, Ethiopia. *Science.* 365 (6453), 583–587. DOI: 10.1126/science.aaw8942.
40. Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martinez-Meyer, E., Nakamura, M., and Araújo, M.B., 2011. *Ecological Niches and Geographic Distributions.* Monographs in Population Biology -49. Princeton University Press, Princeton, and Oxford, PP. 314. ISBN 978-0-691-13688-2.
41. QGIS Development Team, 2018. QGIS Geographic Information System. Open-Source Geospatial Foundation Project. <http://qgis.osgeo.org>.
42. Razgour, O., Kasso, M., Santos, H., and Juste, J., 2020. Up in the air: Threats to Afromontane biodiversity from climate change and habitat loss revealed by genetic monitoring of the Ethiopian Highlands bat. *Evol Appl.* 00,1–13. <https://doi.org/10.1111/eva.13161>.
43. R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing [Internet]. <http://www.R-project.org/>.
44. Sarmiento, G., 1986. Ecological Feature of Climate in High Tropical Mountains. In *High Mountains Tropical Biogeography.* Eds. Vuilleumier F and Monasterio M. Published by Oxford University Press and the American Museum of Natural History. Oxford University Press. New York.
45. Smith, A.P., and Young, T.P., 1987. Tropical alpine plant ecology. *Annual Review of Ecology and Systematics.* 18, 137- 158.
46. Steinbauer, M., Field, R., Grytnes, J.A., Trigas, P., Ah-Peng, C., Attorre, F., Birks, H.J.B., Borges, P.A.V., Cardoso, P., Chou, C-H., De Sanctis, M., Sequera, M.M., Duarte, M.C., Elias, R.B., Fernandez-Palacios, J.M., Gabriel, R., Gereau, R.E., Gillespie, R.G., Greimler, J., Harter, D., Huang, T-J., Irl, S., Jeanmonod, D., Jentsch, A., Jump, A.S., Kueffer, C., Nogué, S., Otto, R., Price, J., Romeiras, M.M., Strasberg, D.,

- Stuessy, T., Svenning, J.C., Vetaas, O.R., Beierkuhnlein, C., 2016. Topography-driven isolation, speciation and a global increase of endemism with elevation, *Global Ecology and Biogeography*. 25(9), 1097–1107. doi: 10.1111/geb.12469.
47. Steinbauer, M.J., Grytnes, J.A., Jurasinski, J., Kulonen, A., et al., 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*. <https://doi.org/10.1038/s41586-018-0005-6>.
48. Testolin, R., Attorre, F., Borchardt, P., Brand, R.F., Bruelheide, H., Chytrý, M., De Sanctis, M., Dolezal, J., Finckh, M., Haider, S., Hemp, A., Jandt, U., Kessler, M., Korolyuk, A.Y., Lenoir, J., Makunina, N., Malanson, N.P., Montesinos-Tubée, D.B., Noroozi, J., Nowak, A., Peet, R.K., Peyre, G., Sabatini, F.M., Šibík, J., Sklenář, P., Sylvester, S.P., Vassilev, K., Virtanen, R., Willner, W., Wiser, S.K., Zibzeev, E.V., and Jiménez-Alfaro, B., 2021. Global patterns and drivers of alpine plant species richness. *Global Ecol Biogeogr.* 00, 1–14. DOI: 10.1111/geb.13297.
49. Uhlig, S., and Uhlig, K., 1991. Mountain Chronicles. Studies on the Altitudinal Zonation of Forests and Alpine Plants in the Central Bale Mountains, Ethiopia. *Mountain Research and Development*. 11, 153-256.
50. Umer, M., Lamb, H.F., Bonnefille, R., Lezine, A.M., Tiercelin, J.J., Gibert, E., Cazet, J.P., Watrin, J., 2007. Late Pleistocene Holocene vegetation history of the Bale Mountains, Ethiopia. *Quatern Sci Rev* .26, 2229–2246.
51. United States Geological Survey (USGS). 2018. Landsat Archive. Landsat standard data products. <http://landsat.usgs.gov>. Accessed July 17, 2018.
52. Urban, M.C., 2015. Accelerating extinction risk from climate change. *Science* 348, 571–573. DOI: 10.1126/science.aaa4984
53. Vuilleumier, F., and Monasterio, M., 1986. Introduction: High tropical Mountain Biota of the World. In Vuilleumier, F., and Monasterio, M. (Eds) *High Mountains Tropical Biogeography*. Oxford University Press. New York.
54. Wana, D; Beierkuhnlein, C. 2010. Plant species and growth form richness along altitudinal gradients in the south-west Ethiopian Highlands, *Journal of Vegetation Science*. **21**, 617-626. doi:10.1111/j.1654-1103.2010.01177.x
55. Warren, R., VanDerWal, J., Price, J., Welbergen, J.A., Atkinson, I., Ramirez-Villegas, J., Osborn, T.J., Jarvis, A., Shoo, L.P., Williams, S.E., and Lowe, J., 2013. Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. *Nature Climate Change*. 3, 678-682. DOI: 10.1038/NCLIMATE1887
56. Wegmann, M., Leutner, B., and Dech, S., 2016. *Remote Sensing and GIS for Ecologists: Using Open Software*. Exeter: Pelagic Publishing, UK.
57. Wesche, K., Cierjacks, A., Assefa, Y., Wagner, S., Fetene, M., and Hensen, I., 2008. Recruitment of trees at tropical alpine treelines: *Erica* in Africa versus *Polylepis* in South America. *Plant Ecology & Diversity*. 1, 35–46. doi.org/10.1080/17550870802262166.

