Subalpine Birches (*Betula* spp.) of the South Caucasus:

Spatial Structure in the Context of Global Climate Change

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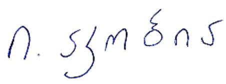
Statement

As the author of the submitted dissertation, I declare that the work represents my original research and does not contain materials previously published, accepted for publication, or submitted for defense by other authors that are not properly referenced or cited in accordance with the relevant rules.

Ilia Akobia



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Abstract

Treeline birches (*Betula* spp.) represent a structurally and functionally important component of subalpine forests in the Caucasus, providing critical ecosystem services while facing increasing vulnerability under ongoing climate change. This dissertation applies ecological niche modeling using the Maximum Entropy (MaxEnt) approach to reconstruct and project habitat dynamics of subalpine birch forests across multiple temporal horizons, including the Last Glacial Maximum (LGM), the Mid-Holocene (MH), present climatic conditions and future projections for 2100 under three Shared Socioeconomic Pathways (SSP126, SSP370, SSP585), based on MIROC and CMCC-ESM2 climate models. Model performance was high (Area Under the Curve (AUC) > 0.97), indicating strong predictive capacity. Seasonal thermal variables such as the mean temperature of the warmest quarter (BIO10) and coldest quarter (BIO11) emerged as the dominant climatic controls, supplemented by precipitation of the warmest and coldest quarters (BIO18 and BIO19). Paleoclimatic reconstructions indicate confinement of birch habitats to refugial zones in Colchis and Hyrcania during the LGM, followed by expansion under wetter Mid-Holocene conditions. Present climatic suitability reflects a regional ecological optimum, characterized by relatively continuous treeline belts along the Greater Caucasus and fragmented distributions in the Lesser Caucasus. Future projections reveal pronounced emission-dependent vulnerability: relative stability is maintained under SSP126, whereas SSP370 and SSP585 project severe habitat shrinkage exceeding 80 – 95%, with persistence restricted to isolated high-elevation refugia. These results support a long-term refugia – recolonization– optimum – shrinkage trajectory and identify the Caucasus as both a historical refugial system and a climate-sensitive hotspot. The findings underline that warming may lead not to uniform upslope advance but to contraction and fragmentation of treeline ecosystems. Effective conservation and management strategies should therefore prioritize climatically stable refugial strongholds, maintain ecological connectivity and integrate climate-adaptive planning into high-mountain forest governance.

Key Words: Treeline belt, Birches, *Betula* spp., Ecological niche modelling, MaxEnt, Mountain ecosystems, Climate change, Climate refugia, Caucasus ecoregion

აბსტრაქტი

ტყის ზედა საზღვრის არყნარები (*Betula* spp.) კავკასიის სუბალპური ტყეების სტრუქტურულად და ფუნქციურად მნიშვნელოვან კომპონენტს წარმოადგენენ. ისინი უზრუნველყოფენ კრიტიკულად პრიორიტეტულ ეკოსისტემურ სერვისებს და, ამავდროულად, კლიმატის მიმდინარე გლობალური ცვლილების პირობებში მზარდი მოწყვლადობით ხასიათდებიან. წინამდებარე სადისერტაციო ნაშრომში გამოყენებულია ეკოლოგიური ნიშის მოდელირება (MaxEnt) ალგორითმის საფუძველზე სხვადასხვა დროით ჰორიზონტში სუბალპური არყნარების ჰაბიტატის დინამიკის რეკონსტრუქციისა და პროექცირების მიზნით. კვლევა მოიცავს უკანასკნელი გამყინვარების მაქსიმუმს (LGM), შუა ჰოლოცენს (MH), თანამედროვე კლიმატურ პირობებსა და 2100 წლის საპროგნოზო სცენარებს სამი სოციო-ეკონომიკური პროგნოზის (SSP126, SSP370, SSP585) მიხედვით, MIROC და CMCC-ESM2 კლიმატური მოდელების გამოყენებით. მოდელის ეფექტიანობის მაჩვენებელი მაღალია (AUC > 0.97), რაც მის ძლიერ პროგნოზირებად უნარზე მიუთითებს. წამყვან კლიმატურ ფაქტორებად გამოიკვეთა სეზონური თერმული ცვლადები: ყველაზე თბილი (BIO10) და ყველაზე ცივი (BIO11) კვარტლების საშუალო ტემპერატურები, რასაც ავსებს ყველაზე თბილი და ცივი კვარტლების ნალექების მონაცემები (BIO18 და BIO19). პალეოკლიმატური რეკონსტრუქციები ცხადყოფს, რომ LGM-ის პერიოდში არყის ჰაბიტატები შემოფარგლული იყო კოლხეთისა და ჰირკანის რეფუგიალური ზონებით, რასაც მოჰყვა მათი ექსპანსია შუა ჰოლოცენის შედარებით თბილ და ნოტიო პირობებში. თანამედროვე კლიმატური შესაფერისობა ასახავს რეგიონულ ეკოლოგიურ ოპტიმუმს, რაც ხასიათდება ტყის ზედა საზღვრის უწყვეტი სარტყლებით დიდი კავკასიონის გასწვრივ და ფრაგმენტული გავრცელებით მცირე კავკასიონზე. სამომავლო

პროექციები ავლენს მკვეთრ, ემისიებზე დამოკიდებულ მოწყვლადობას: შედარებითი სტაბილურობა ნარჩუნდება მხოლოდ SSP126 სცენარით, მაშინ როდესაც SSP370 და SSP585 სცენარების პირობებში მოსალოდნელია ჰაბიტატის მკვეთრი შემცირება (80–95%-ით), სადაც სახეობის გადარჩენა მხოლოდ იზოლირებული მაღალმთიანი რეფუგიუმებით შემოიფარგლება. მიღებული შედეგები ამყარებს „რეფუგიუმი – რეკოლონიზაცია – ოპტიმუმი – შეკუმშვის" ტრაექტორიას, რაც მიგვანიშნებს კავკასიის რეფუგიალურ მემკვიდრეობაზე და წარმოაჩენს, რომ რეგიონი, როგორც ბიომრავალფეროვნების ცხელი წერტილი, კლიმატის ცვლილებების მიმართ მოწყვლადია. კვლევის მიგნებები ცხადყოფს, რომ დათბობამ შესაძლოა გამოიწვიოს არა ტყის საზღვრის ერთგვაროვანი აღმავალი გადანაცვლება, არამედ ტყის ზედა საზღვრის ეკოსისტემების შეკუმშვა და ფრაგმენტაცია. შესაბამისად, კონსერვაციისა და მართვის ეფექტურმა სტრატეგიებმა პრიორიტეტი უნდა მიანიჭოს კლიმატურად სტაბილურ რეფუგიალურ ზონებს, ეკოლოგიური კავშირების შენარჩუნებას და კლიმატთან ადაპტირებული დაგეგმარების ინტეგრირებას სუბალპური ტყეების მართვის პოლიტიკაში.

ძირითადი საძიებო სიტყვები: ტყის ზედა საზღვრის სარტყელი, არყნარები, *Betula* spp., ეკოლოგიური ნიშის მოდელირება, MaxEnt, მთის ეკოსისტემები, კლიმატის ცვლილება, კლიმატური რეფუგიუმი, კავკასიის ეკორეგიონი.

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Kazbegi region. His expertise in mountain ecology and treeline dynamics significantly contributed to the refinement of this research.

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Table of Contents

List of Tables

List of Figures

Abbreviations

AUC	Area Under the Curve
BIO1 – BIO19	Bioclimatic Variables from WorldClim
BIOCLIM	Bioclimatic Variables (climate-related predictors used in modeling)
CCSM	Community Climate System Model
CMCC-ESM2	Climate System Model developed by the Euro-Mediterranean Center
CMIP6	Coupled Model Intercomparison Project Phase 6
GBIF	Global Biodiversity Information Facility
LGM	Last Glacial Maximum
MaxEnt	Maximum Entropy Model
MH	Middle Holocene
MIROC	Model for Interdisciplinary Research on Climate
NFI	National Forest Inventory (Georgia)
QGIS	Quantum Geographic Information System
REML	Restricted Maximum Likelihood
ROC	Operating Characteristic Curve
SD	Standard Deviation (used in descriptive statistics)
SDM	Species Distribution Model
SSP126	Shared Socioeconomic Pathway 126 (low emission scenario)
SSP370	Shared Socioeconomic Pathway 370 (intermediate emission scenario)
SSP585	Shared Socioeconomic Pathway 585 (high emission scenario)
TSS	Training Sensitivity plus Specificity
WWF	World Wildlife Fund

Introduction

In the Caucasus, the treeline belt is predominantly formed by subalpine birch forests (*Betula* spp.), which represent a distinctive ecological formation within the transitional zone between subalpine (treeline) forests and alpine grassland ecosystems (Dolukhanov 2010; Nakhutsrishvili 2000; 2013). These forests represent a structurally and functionally important component of high-mountain ecosystems, where climatic constraints strongly limit tree growth, regeneration and long-term persistence (Körner 2012). Subalpine birch forests play a crucial role in slope stabilization, regulation of hydrological processes, protection of freshwater resources and maintenance of biodiversity in upper hypsometric zones (Bebi, Kienast, and Schönenberger 2001; Fagre 2009; Price et al. 2011; Mina et al. 2017). By creating habitat mosaics for alpine and subalpine species, they contribute significantly to maintaining the ecological integrity of mountain landscapes (Körner 2008; Smith et al. 2009).

High-mountain subalpine birch forests, as treeline ecosystems, are particularly sensitive and vulnerable to both anthropogenic pressures and climate change due to their borderline position at the climatic limit of tree growth (Körner 2008; Larcher 2003; Nakhutsrishvili 2013; Smith et al. 2009). During the 20th century, extensive logging and intensive grazing severely disrupted the structure and spatial continuity of subalpine birch forests across much of the Caucasus (Wiesmair et al. 2016; Rizayeva et al. 2025). As a result, their natural distribution area declined and in many regions, the upper forest limit was artificially lowered (Dolukhanov 1978). The legacy of historical land use remains visible today in fragmented forest belts, structurally impoverished stands and extensive secondary grasslands that were formerly forested.

At the same time, an opposite trend has emerged in recent decades, namely, birch forests are expanding upward and colonizing higher elevations (Gottfried et al. 2012; Pauli et al. 2012; Togonidze and Akhalkatsi 2015; Hansen et al. 2018). This process is often interpreted as a climate-driven advance of the treeline (Arekhi et al. 2018), consistent with the hypothesis that global warming shifts subalpine and alpine species upward along altitudinal gradients (Gottfried et al. 2012; Pauli et al. 2012). Studies conducted in the Kazbegi region of the Central Caucasus also indicate ongoing natural reforestation in subalpine zones (Togonidze and Akhalkatsi 2015).

Post-Soviet socio-economic transformations led to a decline in livestock numbers and abandonment of many high-mountain pastures, substantially reducing grazing pressure and initiating forest regeneration processes (Akhalkatsi et al. 2006; Hughes et al. 2009). Consequently, the upward expansion of birch forests reflects the combined effects of climate change and land-use transformation. Disentangling these drivers based solely on short-term observations is difficult, as the present pattern represents only a small segment of a long-term ecological trajectory characterized by repeated cycles of shrinkage and expansion driven by both natural climatic oscillations and human activity. Therefore, contemporary changes must be interpreted within a broader historical and ecological framework to properly assess the future dynamics and conservation needs of subalpine ecosystems.

During the Pleistocene and Holocene, climatic fluctuations repeatedly reshaped the distribution of mountain forests in the Caucasus (Shatilova et al. 2011). Due to its complex topography, steep altitudinal gradients and proximity to the Black and Caspian Seas, the Caucasus is widely recognized as one of the principal glacial refugia for temperate vegetation (Tarkhnishvili, Gavashelishvili, and Mumladze 2012; Connor and Kvavadze 2009). These conditions enabled forest taxa to persist locally during cold phases, while large parts of northern Eurasia remained unsuitable for forest development. As a result, the region today harbors both relict lineages and postglacial migrants, making it a natural laboratory for studying long-term vegetation responses to climatic oscillations. Subalpine birch forests represent an important component of this refugial system and likely experienced repeated cycles of contraction into climatically favorable microsites during cold phases and expansion during interglacials (Connor et al. 2004; Connor and Kvavadze 2009). Thus, their present distribution reflects not only current climatic conditions but also historical range dynamics shaped by glacial–interglacial cycles.

From a theoretical perspective, the treeline represents an ecotonal system formed through the interaction of physiological limits, demographic processes and landscape-scale constraints. Classical theory emphasizes temperature as the principal control of tissue formation and rapid tree growth (Körner 2008; 2012). However, contemporary research highlights that treeline position and dynamics cannot be explained by temperature alone but rather result from the combined effects of climatic control, recruitment limitations, disturbance regimes, and biotic interactions (Myers-Smith et al. 2020; Shrestha, Gautam, and Bawa 2012; Andrus et al. 2021; Sigdel et al. 2024). Seedling establishment often depends on protective microhabitats that buffer against frost, wind and desiccation, while adult tree persistence depends on long-term carbon balance and resistance to hydraulic stress.

Treeline ecotones are also characterized by temporal lags in response to climate change. Temperature thresholds are frequently incorporated into statistical models simulating treeline responses to climate warming (Xie et al. 2024). However, observed upward shifts in treeline elevation often lag behind the rate of climate warming by at least 50 years (Körner 2012; Rees et al. 2020; Hansson et al. 2023; Kullman 2022). Consequently, current treeline positionality may reflect historical climatic conditions more strongly than present climatic optima. This decoupling between climatic forcing and vegetation response suggests that treeline shifts should not be interpreted solely as direct indicators of ongoing climate change but rather evaluated within a long-term ecological context. Ecological niche modeling provides an effective analytical framework for addressing this complexity, as it allows the climatic component to be separated from non-climatic constraints and examined across multiple temporal horizons.

Forest recovery following disturbance depends on several interacting factors. When anthropogenic pressure declines, agricultural lands are abandoned, grazing intensity decreases and climatic conditions shift, forests gain opportunities for natural regeneration (Satake et al. 2007). Evidence from Scandinavian countries shows that, under reduced grazing and logging pressure combined with contemporary climate change, birch forests expand gradually (Sonesson and Hoogesteger 1983; Kullman 2000, 2002). Improved climatic conditions have also been associated with faster birch growth and more developed crown structures. Overall, birch forest structure and development are shaped by the combined influences of climate, human activity, grazing pressure and insect dynamics (Holtmeier 2002; Oksanen et al. 1995).

Similar regenerative processes have been observed in Georgia. In recent decades, birch regeneration on former pastures and hayfields has gradually led to the reforestation of mountain slopes. In some areas, regeneration have already reached heights of 3-4 meters (Nakhutsrishvili et al. 2004a,b; Nakhutsrishvili et al. 2006; Akhalkatsi et al. 2006; Hughes et al. 2009). This expansion is interpreted as natural regeneration driven by reduced grazing intensity (Körner et al. 2006) and global climate change (Nakhutsrishvili et al. 2004a,b; Akhalkatsi et al. 2006), or by the combined effects of both.

Despite the ecological and biogeographical significance of subalpine birch forests, there is currently no integrated regional assessment that combines paleoclimatic reconstructions, present-day distributions and future climate projections within a unified analytical framework. Most existing studies are spatially localized and focus either on contemporary vegetation structure or short-term dynamics (Abdaladze et al. 2005; Akhalkatsi et al. 2018; Akhalkatsi et al. 2004, 2006; Hansen et al. 2018; Hughes et al. 2009; Nakhutsrishvili et al. 2004a,b). This knowledge gap limits the ability to assess long-term niche dynamics, identify climatically stable refugial areas and predict large-scale shifts of birch forest belts.

The **aim of this dissertation** is to reconstruct and project the spatial distribution and ecological niche dynamics of subalpine birch forests (*Betula* spp.) in the Caucasus from the Last Glacial Maximum to the end of the 21st century, in the context of ongoing global climate change.

By integrating paleoclimatic reconstructions, present-day distribution data and future climate scenarios within an ecological niche modeling framework, this **research seeks to**: (1) Identify long-term climatic constraints shaping birch forest distribution; (2) Quantify temporal shifts in suitable habitat across glacial, interglacial, and projected future conditions; (3) Assess regional differentiation in ecological responses; and (4) Provide a scientific basis for adaptive management and conservation planning in high-mountain ecosystems.

Drawing on ecological niche theory, paleoclimatic reconstructions, and contemporary bioclimatic analyses, this dissertation advances the following **hypotheses**:

H1. Projected climate change, particularly shifts in temperature regimes and moisture availability, will significantly alter the ecological niche and potential spatial distribution of subalpine birch forests in the Caucasus.

H2. The effects of climate change will be spatially heterogeneous. Birch forests in Colchis, the Eastern Caucasus and the southern Caucasus (Samtskhe–Javakheti and northern Armenia) will exhibit regionally differentiated responses due to contrasting climatic regimes, topographic complexity and historical land-use legacies.

H3. Even within a single ecoregion, structurally and compositionally similar subalpine birch forest ecosystems may respond differently to climatic shifts as a consequence of microclimatic buffering, local moisture balance, edaphic conditions and demographic inertia. Therefore, future distributional changes will not follow a uniform upward or latitudinal shift pattern.

To test these hypotheses, the dissertation addresses the following **questions**:

1) How did the ecological niche and spatial distribution of subalpine birch forests change from the Last Glacial Maximum through the mid-Holocene to the present, and which regions functioned as long-term climatic refugia?

2) Which temperature and moisture-related variables most strongly determined birch forest distribution across different time periods, and how stable were these climatic constraints over time?

3) To what extent do potential distribution areas derived from ecological niche models correspond to field observations, and where do discrepancies indicate dispersal limitations, disturbance effects, or historical legacies?

4) How do past and projected niche shifts differ among Colchis, the Eastern Caucasus, and the southern Caucasus, and what explains inter-regional contrasts in response magnitude and direction?

5) How might climate scenarios for the end of the 21st century alter the ecological niche and spatial distribution of subalpine birch forests relative to their Pleistocene and Holocene ranges? Which areas are most likely to function as future climatic refugia or long-term conservation zones?

This dissertation examines the long-term ecological niche dynamics and spatial distribution of subalpine treeline birches (*Betula* spp.) in the Caucasus through an integrated paleoclimatic – present – future modelling framework. The **Literature Review** establishes the taxonomic, phylogenetic and biogeographic background of the genus *Betula* and synthesizes the ecological significance, historical development and climate sensitivity of subalpine birch forests within the Caucasus refugial system. It further contextualizes regional climate change trends and contemporary treeline theory, emphasizing multidimensional climatic controls and niche conservatism. The **Materials and Methods** chapter describes the study area, the compilation of 165 verified occurrence records, the selection of ecologically relevant bioclimatic predictors (BIO10, BIO11, BIO18, BIO19) and the application of the Maximum Entropy (MaxEnt) modelling approach. The modelling framework integrates the Last Glacial Maximum, the Mid-Holocene, present climate and future projections for 2100 under three Shared Socioeconomic Pathways (SSP126, SSP370, SSP585) using MIROC, CCSM and CMCC-ESM2 climate models, allowing reconstruction of spatiotemporal habitat transitions. The **Results** demonstrate high model performance, identify seasonal temperature as the dominant climatic control, reveal LGM confinement to Colchic and Hyrcanian refugia, Holocene expansion and present-day climatic optimum, and project strong scenario-dependent future shrinkage and fragmentation under higher-emission pathways. The **Discussion** interprets these findings within the broader framework of Quaternary biogeography and treeline ecology, highlighting a refugia – recolonization – optimum – shrinkage trajectory and challenging assumptions of uniform upslope advance under warming. The **concluding** chapter synthesizes the ecological implications of emission-dependent vulnerability and formulates conservation and management recommendations focused on the protection of climatically stable refugial strongholds, maintenance of ecological connectivity and integration of climate-adaptive strategies into high-mountain forest governance across the Caucasus region.

Literature Review

Taxonomy, Phylogeny and Biogeography of the Genus Betula

Birch species and birch forest communities (*Betuleta*) occur across the Arctic regions of the Northern Hemisphere, in high-mountain systems, subalpine forests and primary natural landscapes (Ashburner and McAllister 2013). Species of *Betula* are deciduous trees reaching up to 25 meters in height and only rarely exceeding 30 meters (Furlow 1990; Vakkari 2009). Numerous taxa are considered threatened and are included in the IUCN Red List, reflecting both their ecological vulnerability and ongoing taxonomic uncertainties (Ashburner and McAllister 2013; Shaw et al. 2014).

The taxonomy of *Betula* remains complex and controversial. Since the 19th century, multiple classification systems have been proposed (Regel 1865; Winkler 1904; Hutchinson 1964; Furlow 1990; De Jong 1993; Skvortsov 2002). The number of recognized species varies considerably among authors, ranging from 35 to 100 (Ashburner 1980; Furlow 1990). Ashburner and McAllister (2013) recognize approximately 40-50 species, whereas the World Checklist lists 65 species (Royal Botanic Gardens Kew 2026). Additional taxa have been described in recent decades (Zeng et al. 2014; Zeng, Li, and Chen 2008; McAllister and Rushforth 2011), indicating that species delimitation remains unresolved.

The principal causes of taxonomic complexity are frequent hybridization and pronounced morphological plasticity. Species boundaries are obscured by variation in growth form, bark coloration and leaf morphology, as well as by continuous interspecific gene flow (Williams and Arnold 2001; Thórsson, Salmela, and Anamthawat-Jónsson 2001; Palme et al. 2004; Nagamitsu, Kawahara, and Kanazashi 2006; Wang et al. 2016). Discrepancies between morphological and molecular classifications are largely the result of recurrent hybridization occurring both within and between sections and subgenera (Dehond and Campbell 1987, 1989; Dancik and Barnes 1972; Nagamitsu et al. 2006; Czernicka et al. 2014; Thomson et al. 2015).

Early classification systems differed substantially in their interpretation of infrageneric structure. Regel (1865) divided the genus into the subgenera *Alnaster* and *Eubetula*, whereas Winkler (1904) revised the system and reorganized sections and subsections. De Jong (1993) proposed five subgenera: *Betula, Betulaster, Betulenta, Chamaebetula* and *Neurobetula*. Based on North Asian material, Skvortsov (2002) recognized four subgenera and eight sections. The most recent revision by Ashburner and McAllister (2013) also recognizes four subgenera and eight sections, largely following Skvortsov's (2002) system, though the rank and placement of certain groups were modified and *Sinobetula* was excluded due to insufficient evidence.

Molecular studies of Betulaceae consistently demonstrate that *Betula* forms a sister clade to *Alnus*, while *Carpinus, Corylus, Ostryopsis*, and *Ostrya* constitute a separate clade (Bousquet, Strauss, and Li 1992; Chen, Manchester, and Sun 1999; Forest et al. 2005; Grimm and Renner 2013). Within *Betula* itself, however, phylogenetic reconstructions remain incomplete and are often based on limited sampling (Jarvinen et al. 2004; Li, Shoup, and Chen 2005; Nagamitsu, Kawahara, and Kanazashi 2006; Schenk et al. 2008). Some taxa have not yet been included in molecular analyses and the phylogenetic position of certain species, such as *B. schmidtii*, remains debated (Jarvinen et al. 2004; Li, Shoup, and Chen 2005).

Evolutionary evidence suggests that the subgenera *Betulenta* and *Betulaster* represent ancient lineages dating back to the Eocene (De Jong 1993). Molecular dating indicates that *Betula* diverged from other Betulaceae approximately 75 million years ago, with subsequent diversification during the Oligocene and Miocene (Bina et al. 2016). The subgenus *Betula* appears to be older than *Neurobetula*, contradicting the hypothesis proposed by Keinänen et al. (1999).

Overall, *Betula* represents an evolutionarily dynamic and taxonomically complex genus characterized by wide geographic distribution, strong ecological adaptability and reticulate evolution. These features make it an important model system for studying phylogeny, speciation processes and climate-driven distributional dynamics.

Subalpine Birch Forests in the Caucasus: Ecological Significance, Historical Dynamics and Climate-Driven Transformations

Birch forests (*Betuleta*) represent one of the most widespread formations of the subalpine forest belt in the Caucasus. Subalpine (upper treeline) forests develop on the humid and moist slopes of the Greater and Lesser Caucasus (Dolukhanov 1978; 2010; Nakhutsrishvili 2013). Vegetation within this belt plays a crucial role in regulating natural processes, particularly hydrological regimes (Nakhutsrishvili 2000; 2013). Subalpine forests provide essential ecosystem services, including water regulation, soil protection, climate regulation, recreation and other important ecological functions (Körner 2008; Smith et al. 2009; Fagre 2009; Price et al. 2011; Mina et al. 2017).

The upper part of the subalpine belt in western Transcaucasia and the mountainous regions of northeastern Turkey (Rize and Artvin) are rich in relict and endemic dendrofloral elements. These areas are influenced by Mediterranean, Irano-Turanian, and Euro-Siberian floristic centers (Davis 1965; Olson and Dinerstein 2002; Eminağaoğlu and Anşin 2004; Eminağaoğlu et al. 2006). Of particular importance is the Colchic subalpine birch forest, characterized by a humid and mild climate. Endemic and relict birch species occur here, including *Betula medwedewii* and *Betula megrelica* (Dolukhanov 1980, 2010; Browicz 1975; Eminagaoglu et al. 2006; Zazanashvili 1999; Nakhutsrishvili 2013; Ashburner and McAllister 2007, 2013; Shaw et al. 2014). The majority of tree and shrub species within the subalpine belt of the Caucasus are endemic to the Caucasus region and adjacent southern mountain systems (Dolukhanov 1980; Nakhutsrishvili 2000, 2013). Of the five birch species occurring in the Caucasus (Figure 1-4): *Betula litwinowii* Doluch., *B. pendula* Roth, *B. medwediewii* Regel, *B. megrelica* Sosn. and *B. raddeana* Trautv., four are regional endemics (Ashburner and McAllister 2013; Nakhutsrishvili 2013; Shaw et al. 2014). *Betula megrelica* is a narrow local endemic of the southwestern (North Colchic) Caucasus, while *B. medwedewii* and *B. raddeana* are included in the Red List of Georgia; *B. megrelca* is classified as Endangered (EN) in the IUCN Red List.

Figure 1. *Betula litwinowii* Doluch. in the subalpine belt of Kazbegi region, Georgia. Photograph by the author (2023).