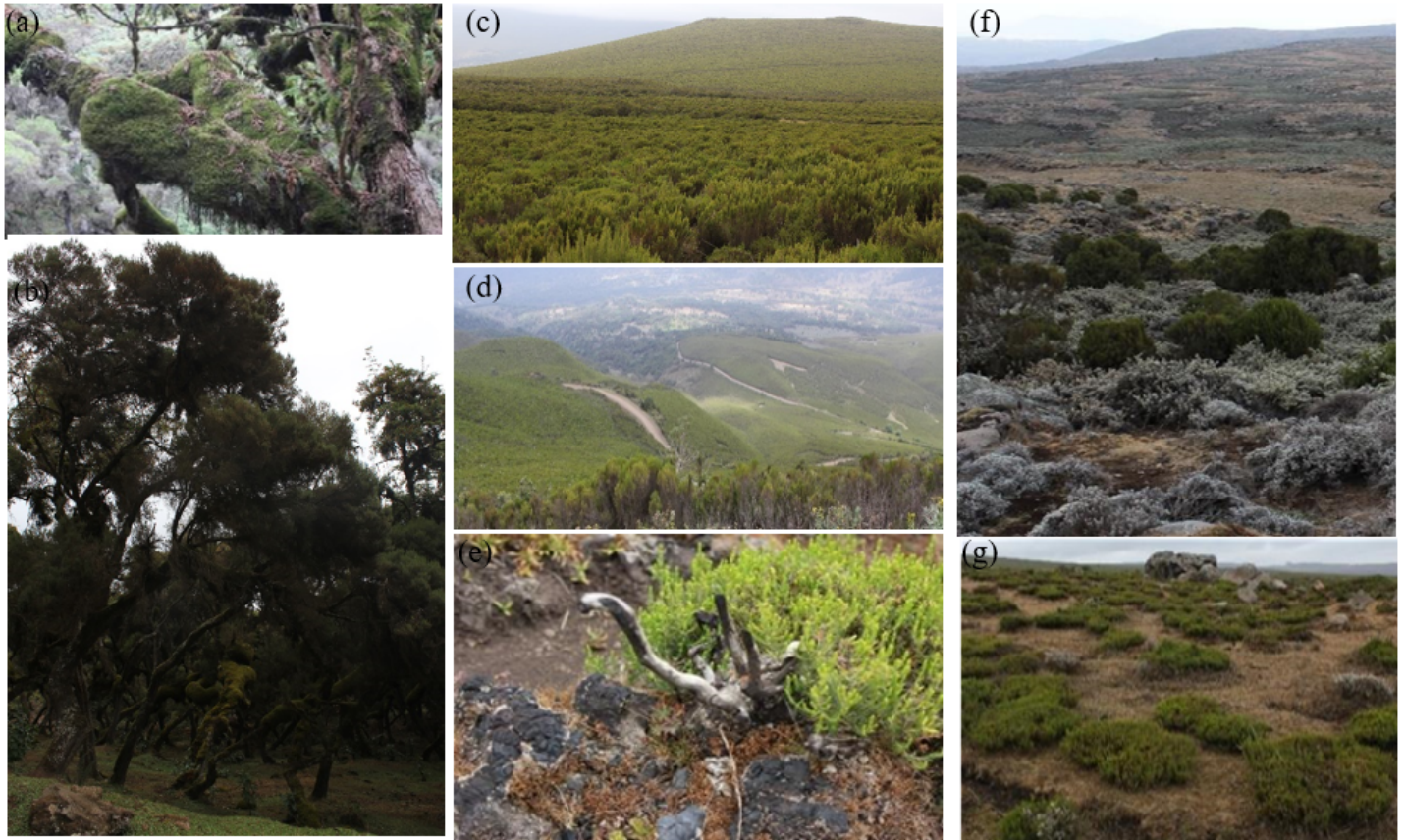
58. Wesche, K., Miehe, G., and Kaeppli, M., 2000. The significance of fire for Afroalpine ericaceous vegetation. *Mountain Research and Development*. 20, 340-347. [OI:10.1659/0276-4741\(2000\)020\[0340:TsoFFA\]2.0.CO;2](https://doi.org/10.1659/0276-4741(2000)020[0340:TsoFFA]2.0.CO;2)
59. Wesche, K., 2003. The importance of occasional droughts for Afroalpine landscape ecology. *Journal of Tropical Ecology*. 19, 197-208. [doi.org/10.1017/S0266467403003225](https://doi.org/10.1017/S0266467403003225)
60. Winkler, M., Lamprecht, A., Steinbauer, K., Hülber, K., Theurillat, J.P., et al., 2016. The rich sides of mountain summit a pan-European view on aspect preferences of alpine plants. *Journal of Biogeography*. 43 (11), 2261-2273. [doi.org/10.1111/jbi.12835](https://doi.org/10.1111/jbi.12835).

## Figures



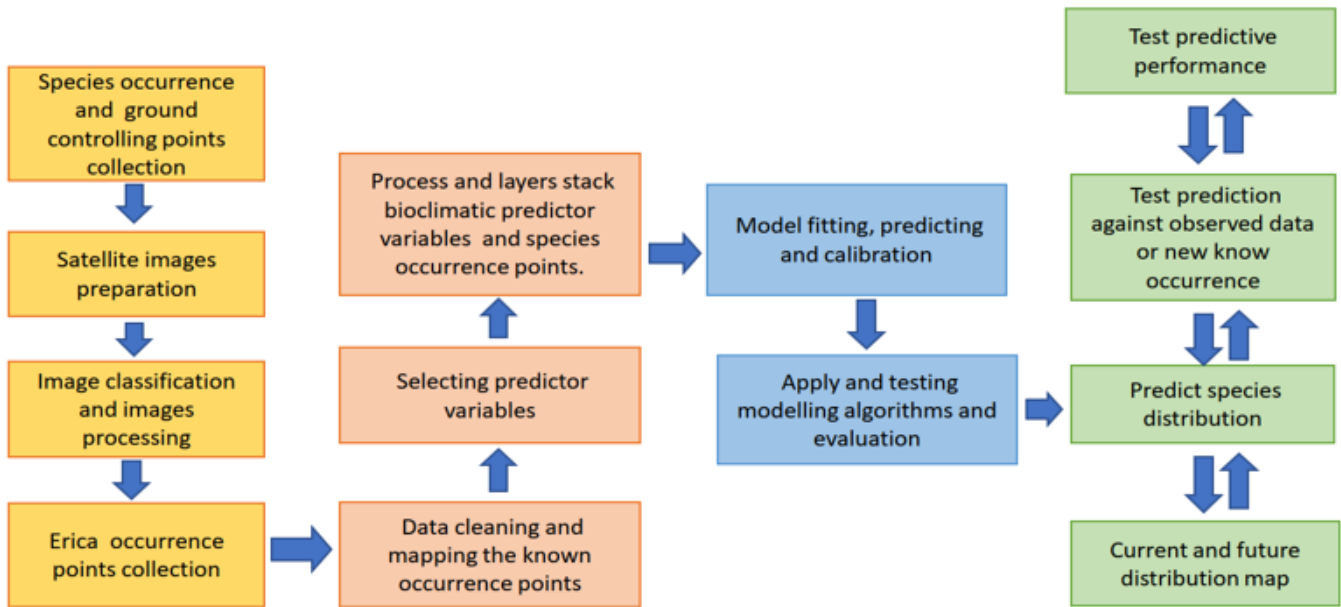
**Figure 1**

Map of the study area, including the transect sampling plots' location, ground controlling points, and the Bale Mountain National Park (BMNP) boundaries. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