Figure 2. *Betula pendula* Roth. in the subalpine belt of the Svaneti region, Georgia. Photograph by the author (2019).

Figure 3. *Betula medwediewii* Regel. in the subalpine belt of Gubazeuli Valley, Bakhmaro, Georgia. Photograph by the author (2019).

Figure 4. *Betula megrelica* Sosn. in the subalpine belt of Egrisi ridge, Migaria, Georgia. Photograph by the author (2025).

Regarding the origin of birch forests, Grossheim (1936, 1948) proposed that the "Mediterranean–Turgai flora," which formed during the Arcto-Tertiary period, served as the foundation for many modern species considered Tertiary relicts, including *Betula medwedewii*. The presence of conservative relict taxa adapted to high-mountain conditions within the subalpine dendroflora suggests an ancient origin for subalpine birch forests (Dolukhanov 1980). Within the Caucasus ecoregion, the southern distribution limit of birch forests extends into northern Iran, including small fragmented areas within the Hyrcanian forests (Bina et al. 2018). *Betula pendula* was previously recorded in the local flora (Browicz 1971, 1982) and is considered an ancient species in Iran, with ancestral origins linked to the Pliocene (Bina et al. 2018). *Betula litwinowii* represents a more recent record in the flora of Iran and occurs in the Hyrcanian forests on the northern slopes of the Elburz Mountains, in contrast to *B. pendula*, which is primarily found on southern slopes (Zare et al. 2010).

Palynological studies indicate that birch pollen grains are already recorded during cooling phases of the Pliocene (Palibin 1930; Mchedlishvili 1954; Shatilova et al. 2007; Shatilova et al. 2011). During the Pleistocene and early–middle Holocene, the proportion of birch pollen increases in sediment records (Margalitadze 1970; Margalitadze and Ramishvili 1972; Margalitadze 1977, 1985, 1995; Kvavadze and Rukhadze 1989; Connor et al. 2004; Connor and Kvavadze 2008). At the beginning of the Holocene (approximately 10 - 12 thousand years ago), when the climate remained relatively cold and glaciers were retreating, birch forests dominated by *Betula litwinowii* and *B. pendula* became widely distributed in Georgia (Margalitadze 1970, 1995; Kvachakidze 2010; Shatilova et al. 2011). These data demonstrate that subalpine birch forests of the Caucasus represent primary natural ecosystems composed of relict and endemic species, thereby increasing their ecological and conservation significance (Thompson et al. 2009).

In the Caucasus, treeline birch stands consist of several *Betula* species, primarily composed by *Betula litwinowii* Doluch., with co-occurrence of *Betula pendula* Roth, *B. medwedewii* Regel, *B. megrelica* Sosn., and *B. raddeana* Trautv. (Ashburner and McAllister 2013; Nakhutsrishvili 2013; Shaw et al. 2014). Subalpine birch forests are widely distributed throughout the Greater Caucasus and across much of the Lesser Caucasus (Dolukhanov 1978, 2010; Nakhutsrishvili 2013). Due to their high-elevation distribution, they are particularly sensitive to both anthropogenic and natural stressors. During the Soviet period, stands of *Betula litwinowii* were significantly degraded due to intensive logging and overgrazing (Wiesmair et al. 2016; Rizayeva et al. 2025), resulting in habitat reduction and a downward shift of the upper forest limit (Dolukhanov 1978). Timber extraction, road construction, excessive grazing and the development of mountain ski resorts negatively affected high-mountain biodiversity (Thannheiser et al. 2005). Consequently, the area of birch forests in Georgia declined (Nakhutsrishvili et al. 2004a,b).

In recent decades, an opposite trend has been observed: birch species are recolonizing higher elevations, likely associated with climatic warming and reduced grazing pressure (Gottfried et al. 2012; Pauli et al. 2012; Togonidze and Akhalkatsi 2015; Hansen et al. 2018). Similar upward shifts have been documented in Turkey (Arekhi et al. 2018), on the Iranian Plateau (Shamsabad et al. 2018), and in the Pontic Mountains (Kurt et al. 2015). European studies indicate that post-disturbance regeneration is determined by reduced anthropogenic pressure, land-use change and climatic effects (Satake et al. 2007). Data from Scandinavia also demonstrate birch forest expansion associated with reduced grazing and logging, together with climate change (Sonesson and Hoogesteger 1983; Kullman 2000, 2002).

The dynamics of subalpine birch forests in the Caucasus reflect the combined influence of historical land use, contemporary climate change and socio-economic pressures. While past anthropogenic impacts led to degradation, recent warming and reduced grazing have activated processes of natural regeneration and upward expansion.

Recent Trends in Climate Change and Temperature Extremes in the Caucasus Region

Since the 1960s, climate change in the Caucasus, particularly in Georgia, has demonstrated by an increase in mean temperatures and a higher frequency of extreme thermal events (Keggenhoff et al. 2014, 2015). Climate extremes are defined as values that exceed historically recorded upper or lower limits (IPCC 2012) and it is widely recognized that anthropogenic warming has substantially altered the intensity and duration of such events (IPCC 2007).

Although global mean surface temperature increased by 0.85°C between 1880 and 2012 (IPCC, 2013), extreme events often respond more sensitively, exhibiting sharper variability and accelerated trends (Katz and Brown 1992; Easterling et al. 1997, 2000; Kunkel et al. 1999; New et al. 2006; Aguilar et al. 2009). Various studies systematically link global warming to changes in temperature extremes (Peterson et al. 2002; Griffiths et al. 2005; Zhang et al. 2005; Haylock et al. 2006; Klein et al. 2006; Moberg and Jones 2005). In Georgia, these changes are reflected in the increased vulnerability of both mountainous and lowland ecosystems (MOE 2009; IPCC 2012).

Analysis of homogenized daily temperature data for 1961-2010 reveals statistically significant warming trends in both annual and seasonal mean values across the Caucasus region (Keggenhoff et al. 2015). This warming has accelerated in recent decades: between 1981 and 2010, annual minimum temperatures increased by 0.39°C per decade, while annual maximum temperatures rose by 0.47°C per decade. Notably, summer maximum temperatures increased by 0.84°C per decade, which is almost twice the rate of the annual mean increase. Autumn seasons also show a pronounced rise in warm nights and warm days (Elizbarashvili et al. 2012, 2013). When extreme heat events increase more rapidly than cold extremes, this indicates greater temperature variability, particularly in the eastern and southern lowlands of the region. Whereas long-term data for 1906-1995 exhibited regional heterogeneity and even slight cooling in western Georgia, recent decades reveal a uniform warming signal across the country (Elizbarashvili et al. 2007, 2009a).

The physical consequences of warming are widely observed in the Caucasus region. Between 1986 and 2014, Caucasian glaciers decreased by an average of 0.69% annually (Tielidze and Wheate 2018) and significant reductions in snow cover have been documented in both the Greater Caucasus and the Zagros Mountains (Notarnicola 2020). Although the rate of warming in the Caucasus is lower than in the Pontic or Arabian mountain ranges, it remains sufficient to drive ecological changes, including upward species migration and increased biodiversity in high-mountain zones (Donat et al. 2014; Elumeeva et al. 2013; Gigauri et al. 2013). In particular, subalpine birch forests (mainly composed of *Betula litwinowii*) are expanding toward higher elevations due to the combined effects of climate warming and land-use change (Akatov 2009; Hansen et al. 2018), mirroring similar trends in the Iranian Plateau and the Pontic Mountains (Kurt et al. 2015; Shamsabad et al. 2018).

Possible ecological perspectives of climate change in the high mountains of Georgia and some trends of expected vegetation transformation, including changes in vertical zonation of vegetation and the structure of natural ecosystems, xerophytization, etc., are analyzed in various studies and national reports (Nakhutsrishvili et al. 1999a,b; Gigauri et al. 2013, 2016; Georgia's Second, Third, and Fourth National Communications to the UNFCCC 2009, 2016, 2021). However, data limitations remain a significant challenge. Following the end of the Soviet Union, the number of meteorological stations declined sharply, creating spatial gaps and metadata inconsistencies (Elizbarashvili et al. 2013). Thus, future research should strengthen monitoring networks and link temperature extreme indices with large-scale atmospheric circulation patterns to better assess the ecological impacts of intensifying heat extremes on various terrestrial ecosystems.

Climate Change and Treeline Forest Responses in Mountain Ecosystems

Under conditions of global climate change, shifts in species distribution boundaries are driven by interactions between thermal and other ecological niche axes. Climate change causes significant alterations in vegetation cover (Myers-Smith et al. 2020), the structural composition of plant communities (Steinbauer et al. 2018) and the geographical limits of species distributions (Grytnes et al. 2014). Under conditions of climatic variability and human pressure, species ranges may expand or shrink (Roces-Díaz et al. 2018; Scheffers et al. 2016). Predictive models indicate that mountain regions are among the most vulnerable ecosystems prone to climate change (Halloy and Mark 2003; Thuiller et al. 2005). High-mountain plants are particularly at risk, as they may lose a large proportion of their potentially suitable habitats by the end of the 21st century, especially when temperature increases are accompanied by declining precipitation (Engler et al. 2011; Tovar et al. 2013; Van De Ven et al. 2007).

Global climate change is characterized not only by rising temperatures but also by shifts in precipitation regimes, nitrogen deposition and other environmental factors (IPCC 2023). These environmental changes may either facilitate or constrain species range shifts, depending on interactions among multiple dimensions of the ecological niche (Sanczuk et al. 2024). For example, along the moisture-related niche axis, some forest boundaries are simultaneously constrained by temperature and soil moisture; therefore, warming alone does not automatically enhance growth and recruitment, which contributes to the relative stability of the treeline belt (Moyes et al. 2015; Elliott et al. 2021). Similarly, if nutrient availability in newly suitable areas does not meet the requirements of particular species, expansion driven by warming may be limited (Hagedorn et al. 2019).

Rising temperatures are often accompanied by increased soil water evaporation, intensified droughts and accelerated photosynthesis. Under such conditions, spring drought stress that arises from the combined effects of water deficit and heat, negatively affects tree growth and survival (Liu et al. 2013; Wu et al. 2013). Empirical studies show that drought stress intensifies under high-temperature conditions (Xu et al. 2013; Bailey et al. 2021). These findings underline the importance of hydrothermal interactions in regulating treeline dynamics.

The contrasting relationships between spring and summer temperatures and treeline elevation further indicate that interactions between temperature and moisture are key predictive factors in alpine regions. Evidence supporting this interpretation demonstrates the combined influence of temperature and moisture on seedling establishment in treeline ecotones (Moyes et al. 2015; Bailey et al. 2021). Hydrothermal interactions may also influence seedling spatial distribution and competitive dynamics within ecotones, ultimately determining treeline position and structure (Sigdel et al. 2020; Bader et al. 2021).

Early observations since the 1850s highlighted the dominant role of temperature in determining vegetation distribution limits. At that time, the idea emerged that plant distribution in mountain ecosystems, in particular, the treeline belt, was closely linked to climatic conditions. Later, in the 1930s, research focused on physiological and ecological mechanisms underlying temperature effects on treeline formation and stability (Tranquillini 1979; Holtmeier and Broll 2020). Global data indicate that the treeline is typically associated with a mean growing-season soil temperature threshold of approximately 6.4°C (Körner and Paulsen 2004; Shi et al. 2008). Accordingly, temperature is considered a primary determinant of treeline elevation (Jobbágy and Jackson 2000; Körner 2012), as primary and secondary growth processes at high elevations are directly dependent on thermal conditions. However, despite the dominant role of temperature, additional climatic factors can modulate this relationship. For instance, in monsoon-influenced regions, simultaneous increases in summer precipitation and temperature may enhance photosynthetic activity in temperature-limited ecosystems. Such conditions facilitate carbohydrate accumulation, biomass growth and plant survival, therefore influencing treeline dynamics (Jiang et al. 2017).

Solar radiation also plays an important role. A moderate but statistically significant positive correlation ($P < 0.05$) between treeline elevation and relative radiation index indicates that treelines tend to occur at higher elevations on sunnier slopes. Sunlight exposition influences not only tree growth but also the spatial structure and age distribution of treeline ecosystems (Elliott and Kipfmueller 2010). Beyond its central role in photosynthesis (Bansal and Germino 2009), light acts as an environmental signal regulating seed germination and phenological rhythms (Willis et al. 2014) and improves microhabitat thermal conditions on sun-exposed mountain slopes (Körner 1999).

Despite global warming, more than one-third of treeline ecosystems worldwide have not shifted upward (Harsch et al. 2009; Hansson et al. 2021). The Himalayas, which are the home to some of the highest and most diverse treeline systems, represent a global hotspot for treeline research under climate change. Studies indicate that treeline advance in the central Himalayas is constrained by pre-monsoon drought (Liang et al. 2014). Similarly, no consistent upward trend has been observed in the southeastern Tibetan Plateau and eastern Himalayan regions, as seedling establishment above the treeline remains limited (Shen et al. 2018).

Additionally, snow cover exerts the following complex effects: on one hand, it protects plants from early frost and excessive solar radiation (Shen et al. 2017), while meltwater reduces spring drought stress (Körner 2012; Li et al. 2021). On the other hand, prolonged snow cover may increase the risk of fungal infections in seedlings (Senn 1999) and shorten the growing season (Wipf and Rixen 2010). In high-mountain environments, growing-season length is a critical limiting factor, directly influencing biomass accumulation and resilience to environmental stress.

The evidence reviewed above demonstrates that treeline ecotone responses to climate change cannot be explained by temperature alone. They result from interactions among multiple niche dimensions, including temperature, moisture, nutrient availability, radiation and snow dynamics, that operate across spatial and temporal scales. Understanding this multidimensional control is essential for accurate predictions of future treeline dynamics under global environmental change.

Materials and Methods

Study Area

The study area encompasses the Caucasus Ecoregion, covering approximately 580,000 km² across Armenia, Azerbaijan, and Georgia (South Caucasus), as well as parts of northeastern Turkey (Transcaucasia), the northern slopes of the Greater Caucasus within the Russian Federation (Ciscaucasia) and northwestern Iran (Figure 5).

Figure 5. Physical map of the Caucasus ecoregion. (Source: Kurtubadze, M. (2008). The Caucasus ecoregion, Physical map. GRID-Arendal. Available at: https://www.grida.no/resources/7902/)

The region is internationally recognized as one of the world's most significant biodiversity centers. It is designated as a global Biodiversity Hotspot by Conservation International (Mittermeier et al. 2004; Conservation International 2025) and listed among WWF's Global

200 priority ecoregions (Olson and Dinerstein 2002), reflecting the coexistence of exceptional species richness and high levels of anthropogenic threat (Zazanashvili et al. 2012, 2020). As part of the broader Greater Black Sea region, the Caucasus has also been identified among WWF's Priority Places of global conservation importance (WWF 2008).

Geologically, the Caucasus Isthmus forms part of the extensive Alpine–Himalayan orogenic belt that stretches from the Pyrenees and Atlas Mountains in the west to Southeast Asia in the east (Maruashvili 1975). The region is characterized by pronounced geomorphological complexity and sharp elevational gradients. Its major physiographic units include the Greater Caucasus Range forming the northern mountainous barrier, the South Caucasian Depression extending from the Colchic lowlands along the Black Sea to the Absheron Peninsula on the Caspian Sea, the Lesser Caucasus Mountain Chain and the South Caucasian Uplands encompassing portions of the Armenian and Iranian highlands (Maruashvili 1975, 1981). Relief diversity is reflected in tectonic, erosional, volcanic, glacial and karst landforms. Glaciers are concentrated primarily in the Greater Caucasus, historically numbering over 2,000 and covering approximately 1,450 km^2, although substantial retreat has occurred during recent decades (Tielidze et al. 2023). This extreme topographic heterogeneity creates strong microclimatic gradients that play a fundamental role in structuring vegetation belts and species distributions.

Climatically, the Caucasus exhibits pronounced west-east and altitudinal gradients. Mean annual precipitation exceeds 2,000 mm along the southwestern Black Sea coast and can reach up to 4,500 mm in parts of the Colchic region, whereas southeastern Caspian lowlands receive less than 200 mm annually (Zazanashvili et al. 2000). Mean annual temperatures in coastal sectors of the Southern Caucasus approximate 15°C, declining with increasing continentality, latitude, and altitude. This climatic variability underpins the coexistence of humid temperate rainforests, xeric continental landscapes, subalpine forests, alpine systems and semi-arid environments within relatively short spatial distances. The combination of topographic isolation and climatic buffering has allowed the region to function as a long-term refugium during Quaternary climatic oscillations.

Biogeographically, the Caucasus is considered one of the most biologically rich temperate regions globally (Mittermeier et al. 2004; Zazanashvili et al. 2012, 2020). The largest natural forest complexes belong to the Caucasus–Anatolia–Hyrcanian temperate rainforest belt (Zazanashvili and Mallon 2009). These forest systems harbor a high proportion of endemic and relict plant taxa, many of which occur as dominants or co-dominants in subalpine communities, particularly in western Georgia and adjacent areas (Bohn et al. 2003; Nakhutsrishvili 2013; Williams et al. 2006; Zazanashvili 1999). The refugial character of the region has facilitated the persistence of Tertiary relicts and promoted speciation processes under conditions of geographic and ecological isolation.

Within this complex environmental framework, subalpine forest belts occupy upper montane elevations of both the Greater and Lesser Caucasus. These forests form transitional ecotones between closed montane forests and alpine grasslands and play critical roles in slope stabilization, hydrological regulation, carbon sequestration, and biodiversity maintenance (Nakhutsrishvili 2013; Mina et al. 2017). Their spatial configuration reflects the interaction of climatic gradients, geological history and long-term human land use.

Data Collection and Sampling Design

In order to ensure spatial representativeness of subalpine birch forest distribution across the Caucasus Ecoregion, six regional study areas were selected to capture the major biogeographic, climatic and physiographic gradients of the region. These included the eastern Greater Caucasus (Lagodekhi), the central Greater Caucasus (Kazbegi), the southern Lesser Caucasus (Samtskhe-Javakheti), northern Armenia and the subalpine zones of Samegrelo, Upper Svaneti and Adjara. These areas collectively represent humid western sectors, continental eastern slopes and transitional southern mountain systems, thereby encompassing the full environmental scale within which subalpine birch forests occur.

Prior to field investigations, a comprehensive review of scientific literature was conducted alongside an analysis of historical forest stand plans and national forest inventory maps of Georgia (1980-1992; 2003-2005). These materials included forest formation polygon maps, allowing the preliminary delineation of potential birch forest areas. This preparatory phase provided a spatial framework for identifying priority sampling zones and ensured that subsequent fieldwork targeted both core and marginal distribution areas.

Field data collection was carried out through systematic expeditions across the selected regions from 2019-2022. In total, 105 field plots were established and investigated. Plots were selected randomly within identified birch formation polygons to reduce sampling bias, while maintaining a minimum distance of 1 km between plots to minimize spatial autocorrelation and ensure statistical independence of observations. Each sampling unit consisted of a permanent square plot measuring 20 × 20 m (400 m^2).

For each plot, geographic coordinates were recorded using GPS devices with an accuracy of approximately 3m. In addition, environmental and structural variables were documented, including slope inclination, exposition (aspect), elevation above sea level and dominant tree species and forest type (formation) composition. This standardized protocol ensured comparability across regions and provided environmental descriptors necessary for subsequent ecological niche modeling.

To strengthen the spatial and environmental coverage of the dataset, field observations were supplemented with presence-only occurrence records from multiple independent sources. National Forest Inventory (NFI) data collected between 2019 and 2021 were incorporated (MEPA 2023), contributing 26 verified records. For the northern Caucasus and areas beyond direct field accessibility, additional occurrence data were obtained from the Global Biodiversity Information Facility (GBIF.org 2021). An initial set of 78 GBIF records was downloaded and subjected to manual quality control. Occurrences located in urban green spaces, parks, botanical gardens, museums, institutional collections and other non-natural locations were excluded to avoid artificial or cultivated records. After filtering, 26 high-confidence records were retained. Furthermore, 8 georeferenced records were obtained from the herbarium collection of the Botanical Institute at Ilia State University.

In total, the compiled dataset consisted of 165 occurrence records: 105 from field expeditions, 26 from the National Forest Inventory, 26 from the filtered GBIF dataset and 8 from herbarium materials (Figure 6). The integration of primary field data with verified secondary occurrence datasets allowed for enhanced spatial coverage across the Caucasus while maintaining data reliability. This combined sampling framework ensured adequate representation of both western humid and eastern continental sectors, as well as altitudinal and ecological gradients relevant to subalpine birch forest distribution.

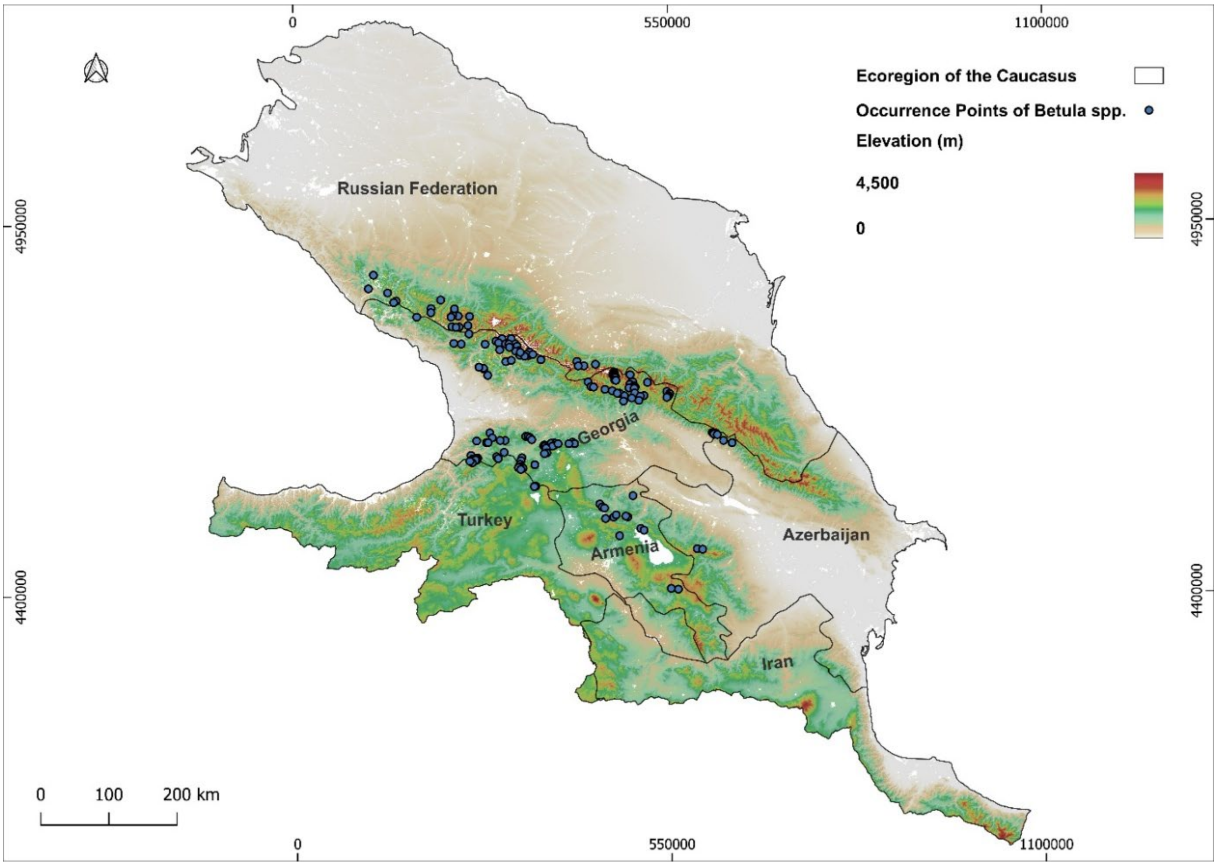

Figure 6. Spatial distribution of *Betula* spp. occurrence records within the Caucasus Ecoregion. Blue circles indicate verified presence locations (n = 165) compiled from field expeditions, National Forest Inventory data (2019–2021), GBIF records and herbarium collections, that are used for ecological niche model calibration and validation. The background layer represents regional topography, with elevation visualized as a gradient from lowland areas (green) to high mountain zones (brown to white).

Climatic Predictors and Variable Selection

To characterize the climatic constraints shaping the distribution of subalpine birch forests across the Caucasus Ecoregion, we used high-resolution bioclimatic predictors derived from the WorldClim 2.1 database (Fick and Hijmans 2017). All climatic layers were obtained at 30 arc-second spatial resolution (~1 km²), ensuring compatibility with the spatial resolution of the occurrence dataset and minimizing scale-related inconsistencies between environmental predictors and presence records.

Selection of appropriate predictor variables represents a critical step in species distribution modelling, as multicollinearity among environmental variables can inflate model performance metrics and obscure ecological interpretation (Elith and Leathwick 2009; Warren et al. 2010). Initially, all 19 standard bioclimatic variables available in the WorldClim dataset were downloaded and examined (Table 1). To reduce redundancy and avoid overparameterization, pairwise Pearson correlation coefficients were calculated, applying a threshold of $-0.7 < r < 0.7$ (Warren et al. 2010) (Figure 7). This filtering step supported the selection of quarterly temperature and precipitation variables (BIO10, BIO11, BIO18, BIO19), which showed acceptable levels of intercorrelation and strong ecological interpretability.

Table 1. WorldClim 2.1 bioclimatic variables used in this study. All 19 predictors were initially evaluated, and the four quarterly variables selected for the final model (BIO10, BIO11, BIO18, BIO19) are highlighted and in bold.