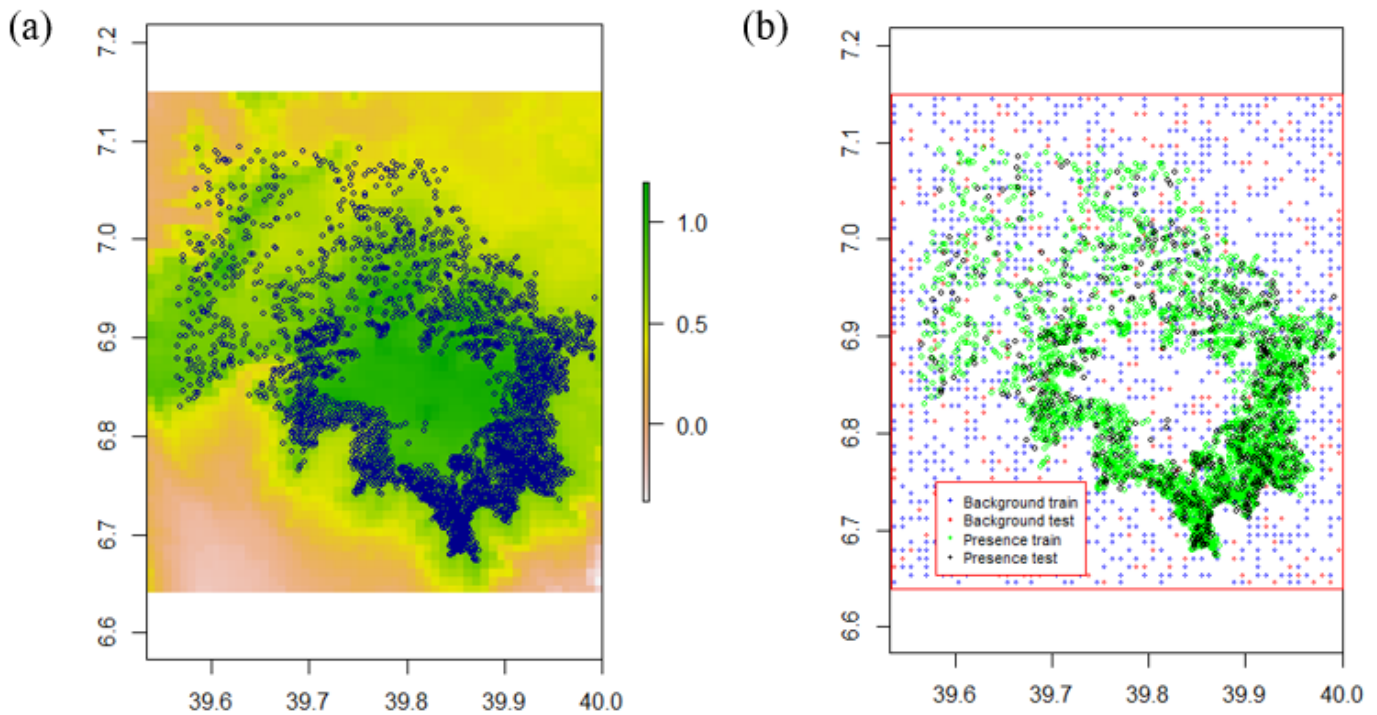
**Figure 2**

Erica succession and distribution patterns along the Bale Mountains. a) and b) Old Erica tree stand up to 12 m high with thick *Breutelia* spp. Moss on the stem. c) and d) Ericaceous Belt: young Erica brush 1 to 5 years old (1m to 3m high). e) Erica lignotubers regeneration after a fire, and f) and g) Isolated Erica grooves at the Erica/Afroalpine grassland ecotone: dominated by isolated Erica stands and different grasses and shrubs.