Code	Variable Name	Description	Used in Final Model
BIO1	Annual Mean Temperature	Mean annual temperature	No
BIO2	Mean Diurnal Range	Mean of monthly (max temp – min temp)	No
BIO3	Isothermality	(BIO2 / BIO7) × 100	No
BIO4	Temperature Seasonality	Standard deviation of monthly temperature ×100	No
BIO5	Max Temperature of Warmest Month	Maximum temperature of the warmest month	No
BIO6	Min Temperature of Coldest Month	Minimum temperature of the coldest month	No
BIO7	Temperature Annual Range	BIO5 – BIO6	No
BIO8	Mean Temperature of Wettest Quarter	Mean temperature during the wettest quarter	No
BIO9	Mean Temperature of Driest Quarter	Mean temperature during the driest quarter	No

Code	Variable Name	Description	Used in Final Model
BIO10	**Mean Temperature of Warmest Quarter**	Mean temperature of the warmest quarter	**Yes**
BIO11	**Mean Temperature of Coldest Quarter**	Mean temperature of the coldest quarter	**Yes**
BIO12	Annual Precipitation	Total annual precipitation	No
BIO13	Precipitation of Wettest Month	Total precipitation of the wettest month	No
BIO14	Precipitation of Driest Month	Total precipitation of driest month	No
BIO15	Precipitation Seasonality	Coefficient of variation of monthly precipitation	No
BIO16	Precipitation of Wettest Quarter	Total precipitation of the wettest quarter	No
BIO17	Precipitation of Driest Quarter	Total precipitation of the driest quarter	No
BIO18	**Precipitation of Warmest Quarter**	Total precipitation of the warmest quarter	**Yes**
BIO19	**Precipitation of Coldest Quarter**	Total precipitation of the coldest quarter	**Yes**

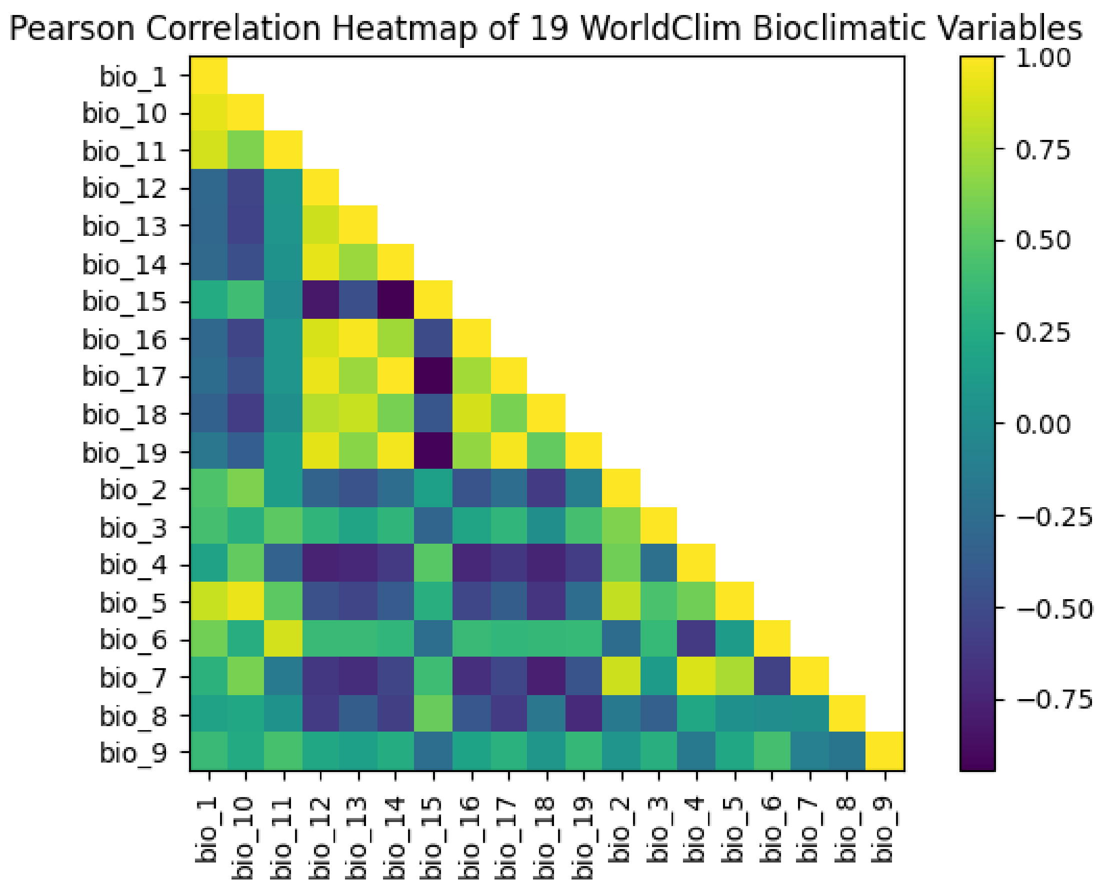

Figure 7. Pearson correlation matrix of the 19 WorldClim bioclimatic variables (BIO1–BIO19). Color gradients indicate the strength and direction of pairwise correlations. Highly correlated variables were excluded to minimize multicollinearity prior to model construction.

From the subset of eight variables retained after correlation filtering, four quarterly bioclimatic variables were selected based on ecological relevance to treeline dynamics and interpretability in a high-mountain context. These included two temperature-related variables: **BIO10** (Mean Temperature of Warmest Quarter) and **BIO11** (Mean Temperature of Coldest Quarter), and two precipitation-related variables: **BIO18** (Precipitation of Warmest Quarter) and **BIO19** (Precipitation of Coldest Quarter).

These quarterly variables were chosen because they directly reflect seasonal thermal and moisture constraints that regulate growth, seasonal survival and recruitment processes in subalpine treeline ecosystems. Temperature during the warmest quarter governs primary productivity and cambial activity, while cold-quarter temperature influences overwinter survival and frost tolerance. Similarly, precipitation during the warmest and coldest quarters captures seasonal moisture availability and winter snow-related hydrological inputs, both of which are critical for treeline forest persistence.

Ecotopological variables, including elevation and aspect, were tested in multiple combinations with the selected bioclimatic predictors. However, their inclusion did not improve the explanatory strength or ecological plausibility of predicted birch distributions. Because elevation is strongly correlated with temperature gradients and may artificially constrain projections across temporal scenarios, its inclusion risked introducing redundant or circular predictors. Aspect similarly showed limited additional explanatory power beyond the selected climatic variables. Consequently, both elevation and aspect were excluded from the final predictor set, and the analysis relied exclusively on the four selected bioclimatic variables.

The final predictor set thus consisted of BIO10, BIO11, BIO18 and BIO19. This combination minimized multicollinearity while preserving ecologically meaningful gradients relevant to subalpine birch forests. The selected variables have previously demonstrated strong predictive capacity for birch habitats in the Caucasus (Akobia et al. 2022) and for other deciduous forest systems in the region (Metreveli et al. 2023, 2025), supporting their robustness and ecological validity.

Ecological Niche Modelling and Model Evaluation

Ecological niche modelling was performed using the Maximum Entropy (MaxEnt) algorithm (Phillips et al., 2006; version 3.3.3k), a widely applied method for presence-only data that estimates the probability distribution of maximum entropy constrained by environmental predictors (Elith et al., 2011). One occurrence record per pixel was retained to match the 1-km spatial resolution of climatic layers. Climatic data processing was conducted in QGIS Desktop 3.4.5 "Madeira" (QGIS Development Team 2019), and statistical analyses were performed in R (R Core Team 2018).

Models were run with a maximum of 2,500 iterations, allowing quadratic and hinge feature classes, while retaining default convergence thresholds and regularization settings (Phillips and Dudík 2008; Merow et al. 2013; Kuemmerle et al. 2020). The dataset was randomly partitioned, with 75% of occurrence records used for training and 25% reserved for testing. A total of 10,120 background points were sampled across the study area to characterize environmental availability.

Model performance was evaluated using the Receiver Operating Characteristic (ROC) curve and the Area Under the Curve (AUC), complemented by Training Sensitivity plus Specificity. The models demonstrated very high predictive performance (AUC consistently > 0.971), indicating strong discriminatory capacity. Variable importance was assessed through percent contribution, permutation importance, and jackknife tests (Phillips et al. 2006).

The modelling framework enabled integration of multiple climatic time slices, including paleoclimatic conditions (Last Glacial Maximum and Mid-Holocene), present climate and future emission scenarios (SSP126, SSP370, SSP585). This unified modelling approach allowed reconstruction of a refugia-expansion-optimum-shrinkage trajectory for Caucasian birch forests, highlighting both the sensitivity of treeline systems to climatic shifts and their dependence on emission pathways.

For model calibration, the occurrence dataset was expanded from the original 160 records (reported in Akobia et al. (2022)) to 165 records following additional field validation and quality control. All records were subjected to spatial thinning at a minimum distance of 1 km to reduce sampling bias and spatial autocorrelation, consistent with the spatial resolution of the WorldClim layers (30 arc-seconds, ~1 km^2).

To evaluate the effect of dataset expansion, models constructed with 165 records were compared to those based on the original 160 records. The comparison revealed no substantive differences in predictive performance (AUC = 0.971 vs. 0.970; Training Sensitivity plus Specificity = 0.148 vs. 0.122), nor in the ranking of predictor importance. In both cases, BIO10 (Mean Temperature of Warmest Quarter) and BIO11 (Mean Temperature of Coldest Quarter) remained the dominant predictors, while BIO18 and BIO19 contributed secondary but consistent effects. These results indicate that the ecological signal is robust to minor changes in sample size, consistent with previous studies demonstrating that

MaxEnt models stabilize once a minimum occurrence threshold is exceeded (Hernandez et al. 2006; Pearson et al. 2007; Wisz et al. 2008). Therefore, the 165-record dataset was retained for all primary analyses.

All 165 occurrence points were used in conjunction with the selected bioclimatic predictors (BIO10, BIO11, BIO18, BIO19) to construct the ecological niche models. The treeline belt of the Caucasus region is composed of several birch taxa, with *Betula litwinowii* Doluch. being the dominant and most widespread species. In this study, modelling was conducted at the habitat level (birch-dominated subalpine treeline forests) rather than at the scale of individual species micro-niches. Consequently, the dataset primarily reflects the distribution of *B. litwinowii*, supplemented by records of *Betula pendula* Roth, which frequently co-occurs in mixed stands (Figure 6).

Niche Conservatism and Spatiotemporal Projection Framework

The reconstruction of past and future distribution patterns of Caucasian treeline birches is grounded in the assumption that their fundamental climatic niche has remained relatively stable across late Quaternary time. Under this framework, present-day environmental relationships are used to infer the climatic envelope within which birch-dominated subalpine forests can persist. This approach does not assume static geographic distributions, but rather stability in the species' physiological and climatic tolerances over evolutionary time scales (Peterson et al. 1999; Wiens and Graham 2005).

The stability assumption is particularly relevant in mountain systems where long-lived tree taxa exhibit broad climatic tolerances and slow evolutionary rates relative to glacial–interglacial climatic oscillations. While distributional shifts are expected in response to climate change, available paleoecological evidence suggests that temperate tree species generally track suitable climates rather than undergoing rapid niche evolution (Martínez-Meyer and Peterson 2006). Therefore, modelling present-day climate–occurrence relationships provides a defensible basis for projecting potential suitability onto paleoclimatic and future climate layers.

Palynological archives offer important insights into vegetation history, yet pollen records represent regional signals influenced by species-specific production rates and dispersal mechanisms. Wind transport, hydrological redistribution and basin characteristics may alter pollen deposition patterns, meaning that sedimentary pollen percentages cannot be interpreted as direct measures of local vegetation abundance (Prentice 1988; Jackson and Williams 2004). Integrating ecological niche modelling with paleovegetation knowledge provides a more comprehensive framework for interpreting long-term dynamics (Dawson et al. 2016).

Using the contemporary occurrence dataset (n = 165), the calibrated MaxEnt model was projected onto reconstructed paleoclimate layers representing the Last Glacial Maximum (~21 ka BP) and the Mid-Holocene (~6 ka BP), as well as future climate scenarios for the year 2100 under alternative Shared Socioeconomic Pathways (SSP126, SSP370, SSP585). By maintaining identical predictor variables across all time slices, the projections ensured methodological consistency and comparability. This design allowed identification of climatically stable areas (putative refugia), zones of postglacial expansion, Holocene suitability optima and potential contraction or altitudinal displacement under projected warming.

Such spatiotemporal projections do not imply that realized historical or future distributions perfectly match modeled suitability. Biotic interactions, dispersal constraints, disturbance regimes and anthropogenic pressures may restrict range shifts even when climatic conditions are favorable (Guisan and Thuiller 2005; Araújo and Peterson 2012). Nevertheless, this framework provides a coherent basis for evaluating long-term climatic sensitivity and emission-dependent vulnerability of treeline ecosystems in the Caucasus. Comparable modelling strategies have been widely applied in Quaternary biogeography and climate-change risk assessment studies (Waltari et al. 2007; Nogués-Bravo 2009; Svenning et al. 2011).

Climate Models and Emission Scenarios

To reconstruct past, present and future suitability patterns of Caucasian treeline birches, climatic projections were derived from established paleoclimate simulations and contemporary General Circulation Models (GCMs). The modelling framework integrates multiple temporal horizons in order to evaluate long-term climatic stability, postglacial dynamics, and emission-dependent future vulnerability within a unified methodological design.

Past climatic conditions were represented by two key Quaternary intervals: the **Last Glacial Maximum** (LGM; ~21,000 years before present) and the **Mid-Holocene** (MH; ~6,000 years before present). These paleoclimatic reconstructions were obtained from Phase II of the Paleoclimate Modelling Intercomparison Project (PMIP2) (Braconnot et al. 2007).

Two widely used global climate models were selected for paleoprojections: the Community Climate System Model (CCSM) and the Model for Interdisciplinary Research on Climate (MIROC). These models have been extensively applied in biogeographic and phylogeographic studies of the Caucasus and adjacent regions (e.g., Tarkhnishvili et al., 2012). Their selection was motivated by the availability of downscaled layers at 30 arc-second spatial resolution (~1 km), ensuring consistency with contemporary WorldClim predictors and allowing direct comparability across time slices. The inclusion of both CCSM and MIROC reduces model-specific uncertainty and provides a more robust estimate of potential refugial areas during glacial and early Holocene periods.

Future climatic suitability was projected to the year 2100 under alternative greenhouse gas emission trajectories defined within the CMIP6 framework. Two Earth System Models were used: MIROC and CMCC-ESM2. The latter, developed by the Euro-Mediterranean Center on Climate Change, has demonstrated strong performance in reproducing temperature and precipitation dynamics across the Mediterranean–Black Sea region (Scoccimarro and Gualdi, 2020), making it particularly relevant for the Caucasus.

Future projections were generated under three Shared Socioeconomic Pathways (SSPs), representing contrasting emission and socio-economic development trajectories (Collins et al., 2013; IPCC AR6, 2021):

- **SSP126** – low-emission mitigation pathway (~+1.0 – 1.8 °C by 2100)
- **SSP370** – intermediate stabilization pathway (~+2.8 – 3.6 °C)
- **SSP585** – high-emission pathway (~+3.3 – 5.7 °C)

These scenarios span a broad range of plausible climate futures and allow assessment of emission-dependent shifts in suitable habitat. By applying identical predictor variables across paleoclimate and future simulations, the modelling framework maintains internal consistency and facilitates comparison of refugial persistence, Holocene expansion and projected shrinkage or altitudinal displacement under warming scenarios. The use of multiple GCMs and emission pathways allows explicit evaluation of structural uncertainty associated with climate model selection and scenario choice, therefore strengthening the robustness of long-term projections.

Habitat Suitability Change and Spatial Transition Analysis

To quantify the impact of projected climate change on treeline birch habitats in Caucasus, spatial comparisons were conducted between present-day suitability and future projections under alternative emission scenarios. The objective was to identify areas of persistence, shrinkage and potential expansion within the modeled climatic envelope.

MaxEnt outputs were initially generated as continuous probability surfaces representing relative habitat suitability. To enable spatial comparison across time slices, these continuous predictions were converted into binary suitability maps. Threshold selection followed a species-specific criterion based on the maximum training sensitivity plus specificity value (0.148), ensuring an optimal balance between omission and commission errors. This thresholding approach is widely applied in species distribution modelling to produce ecologically interpretable presence–absence maps (Phillips et al. 2006; Elith et al. 2011).

Binary maps representing current and future climatic suitability were then spatially overlaid at the grid-cell level. For each pixel, temporal transitions were classified into three categories:

- **Habitat Loss** (1 → 0): areas currently suitable but projected to become unsuitable under future climate conditions;
- **Habitat Stability** (1 → 1): areas maintaining suitability across time slices;
- **Habitat Gain** (0 → 1): areas currently unsuitable but projected to become climatically suitable.

This transition-based framework allows direct identification of climatically stable cores, emerging suitable zones and areas at risk of shrinkage. By applying identical thresholds and spatial resolution across scenarios, the analysis ensures methodological comparability and minimizes artificial differences caused by scaling effects.

All spatial calculations, raster overlays and reclassification procedures were performed in R (R Core Team 2018) and QGIS 3.4 (QGIS Development Team 2019). The resulting change maps were subsequently used to quantify proportional shifts in suitable habitat area under each emission pathway. This approach follows established protocols in climate-driven species distribution change analyses (Thuiller et al. 2005; Elith et al. 2011), while explicitly emphasizing transition dynamics rather than solely area-based comparisons.

Results

Model Performance and Climatic Determinants

The MaxEnt model demonstrated very high predictive performance for treeline birch habitats in the Caucasus. The Receiver Operating Characteristic (ROC) curve (Figure 8) shows strong separation between suitable and unsuitable environmental conditions. The training AUC reached 0.971, while the test AUC was 0.959 ± 0.008, indicating excellent discriminatory capacity and robust generalization ability. Considering that an AUC value of 0.5 represents random prediction and values above 0.9 are regarded as highly accurate, these results confirm that the selected climatic predictors effectively capture the environmental constraints governing birch distribution across the Caucasus region.

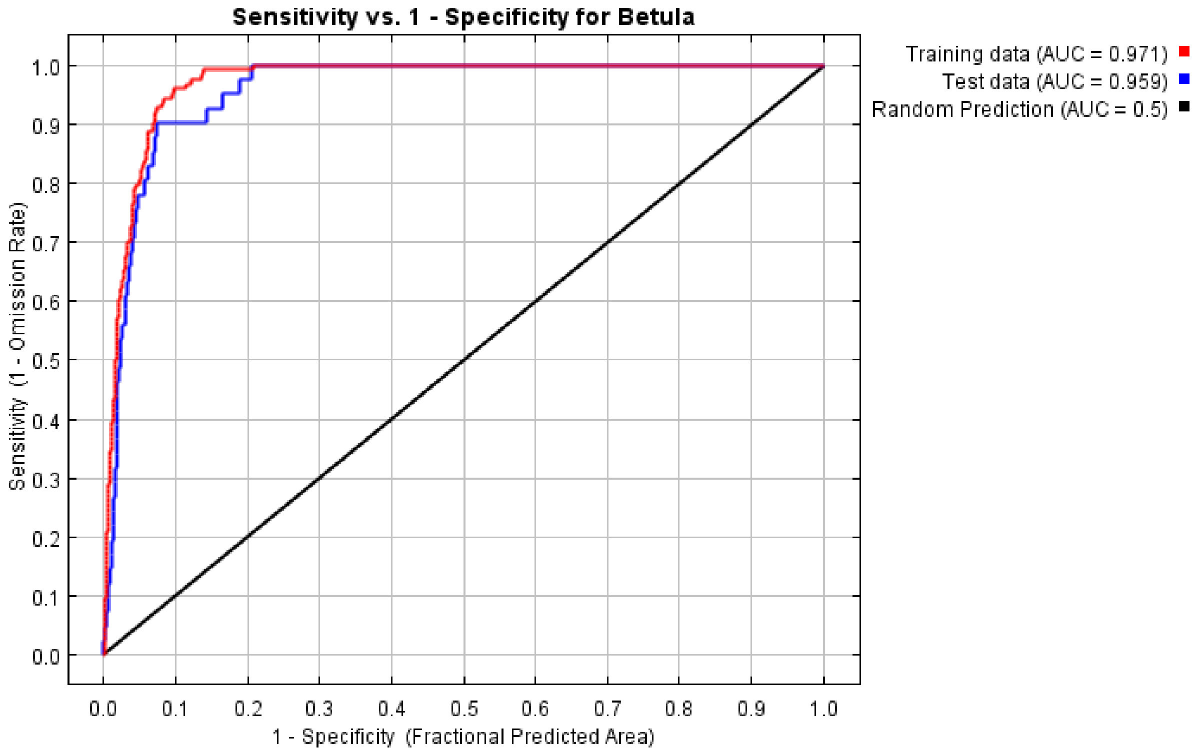

Figure 8. Receiver Operating Characteristic (ROC) curve for the MaxEnt model of *Betula* spp. in the Caucasus. The curve illustrates high model performance, AUC = 0.971, relative to random expectation (AUC = 0.5).

Analysis of variable importance reveals a clear dominance of thermal controls over precipitation-related predictors (Table 2). Among the selected bioclimatic variables, BIO10 (Mean Temperature of Warmest Quarter) showed the strongest influence, accounting for 70.4% of total model contribution and 36% permutation importance. This indicates that summer thermal conditions represent the principal climatic driver of subalpine birch habitat suitability. Although BIO11 (Mean Temperature of Coldest Quarter) contributed a smaller proportion to overall model gain (11.1%), it exhibited the highest permutation importance (46.2%).

Table 2. Relative contribution (%) and permutation importance (%) of predictor variables in the MaxEnt model for *Betula* spp. in the Caucasus.

Predictor variable	Description	Contribution (%)	Permutation importance (%)
BIO10	Mean Temperature of Warmest Quarter	70.4	36.0
BIO11	Mean Temperature of Coldest Quarter	11.1	46.2
BIO18	Precipitation of Warmest Quarter	10.6	11.7
BIO19	Precipitation of Coldest Quarter	7.9	6.1

The jackknife tests reinforce this interpretation. When used in isolation, BIO10 produced the highest training gain (Figure 9), confirming its dominant explanatory power. Conversely, omission of BIO11 caused the strongest decline in model gain, demonstrating that winter temperature plays a critical role in shaping habitat suitability. Similar patterns were observed when variable importance was evaluated using test gain and test AUC, indicating stable predictor ranking under independent validation.

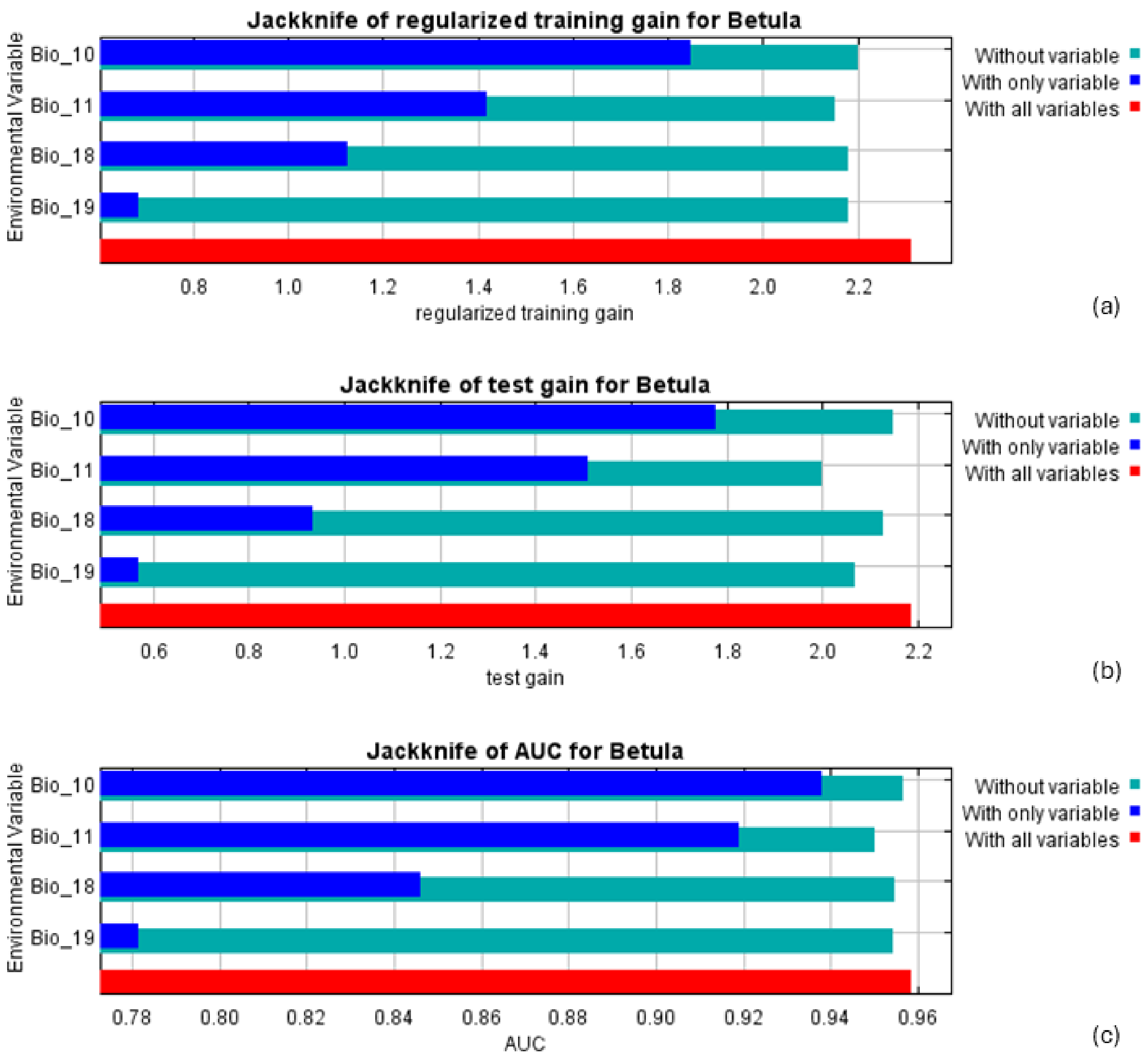

Figure 9. Jackknife evaluation of predictor importance in the MaxEnt model for *Betula* spp. in the Caucasus. Panels show jackknife results based on (a) training gain, (b) test gain and (c) test AUC. Blue bars indicate model performance when each predictor variable is used in isolation, turquoise bars represent performance when the variable is omitted, and the red bar shows model performance using all variables simultaneously.

Precipitation-related variables played a secondary but non-negligible role. BIO18 (Precipitation of Warmest Quarter) contributed 10.6% to overall model gain, while BIO19 (Precipitation of Coldest Quarter) accounted for 7.9% (Table 2). Their lower relative importance suggests that moisture availability controls habitat suitability primarily within a broader temperature-defined niche envelope rather than acting as the primary limiting factor.

Response curves (Figure 10) illustrate the relationship between each bioclimatic predictor and predicted habitat suitability. Suitability increases sharply with increasing values of BIO10 (Mean Temperature of Warmest Quarter) up to an optimal range, after which it stabilizes. In contrast, suitability declines under very low values of BIO11 (Mean Temperature of Coldest Quarter). The precipitation variables (BIO18 and BIO19) show more gradual response patterns, with moderate increases in suitability across intermediate precipitation ranges. Overall, thermal variables display steeper and more pronounced response gradients than precipitation variables.

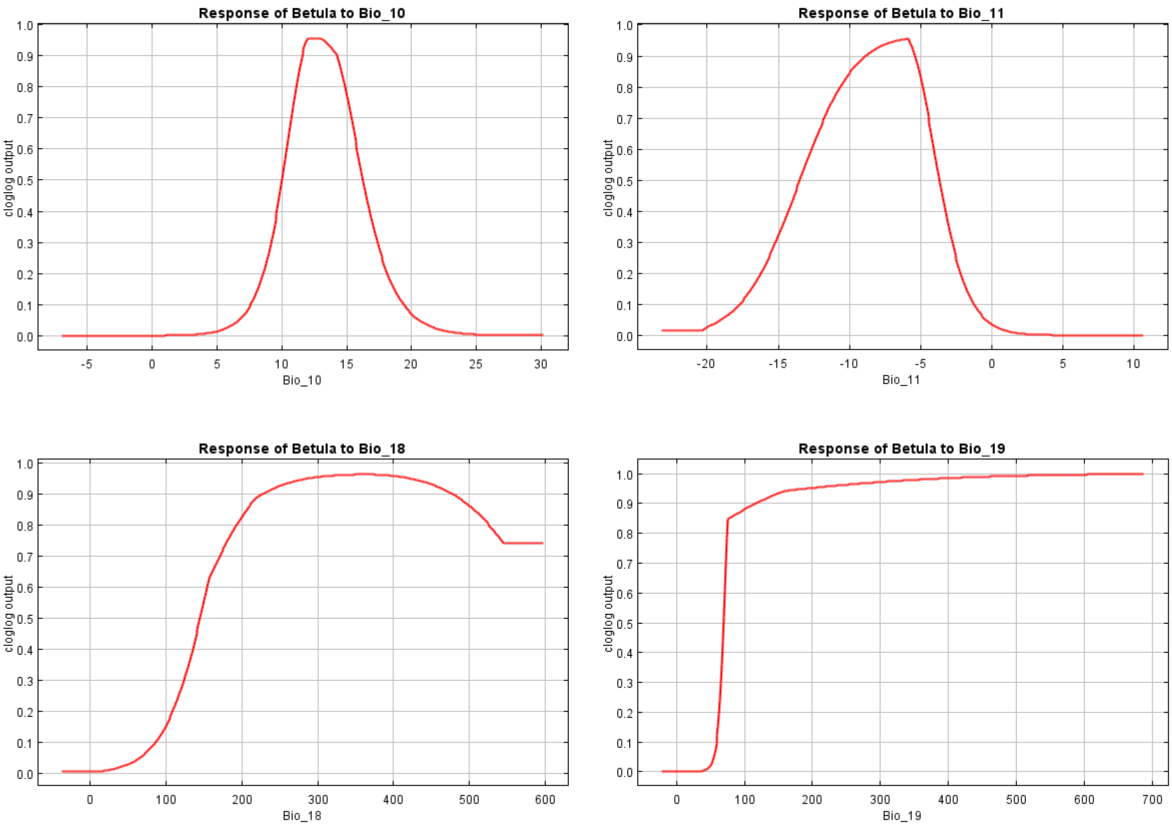

Figure 10. Response curves of the selected bioclimatic predictors in the MaxEnt model for *Betula* spp. in the Caucasus. Curves represent the marginal effect of each variable (BIO10, BIO11, BIO18 and BIO19) on predicted habitat suitability while holding other predictors constant.

Paleoclimatic Projections

Paleoclimatic projections reveal substantial spatiotemporal variation in the climatic suitability of treeline birches across the Caucasus during the Late Quaternary (Figure 11). Model outputs for the Last Glacial Maximum (LGM, ~21 ka BP) indicate extremely restricted and spatially fragmented areas of suitable habitat. Under both MIROC and CCSM simulations, predicted suitability values remain close to zero across most of the Greater and Lesser Caucasus. Interior mountainous regions exhibit virtually no modeled probability of occurrence. Suitable habitat during the LGM is confined almost exclusively to two humid peripheral regions: (1) the Black Sea coastal zone (Colchis) and (2) the southern Caspian region (Hyrcanian). These areas display the only detectable pockets of non-zero suitability under both climate models. Mean predicted suitability values remain extremely low (MIROC: 0.000147; CCSM: 0.001172), confirming the severe climatic constraints imposed during glacial conditions. Although both models agree on the geographic concentration of refugial areas, the CCSM simulation produces slightly higher suitability values relative to MIROC, suggesting minor inter-model variability in the magnitude of projected suitability.

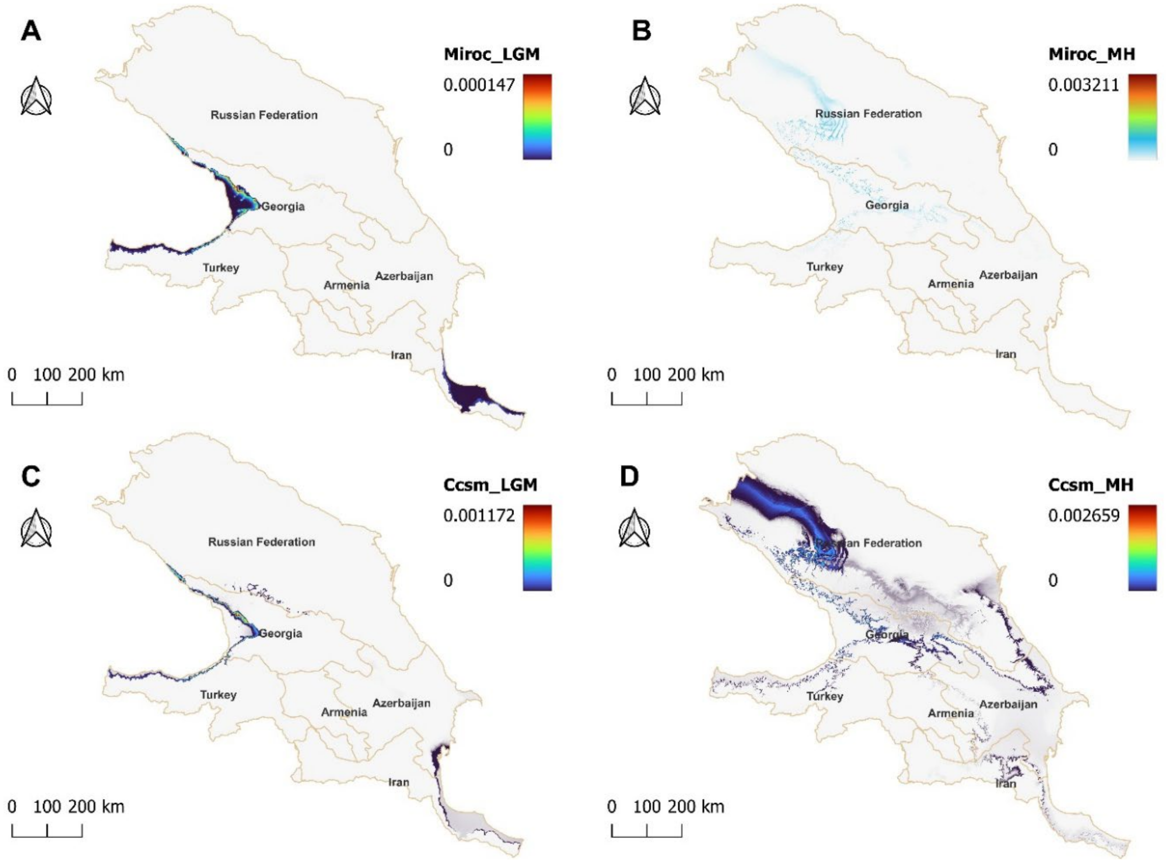

Figure 11. Paleoclimatic projections of *Betula* spp. distribution in the Caucasus during the Last Glacial Maximum and the Mid-Holocene. Panels show predicted climatic suitability under MIROC (A-B) and CCSM (C-D) paleoclimate simulations. Warmer colors represent higher probabilities of suitability, while cooler colors indicate lower probabilities.

In contrast, projections for the Mid-Holocene (MH, ~6 ka BP) demonstrate a pronounced increase in both the magnitude and spatial continuity of climatically suitable habitats. Relative to the LGM, suitability values increase several-fold across large portions of the Caucasus. Under CCSM, suitable areas form more continuous elevational belts along the Greater Caucasus and extend into segments of the Lesser Caucasus, with a mean suitability of 0.002659. The MIROC simulation yields slightly higher overall mean suitability (0.003211) and projects geographically broader but more fragmented patches of climatically favorable areas. Compared to the LGM, the MH projections display (1) greater spatial connectivity among mountainous regions, (2) expanded elevational belts of suitability and (3) increased probability values across central and western parts of the Greater Caucasus. Both models consistently indicate that the Mid-Holocene climatic regime supported a markedly wider potential distribution of birch habitats relative to glacial conditions.

Despite differences in spatial continuity and fragmentation patterns between MIROC and CCSM, the two paleoclimatic simulations converge on the same general trajectory: highly restricted suitability during the LGM followed by a substantial expansion during the Mid-Holocene. The magnitude of increase in predicted suitability and the expansion of climatically suitable belts illustrate a strong contrast between glacial refugial persistence and post-glacial distributional expansion.

Present Climatic Suitability

Projections under current climatic conditions reveal the highest overall suitability values across the entire temporal framework analyzed (Figure 12). Compared to paleoclimatic simulations, present-day projections display substantially greater spatial continuity and higher mean probability values, indicating that contemporary climatic conditions are highly favorable for treeline birch habitats in the Caucasus. Climatic suitability is predominantly concentrated along the Greater Caucasus mountain range, where continuous elevational belts of high-probability areas extend from western Georgia eastward through the central and eastern sectors. The Colchic region along the eastern Black Sea coast also exhibits notable areas of suitability, particularly within humid montane and subalpine belts. In addition, fragmented but clearly delineated patches of suitable habitat are projected within the Lesser Caucasus, particularly in the Samtskhe–Javakheti region.

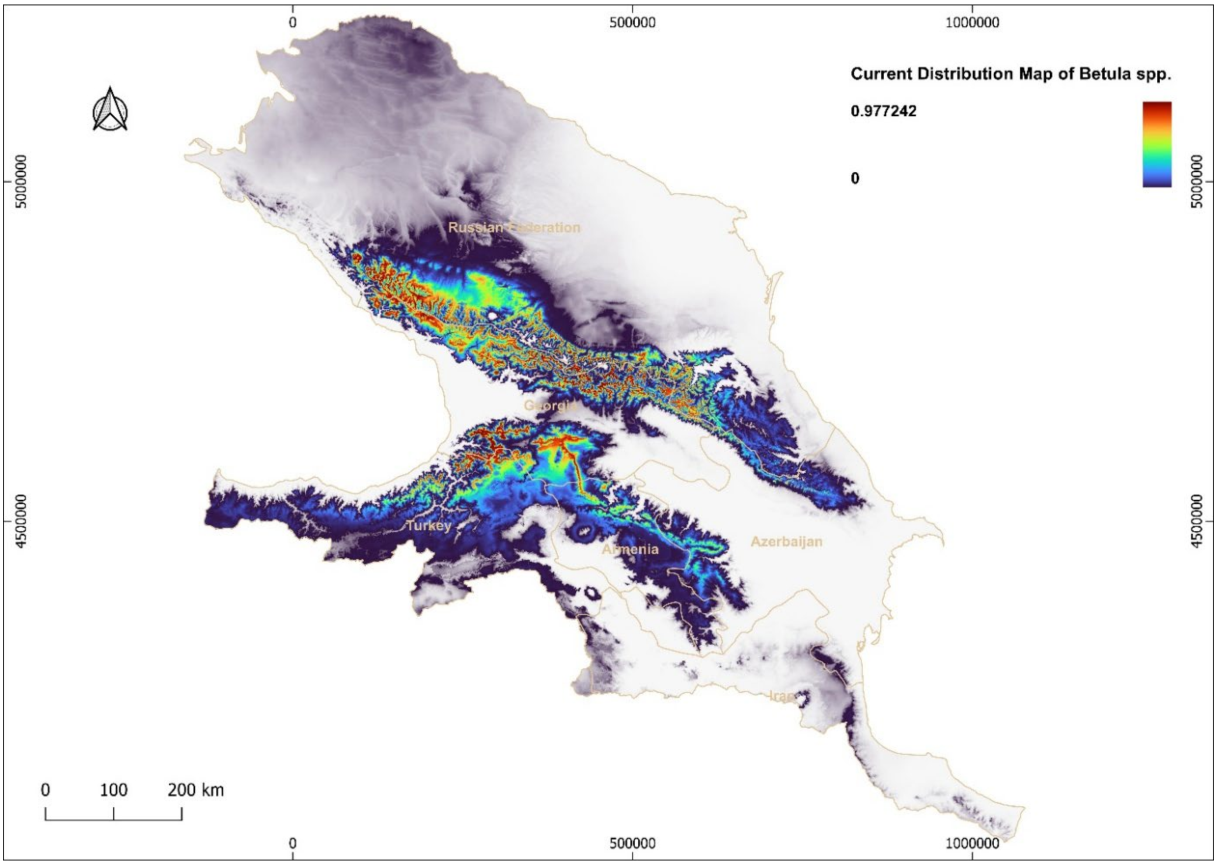

Figure 12. Present climatic suitability of *Betula* spp. distribution in the Caucasus based on MaxEnt model. The map shows the predicted probability of occurrence under current climatic conditions. Warmer colors indicate higher suitability values, while cooler colors represent lower probabilities.

The model consistently excludes permanent glaciers and subnival/nival zones from suitable habitat projections, indicating that extremely cold high-elevation environments remain climatically unsuitable. Similarly, lowland regions, including Kolkheti Plain, the Alazani Valley and the Eldari lowlands, show negligible or zero predicted suitability, reflecting clear elevational and climatic constraints. In the eastern Greater Caucasus (Kakheti region), the model identifies climatically suitable areas that correspond closely with known treeline zones. These projections are consistent with field observations and verified occurrence records, including small birch stands documented within Lagodekhi Protected Areas. The spatial correspondence between modeled suitability and empirical field plots further supports the reliability of the present-day projection.

Future Distribution Patterns

Future projections to the year 2100 reveal pronounced scenario-dependent changes in the climatic suitability of treeline birch habitats across the Caucasus (Figures 13-14; Table 3). Compared to present climatic conditions, which show the highest overall mean suitability values, future projections indicate progressive shrinkage and fragmentation of suitable habitats under increasing emission pathways.

Table 3. Projected changes in *Betula* spp. distribution in the Caucasus by 2100 under different SSP scenarios (MIROC and CMCC models).

Scenario (SSP)	Model	Loss (%)	Loss (km²)	Stable (%)	Stable (km²)	Gain (%)	Gain (km²)
SSP126 (low)	MIROC	44.8	24,212	55.2	29,815	21.5	11,599
	CMCC	69.2	37,361	30.9	16,666	28.0	15,111
SSP370 (med-high)	MIROC	82.7	44,667	17.3	9,361	24.4	13,190
	CMCC	89.3	48,227	10.7	5,800	21.9	11,845
SSP585 (high)	MIROC	95.7	51,701	4.3	2,326	19.6	10,589
	CMCC	99.8	53,901	0.2	126	13.9	7,489

Under the low-emission scenario SSP126, both MIROC and CMCC simulations project relatively moderate changes in distribution patterns (Figure 13). Suitability remains continuous across large portions of the Greater Caucasus, particularly in western and central regions, while some reductions are visible in the eastern Caucasus and parts of Armenia. Quantitative analysis (Table 3) indicates that stable habitat comprises 55.2% of the current range under MIROC and 30.9% under CMCC. Corresponding habitat losses reach 44.8% (MIROC) and 69.2% (CMCC). Projected habitat gains range between 21.5% and 28.0%, largely confined to higher elevations. Despite moderate losses, SSP126 maintains substantial continuity of climatically suitable areas within major mountain belts.

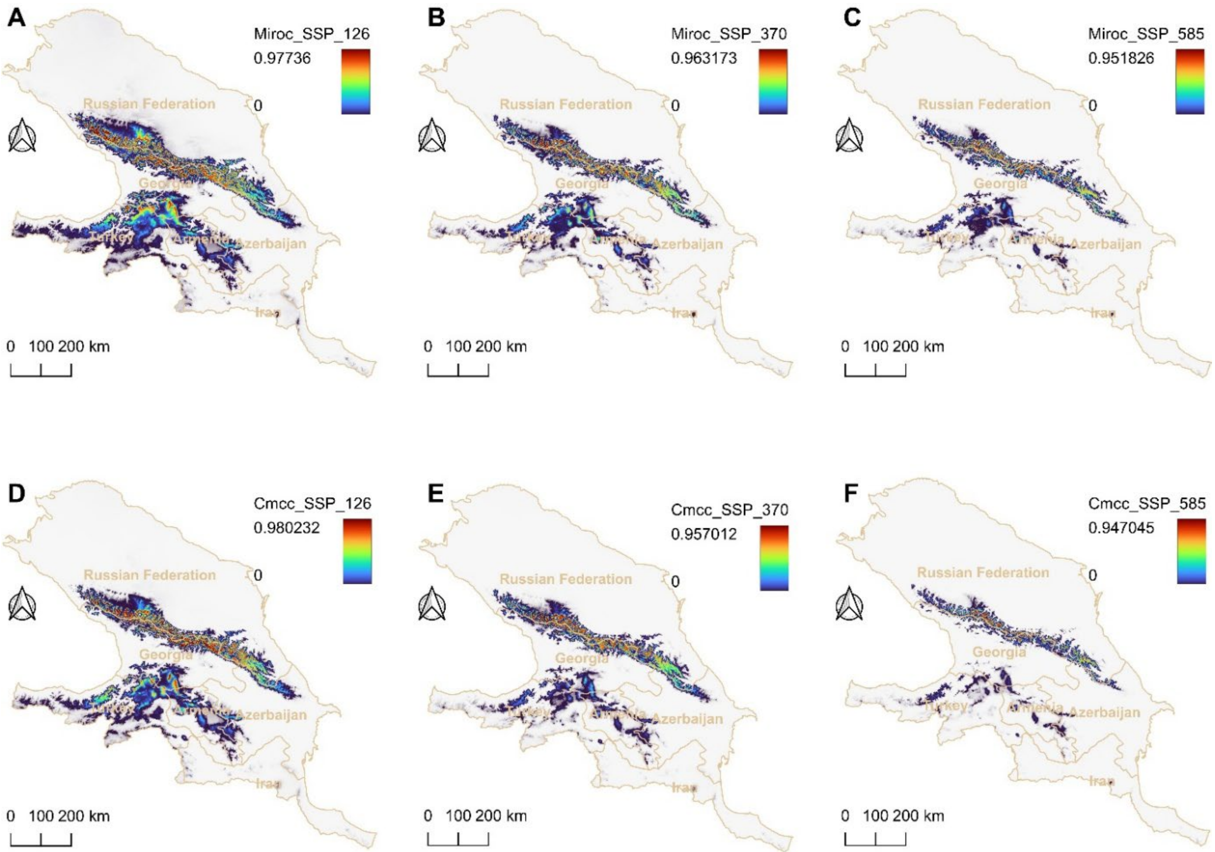

Figure 13. Future climatic suitability of *Betula* spp. in the Caucasus under SSP126, SSP370 and SSP585 scenarios based on MIROC and CMCC models. Maps illustrate the predicted probability of occurrence for 2100. Panels A-C show the MIROC model and panels D–F show the CMCC model. Warmer colors indicate higher suitability, while cooler colors represent lower probabilities.

Under the intermediate scenario SSP370, shrinkage becomes more pronounced. Both models indicate substantial reduction and fragmentation of suitable habitat. Losses exceed 80% under MIROC (82.7%) and approach 90% under CMCC (89.3%). Stable areas decline to 17.3% and 10.7%, respectively. Spatially, persistence becomes increasingly restricted to higher elevations of the Greater Caucasus, while suitability in the Lesser Caucasus and eastern ranges declines sharply. Projected gains (approximately 22-24%) remain spatially fragmented and do not compensate for widespread habitat loss. Compared to SSP126, suitable areas under SSP370 become more discontinuous and geographically isolated.

The high-emission scenario SSP585 produced the most severe reductions in climatic suitability. MIROC projects 95.7% habitat loss, while CMCC indicates near-complete loss (99.8%) of currently suitable areas. Stable habitat declines to 4.3% (MIROC) and 0.2% (CMCC), confined to narrow and isolated high-elevation patches primarily within the central and western Greater Caucasus. Habitat gains decrease further (13.9–19.6%) and remain spatially fragmented. Across the South Caucasus, most currently suitable areas become climatically unsuitable by 2100 under SSP585.

Spatial change analysis (Figure 14) confirms that future distributional dynamics are dominated by habitat loss rather than redistribution. Red zones (loss) expand progressively from SSP126 to SSP585, particularly across the Lesser Caucasus and eastern parts. Green zones (stable habitat) contract upward into higher elevations, while blue zones (gains) remain limited in extent and scattered. Across all scenarios, MIROC consistently projects slightly less severe declines compared to CMCC. Nevertheless, both models display the same overall trajectory: increasing shrinkage, fragmentation and isolation of climatically suitable birch habitats with intensifying emission pathways.

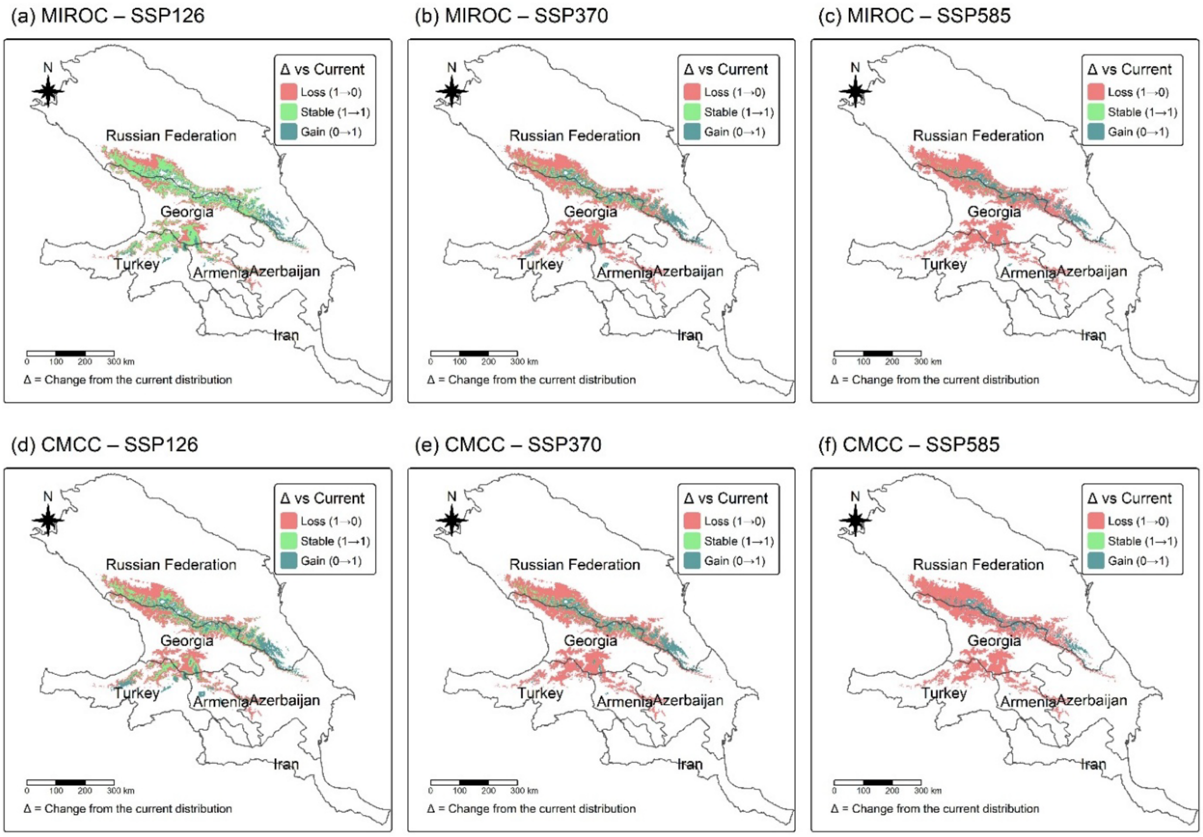

Figure 14. Spatial habitat change (Loss-Stable-Gain) of *Betula* spp. in the Caucasus by 2100 under future SSP scenarios. Red areas indicate habitat loss, green areas indicate stability and blue areas indicate gains relative to present conditions. Panels correspond to MIROC and CMCC projections under SSP126, SSP370 and SSP585.

Temporal Dynamics of Habitat Suitability

To quantitatively compare modeled habitat suitability of *Betula* spp. across paleoclimatic, present and future scenarios, the distribution of MaxEnt-derived suitability values was summarized using boxplots (Figure 15). For each grid cell within the study area, mean suitability probabilities were extracted from model outputs. To reduce right-skewness and accommodate zero values, probabilities were log-transformed using log (probability + 1e-06) following standard recommendations for proportional ecological data (Warton 2005).