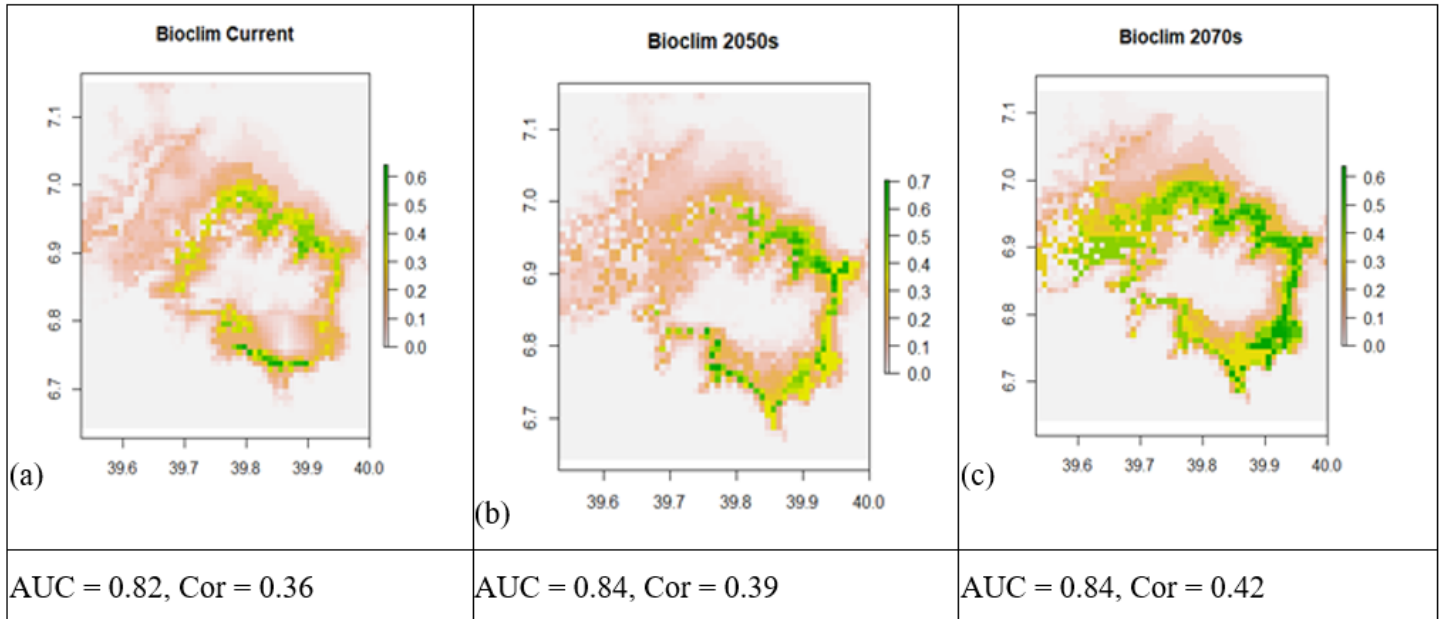
**Figure 3**

Flow diagram detailing the main data preparation steps and modeling processes when building and validating the Erica SDMs.