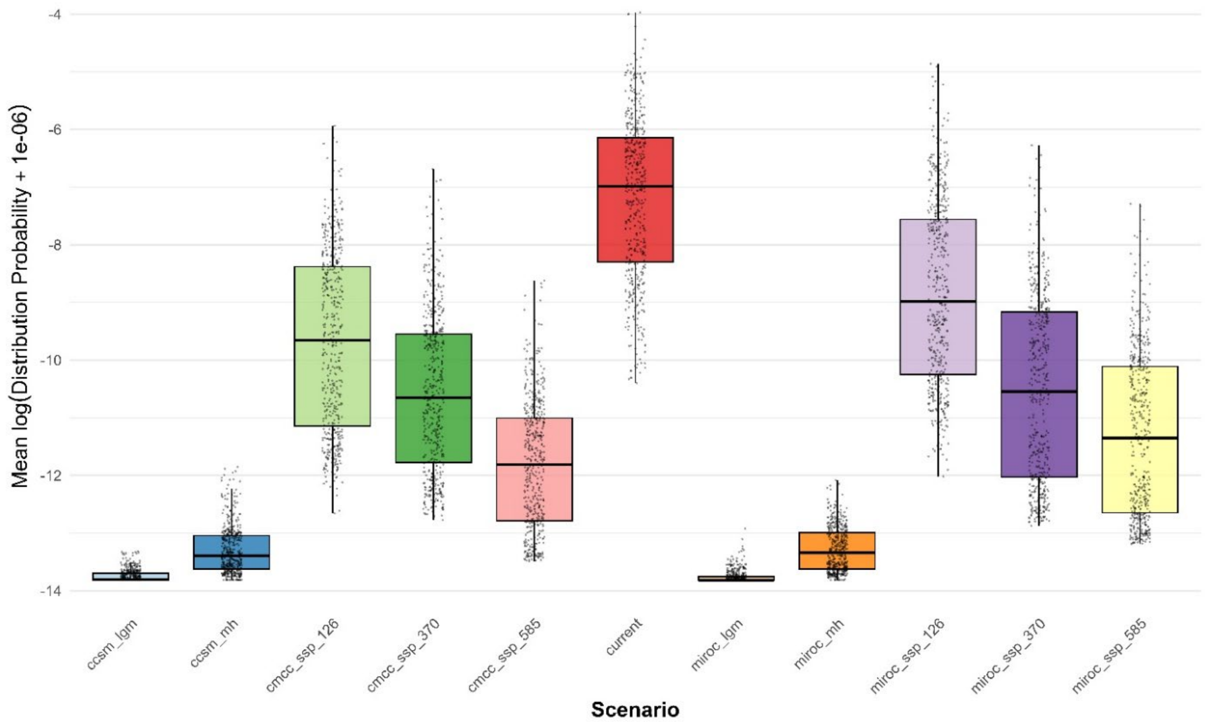

Figure 15. Spatiotemporal shifts in predicted habitat suitability for *Betula* spp. in the Caucasus from the Last Glacial Maximum to 2100. Each box represents the distribution of MaxEnt-derived suitability probabilities (log-transformed as log(probability + 1e-06)) for individual grid cells under the LGM, MH, current climate and future SSP scenarios (SSP126, SSP370, SSP585) based on CCSM, MIROC, and CMCC models. Boxes show interquartile ranges with median values indicated; whiskers represent the range of values and points denote individual grid-cell probabilities.

The boxplot distributions reveal clear and consistent temporal contrasts in habitat suitability across climatic intervals. The lowest suitability values occur under Last Glacial Maximum (LGM) conditions in both paleoclimate models (ccsm_lgm and miroc_lgm). Median values remain close to zer and the interquartile ranges are narrow, reflecting the highly restricted spatial extent of suitable climatic conditions during the glacial period. Under Mid-Holocene (MH) conditions (ccsm_mh and miroc_mh), median suitability values increase relative to the LGM. The interquartile ranges expand, indicating a broader distribution of moderate suitability across the landscape. Nevertheless, median values remain lower than those observed under current climatic conditions, demonstrating that suitability during the MH, although improved relative to the LGM, did not reach present-day levels. Current climate projections exhibit the highest median suitability values and the widest interquartile ranges among all temporal intervals. The broader spread of values indicates widespread and spatially continuous suitable conditions across the montane and subalpine belts of the Caucasus. The upper quartile values are also markedly higher than in paleoclimatic scenarios, confirming that present climatic conditions represent the most favorable suitability regime within the analyzed timeframe.

Future projections show clear scenario-dependent declines. Under SSP126, median suitability values remain relatively close to present-day conditions in both MIROC and CMCC models (although slight downward shifts are visible). Interquartile ranges contract moderately, indicating a partial reduction in overall suitability but persistence of relatively broad suitable areas. Under SSP370, a pronounced downward shift in median suitability values is observed. The interquartile range narrows considerably compared to SSP126 and present conditions, reflecting substantial contraction and fragmentation of suitable habitats. Suitability distributions shift toward lower probability values, particularly under the CMCC model. The SSP585 scenario shows the most pronounced reduction across all future projections. Median suitability values decline sharply, approaching levels observed under glacial conditions in some model runs. Interquartile ranges are narrow and concentrated at low probability values, indicating extensive loss of climatically suitable habitat. Variability among grid cells is reduced, consistent with the spatial restriction of suitability to isolated high-elevation areas. Across all scenarios, MIROC consistently produces slightly higher median suitability values than CMCC. However, both models display the same overall trajectory, showing minimal suitability during the LGM, moderate recovery during the Mid-Holocene, peak suitability under current conditions and progressive decline under increasing emission pathways.

Discussion

Climatic Controls and Ecological Interpretation of Treeline Birch Distribution

The high predictive performance of the MaxEnt model indicates that the selected climatic variables successfully capture the major environmental gradients structuring treeline birch distribution in the Caucasus. Such performance levels suggest that the real distribution of subalpine birch forests is tightly linked to seasonal climatic controls, supporting the long-established view that temperature and moisture define the upper forest boundary in mountain ecosystems (Holtmeier 2009; Körner 2012).

Among the selected predictors, growing-season temperature (BIO10) emerged as the dominant explanatory variable, accounting for 70.4% of total model contribution. This result is consistent with global treeline theory, which identifies summer warmth as the principal determinant of tree growth at high elevations. Cambial activity, xylem formation and carbon assimilation are strongly temperature-dependent processes and treeline position worldwide closely follows growing-season isotherms (Körner and Paulsen, 2004; Körner, 2012). Recent regional dendroclimatic studies in the Caucasus ecoregion confirm that radial growth in different tree species correlates strongly with warm-season temperature (Dhyani et al. 2025; Kvaratskhelia and Gavashelishvili 2025), reinforcing the ecological realism of BIO10 as a primary driver.

However, the high permutation importance of winter temperature (BIO11), despite its lower overall contribution, highlights an equally important but distinct mechanism. Winter severity regulates frost damage, snow insulation and seedling survival – processes that frequently determine recruitment success rather than adult tree persistence (Holtmeier and Broll 2005, 2019). The jackknife results, showing a marked decline in model gain when BIO11 is omitted, demonstrate that cold-season temperature provides unique explanatory information not redundant with summer warmth. This pattern supports the interpretation that treeline birch dynamics in the Caucasus are governed by a dual thermal constraint. Summer temperature controls growth potential, while winter conditions define survival thresholds.

Seasonal precipitation variables (BIO18 and BIO19) contributed to secondary but ecologically meaningful influences. Growing-season precipitation (BIO18) contributed to model performance and aligns with evidence that summer moisture availability controls productivity, particularly in more continental eastern parts of the Caucasus, where drought stress can intensify under warm conditions (Nakhutsrishvili et al. 2015; Sagheb Talebi et al. 2014). Winter precipitation (BIO19), which partly reflects snowpack dynamics, influences soil insulation and spring moisture supply. Although precipitation did not dominate the model, its consistent contribution suggests that hydrothermal interactions refine the climatic niche rather than independently determining treeline position.

Comparable patterns have been documented in other mountain systems. In the Himalaya, *Betula utilis* distribution is constrained by growing-season temperature and snow-related moisture (Bobrowski et al. 2017; Bhatta et al. 2018). In the Pyrenees, treeline shifts respond to interactions between summer temperature (BIO10) and precipitation during the growing season (Batllori et al. 2013). Fennoscandian mountain birch treeline ecosystems similarly track summer isotherms but remain sensitive to winter severity and snow conditions (Hofgaard et al. 2013; Körner and Paulsen 2004). The Caucasus therefore, fits within a broader global pattern in which temperature defines the primary climatic envelope of treeline systems, while moisture and snowpack define local persistence and recruitment dynamics.

The response curves further illustrate that temperature variables produce steeper and more threshold-like relationships with habitat suitability compared to precipitation predictors. Such response shapes are characteristic of physiological limits, where suitability increases rapidly within an optimal thermal range but declines sharply beyond lower temperature thresholds. Precipitation responses are comparatively gradual, suggesting that moisture acts as a modifying factor within a thermally defined niche space.

Late Quaternary Dynamics: Refugia and Postglacial Expansion

The paleoclimatic projections provide strong evidence that the distribution of birches in the Caucasus has been tightly linked to Late Quaternary climatic oscillations. The modeled contrast between the Last Glacial Maximum (LGM, ~21 ka BP) and the Mid-Holocene (~6 ka BP) reveals a clear refugial-expansion trajectory, consistent with independent palaeoecological records from the region. During the LGM, both MIROC and CCSM simulations indicate extremely restricted and spatially fragmented climatically suitable areas, confined almost exclusively to the humid coastal refugia of Colchis along the eastern Black Sea and the Hyrcanian region south of the Caspian Sea. Interior parts of the Greater and Lesser Caucasus show near-zero modeled suitability, reflecting the combined effects of low temperatures, strong continentality and widespread aridity under glacial conditions.

This spatial shrinkage aligns closely with palynological evidence from Georgia and adjacent regions, where arboreal pollen percentages during the LGM were minimal and *Betula* typically contributed less than 5% of the spectra (Connor et al. 2007; Shatilova et al. 2011). Vegetation assemblages were dominated by steppe and semi-desert taxa such as *Artemisia*, Chenopodiaceae, and *Ephedra*, indicating open landscapes and pronounced moisture limitation. Sedimentological and geomorphological reconstructions further demonstrate that the upper treeline limit was depressed by approximately 800–850 m relative to present elevations (Kvavadze and Connor 2005), while the lowered Black Sea level reflects reduced effective moisture during glacial intervals (Tvalchrelidze et al. 2004). Together, these records confirm that birch persistence during the LGM depended on localized, climatically buffered refugia rather than continuous elevational belts (Tarkhnishvili et al. 2012; Dering et al. 2021). The extremely low modeled suitability values do not imply complete regional absence, but rather indicate that survival was spatially constrained to microrefugia characterized by maritime influence, topographic shelter and relatively stable hydrological regimes.

In contrast, the Mid-Holocene projections demonstrate a pronounced expansion in both the magnitude and spatial continuity of climatically suitable habitats. Under warmer and more humid conditions, suitability values increase several-fold relative to glacial simulations and continuous elevational belts re-emerge along the Greater Caucasus, with extensions into parts of the Lesser Caucasus. This modeled expansion corresponds closely to palynological records documenting substantial increases in birch abundance during the Early and Mid-Holocene, with *Betula* percentages rising to 30–50% in many sediment sequences (Connor et al. 2004; Connor and Kvavadze 2009; Shatilova et al. 2011; Messager et al. 2017). Weighted-averaging reconstructions indicate peak precipitation between approximately 7000-4000 cal yr BP (Connor and Kvavadze 2009), coinciding with the maximum expansion of mesophilous forests. During this period, birch formed extensive stands and participated in mixed forest assemblages including *Corylus*, *Quercus*, *Fagus*, *Carpinus* and *Abies*, reflecting both climatic amelioration and successional dynamics.

The Holocene expansion illustrates birch's ecological flexibility and pioneer capacity under favorable hydrothermal regimes. However, subsequent declines in birch dominance in many regions underline the importance of successional replacement once climatic conditions stabilized and late-successional taxa became competitively dominant. This demonstrates that while climate defines the potential niche envelope, realized distribution is further shaped by interspecific competition and community development. Regional heterogeneity further indicated these dynamics. Coastal Colchis and Hyrcania maintained forest continuity even during glacial maxima due to maritime buffering, whereas interior areas such as Javakheti remained more sensitive to aridity. Palynological sequences from Javakheti region indicate that birch and hazel were among the earliest taxa to expand following glacial retreat, later replaced by fir-beech-oak assemblages in the Mid-Holocene (Connor and Kvavadze 2009; Shatilova et al. 2011). The persistence of small birch remnants today on the northern slopes of Tabatskhuri and Kartsakhi lakes (Akobia et al. 2022) reflects this long-term legacy of climatic filtering and successional turnover.

Present-Day Distribution: Climate, Competition and Historical Legacies

Under contemporary climatic conditions, the modeled suitability patterns indicate that the present climate represents a broadly favorable envelope for treeline birches across the Caucasus. Compared to paleoclimatic simulations, current projections show the highest overall suitability values and substantially greater spatial continuity, particularly along the Greater Caucasus mountain range. Continuous belts of high-probability habitat extend from the humid western parts eastward through the central and eastern Greater Caucasus, closely corresponding to known subalpine and treeline zones. The Colchic region also exhibits elevated suitability within its montane and subalpine belts, reflecting the moderating influence of Black Sea humidity. Fragmented but distinct areas of suitable habitat are projected within the Lesser Caucasus, particularly in Samtskhe-Javakheti. Simultaneously, the model clearly delineates climatic boundaries. Permanent glaciers and subnival/nival belts remain outside the suitable envelope, confirming that extreme cold and prolonged snow-free exposure at the highest elevations limit birch establishment. Similarly, lowland regions such as the Kolkheti Plain, Alazani Valley and Eldari lowlands show insignificant suitability, reflecting strong elevational and thermal constraints. The spatial agreement between modeled suitability and verified field records, which include small birch stands within Lagodekhi Protected Areas, provides further support for the robustness of the projection. The model effectively captures both currently occupied stands and areas that are climatically favorable but not necessarily fully forested, indicating that it approximates the fundamental climatic niche rather than realized distribution alone.

However, present-day birch distribution cannot be interpreted solely through climate. While temperature and precipitation during the warmest and coldest quarters define the principal niche dimensions, actual stand composition is further shaped by interspecific competition, successional dynamics and local site conditions. In the southern and southeastern Caucasus, treeline belts are frequently dominated by conifers such as *Pinus sylvestris* var. *hamata* and drought-tolerant deciduous species such as *Quercus macranthera*, which are better adapted to continental conditions and can competitively limit birch establishment (Zazanashvili et al. 2000). In contrast, the humid western Caucasus which is strongly influenced by the Black Sea, supports mesophilous broad-leaved forests, where *Fagus orientalis* often occupies the upper forest belt and may restrict birch dominance through shading and successional replacement (Dolukhanov 2010; Nakhutsrishvili 2013).

Local-scale ecological interactions further complicate distribution patterns. Understory shrub communities, particularly *Rhododendron caucasicum*, may either inhibit birch regeneration by limiting light availability or facilitate seedling survival under harsh microclimatic conditions, depending on slope exposure and snow dynamics (Akhalkatsi et al. 2006; Bobrowski et al. 2017). Snow cover duration and soil moisture retention, especially on northern and northwestern slopes, are widely recognized as important drivers of *Betula litwinowii* establishment in the Central Caucasus (Hughes et al. 2009; Nakhutsrishvili 1999). Nevertheless, field observations indicate that birches are not strictly confined to northern exposures and can persist on southern and southwestern slopes where sufficient moisture and snow insulation occur. These findings highlight that microtopography, slope inclination and snowpack stability interact with regional climate to determine local suitability.

The Lesser Caucasus presents an informative case. Although the Javakheti Plateau is currently largely unforested due to harsh continental conditions and strong historical anthropogenic pressure (Grossheim 1936; Margalitadze 1970; Messager et al. 2013; Troitsky 1927), climatic conditions alone do not appear to fully limit birch occurrence. Palynological evidence confirms the historical presence of birch in the region (Connor and Kvavadze 2009; Shatilova et al. 2011) and small modern fragments persist on the northern slopes of Tabatskhuri and Kartsakhi lakes (Akobia et al. 2022). This suggests that present-day absence in some climatically suitable areas reflects land-use legacy and successional history rather than purely climatic exclusion.

At the southern borders of the birch distribution, including northern Armenia and the Hyrcanian–Elburz region of Iran, the model identifies only low-probability patches consistent with fragmented stands documented in floristic studies (Bina et al. 2016; Saghatelyan 2006; Zare et al. 2010). These peripheral occurrences likely represent long-term refugial persistence and isolated populations rather than continuous occupancy.

Future Trajectories: Mechanisms of Climatic Shrinkage

Future projections indicate that the current climatic optimum for treeline birches in the Caucasus is likely to be temporary. Across emission pathways (SSP126, SSP370 and SSP585), projected changes follow a consistent trajectory of shrinkage, fragmentation and elevational confinement, with the magnitude of decline closely linked to greenhouse gas emissions. While lower-emission scenarios (SSP126) retain comparatively greater continuity of suitable habitat, intermediate (SSP370) and high-emission (SSP585) pathways produce pronounced shrinkage, suggesting that the stability observed under present climatic conditions will not persist under sustained warming. The projected response is not a simple upward shift of distribution limits. Although warming can theoretically relax thermal constraints and open higher elevations to colonization, several interacting mechanisms limit the compensatory potential of upslope migration.

Firstly, increasing warm-season temperatures intensify evaporative demand and may increase moisture stress where precipitation does not increase proportionally (Moyes et al. 2015; Bailey et al. 2021). This process is particularly relevant in the eastern and southern Caucasus, where continentality and seasonal aridity already constrain regeneration (Nakhutsrishvili et al. 2015; Sagheb Talebi et al. 2014). Under such conditions, higher temperatures may reduce seedling establishment even if adult trees temporarily persist, leading to demographic bottlenecks and long-term population decline. Secondly, winter processes impose additional constraints. Altered snow regimes and increased variability in freeze-thaw cycles can reduce the insulating function of snowpack, exposing seedlings to frost damage and early-season drought (Holtmeier and Broll 2005, 2019). Winter severity and snow cover duration are critical for treeline dynamics because they regulate soil moisture retention and protect overwintering tissues. If warming leads to reduced snow stability without sufficient compensation in moisture availability, recruitment may decline even where mean annual temperatures become more favorable (Huang et al. 2023). Third, successional and competitive dynamics may amplify climatic effects. Birch species, particularly *Betula litwinowii*, function as pioneer or early-successional taxa in many Caucasian subalpine systems. Under warming, late-successional competitors that include mesophilous broad-leaved species in humid regions and drought-tolerant taxa in continental sectors may gain an advantage, while suppressing birch regeneration through shading and competition for soil moisture (Lyu and Alexander 2022; Zheng et al. 2026). Evidence from other mountain systems shows that conifers and late-successional species often advance upslope more rapidly than birches under warming, resulting in reduced birch recruitment despite rising temperatures (Sigdel et al. 2024). Similar dynamics are likely to occur in the Caucasus, where both coniferous and broad-leaved competitors are well established along subalpine belts.

Topographic constraints further intensify vulnerability. The steep elevational gradients of the Caucasus limit the availability of continuous land area at higher elevations. Soil development, slope stability and microhabitat continuity decline rapidly toward summit zones, creating a pronounced “mountain squeeze” effect in which potential high-elevation gains are spatially restricted and fragmented. This phenomenon has been widely documented in alpine systems and is considered a major driver of range contraction under climate change (Holtmeier and Broll 2019; Myers-Smith et al. 2020). As lower belts become unsuitable and higher belts offer limited colonizable space, the net outcome is a reduction rather than an expansion of climatically viable habitat.

Importantly, differences between climate models do not alter the overall trajectory. Although structural variations among general circulation models influence the magnitude of projected loss, particularly through differences in precipitation seasonality and winter severity, the convergence of independent simulations on the same shrinkage-fragmentation pattern strengthens confidence in the robustness of the projected trend. Higher emission pathways consistently amplify habitat loss and spatial isolation, underlying the sensitivity of treeline birch ecosystems to sustained warming.

When interpreted in the context of past dynamics, the future projections suggest a partial return to a refugial configuration, although driven by warming rather than cooling. During the Last Glacial Maximum, birches persisted in localized coastal refugia under cold-arid conditions; under high-emission futures, suitability becomes confined to isolated high-elevation refugia under warm-dry stress. In both cases, persistence is spatially constrained and fragmented. The difference lies in the direction of climatic forcing, but the structural outcome as a restricted and discontinuous distribution, remains comparable.

Taken together, these findings indicate that treeline birches in the Caucasus face substantial vulnerability under climate change. Even under moderate emission scenarios, losses are considerable, and under high-emission futures, suitable habitat becomes severely fragmented and geographically restricted. The combined influence of moisture limitation, altered snow regimes, competitive displacement, and strong topographic constraints suggests that future dynamics will be governed not by simple upward migration, but by contraction into increasingly isolated high-elevation refugia. Such fragmentation may reduce connectivity among stands, limit genetic exchange, and diminish ecosystem resilience, with cascading consequences for subalpine biodiversity and ecosystem functioning in the Caucasus.

Conclusion and Recommendations

Conclusion

This research provides the first integrated spatiotemporal reconstruction of subalpine treeline birch (*Betula* spp.) habitat dynamics in the Caucasus from the Last Glacial Maximum to projected conditions in 2100. By combining field-validated occurrence data, high-resolution bioclimatic predictors, paleoclimatic simulations and CMIP6 future scenarios within a unified ecological niche modelling framework, the study clarifies both the long-term climatic sensitivity and the emission-dependent vulnerability of treeline ecosystems in the Caucasus.

The results demonstrate that the distribution of subalpine birch forests has been highly responsive to late Quaternary climatic oscillations. During the Last Glacial Maximum, climatically suitable habitats were strongly restricted and largely confined to humid refugial sectors, particularly within the Colchic and Hyrcanian lowlands and adjacent foothill systems. These areas likely functioned as long-term microrefugia, enabling persistence of birch taxa under cold and relatively dry glacial conditions. With the onset of the Holocene and the improvement of hydrothermal regimes, birch expanded rapidly, occupying newly available montane and subalpine environments. The Early to Mid-Holocene represents a regional climatic optimum, characterized by the broadest extent of suitable habitats and enhanced ecological connectivity across the Greater and Lesser Caucasus. These findings align with palynological evidence indicating increased birch representation during postglacial warming and confirm the Caucasus as both a refugial stronghold and a center of postglacial recolonization.

Under present climatic conditions, treeline birches occupy an apparent thermal-moisture optimum across large portions of the Greater Caucasus and western humid sectors. Model performance and variable contribution analyses indicate that this distribution is primarily governed by seasonal thermal constraints, especially summer temperature (BIO10) and winter temperature (BIO11), while seasonal precipitation (BIO18 and BIO19) plays a secondary but ecologically meaningful role. The dominance of thermal predictors confirms the central role of growing-season warmth in regulating productivity and cambial activity, as well as the importance of winter temperature in controlling frost tolerance and survival at high elevations. Nevertheless, the contribution of precipitation variables underlines that treeline dynamics in the Caucasus are shaped by hydrothermal interactions rather than temperature alone.

However, this contemporary climatic optimum appears temporary. Future projections reveal pronounced scenario-dependent divergence. Under the low-emission pathway (SSP126), habitat suitability remains relatively stable, with limited shrinkage and preservation of most current distribution cores. In contrast, intermediate (SSP370) and high-emission (SSP585) scenarios indicate progressive shrinkage and fragmentation of climatically suitable areas. Under SSP585 in particular, suitable habitats become increasingly restricted to isolated high-elevation refugial patches, especially in the central Greater Caucasus and localized humid sectors. Rather than exhibiting a uniform upslope shift, birch treeline habitats show patterns of shrinkage and spatial fragmentation, suggesting that warming does not necessarily translate into continuous altitudinal expansion. Instead, excessive thermal stress combined with changing moisture regimes may compress suitable climatic space, leading to habitat loss at lower and mid-elevations without fully compensatory gains at higher altitudes.

The findings have important theoretical implications. First, they reinforce the concept of climatic niche conservatism across late Quaternary timescales, as the same seasonal thermal constraints that shaped glacial persistence also determine future vulnerability. Second, they demonstrate that treeline ecosystems cannot be interpreted solely through a linear „warming equals upslope advance" paradigm. The Caucasus example highlights the multidimensional nature of ecological limits, where hydrothermal balance, seasonal extremes and demographic inertia interact to regulate distributional outcomes. Third, the results emphasize regional heterogeneity while western humid sectors, eastern continental slopes and southern Caucasus highlands respond differently to projected climate trajectories, reflecting underlying differences in moisture regimes, topographic buffering, and historical land use.

From a conservation perspective, the Caucasus emerges simultaneously as a long-term refugial region and a climate-sensitive hotspot. The same topographic complexity that facilitated glacial persistence now offers potential microclimatic buffering under moderate warming, yet extreme emission trajectories threaten to exceed these buffering capacities. Anticipated shrinkage and fragmentation of treeline birch habitats may have cascading consequences for slope stabilization, hydrological regulation, carbon storage and alpine biodiversity. As keystone components of the upper forest belt, subalpine birch forests support endemic and relict taxa dependent on structurally complex forest-alpine ecotones. Habitat fragmentation under high-emission scenarios may therefore amplify risks to regional biodiversity and ecosystem resilience.

Subalpine birch forests of the Caucasus follow a long-term refugia – expansion – optimum – shrinkage trajectory under climatic forcing. Past glacial confinement, Holocene expansion and present stability under higher emission pathways are succeeded by projected contraction and spatial fragmentation. The magnitude of future habitat loss is strongly dependent on global mitigation trajectories. Low-emission scenarios allow relative persistence of current distribution cores, whereas high-emission scenarios confine birch habitats to isolated high-elevation refugia. The future of treeline ecosystems in the Caucasus is therefore not predetermined by warming alone, but contingent upon the interaction between climatic intensity, regional hydrothermal regimes and global emission pathways. Integrating paleoclimatic perspectives with future projections provides a coherent framework for anticipating ecological risk and guiding adaptive conservation strategies in one of the world's most complex and biodiverse mountain systems.

Conservation and Management Recommendations

The projected shrinkage and fragmentation of subalpine birch treeline habitats under future climate scenarios carry significant implications for high-mountain ecosystem stability in the Caucasus. Treeline forests are not merely distributional boundaries of woody vegetation. They represent structurally and functionally critical ecological systems. Subalpine birch stands contribute to slope stabilization, regulation of hydrological processes, carbon storage, soil development and the maintenance of alpine-subalpine biodiversity mosaics. Disruption of treeline continuity therefore has cascading ecological consequences extending beyond the birch communities themselves.

Under intermediate and high-emission scenarios, projected shrinkage and spatial fragmentation may reduce the ecological resilience of the upper forest belt. Loss of continuous forest cover increases susceptibility to soil erosion, shallow landslides and accelerated surface runoff, particularly on steep Caucasian mountain slopes characterized by thin soils and high precipitation gradients. In addition, fragmentation may alter microclimatic buffering capacity at the forest-alpine ecotone, intensifying exposure to temperature extremes and wind stress. Such structural degradation can destabilize not only birch populations but also associated endemic and relict taxa dependent on subalpine forest habitats. Habitat fragmentation also poses demographic and genetic risks. As climatically suitable areas become confined to isolated high-elevation patches, population connectivity may decline. Reduced gene flow and smaller effective population sizes increase vulnerability to stochastic disturbances, including drought events, pest outbreaks and extreme winters. Pioneer species such as birch depend on episodic recruitment windows under favorable hydrothermal conditions. Thus, fragmentation may limit dispersal pathways and reduce colonization opportunities in newly suitable habitats. Where topography restricts further upslope migration, local extinctions may become more probable, particularly under high-emission scenarios.

The spatial loss – stability – gain analysis provides a practical framework for identifying priority conservation areas. Regions demonstrating climatic stability across temporal projections represent critical refugial cores for long-term persistence. In particular, the humid Colchic sector, Hyrcanian fringe systems and high-elevation zones of the central and western Greater Caucasus consistently show comparatively higher stability under low-emission pathways. These areas function simultaneously as historical glacial refugia and potential future climatic refuges. Their protection should therefore constitute a central pillar of conservation strategy.

Based on the projected patterns of vulnerability, the following strategic directions are recommended: (1) Prioritization of protecting climatically stable refugial strongholds; (2) Maintenance and restoration of ecological connectivity; (3) Integration of climate projections into forest management and protected area planning processes; (4) Strengthening of monitoring systems; (5) Reduction of non-climatic stressors to enhance resilience; and (6) Promotion transboundary cooperation.

Importantly, emission pathway dependency highlights the broader context of global mitigation. Under low-emission scenarios, large portions of the current treeline distribution remain stable, suggesting that climate mitigation policies directly influence conservation outcomes at regional scales. Conversely, under high-emission trajectories, even well-protected areas may experience substantial habitat contraction. Therefore, regional conservation strategies must be aligned with international climate mitigation efforts.

References

Abdaladze, Otar, George Nakhutsrishvili, Maia Akhalkatsi, and William. K. Smith. 2005. "Treeline Ecotone Structure and Some Ecological Features of Betula Litwinowii in the Central Greater Caucasus." *Proccessing of Georgian Acadamy Science* 3 (2): 57–65.

Abdaladze, Otar, Gia Nakhutsrishvili, Ketevan Batsatsashvili, Khatuna Gigauri, Tamar Jolokhava, and George Mikeladze. 2015. "Sensitive Alpine Plant Communities to the Global Environmental Changes (Kazbegi Region, the Central Great Caucasus)." *American Journal of Environmental Protection 2015, Volume 4, Page 93* 4 (3): 93–100. https://doi.org/10.11648/J.AJEP.S.2015040301.25.

Aguilar, Enric, Thomas C. Peterson, Pedro R. Obando, Raúl Frutos, José A. Retana, Marta Solera, et al. 2005. "Changes in Precipitation and Temperature Extremes in Central America and Northern South America, 1961–2003." *Journal of Geophysical Research: Atmospheres* 110 (D23). https://doi.org/10.1029/2005JD006119.

Akatov, P. V. 2009. "Changes in the Upper Limits of Tree Species Distribution in the Western Caucasus (Belaya River Basin) Related to Recent Climate Warming." *Russian Journal of Ecology* 40 (1): 33–38. https://doi.org/10.1134/S1067413609010056/METRICS.

Akhalkatsi, Maia, Otar Abdaladze, George Nakhutsrishvili, and William. K. Smith. 2004. "Global Warming Effect on Birch Seedling Establishment at Tree Line in the Central Caucasus." *Botanikertagung, Braunschweig* 386 (05).

———. 2006a. "Facilitation of Seedling Microsites by Rhododendron Caucasicum Extends the Betula Litwinowii Alpine Treeline." *Arctic, Antarctic, and Alpine Research* 38 (4): 481–88. https://doi.org/10.1657/1523-0430(2006)38.

Akhalkatsi, Maia, Otar Abdaladze, George Nakhutsrishvili, and William K Smith. 2006b. "Facilitation of Seedling Microsites by Rhododendron Caucasicum Extends the Betula Litwinowii Alpine Treeline, Caucasus Mountains, Republic of Georgia." *Arctic, Antarctic, and Alpine Research* 38 (4): 481–88. https://doi.org/10.1657/1523-0430(2006)38.

Akhalkatsi, Maia, Natalia Togonidze, Giorgi Arabuli, Nana Goginashvili, and William. K. Smith. 2018. "Birch Forest and Rhododendron on North-Facing Slopes in Central Greater Caucasus." *International Journal of Research Studies in Science, Engineering and Technology* 5 (6): 14.

Akkemik, Ünal, Besim Seratok, and Ferdi Akarsu. 2017. "Distribution of Betula Pendula during Late Quaternary to the Present and Characteristics of Its Lowest Growing Area in Turkey." *Eurasian Journal of Forest Science* 5 (2): 1–18. https://doi.org/10.31195/EJEJFS.351279.

Akobia, Ilia. 2013. "Prospects for Forest Restoration in Javakheti National Park." Tbilisi: Ilia State University (in Georgian).

Akobia, Ilia, Zurab Janiashvili, Vasil Metreveli, Nugzar Zazanashvili, Ketevan Batsatsashvili, and Ketevan Ugrekhelidze. 2022. "Modelling the Potential Distribution of Subalpine Birches (Betula Spp.) in the Caucasus." *Community Ecology* 23 (2): 209–18. https://doi.org/10.1007/S42974-022-00097-4/METRICS.

Andrus, Robert A., Rachel K. Chai, Brian J. Harvey, Kyle C. Rodman, and Thomas T. Veblen. 2021. "Increasing Rates of Subalpine Tree Mortality Linked to Warmer and Drier Summers." *Journal of Ecology* 109 (5): 2203–18. https://doi.org/10.1111/1365-2745.13634.

Araújo, Miguel B., and A. Townsend Peterson. 2012. "Uses and Misuses of Bioclimatic Envelope Modeling." *Ecology* 93 (7): 1527–39. https://doi.org/10.1890/11-1930.1.

Arekhi, Maliheh, Ahmet Yesil, Ulas Yunus Ozkan, and Fusun Balik Sanli. 2018. "Detecting Treeline Dynamics in Response to Climate Warming Using Forest Stand Maps and Landsat Data in a Temperate Forest." *Forest Ecosystems* 5 (1): 1–14. https://doi.org/10.1186/S40663-018-0141-3/TABLES/3.

Ashburner, Kenneth, and Hugh McAllister. 2013. *The Genus Betula - a Taxonomic Revision of Birches*. Botanical Magazine Monograph, vol. 5, Royal Botanic Gardens, Kew .

Batllori, Enric, Marc André Parisien, Meg A. Krawchuk, and Max A. Moritz. 2013. "Climate Change-Induced Shifts in Fire for Mediterranean Ecosystems." *Global Ecology and Biogeography* 22 (10): 1118–29. https://doi.org/10.1111/GEB.12065.

Bebi, Peter, Felix Kienast, and Walter Schönenberger. 2001. "Assessing Structures in Mountain Forests as a Basis for Investigating the Forests' Dynamics and Protective Function." *Forest Ecology and Management* 145 (1–2): 3–14. https://doi.org/10.1016/S0378-1127(00)00570-3.

Bhatta, Kuber Prasad, John Arvid Grytnes, and Ole Reidar Vetaas. 2018. "Downhill Shift of Alpine Plant Assemblages under Contemporary Climate and Land-Use Changes." *Ecosphere* 9 (1): e02084. https://doi.org/10.1002/ECS2.2084.

Bina, Hamid, Hamed Yousefzadeh, Syed Shujait Ali, and Mohammad Esmailpour. 2016. "Phylogenetic Relationships, Molecular Taxonomy, Biogeography of Betula, with

Emphasis on Phylogenetic Position of Iranian Populations." *Tree Genetics & Genomes* 12 (84): 1–17. https://doi.org/10.1007/S11295-016-1037-4.

Bobrowski, Maria, Lars Gerlitz, and Udo Schickhoff. 2017. "Modelling the Potential Distribution of Betula Utilis in the Himalaya." *Global Ecology and Conservation* 11 (July): 69–83. https://doi.org/10.1016/J.GECCO.2017.04.003.

Bohn, Udo, Gisela Gollub, Christoph Hettwer, Zdenka Neuhäuslová, Thomas Raus, Heinz Schlüter, and Herbert Weber. 13523. "Karte Der Natürlichen Vegetation Europas / Map of the Natural Vegetation of Europe. Maßstab / Scale 1 : 2 500 000." Münster (Landwirtschaftsverlag). www.lv-h.de/bfn.

Bousquet, Jean, Steven H. Strauss, and Peng Li. 1992. "Complete Congruence between Morphological and RbcL-Based Molecular Phylogenies in Birches and Related Species (Betulaceae)." *Molecular Biology and Evolution* 9 (6): 1076–88. https://doi.org/10.1093/oxfordjournals.molbev.a040779.

Braconnot, P., B. Otto-Bliesner, S. Harrison, S. Joussaume, J. Y. Peterchmitt, A. Abe-Ouchi, M. Crucifix, et al. 2007. "Results of PMIP2 Coupled Simulations of the Mid-Holocene and Last Glacial Maximum – Part 1: Experiments and Large-Scale Features." *Climate of the Past* 3 (2): 261–77. https://doi.org/10.5194/CP-3-261-2007.

Camarero, J. J., and E. Gutiérrez. 2002. "Plant Species Distribution across Two Contrasting Treeline Ecotones in the Spanish Pyrenees." *Plant Ecology* 162 (2): 247–57. https://doi.org/10.1023/A:1020367918521/METRICS.

Chen, Zhi Duan, Steven R. Manchester, and Hai Ying Sun. 1999. "Phylogeny and Evolution of the Betulaceae as Inferred from DNA Sequences, Morphology, and Paleobotany." *American Journal of Botany* 86 (8): 1168–81. https://doi.org/10.2307/2656981.

"Colchic and Hyrcanian Forests of the Caucasus: Similarities, Differences and Conservation Status." n.d. Accessed September 28, 2025. https://herbmedit.org/papers/b1ff946f-e605-4d5c-b7d8-f586b09037e0.

Collins, Matthew, Reto Knutti, Julie Arblaster, Jean-Louis Dufresne, Thierry Fichefet, Pierre Friedlingstein, Xuejie Gao, et al. 2013. "Long-Term Climate Change: Projections, Commitments and Irreversibility." Cambridge University Press. https://research.monash.edu/en/publications/long-term-climate-change-projections-commitments-and-irreversibil.

Cong, Yu, Yongfeng Gu, Wen J. Wang, Lei Wang, Zhenshan Xue, Yingyi Chen, Yinghua Jin, et al. 2024. "The Interaction between Temperature and Precipitation on the Potential Distribution Range of Betula Ermanii in the Alpine Treeline Ecotone on the

Changbai Mountain." *Forest Ecosystems* 11 (January): 100166. https://doi.org/10.1016/J.FECS.2024.100166.

Connor, Simon E., and Eliso V. Kvavadze. 2009a. "Modelling Late Quaternary Changes in Plant Distribution, Vegetation and Climate Using Pollen Data from Georgia, Caucasus." *Journal of Biogeography* 36 (3): 529–45. https://doi.org/10.1111/J.1365-2699.2008.02019.X.

———. 2009b. "Modelling Late Quaternary Changes in Plant Distribution, Vegetation and Climate Using Pollen Data from Georgia, Caucasus." *Journal of Biogeography* 36 (3): 529–45. https://doi.org/10.1111/J.1365-2699.2008.02019.X.

Connor, Simon E., Ian Thomas, and Eliso V. Kvavadze. 2007. "A 5600-Yr History of Changing Vegetation, Sea Levels and Human Impacts from the Black Sea Coast of Georgia." *The Holocene* 17 (1): 25–36. https://doi.org/10.1177/0959683607073270.

Connor, Simon E., Ian Thomas, Eliso V. Kvavadze, Giorgi J. Arabuli, Genia S. Avakov, and Antonio Sagona. 2004. "A Survey of Modern Pollen and Vegetation along an Altitudinal Transect in Southern Georgia, Caucasus Region." *Review of Palaeobotany and Palynology* 129 (4): 229–50. https://doi.org/10.1016/J.REVPALBO.2004.02.003.

Conservation International. 2025. "Biodiversity Hotspots, Targeted Investment in Nature's Most Important Places." 2025. https://www.conservation.org/priorities/biodiversity-hotspots.

Davis, P.H. 1965. *Flora of Turkey*. Edinburgh: Edinburgh University Press.

Dawson, Andria, Christopher J. Paciorek, Jason S. McLachlan, Simon Goring, John W. Williams, and Stephen T. Jackson. 2016. "Quantifying Pollen-Vegetation Relationships to Reconstruct Ancient Forests Using 19th-Century Forest Composition and Pollen Data." *Quaternary Science Reviews* 137 (April): 156–75. https://doi.org/10.1016/J.QUASCIREV.2016.01.012.

DeLong, Elizabeth R., David M. DeLong, and Daniel L. Clarke-Pearson. 1988a. "Comparing the Areas under Two or More Correlated Receiver Operating Characteristic Curves: A Nonparametric Approach." *Biometrics* 44 (3): 845. https://doi.org/10.2307/2531595.

———. 1988b. "Comparing the Areas under Two or More Correlated Receiver Operating Characteristic Curves: A Nonparametric Approach." *Biometrics* 44 (3): 837. https://doi.org/10.2307/2531595.

Dering, M., M. Baranowska, B. Beridze, I. J. Chybicki, I. Danelia, G. Iszkuło, G. Kvartskhava, et al. 2021. "The Evolutionary Heritage and Ecological Uniqueness of Scots Pine in the Caucasus Ecoregion Is at Risk of Climate Changes." *Scientific Reports*

11 (1): 1–17. https://doi.org/10.1038/S41598-021-02098-1;SUBJMETA.

Dhyani, Rupesh, Dario Martin-Benito, Mehmet Doğan, Revaz Kvaratskhelia, Nesibe Köse, Hüseyin Tuncay Güner, and Lea Schneider. 2025. "Consistent Summer Temperature Signals in a Latewood Blue Intensity Network from the Upper Tree Line in the Caucasus." *Dendrochronologia* 92 (August): 126372. https://doi.org/10.1016/J.DENDRO.2025.126372.

Dirnböck, Thomas, Franz Essl, and Wolfgang Rabitsch. 2011. "Disproportional Risk for Habitat Loss of High-Altitude Endemic Species under Climate Change." *Global Change Biology* 17 (2): 990–96. https://doi.org/10.1111/J.1365-2486.2010.02266.X.

Dolukhanov, A. G. 1980. *Colchic Underwood*. Tbilisi. (in Russian).

———. 2010. *Forest Vegetation of Georgia*. Universal, Tbilisi. (in Russian).

Dolukhanov, Armen. 1978. "The Timberline and the Subalpine Belt in the Caucasus Mountains, USSR." *Arctic and Alpine Research* 10 (2): 409–22. https://doi.org/10.1080/00040851.1978.12003977.

Donat, Markus G., Jana Sillmann, Simon Wild, Lisa V. Alexander, Tanya Lippmann, and Francis W. Zwiers. 2014. "Consistency of Temperature and Precipitation Extremes across Various Global Gridded In Situ and Reanalysis Datasets." *Journal of Climate* 27 (13): 5019–35. https://doi.org/10.1175/JCLI-D-13-00405.1.

Elith, Jane, and John R. Leathwick. 2009. "Species Distribution Models: Ecological Explanation and Prediction Across Space and Time." *Annual Review of Ecology, Evolution, and Systematics* 40 (December): 677–97. https://doi.org/10.1146/ANNUREV.ECOLSYS.110308.120159.

Elith, Jane, Steven J. Phillips, Trevor Hastie, Miroslav Dudík, Yung En Chee, and Colin J. Yates. 2011. "A Statistical Explanation of MaxEnt for Ecologists." *Diversity and Distributions* 17 (1): 43–57. https://doi.org/10.1111/J.1472-4642.2010.00725.X.

Elizbarashvili, E. S., R. S. Meskhiya, and M. E. Elizbarashvili. 2007. "Dynamics of Occurrence Frequency of Extreme Anomalies of Monthly Mean Air Temperature in Georgia in the 20th Century and Its Effect on Precipitation and on the River Water Discharge." *Russian Meteorology and Hydrology* 32 (1): 71–74.

Elizbarashvili, E. S., M. R. Tatishvili, M. E. Elizbarashvili, S. E. Elizbarashvili, and R. S. Meskhiya. 2013. "Air Temperature Trends in Georgia under Global Warming Conditions." *Russian Meteorology and Hydrology* 38 (4): 234–238.

Elizbarashvili, E. S., O. S. Varazanashvili, N. S. Tsereteli, M. E. Elizbarashvili, and S. E. Elizbarashvili. 2012. "Dangerous Fogs on the Territory of Georgia." *Russian Meteorology and Hydrology* 37 (2): 106–111.

Elizbarashvili, Mariam, Elizbar Elizbarashvili, Marika Tatishvili, Shalva Elizbarashvili, Ramaz Meskhia, Nato Kutaladze, Lorenz King, Ina Keggenhoff, and Tamar Khardziani. 2017. "Georgian Climate Change under Global Warming Conditions." *Annals of Agrarian Science* 15 (1): 17–25. https://doi.org/10.1016/J.AASCI.2017.02.001.

Elumeeva, Tatiana G., Vladimir G. Onipchenko, Aleksey V. Egorov, Anzor B. Khubiev, Dzhamal K. Tekeev, Nadejda A. Soudzilovskaia, and Johannes H.C. Cornelissen. 2013. "Long-Term Vegetation Dynamic in the Northwestern Caucasus: Which Communities Are More Affected by Upward Shifts of Plant Species?" *Alpine Botany* 123 (2): 77–85. https://doi.org/10.1007/S00035-013-0122-7/METRICS.

Eminağaoğlu, Özgür, and Rahim Anşin. 2004. "Flora of the Karagöl-Sahara National Park (Artvin) and Its Environs." *Turkish Journal of Botany* 28 (6): 557–90. https://doi.org/-.

Eminağaoğlu, Özgür, Hamdi Güray Kutbay, Ali Bilgin, and Erkan Yalçin. 2006. "CONTRIBUTION TO THE PHYTOSOCIOLOGY AND CONSERVATION OF TERTIARY RELICT SPECIES IN NORTHEASTERN ANATOLIA (TURKEY)." *Belgian Journal of Botany* 139 (1): 124–30. https://www.jstor.org/stable/20794600?seq=1.

Engler, Robin, Christophe F. Randin, Wilfried Thuiller, Stefan Dullinger, Niklaus E. Zimmermann, Miguel B. Araújo, Peter B. Pearman, et al. 2011. "21st Century Climate Change Threatens Mountain Flora Unequally across Europe." *Global Change Biology* 17 (7): 2330–41. https://doi.org/10.1111/J.1365-2486.2010.02393.X.

Fagre, Daniel B. 2009a. "Chapter 1 Introduction: Understanding the Importance of Alpine Treeline Ecotones in Mountain Ecosystems." *Developments in Earth Surface Processes* 12 (January): 1–9. https://doi.org/10.1016/S0928-2025(08)00201-0.

———. 2009b. "Chapter 1 Introduction: Understanding the Importance of Alpine Treeline Ecotones in Mountain Ecosystems." In *Developments in Earth Surface Processes*, 12:1–9. Elsevier. https://doi.org/10.1016/S0928-2025(08)00201-0.

Fick, Stephen E., and Robert J. Hijmans. 2017. "WorldClim 2: New 1-Km Spatial Resolution Climate Surfaces for Global Land Areas." *International Journal of Climatology* 37 (12): 4302–15. https://doi.org/10.1002/JOC.5086.

Forest, Félix, Vincent Savolainen, Mark W. Chase, Richard Lupia, Anne Bruneau, and Peter R. Crane. 2005. "Teasing Apart Molecular- Versus Fossil-Based Error Estimates When Dating Phylogenetic Trees: A Case Study in the Birch Family (Betulaceae)." *Systematic*

Botany 30 (1): 118–33. https://doi.org/10.1600/036364405366185.

Franklin, Janet, and Jennifer A. Miller. 2010. "Mapping Species Distributions: Spatial Inference and Prediction." *Mapping Species Distributions: Spatial Inference and Prediction*, January, 1–320. https://doi.org/10.1017/CBO9780511810602.

Furlow, John J. 1990. "THE GENERA OF BETULACEAE IN THE SOUTHEASTERN UNITED STATES." *Journal of the Arnold Arboretum* 71 (1): 1–67. https://www.jstor.org/stable/43782230.

Gavashelishvili, Alexander, and David Tarkhnishvili. 2016. "Biomes and Human Distribution during the Last Ice Age." *Global Ecology and Biogeography* 25 (5): 563–74. https://doi.org/10.1111/GEB.12437.

GBIF.org. 2021. "GBIF Occurrence Download." 2021. https://www.gbif.org/occurrence/download/0200709-200613084148143.

Gent, Peter R., Gokhan Danabasoglu, Leo J. Donner, Marika M. Holland, Elizabeth C. Hunke, Steve R. Jayne, David M. Lawrence, et al. 2011. "The Community Climate System Model Version 4." *Journal of Climate* 24 (19): 4973–91. https://doi.org/10.1175/2011JCLI4083.1.

Gigauri, Khatuna, Maia Akhalkatsi, George Nakhutsrishvili, and Otar Abdaladze. 2013. "Monitoring of Vascular Plant Diversity in a Changing Climate in the Alpine Zone of the Central Greater Caucasus." *Turkish Journal of Botany* 37 (6): 1104–14. https://doi.org/10.3906/bot-1301-38.

Gigauri, Khatuna, Maia Akhalkatsi, Otar Abdaladze, and George Nakhutsrishvili. 2016. "Alpine Plant Distribution and Thermic Vegetation Indicator on GLORIA Summits in the Central Greater Caucasus." *Pakistan Journal of Botany* 48 (5): 1893–1902.

Goberville, Eric, Grégory Beaugrand, Nina Coralie Hautekèete, Yves Piquot, and Christophe Luczak. 2015. "Uncertainties in the Projection of Species Distributions Related to General Circulation Models." *Ecology and Evolution* 5 (5): 1100–1116. https://doi.org/10.1002/ECE3.1411.

Gottfried, Michael, Harald Pauli, Andreas Futschik, Maia Akhalkatsi, Peter Barančok, José Luis Benito Alonso, Gheorghe Coldea, et al. 2012. "Continent-Wide Response of Mountain Vegetation to Climate Change." *Nature Climate Change 2012 2:2* 2 (2): 111–15. https://doi.org/10.1038/nclimate1329.

Grimm, Guido W., and Susanne S. Renner. 2013. "Harvesting Betulaceae Sequences from GenBank to Generate a New Chronogram for the Family." *Botanical Journal of the Linnean Society* 172 (4): 465–77. https://doi.org/10.1111/boj.12065.

Grossgeim, A. A. 1936. *Analiz flory Kavkaza* [Analysis of the Flora of the Caucasus]. Baku: Izdatel'stvo Azerbaidzhanskogo filiala Akademii nauk SSSR.

———. 1948. *Rastitel'nyi pokrov Kavkaza* [Vegetation Cover of the Caucasus]. Materialy k poznaniiu fauny i flory SSSR, novaia seriia, otdel botaniki, vyp. 4 (12). Moscow: Moskovskoe obshchestvo ispytatelei prirody.

Grossheim, A. A., D. I. Sosnovski, and Troytski N. A. 1928. *Vegetation of Georgia*. Publish house Georg. SSR Planing Commision, Tbilisi. (in Russian).

Grytnes, John Arvid, Jutta Kapfer, Gerald Jurasinski, Hilary H. Birks, Hanne Henriksen, Kari Klanderud, Arvid Odland, Mikael Ohlson, Sonja Wipf, and H. John B. Birks. 2014. "Identifying the Driving Factors behind Observed Elevational Range Shifts on E Uropean Mountains." *Wiley Online LibraryJA Grytnes, J Kapfer, G Jurasinski, HH Birks, H Henriksen, K Klanderud, A Odland, M OhlsonGlobal Ecology and Biogeography, 2014•Wiley Online Library* 23 (8): 876–84. https://doi.org/10.1111/GEB.12170.

Guisan, Antoine, and Wilfried Thuiller. 2005. "Predicting Species Distribution: Offering More than Simple Habitat Models." *Ecology Letters* 8 (9): 993–1009. https://doi.org/10.1111/J.1461-0248.2005.00792.X.

Halloy, Stephan R P, and Alan F Mark. 2003. "Climate-Change Effects on Alpine Plant Biodiversity: A New Zealand Perspective on Quantifying the Threat." *Arctic, Antarctic, and Alpine Research* 35 (2): 248–54. https://doi.org/10.1657/1523-0430(2003)035.

Hamid, Maroof, Anzar A. Khuroo, Bipin Charles, Rameez Ahmad, C. P. Singh, and N. A. Aravind. 2019. "Impact of Climate Change on the Distribution Range and Niche Dynamics of Himalayan Birch, a Typical Treeline Species in Himalayas." *Biodiversity and Conservation* 28 (8–9): 2345–70. https://doi.org/10.1007/S10531-018-1641-8/METRICS.

Hansen, Wiebke, Anja Magiera, Tim Theissen, Rainer Waldhardt, and Annette Otte. 2018. "Analysing Betula Litwinowii Encroachment and Reforestation in the Kazbegi Region, Greater Caucasus, Georgia." *Journal of Vegetation Science* 29 (1): 110–23. https://doi.org/10.1111/JVS.12589.

Hansson, Amanda, Jamie Shulmeister, Paul Dargusch, and Genia Hill. 2023. "A Review of Factors Controlling Southern Hemisphere Treelines and the Implications of Climate Change on Future Treeline Dynamics." *Agricultural and Forest Meteorology* 332 (1): 109375. https://doi.org/10.1016/j.agrformet.2023.109375.

Harsch, Melanie A., Philip E. Hulme, Matt S. McGlone, and Richard P. Duncan. 2009. “Are Treelines Advancing? A Global Meta-Analysis of Treeline Response to Climate Warming.” *Ecology Letters* 12 (10): 1040–49. https://doi.org/10.1111/J.1461-0248.2009.01355.X.