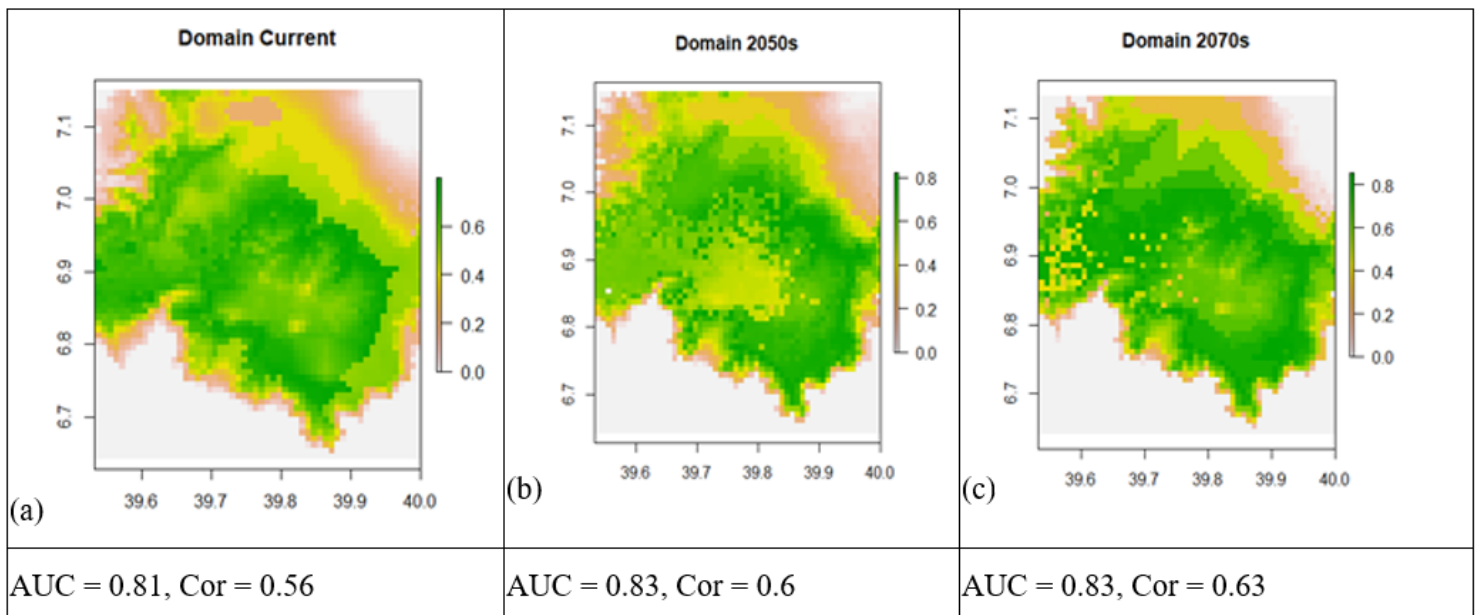
**Figure 4**

(a) Background: Layer stacked environmental predictors variables and sampled Erica (Blue circles) occurrence points, (b) Model fitting map with background train (blue), background test (red), presence train (green), and presence test (black).



**Figure 5**

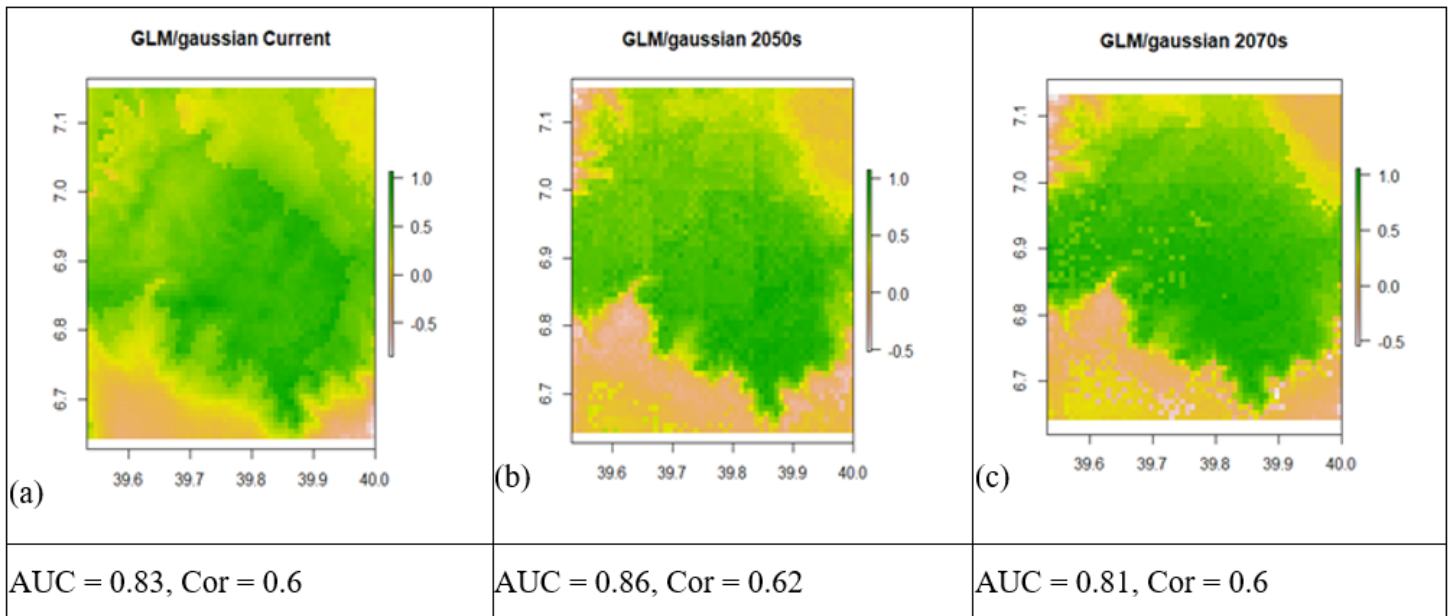
Bioclim model prediction for current (a), future 2050s (b), and future 2070s (c). A gray area represents absolute absence, brown to green indicates presence, while green to yellow indicating stronger hold.