Haylock, Malcolm R., Thomas C. Peterson, Luiz M. Alves, Tercio Ambrizzi, Yara M. Anunciação, Juan Báez, et al. 2006. “Trends in Total and Extreme South American Rainfall in 1960–2000 and Links with Sea Surface Temperature.” *Journal of Climate* 19 (8): 1490–1512. https://doi.org/10.1175/JCLI3695.1.

Hernandez, Pilar A., Catherine H. Graham, Lawrence L. Master, and Deborah L. Albert. 2006. “The Effect of Sample Size and Species Characteristics on Performance of Different Species Distribution Modeling Methods.” *Ecography* 29 (5): 773–85. https://doi.org/10.1111/J.0906-7590.2006.04700.X.

Hofgaard, Annika, Hans Tømmervik, Gareth Rees, and Frank Hanssen. 2013. “Latitudinal Forest Advance in Northernmost Norway since the Early 20th Century.” *Journal of Biogeography* 40 (5): 938–49. https://doi.org/10.1111/JBI.12053.

Holtmeier, Friedrich Karl. 2009. *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. *Advances in Global Change Research*. 2nd ed. Vol. 36. Springer. https://doi.org/10.1657/1523-0430(2004)036[0635:br]2.0.co;2.

Holtmeier, Friedrich Karl, and Gabriele Broll. 2005. “Sensitivity and Response of Northern Hemisphere Altitudinal and Polar Treelines to Environmental Change at Landscape and Local Scales.” *Global Ecology and Biogeography* 14 (5): 395–410. https://doi.org/10.1111/J.1466-822X.2005.00168.X.

———. 2019. “Treeline Research—From the Roots of the Past to Present Time. A Review.” *Forests 2020, Vol. 11, Page 38* 11 (1): 38. https://doi.org/10.3390/F11010038.

Huang, Mengyue, Guoyan Wang, Xiaojuan Bie, Yunqing Jiang, Xiyue Huang, Jing Ji Li, Songlin Shi, Tingbin Zhang, and Pei Hao Peng. 2023. “Seasonal Snow Cover Patterns Explain Alpine Treeline Elevation Better than Temperature at Regional Scale.” *Forest Ecosystems* 10 (January): 100106. https://doi.org/10.1016/J.FECS.2023.100106.

Hughes, Nicole M, Daniel M Johnson, Maia Akhalkatsi, and Otar Abdaladze. 2009. “Characterizing Betula Litwinowii Seedling Microsites at the Alpine-Treeline Ecotone, Central Greater Caucasus Mountains, Georgia.” *Arctic, Antarctic, and Alpine Research* 41 (1): 112–18. https://doi.org/10.1657/1523-0430-41.1.112.

IPCC (Intergovernmental Panel on Climate Change). 2007. *Climate Change 2007: The Physical Science Basis. Summary for Policymakers.* Contribution of Working Group I to the Fourth Assessment Report.

———. 2014. *Climate Change 2014: Synthesis Report. Summary for Policymakers.* Valencia: IPCC.

Jackson, Stephen T., and John W. Williams. 2004. "Modern Analogs in Quaternary Paleoecology: Here Today, Gone Yesterday, Gone Tomorrow?" *Annual Review of Earth and Planetary Sciences* 32 (Volume 32, 2004): 495–537. https://doi.org/10.1146/ANNUREV.EARTH.32.101802.120435/CITE/REFWORKS.

Jarvinen, Pia, Anna Palmé, Luis Orlando Morales, Mika Lannenpaa, Markku Keinanen, Tuomas Sopanen, and Martin Lascoux. 2004. "Phylogenetic Relationships of Betula Species (Betulaceae) Based on Nuclear ADH and Chloroplast MatK Sequences." *American Journal of Botany* 91 (11): 1834–45. https://doi.org/10.3732/ajb.91.11.1834.

Keggenhoff, Inga, Mikheil Elizbarashvili, and Lewis King. 2015. "Heat Wave Events over Georgia since 1961: Climatology, Changes and Severity." *Climate* 3 (2): 308–328. https://doi.org/10.3390/cli3020308.

Keggenhoff, Inga, Mikheil Elizbarashvili, Azadeh Amiri-Farahani, and Lewis King. 2014. "Trends in Daily Temperature and Precipitation Extremes over Georgia, 1971–2010." *Weather and Climate Extremes* 4: 75–85. https://doi.org/10.1016/j.wace.2014.05.001.

Keinänen, Markku, Riitta Julkunen-Tiitto, Pia Mutikainen, Mari Walls, Jari Ovaska, and Elina Vapaavuori. 1999. "TRADE-OFFS IN PHENOLIC METABOLISM OF SILVER BIRCH: EFFECTS OF FERTILIZATION, DEFOLIATION, AND GENOTYPE." *Ecology* 80 (6): 1970–86. https://doi.org/https://doi.org/10.1890/0012-9658(1999)080[1970:TOIPMO]2.0.CO;2.

Ketskhoveli, Niko. 1960. *Vegetation Cover of Georgia*. Metsniereba, Tbilisi. (in Georgian).

Klein Tank, Albert M. G., Thomas C. Peterson, D. A. Quadir, S. Dorji, X. Zou, H. Tang, et al. 2006. "Changes in Daily Temperature and Precipitation Extremes in Central and South Asia." *Journal of Geophysical Research: Atmospheres* 111 (D16). https://doi.org/10.1029/2005JD006316.

Körner, Christian. 2008. "Winter Crop Growth at Low Temperature May Hold the Answer for Alpine Treeline Formation." *Plant Ecology & Diversity* 1 (1): 3–11. https://doi.org/10.1080/17550870802273411.

———. 2012. "High Elevation Treelines." In *Alpine Treelines*, 1–10. Springer, Basel. https://doi.org/10.1007/978-3-0348-0396-0_1.

Körner, Christian, and Jens Paulsen. 2004. "A World-Wide Study of High Altitude Treeline Temperatures." *Journal of Biogeography* 31 (5): 713–32. https://doi.org/10.1111/J.1365-2699.2003.01043.X.

Kuemmerle, Tobias, Hendrik Bluhm, Arash Ghoddousi, Marine Arakelyan, Elshad Askerov, Benjamin Bleyhl, Mamikon Ghasabian, et al. 2020. "Identifying Priority Areas for Restoring Mountain Ungulates in the Caucasus Ecoregion." *Conservation Science and Practice* 2 (11): e276. https://doi.org/10.1111/CSP2.276.

Kullman, Leif. 2022. "Forest-Limit (Betula Pubescens Ssp. Czerepanovii) Performance in the Context of Gentle Modern Climate Warming." *European Journal of Applied Sciences* 10 (3): 168–85. https://doi.org/10.14738/aivp.103.12369.

Kunkel, Kenneth E., Roger A. Pielke Jr., and Stanley A. Changnon. 1999. "Temporal Fluctuations in Weather and Climate Extremes That Cause Economic and Human Health Impacts: A Review." *Bulletin of the American Meteorological Society* 80 (6): 1077–1098.

Kurt, L., O. Ketenoglu, G. N. Tug, and F. Sekerciler. 2015. "Highland Vegetation of Inner and Eastern Anatolia and the Effects of Global Warming." *Climate Change Impacts on High-Altitude Ecosystems*, January, 275–88. https://doi.org/10.1007/978-3-319-12859-7_11.

Kvachakidze, Revaz. 2010. *The Vegetation of Georgia, State Reserve*. Tbilisi. (in Georgian).

Kvaratskhelia, Revaz, and Alexander Gavashelishvili. 2025. "Common Yew (Taxus Baccata) as a Climate Archive: Reconstructing 200 Years of Temperature Change in Georgia (Caucasus)." *Dendrochronologia* 89 (February): 126285. https://doi.org/10.1016/J.DENDRO.2024.126285.

Kvavadze, E. V., and L. Rukhadze. 1989. *Rastitel'nost' i klimat golotsena Abkhazii* [Vegetation and Climate of the Holocene in Abkhazia]. Tbilisi: Metsniereba.

Kvavadze, Eliso, and Kakha Kakhiani. 2010. "Palynology of the Paravani Burial Mound (Early Bronze Age, Georgia)." *Vegetation History and Archaeobotany* 19 (5): 469–78. https://doi.org/10.1007/S00334-010-0259-X/METRICS.

Kvavadze, Eliso V., and Simon E. Connor. 2005. "Zelkova Carpinifolia (Pallas) K. Koch in Holocene Sediments of Georgia—an Indicator of Climatic Optima." *Review of Palaeobotany and Palynology* 133 (1–2): 69–89.

https://doi.org/10.1016/J.REVPALBO.2004.09.002.

Larcher, W. 1995. "Photosynthesis as a Tool for Indicating Temperature Stress Events." *Ecophysiology of Photosynthesis*, 261–77. https://doi.org/10.1007/978-3-642-79354-7_13.

Larcher, Walter. 2003. *Physiological Plant Ecology : Ecophysiology and Stress Physiology of Functional Groups*. Springer Science & Business Media.

Lenoir, J., J. C. Gégout, P. A. Marquet, P. De Ruffray, and H. Brisse. 2008. "A Significant Upward Shift in Plant Species Optimum Elevation during the 20th Century." *Science* 320 (5884): 1768–71. https://doi.org/10.1126/SCIENCE.1156831/SUPPL_FILE/1768.MP3.

Li, Jianhua, Suzanne Shoup, and Zhiduan Chen. 2005. "Phylogenetics of Betula (Betulaceae) Inferred from Sequences of Nuclear Ribosomal DNA." *Https://Doi.Org/10.3119/04-14.1* 107 (929): 69–86. https://doi.org/10.3119/04-14.1.

Liang, Jingjing, Thomas W. Crowther, Nicolas Picard, Susan Wiser, Mo Zhou, Giorgio Alberti, Ernst Detlef Schulze, et al. 2016. "Positive Biodiversity-Productivity Relationship Predominant in Global Forests." *Science* 354 (6309). https://doi.org/10.1126/SCIENCE.AAF8957.

Lobo, Jorge M., Alberto Jiménez-Valverde, and Joaquín Hortal. 2010. "The Uncertain Nature of Absences and Their Importance in Species Distribution Modelling." *Ecography* 33 (1): 103–14. https://doi.org/10.1111/J.1600-0587.2009.06039.X.

Lu, Xiaoming, Eryuan Liang, Yafeng Wang, Flurin Babst, and J. Julio Camarero. 2021. "Mountain Treelines Climb Slowly despite Rapid Climate Warming." *Global Ecology and Biogeography* 30 (1): 305–15. https://doi.org/10.1111/GEB.13214.

Lu, Xiaoming, Xiangyu Zheng, Eryuan Liang, Shilong Piao, Flurin Babst, Grant P. Elliott, Shalik Ram Sigdel, et al. 2025. "Patterns, Dynamics and Drivers of Alpine Treelines and Shrublines." *Nature Reviews Earth and Environment* 6 (8): 489–502. https://doi.org/10.1038/S43017-025-00703-9;SUBJMETA.

Mandel, Igor, and Stan Lipovetsky. 2021. "Climate Change Report IPCC 2021 – A Chimera of Science and Politics." *SSRN Electronic Journal*, August. https://doi.org/10.2139/SSRN.3913788.

Margalitadze, Nana. 1970. *The History of Vegetation in the Southern Highlands of Georgia in the Holocene Period Based on the Data of Spore-Pollen Analysis*. Tbilisi: Science (in Georgian).

Margalitadze, N. A. 1973. “Istoriia rastitel'nosti Iuzhno-Gruzinskogo nagor'ia v golotsene” [History of Vegetation of the South Georgian Highland in the Holocene]. In *Palinologiia golotsena i marinopalinologiia* [Holocene Palynology and Marine Palynology].

———. 1977a. “Istoriia lesnoi rastitel'nosti Gornoi Kolkhidy v golotsene” [History of Forest Vegetation of Mountain Colchis in the Holocene]. In *Tezisy dokladov 7-go soveshchaniia* [Abstracts of the 7th Conference]. Novosibirsk.

———. 1977b. “Istoriia rastitel'nosti Dzhavakhetskogo nagor'ia i Tsalkinskogo plato v golotsene” [History of Vegetation of the Javakheti Highland and Tsalka Plateau in the Holocene]. In *Palinologicheskie issledovaniia v Gruzii* [Palynological Studies in Georgia]. Tbilisi.

———. 1985. “Golotsenovaia istoriia lesnoi rastitel'nosti Rachinskogo khrebta” [Holocene History of Forest Vegetation of the Racha Ridge]. In *Geografiia i flora Racha-Lechkhumi* [Geography and Flora of Racha-Lechkhumi]. Tbilisi.

———. 1995. *Istoriia golotsenovoi rastitel'nosti Gruzii* [History of Holocene Vegetation of Georgia]. Tbilisi: Metsniereba.

Martínez-Meyer, E., and A. T. Peterson. 2006. “Conservatism of Ecological Niche Characteristics in North American Plant Species over the Pleistocene-to-Recent Transition.” *Journal of Biogeography* 33 (10): 1779–89. https://doi.org/10.1111/J.1365-2699.2006.01482_33_10.X.

McAllister, Hugh A., and Keith Rushforth. 2011. “706. BETULA ASHBURNERI.” *Curtis's Botanical Magazine* 28 (2): 111–18. https://doi.org/10.1111/j.1467-8748.2011.01735.x.

McAllister, Hugh, and Kenneth Ashburner. 2007. “593. BETULA MEGRELICA.” *Curtis's Botanical Magazine* 24 (3): 174–79. https://doi.org/10.1111/J.1467-8748.2007.00582.X.

Mchedlishvili, P. A. 1954. “Novye dannye o ponticheskikh rastitel'nykh ostatkakh Gruzii” [New Data on Pontic Plant Remains of Georgia]. *Doklady Akademii Nauk SSSR* 96: 185–187.

MEPA. 2023. “ანგარიში ტყის პირველი ეროვნული აღრიცხვა საქართველოში – First National Forest Inventory in Georgia: ანგარიში/Report 2023.” https://mepa.gov.ge/Ge/Reports?page=3&pageSize=9.

Merow, Cory, Matthew J. Smith, and John A. Silander. 2013. “A Practical Guide to MaxEnt for Modeling Species' Distributions: What It Does, and Why Inputs and Settings Matter." *Ecography* 36 (10): 1058–69. https://doi.org/10.1111/J.1600-0587.2013.07872.X.

Messager, Erwan, Soumaya Belmecheri, Ulrich Von Grafenstein, Sébastien Nomade, Vincent Ollivier, Pierre Voinchet, Simon Puaud, et al. 2013a. "Late Quaternary Record of the Vegetation and Catchment-Related Changes from Lake Paravani (Javakheti, South Caucasus)." *Quaternary Science Reviews* 77 (October): 125–40. https://doi.org/10.1016/J.QUASCIREV.2013.07.011.

———. 2013b. "Late Quaternary Record of the Vegetation and Catchment-Related Changes from Lake Paravani (Javakheti, South Caucasus)." *Quaternary Science Reviews* 77 (October): 125–40. https://doi.org/10.1016/J.QUASCIREV.2013.07.011.

Messager, Erwan, Vincent Lebreton, Laurent Marquer, Elda Russo-Ermolli, Ronan Orain, Josette Renault-Miskovsky, David Lordkipanidze, Jackie Despriée, Carlo Peretto, and Marta Arzarello. 2011. "Palaeoenvironments of Early Hominins in Temperate and Mediterranean Eurasia: New Palaeobotanical Data from Palaeolithic Key-Sites and Synchronous Natural Sequences." *Quaternary Science Reviews* 30 (11–12): 1439–47. https://doi.org/10.1016/J.QUASCIREV.2010.09.008.

Messager, Erwan, Sébastien Nomade, Bruno Wilhelm, Sébastien Joannin, Vincent Scao, Ulrich Von Grafenstein, Inga Martkoplishvili, et al. 2017. "New Pollen Evidence from Nariani (Georgia) for Delayed Postglacial Forest Expansion in the South Caucasus." *Quaternary Research* 87 (1): 121–32. https://doi.org/10.1017/QUA.2016.3.

Metreveli, Vasil, Holger Kreft, Ilia Akobia, Zurab Janiashvili, Zaza Nonashvili, Lasha Dzadzamia, Zurab Javakhishvili, and Alexander Gavashelishvili. 2023. "Potential Distribution and Suitable Habitat for Chestnut (Castanea Sativa)." *Forests* 14 (10): 2076. https://doi.org/10.3390/F14102076/S1.

Metreveli, Vasil, Holger Kreft, Zurab Javakhishvili, Ilia Akobia, Sandro Mdivani, Giorgi Chikorashvili, and Alexander Gavashelishvili. 2025. "On the Relationship between Environment and Growth of Sweet Chestnut (Castanea Sativa) in the Caucasus." *Frontiers in Forests and Global Change* 8: 1670459. https://doi.org/10.3389/FFGC.2025.1670459.

Mina, Marco, Harald Bugmann, Thomas Cordonnier, Florian Irauschek, Matija Klopcic, Marta Pardos, and Maxime Cailleret. 2017. "Future Ecosystem Services from European Mountain Forests under Climate Change." *Journal of Applied Ecology* 54 (2): 389–401. https://doi.org/10.1111/1365-2664.12772.

Ministry of Environment Protection and Natural Resources of Georgia. 2009. *Georgia's Second National Communication under the United Nations Framework Convention on Climate Change.* Tbilisi.

Mittermeier, Russell A., Cláudio Valladares-Pádua, Anthony B. Rylands, Ardith A. Eudey, Thomas M. Butynski, Jörg U. Ganzhorn, Rebecca Kormos, John M. Aguiar, and Sally Walker. 2006. "Primates in Peril: The World's 25 Most Endangered Primates, 2004–2006." *Https://Doi.Org/10.1896/0898-6207.20.1.1* 2006 (20): 1–28. https://doi.org/10.1896/0898-6207.20.1.1.

Moberg, Anders, and Philip D. Jones. 2005. "Trends in Indices for Extremes in Daily Temperature and Precipitation in Central and Western Europe, 1901–99." *International Journal of Climatology* 25 (9): 1149–1171. https://doi.org/10.1002/joc.1163.

Müller, Michael, Udo Schickhoff, Thomas Scholten, Simon Drollinger, Jürgen Böhner, and Ram P. Chaudhary. 2016. "How Do Soil Properties Affect Alpine Treelines? General Principles in a Global Perspective and Novel Findings from Rolwaling Himal, Nepal:" *Progress in Physical Geography* 40 (1): 135–60. https://doi.org/10.1177/0309133315615802.

Müller, Michael, Niels Schwab, Udo Schickhoff, Jürgen Böhner, and Thomas Scholten. 2016. "Soil Temperature and Soil Moisture Patterns in a Himalayan Alpine Treeline Ecotone." *Arctic, Antarctic, and Alpine Research* 48 (3): 501–21. https://doi.org/10.1657/AAAR0016-004.

Myers-Smith, Isla H., and David S. Hik. 2018. "Climate Warming as a Driver of Tundra Shrubline Advance." *Journal of Ecology* 106 (2): 547–60. https://doi.org/10.1111/1365-2745.12817.

Myers-Smith, Isla H., Jeffrey T. Kerby, Gareth K. Phoenix, Jarle W. Bjerke, Howard E. Epstein, Jakob J. Assmann, Christian John, et al. 2020. "Complexity Revealed in the Greening of the Arctic." *Nature Climate Change* 10 (2): 106–17. https://doi.org/10.1038/S41558-019-0688-1;TECHMETA.

Nagamitsu, Teruyoshi, Takayuki Kawahara, and Ayako Kanazashi. 2006. "Endemic Dwarf Birch Betula Apoiensis (Betulaceae) Is a Hybrid That Originated from Betula Ermanii and Betula Ovalifolia." *Plant Species Biology* 21 (1): 19–29. https://doi.org/10.1111/j.1442-1984.2006.00147.x.

Nakhutsrishvili, G., N. Zazanashvili, K. Batsatsashvili, and S. C. Montalvo Mancheno. 2015. "Colchic and Hyrcanian Forests of the Caucasus: Similarities, Differences and

Conservation Status." *Flora Mediterranea* Fl. Medit. (Special Issue): 185–92. https://doi.org/doi: 10.7320/FlMedit25SI.185.

Nakhutsrishvili, George. 2000. "Georgia's Basis Biomes." In *Biological and Landscape Diversity of Georgia*. WWF, The World Bank, Tbilisi.

———. 2013. *The Vegetation of Georgia (South Caucasus)*. Springer Science & Business Media.

Nakhutsrishvili, George, Otar Abdaladze, and Maia Akhalkatsi. 2004a. "Concerning the Tree Line Vegetation of the Kazbegi Region (the Central Caucasus)." *Bulletin of the Georgian National Academy of Sciences (Moambe)* 169 (1): 122–25.

———. 2004b. "Global Warming and Treeline." *Proc. Acad. Sci. Biol. Ser. B* 2 (3–4): 87–90.

New, Mark, Bruce Hewitson, David B. Stephenson, Amarela Tsiga, Adriaan Kruger, Anabela Manhique, et al. 2006. "Evidence of Trends in Daily Climate Extremes over Southern and West Africa." *Journal of Geophysical Research: Atmospheres* 111 (D14). https://doi.org/10.1029/2005JD006289.

Nogués-Bravo, David. 2009. "Predicting the Past Distribution of Species Climatic Niches." *Global Ecology and Biogeography* 18 (5): 521–31. https://doi.org/10.1111/J.1466-8238.2009.00476.X.

Notarnicola, C. 2020. "Hotspots of Snow Cover Changes in Global Mountain Regions over 2000–2018." *Remote Sensing of Environment* 243 (June): 111781. https://doi.org/10.1016/J.RSE.2020.111781.

Olson, David M., and Eric Dinerstein. 2002. "The Global 200: Priority Ecoregions for Global Conservation." *Annals of the Missouri Botanical Garden* 89 (2): 199–224. https://doi.org/10.2307/3298564.

Palibin, I. V. 1929. *Razvedochnye raboty polevykh partii geologo-razvedochnogo neftianogo instituta v 1928–1929 gg.* [Exploratory Work of Field Parties of the Geological Exploration Oil Institute in 1928–1929]. 53 pp.

Palme, A. E., Q. Su, S. Palsson, and M. Lascoux. 2004. "Extensive Sharing of Chloroplast Haplotypes among European Birches Indicates Hybridization among Betula Pendula, B. Pubescens and B. Nana." *Molecular Ecology* 13 (1): 167–78. https://doi.org/10.1046/j.1365-294X.2003.02034.x.

Parker, Thomas C., Jens Arne Subke, and Philip A. Wookey. 2015. "Rapid Carbon Turnover beneath Shrub and Tree Vegetation Is Associated with Low Soil Carbon Stocks at a Subarctic Treeline." *Global Change Biology* 21 (5): 2070–81.

https://doi.org/10.1111/GCB.12793.

Pauli, Harald, Michael Gottfried, Stefan Dullinger, Otari Abdaladze, Maia Akhalkatsi, José Luis Benito Alonso, Gheorghe Coldea, et al. 2012. "Recent Plant Diversity Changes on Europe's Mountain Summits." *Science* 336 (6079): 353–55. https://doi.org/10.1126/SCIENCE.1219033/SUPPL_FILE/PAULI.SM.PDF.

Paulsen, Jens, and Christian Körner. 2014. "A Climate-Based Model to Predict Potential Treeline Position around the Globe." *Alpine Botany* 124 (1): 1–12. https://doi.org/10.1007/S00035-014-0124-0/METRICS.

Pearson, Richard G., Christopher J. Raxworthy, Miguel Nakamura, and A. Townsend Peterson. 2007. "Predicting Species Distributions from Small Numbers of Occurrence Records: A Test Case Using Cryptic Geckos in Madagascar." *Journal of Biogeography* 34 (1): 102–17. https://doi.org/10.1111/J.1365-2699.2006.01594.X.

Peterson, A. T., J. Soberón, and V. Sánchez-Cordero. 1999. "Conservatism of Ecological Niches in Evolutionary Time." *Science* 285 (5431): 1265–67. https://doi.org/10.1126/SCIENCE.285.5431.1265.

Peterson, Thomas C., Michael A. Taylor, Reginald Demeritte, Duncombe D. L. Duncombe, Steven Burton, Felicia Thompson, et al. 2002. "Recent Changes in Climate Extremes in the Caribbean Region." *Journal of Geophysical Research: Atmospheres* 107 (D21). https://doi.org/10.1029/2002JD002251.

Phillips, Sharon B., Viney P. Aneja, Daiwen Kang, and S. Pal Arya. 2006. "Maximum Entropy Modeling of Species Geographic Distributions." *Ecological Modelling* 190 (3–4): 231–59. https://doi.org/10.1016/J.ECOLMODEL.2005.03.026.

Phillips, Steven J., and Miroslav Dudík. 2008. "Modeling of Species Distributions with Maxent: New Extensions and a Comprehensive Evaluation." *Ecography* 31 (2): 161–75. https://doi.org/10.1111/J.0906-7590.2008.5203.X.

Prentice, Colin. 1988. "Records of Vegetation in Time and Space: The Principles of Pollen Analysis." *Vegetation History*, 17–42. https://doi.org/10.1007/978-94-009-3081-0_2.

Price, Martin F, Georg Gratzer, Lalisa Alemayehu Duguma, Thomas Kohler, Daniel Maselli, and Rosalaura Romeo. 2011. "Mountain Forests in a Changing World." www.fao.organdwww.mountainpartnership.org.

QGIS Development Team. 2019. "QGIS Geographic Information System. Open Source Geospatial Foundation Project." 2019. http://qgis.osgeo.org.

R Core Team. 2018. "R: A Language and Environment for Statistical Computing. R

Foundation for Statistical Computing, Vienna, Austria.” 2018. https://www.r-project.org/.

Randin, Christophe F., Robin Engler, Signe Normand, Massimiliano Zappa, Niklaus E. Zimmermann, Peter B. Pearman, Pascal Vittoz, Wilfried Thuiller, and Antoine Guisan. 2009. “Climate Change and Plant Distribution: Local Models Predict High-Elevation Persistence.” *Global Change Biology* 15 (6): 1557–69. https://doi.org/10.1111/J.1365-2486.2008.01766.X.

Rees, W. Gareth, Annika Hofgaard, Stéphane Boudreau, David M. Cairns, Karen Harper, Steven Mamet, Ingrid Mathisen, Zuzanna Swirad, and Olga Tutubalina. 2020. “Is Subarctic Forest Advance Able to Keep Pace with Climate Change?” *Global Change Biology* 26 (7): 3965–77. https://doi.org/10.1111/gcb.15113.