**Figure 6**

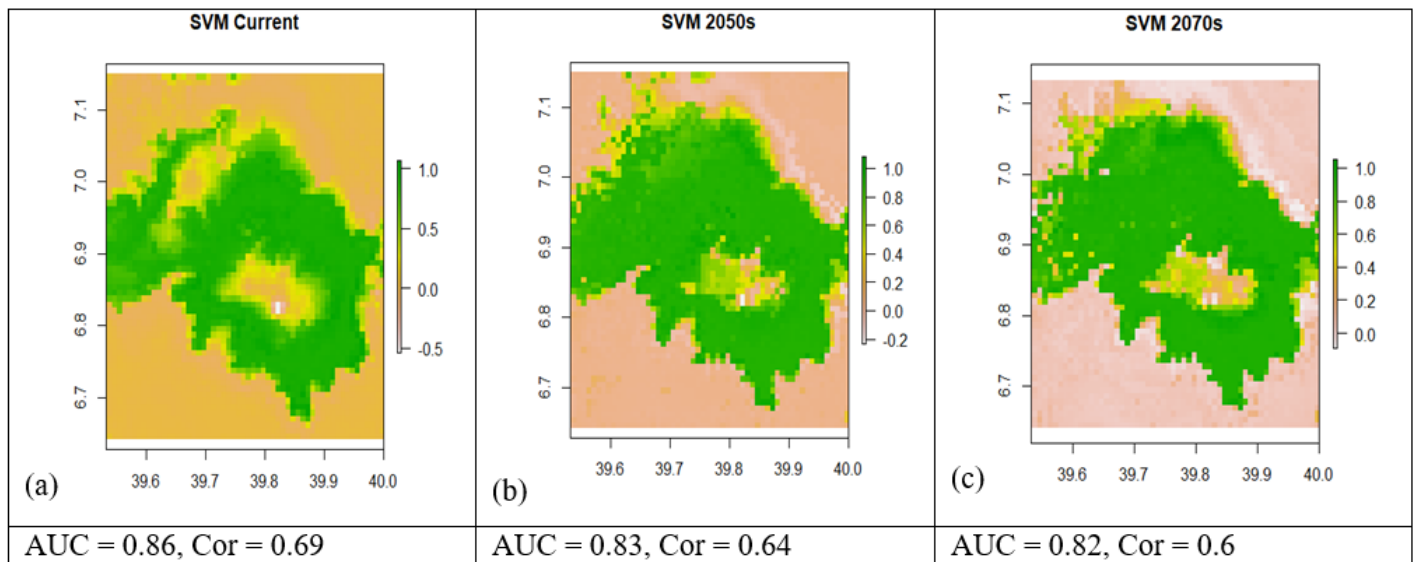
Domain model prediction for current (a), future 2050s (b), and future 2070s (c). Here gray indicates absence (unsuitable habitat) while brown to green indicates suitable habitat (potential presence) and

green and yellow indicating a stronger presence.



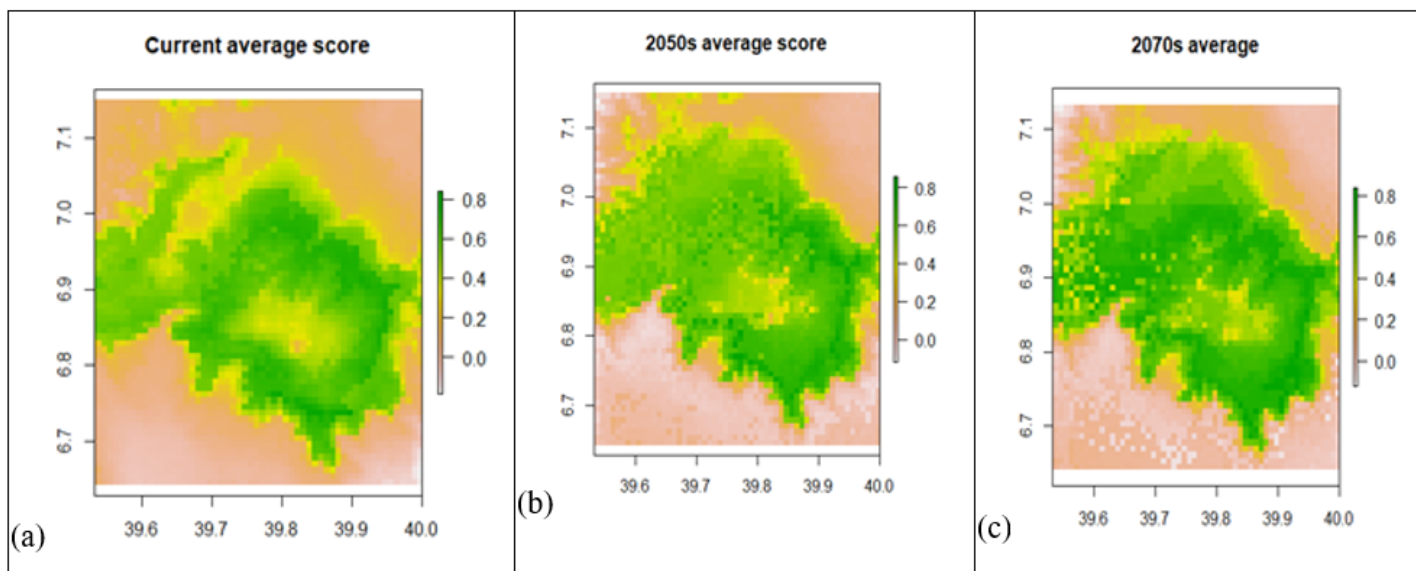
**Figure 7**

GLM model prediction for current (a), future 2050s (b), and future 2070s (c). Here brown indicates absence (unsuitable habitat) while yellow to green indicates presence, and green indicating a stronger presence.



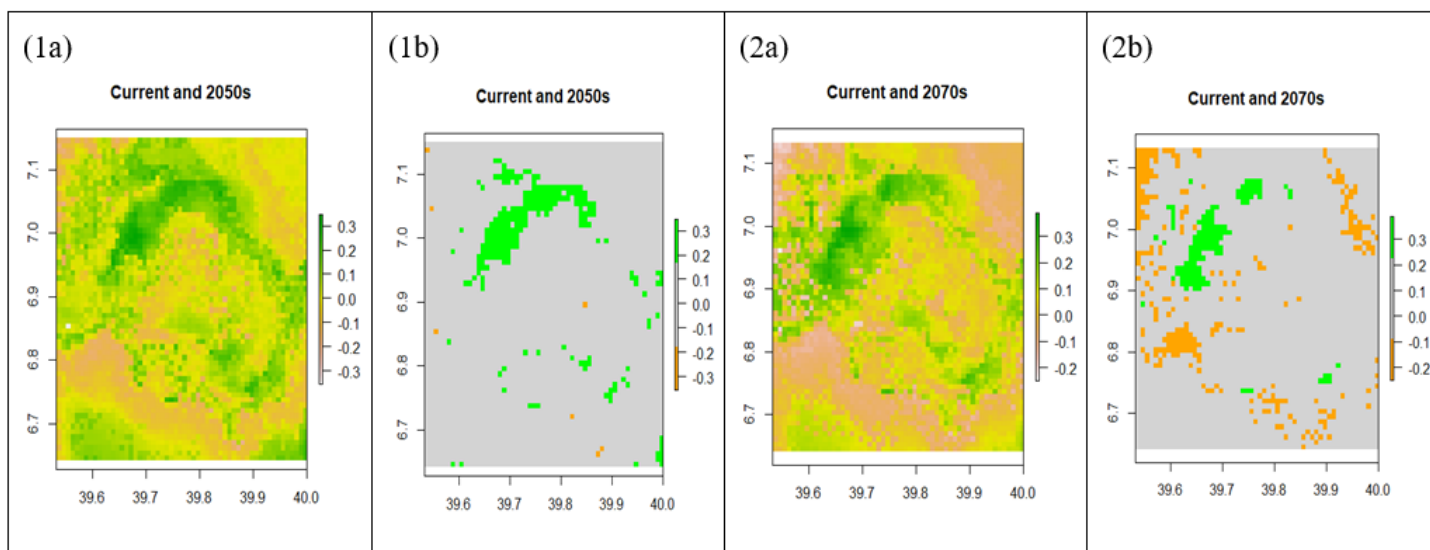
**Figure 8**

SVM model prediction for current (a), future 2050s (b) and future 2070s (c). Here brown area indicates absence (unsuitable habitat) while yellow to green indicates presence.



**Figure 9**

Four Models average of the three-time steps (Current, 2050s, and 2070s). All future predictions indicate strong midaltitude hold, southwest and westward expansion into the current dispersed Erica habitat and towards the Afroalpine habitat, and retreat on all lower ranges.



**Figure 10**

The difference between average models of the different time steps. 1a and 1b) the difference between current and the 2050s, and 2ab and 2b) the difference between current and 2070s.

## Supplementary Files

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