Rizayeva, Afag, Mihai D. Nita, He Yin, Johanna Buchner, Neda Kasraee, Natalia Rogova, Elshad Askerov, et al. 2025. “A Half-Century of Land Cover Changes in the Caucasus Derived from Corona Spy Satellite and Landsat Images.” *Regional Environmental Change* 25 (1): 1–19. https://doi.org/10.1007/S10113-025-02360-6/METRICS.

Roces-Díaz, José V., Borja Jiménez-Alfaro, Milan Chytrý, Emilio R. Díaz-Varela, and Pedro Álvarez-Álvarez. 2018. “Glacial Refugia and Mid-Holocene Expansion Delineate the Current Distribution of Castanea Sativa in Europe.” *ElsevierJV Roces-Díaz, B Jiménez-Alfaro, M Chytrý, ER Díaz-Varela, P Álvarez-ÁlvarezPalaeogeography, Palaeoclimatology, Palaeoecology, 2018•Elsevier* 491 (February): 152–60. https://doi.org/10.1016/J.PALAEO.2017.12.004.

Royal Botanic Gardens Kew. 2026. “Betula L. | Plants of the World Online | Kew Science.” 2026. https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:328387-2#children.

Saghatelyan, A. 2006. “Flora of Armenia: Ist Composition, Analysis and Relationships.” *Turczaninowia* 9 (3): 5–47.

Sagheb Talebi, Khosro, Toktam Sajedi, and Mehdi Pourhashemi. 2014. *Forests of Iran, A Treasure from the Past, a Hope for the Future*. Vol. 10. Plant and Vegetation. Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-94-007-7371-4.

Sakhokia, Mikheil. 1983. *Agrobotanical Review of Pastures and Hay Meadows of the Kazbegi Region*. Tbilisi, Georgia: Metsniereba (in Georgian).

Scheffers, Brett R., Luc De Meester, Tom C.L. Bridge, Ary A. Hoffmann, John M. Pandolfi, Richard T. Corlett, Stuart H.M. Butchart, et al. 2016. “The Broad Footprint of Climate Change from Genes to Biomes to People.” *Science.OrgBR Scheffers, L De Meester, TCL Bridge, AA Hoffmann, JM Pandolfi, RT CorlettScience, 2016•science.Org* 354 (6313).

https://doi.org/10.1126/SCIENCE.AAF7671.

Schenk, Martijn F., Claire Noëlle Thienpont, Wim J.M. Koopman, Luud J.W.J. Gilissen, and Marinus J.M. Smulders. 2008. "Phylogenetic Relationships in Betula (Betulaceae) Based on AFLP Markers." *Tree Genetics & Genomes 2008 4:4* 4 (4): 911–24. https://doi.org/10.1007/s11295-008-0162-0.

Schickhoff, U., M. Bobrowski, J. Böhner, B. Bürzle, R. P. Chaudhary, L. Gerlitz, H. Heyken, et al. 2015. "Do Himalayan Treelines Respond to Recent Climate Change? An Evaluation of Sensitivity Indicators." *Earth System Dynamics* 6 (1): 245–65. https://doi.org/10.5194/ESD-6-245-2015.

Schickhoff, U., Maria Bobrowski, Jürgen Böhner, Birgit Bürzle, Ram Prasad Chaudhary, Lars Gerlitz, Jelena Lange, Michael Müller, Thomas Scholten, and Niels Schwab. 2016. "Climate Change and Treeline Dynamics in the Himalaya." *Climate Change, Glacier Response, and Vegetation Dynamics in the Himalaya: Contributions Toward Future Earth Initiatives*, January, 271–306. https://doi.org/10.1007/978-3-319-28977-9_15.

Schickhoff, Udo. 2005. "The Upper Timberline in the Himalayas, Hindu Kush and Karakorum: A Review of Geographical and Ecological Aspects." *Mountain Ecosystems: Studies in Treeline Ecology*, 275–354. https://doi.org/10.1007/3-540-27365-4_12.

Scoccimarro, Enrico, and Silvio Gualdi. 2020. "Heavy Daily Precipitation Events in the CMIP6 Worst-Case Scenario: Projected Twenty-First-Century Changes." *Journal of Climate* 33 (17): 7631–42. https://doi.org/10.1175/JCLI-D-19-0940.1.

Shamsabad, Mahmoudi M., Mostafa Assadi, and Laura Parducci. 2018. "Impact of Climate Change Implies the Northward Shift in Distribution of the Irano-Turanian Subalpine Species Complex Acanthophyllum Squarrosum." *Journal of Asia-Pacific Biodiversity* 11 (4): 566–72. https://doi.org/10.1016/J.JAPB.2018.08.009.

Shatilova, Irina, Nino Mchedlishvili, Luara Rukhadze, and Eliso Kvavadze. 2011. *The History of the Flora and Vegetation of Georgia (South Caucasus)* . Edited by David Lordkipanidze and Abesalom Vekua. Tbilisi: Georgian National Museum.

Shatilova, I., L. Rukhadze, and N. Mchedlishvili. 2007. "The Main Stages of Development of Family Hamamelidaceae on the Territory of Eurasia." *Proceedings of the Georgian Academy of Sciences* 5: 1.

Shaw, Kirsty, Larry Stritch, Malin Rivers, Shyamali Roy, Becky Wilson, and Rafaël Govaerts. 2014. "The Red List of Betulaceae." https://www.researchgate.net/publication/277988052.

Shrestha, Uttam Babu, Shiva Gautam, and Kamaljit S. Bawa. 2012. "Widespread Climate Change in the Himalayas and Associated Changes in Local Ecosystems." *PLOS ONE* 7 (5): e36741. https://doi.org/10.1371/journal.pone.0036741.

Sigdel, Shalik Ram, Xiangyu Zheng, Flurin Babst, J. Julio Camarero, Shan Gao, Xiaoxia Li, Xiaoming Lu, et al. 2024. "Accelerated Succession in Himalayan Alpine Treelines under Climatic Warming." *Nature Plants* 10 (12): 1909–18. https://doi.org/10.1038/s41477-024-01855-0.

Skvortsov, A. K. 2002. "A New System of the Genus Betula L.—the Birch." *Bull. Mosc. Natur. Soc.* 107 (5): 73–76. http://172.104.19.75/translations/Skv2002Betula.html.

Smith, William K., Matthew J. Germino, Daniel M. Johnson, and Keith Reinhardt. 2009. "The Altitude of Alpine Treeline: A Bellwether of Climate Change Effects." *The Botanical Review 2009 75:2* 75 (2): 163–90. https://doi.org/10.1007/S12229-009-9030-3.

Steinbauer, Manuel J., John Arvid Grytnes, Gerald Jurasinski, Aino Kulonen, Jonathan Lenoir, Harald Pauli, Christian Rixen, et al. 2018. "Accelerated Increase in Plant Species Richness on Mountain Summits Is Linked to Warming." *Nature* 556 (7700): 231–34. https://doi.org/10.1038/S41586-018-0005-6;TECHMETA.

Svenning, Jens Christian, Camilla Fløjgaard, Katharine A. Marske, David Nógues-Bravo, and Signe Normand. 2011. "Applications of Species Distribution Modeling to Paleobiology." *Quaternary Science Reviews* 30 (21–22): 2930–47. https://doi.org/10.1016/J.QUASCIREV.2011.06.012.

Tarkhnishvili, David, Alexander Gavashelishvili, and Levan Mumladze. 2012a. "Palaeoclimatic Models Help to Understand Current Distribution of Caucasian Forest Species." *Academic.Oup.ComD Tarkhnishvili, A Gavashelishvili, L MumladzeBiological Journal of the Linnean Society, 2012•academic.Oup.Com* 105 (1): 231–48. https://doi.org/10.1111/J.1095-8312.2011.01788.X.

———. 2012b. "Palaeoclimatic Models Help to Understand Current Distribution of Caucasian Forest Species." *Biological Journal of the Linnean Society* 105 (1): 231–48. https://doi.org/10.1111/J.1095-8312.2011.01788.X.

Tarkhnishvili, David, Uğur Kaya, Alexander Gavashelishvili, and Irina Serbinova. n.d. "Ecological Divergence between Two Evolutionary Lineages of the Caucasian Salamander: Evidence from GIS Analysis."

Thórsson, ÆH Th, E. Salmela, and K. Anamthawat-Jónsson. 2001. "Morphological, Cytogenetic, and Molecular Evidence for Introgressive Hybridization in Birch."

Journal of Heredity 92 (5): 404–8. https://doi.org/10.1093/jhered/92.5.404.

Thuiller, Wilfried, Sandra Lavorel, Miguel B. Araújo, Martin T. Sykes, and I. Colin Prentice. 2005. "Climate Change Threats to Plant Diversity in Europe." *Proceedings of the National Academy of Sciences* 102 (23): 8245–50. https://doi.org/10.1073/PNAS.0409902102.

Tielidze, Levan G., and Roger D. Wheate. 2018. "The Greater Caucasus Glacier Inventory (Russia, Georgia and Azerbaijan)." *Cryosphere* 12 (1): 81–94. https://doi.org/10.5194/TC-12-81-2018.

Togonidze, Natalia, and Maia Akhalkatsi. 2015. "Variability of Plant Species Diversity during the Natural Restoration of the Subalpine Birch Forest in the Central Great Caucasus." *TURKISH JOURNAL OF BOTANY* 39 (3): 458–71. https://doi.org/10.3906/bot-1404-19.

Tovar, Carolina, Carlos Alberto Arnillas, Francisco Cuesta, and Wouter Buytaert. 2013. "Diverging Responses of Tropical Andean Biomes under Future Climate Conditions." *PLOS ONE* 8 (5): e63634. https://doi.org/10.1371/JOURNAL.PONE.0063634.

Tranquillini, Walter. 1979. "Climatic Resistance and Damage of Trees at Timberline." In *Physiological Ecology of the Alpine Timberline. Ecological Studies (Analysis and Synthesis), Vol 31.*, 91–111. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-67107-4_8.

Troitsky, N. A. 1927. "Remains of Forests in Akhalkalaki District." *Bulletin of Tbilisi Botanical Garden, New Series* 3–4: 107–22.

Tvalchrelidze, M., Z. Lebanidze, and G. Jaoshvili. 2004. "Eustatics of the Black Sea and Sedimentation Peculiarities during the Last 20 000 Years (Georgian Sector of the Black Sea)." *Proceed. of Geological Institute, Georgian Academy of Sciences* new series (119): 656–70.

Vakkari, Pekka. 2009. "EUFORGEN Technical Guidelines for Genetic Conservation and Use for Silver Birch (Betula Pendula)." Rome, Italy. https://hdl.handle.net/10568/104741.

Ven, Christopher M. Van De, S. B. Weiss, and W. G. Ernst. 2007. "Plant Species Distributions under Present Conditions and Forecasted for Warmer Climates in an Arid Mountain Range." *Earth Interactions* 11 (9): 1–33. https://doi.org/10.1175/EI205.1.

Waltari, Eric, Robert J. Hijmans, A. Townsend Peterson, Árpád S. Nyári, Susan L. Perkins, and Robert P. Guralnick. 2007. "Locating Pleistocene Refugia: Comparing

Phylogeographic and Ecological Niche Model Predictions." *PLOS ONE* 2 (7): e563. https://doi.org/10.1371/JOURNAL.PONE.0000563.

Wang, Nian, Hugh A. Mcallister, Paul R. Bartlett, and Richard J.A. Buggs. 2016. "Molecular Phylogeny and Genome Size Evolution of the Genus Betula (Betulaceae)." *Annals of Botany* 117 (6): 1023–35. https://doi.org/10.1093/aob/mcw048.

Warren, Dan L., Richard E. Glor, and Michael Turelli. 2010. "ENMTools: A Toolbox for Comparative Studies of Environmental Niche Models." *Ecography* 33 (3): 607–11. https://doi.org/10.1111/J.1600-0587.2009.06142.X.

Warton, David I. 2005. "Many Zeros Does Not Mean Zero Inflation: Comparing the Goodness-of-Fit of Parametric Models to Multivariate Abundance Data." *Environmetrics* 16 (3): 275–89. https://doi.org/10.1002/ENV.702.

Wielgolaski, F. E. 2005a. "History and Environment of the Nordic Mountain Birch." *Plant Ecology, Herbivory, and Human Impact in Nordic Mountain Birch Forests*, January, 3–18. https://doi.org/10.1007/3-540-26595-3_1.

———. 2005b. "History and Environment of the Nordic Mountain Birch." In *Plant Ecology, Herbivory, and Human Impact in Nordic Mountain Birch Forests*, edited by Caldwell M.M. et al., 3–18. Springer, Berlin, Heidelberg. https://doi.org/10.1007/3-540-26595-3_1.

Wiens, John J., and Catherine H. Graham. 2005. "Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology." *Annual Review of Ecology, Evolution, and Systematics* 36 (Volume 36, 2005): 519–39. https://doi.org/10.1146/ANNUREV.ECOLSYS.36.102803.095431/CITE/REFWORKS.

Wiesmair, Martin, Hannes Feilhauer, Anja Magiera, Annette Otte, and Rainer Waldhardt. 2016. "Estimating Vegetation Cover from High-Resolution Satellite Data to Assess Grassland Degradation in the Georgian Caucasus." *Https://Doi.Org/10.1659/MRD-JOURNAL-D-15-00064.1* 36 (1): 56–65. https://doi.org/10.1659/MRD-JOURNAL-D-15-00064.1.

Williams, Jr, and M. L. Arnold. 2001. "Sources of Genetic Structure in the Woody Perennial Betula Occidentalis." *Https://Doi.Org/10.1086/321921* 162 (5): 1097–1109. https://doi.org/10.1086/321921.

Williams, L, N Zazanashvili, G Sanadiradze, and A Kandaurov. 2006. "Ecoregional Conservation Plan for the Caucasus."

Winkler, Hubert. 1904. *Betulaceae. In: Engler, Das Pflanzenreich IV.* . Verlag von Wilhelm Engelmann .

Wisz, M. S., R. J. Hijmans, J. Li, A. T. Peterson, C. H. Graham, A. Guisan, J. Elith, et al. 2008. "Effects of Sample Size on the Performance of Species Distribution Models." *Diversity and Distributions* 14 (5): 763–73. https://doi.org/10.1111/J.1472-4642.2008.00482.X.

Xie, Yuyang, Zehao Shen, Tao Wang, George P. Malanson, Josep Peñuelas, Xiaoyi Wang, Xiangwu Chen, et al. 2024. "Uppermost Global Tree Elevations Are Primarily Limited by Low Temperature or Insufficient Moisture." *Global Change Biology* 30 (4): e17260. https://doi.org/10.1111/gcb.17260.

Zhang, Xuebin, Enric Aguilar, S. Sensoy, H. Melkonyan, U. Tagiyeva, N. Ahmed, et al. 2005. "Trends in Middle East Climate Extreme Indices from 1950 to 2003." *Journal of Geophysical Research: Atmospheres* 110 (D22). https://doi.org/10.1029/2005JD006181.

Zare, H., M. Akbarinia, S. Hosseini, H. Ejtehadi, and T. A. Eshkevari. 2010. "A New Record of Betula Litwinowii (Betulaceae) and a Review of the Geographical Distribution of the Genus Betula L. In Iran." *Iran J Bot* 16 (2): 237–41.

Zazanashvili, N., M. Garforth, H. Jungius, T. Gamkrelidze, and C. Montalvo. 2012. "Ecoregional Conservation Plan for the Caucasus. 2012 Revised and Updated Edition."

Zazanashvili, N., G. Sanadiradze, M. Garforth, M. Bitsadze, K. Manvelyan, E. Askerov, M. Mousavi, et al. 2020. "Ecoregional Conservation Plan for the Caucasus: 2020 Edition."

Zazanashvili, N, L. Gavashelishvili, C. Montalvo, G. Beruchashvili, A. Heidelberg, J. Neuner, R. Schulzke, and M. Garforth. 2011. "Strategic Guidelines for Responding to Impacts of Global Climate Change on Forests in the Southern Caucasus (Armenia, Azerbaijan, Georgia)." https://wwfint.awsassets.panda.org/downloads/forest_strategy_for_south_caucasus_1.pdf.

Zazanashvili, Nugzar. 1999. "On the Colkhic Vegetation." In *Conference on Recent Shifts in Vegetation Boundaries of Deciduous Forests, Especially Due to General Global Warming*, 181–97. Birkhäuser, Basel. https://doi.org/10.1007/978-3-0348-8722-9_11.

Zazanashvili, Nugzar, Revaz Gagnidze, and George Nakhutsrishvili. 2000. "Main Types of Vegetation Zonation on the Mountains of the Caucasus." *Acta Phytogeographica Suecica* 85: 7–16.

Zazanashvili, Nugzar, and David Mallon. 2009. "Status and Protection of Globally Threatened Species in the Caucasus."

Zeng, Jie, Jian Hua Li, and Zhi Duan Chen. 2008. "A New Species of Betula Section Betulaster (Betulaceae) from China." *Botanical Journal of the Linnean Society* 156 (4):

523–28. https://doi.org/10.1111/j.1095-8339.2007.00764.x.

Zeng, Jie, Bao Qing Ren, Jun Yi Zhu, and Zhi Duan Chen. 2014. "Betula Hainanensis (Betulaster, Betulaceae), a New Species from Hainan Island, China." *Https://Doi.Org/10.5735/085.051.0606* 51 (6): 399–402. https://doi.org/10.5735/085.051.0606.

Appendixes

Appendix 1. Article published: Akobia, I., Janiashvili, Z., Metreveli, V. et al. (2022). Modelling the potential distribution of subalpine birches (*Betula* spp.) in the Caucasus. COMMUNITY ECOLOGY 23, 209–218 https://doi.org/10.1007/s42974-022-00097-4

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ORIGINAL ARTICLE

Modelling the potential distribution of subalpine birches (*Betula* spp.) in the Caucasus

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Abstract
The treeline ecosystems in the Caucasus are mainly composed of birch (*Betuletum*) stands. These high-mountain forests encompass pivotal ecological functions like climate regulation, water retention, soil protection and more. The location of Caucasus birches as part of the treeline communities determines its vulnerability to anthropogenic as well as natural stressors. Therefore, the natural distribution area of birches has been significantly shrunk. Meanwhile, the two contrasting tendencies are also observable in the Caucasus, the lowering of the natural upper limit of the treeline border as well as the widening of the distribution area towards higher elevations. In this research, we aimed to model the actual distribution areas of Caucasus birches according to the factors and patterns of their present distribution. We used the Maxent (Maximum Entropy Model) model based on WorldClim bioclimatic variables—mean temperature of warmest quarter, mean temperature of coldest quarter, precipitation of coldest quarter and precipitation of warmest quarter, and 160 study plots (including 100 field experimental plots). The model demonstrated high predictive power AUC = 0.97. The Maxent algorithm showed the potential distribution areas of Caucasus birches covering the entire Caucasus region and the climatic variables as the main factors contributing to or limiting the distribution of birches in the study region. Understanding the distribution characteristics of birches in the Caucasus can serve as a basis for future research on shifts and changes in treeline forest communities occurring as a result of various impacts, e.g. climate change.

Keywords Caucasus · Treeline · Birches · Potential distribution · Maximum entropy model

Abbreviations

AUC	Area under the curve
GBIF	Global biodiversity information facility
Maxent	Maximum entropy model
NFI	National forest inventory of Georgia
WWF	World wildlife fund

Deceased: Nugzar Zazanashvili.

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Introduction

High-elevation treeline forests are one of the most prominent ecotones (Körner, 2012; Tranquillini, 1979) that have attracted scientific interest for a long time (e.g. Brockmann-Jerosch, 1919; von Humboldt & Bonpland, 1807). These high mountain (Subalpine) forests are a source of various vital ecosystem services, like water retention and regulation, soil protection, climate regulation, recreation and others, essential for the well-being of local upland (rural) as well as lowland communities (Bebi et al., 2001; Fagre, 2009; Price et al. 2011; Mina et al., 2017). Treeline ecotones

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Appendix 2. Article accepted for publication: Akobia, I., Metreveli, V., Ugrekhelidze, K. (2026). Ecological Niche Dynamics of Treeline Birches (*Betula* spp.) under Pleistocene - Holocene - Future Climate Change in the Caucasus. Trees, Forests and People. https://doi.org/10.1016/j.tfp.2026.101192.

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Ecological Niche Dynamics of Treeline Birches (*Betula* spp.) under Pleistocene - Holocene - Future Climate Change in the Caucasus

Ilia Akobia [a b], Vasil Metreveli [b c d], Ketevan Ugrekhelidze [b], Ketevan Batsatsashvili [b], Zurab Javakhishvili [b], Nugzar Zazanashvili [e †]

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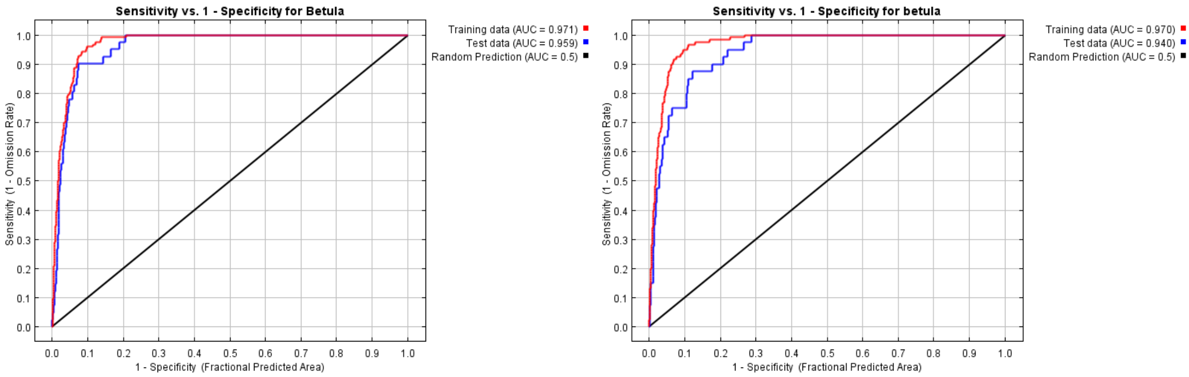
Abstract

Treeline birches (Betula spp.) are key components of subalpine forests in the Caucasus, providing important ecosystem services but facing growing threats from climate change. We applied ecological niche modeling (MaxEnt) to assess birch habitat dynamics across multiple temporal scales: the Last Glacial Maximum (LGM), the Mid-Holocene (MH), the present and future projections for 2100 under three Shared Socioeconomic Pathways (SSP126, SSP370, SSP585), using MIROC and CMCC-ESM2 climate models. Model performance was high (AUC > 0.97). Thermal variables, particularly the mean temperature of the warmest (Bio10) and coldest (Bio11) quarters, were the dominant predictors, complemented by seasonal precipitation (Bio18, Bio19). Paleoclimatic reconstructions showed confinement to refugial areas in Colchis and Hyrcania during the LGM, with expansion during the wetter Mid-Holocene. Present conditions represent the ecological optimum, supporting continuous treeline belts along the Greater Caucasus and fragmented patches in the Lesser Caucasus. Future projections revealed strong scenario-dependent shrinkages: SSP126 maintained relative stability, whereas SSP370 and SSP585 indicated losses exceeding 80-95%, leaving only small, isolated refugia at high elevations. These results demonstrate a refugia – recolonization – optimum – shrinkage trajectory and identify the Caucasus ecoregion as both a long-term refugial zone and a climate-sensitive hotspot. Conservation strategies should prioritize refugial strongholds, ecological connectivity and climate-adaptive management to safeguard birch treelines under future climate warming.

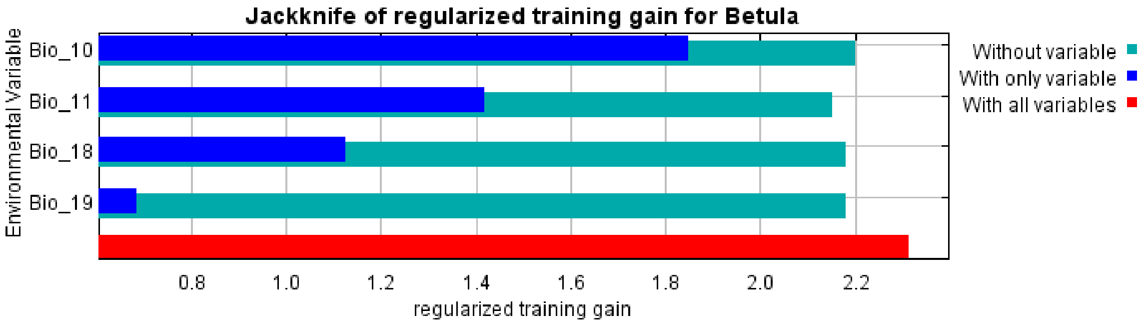
Appendix 3. Figure: Comparison of Training AUC values of the MaxEnt model for *Betula* spp. based on 165 occurrence records (left; AUC = 0.971) and 160 occurrence records (right; AUC = 0.970).



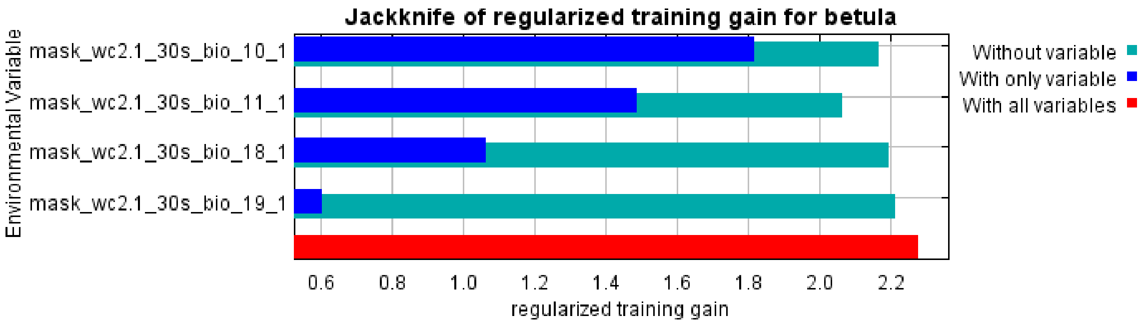
Appendix 4. Table: Relative contribution (%) and permutation importance (%) of environmental variables in the MaxEnt model for *Betula* spp., comparing models calibrated with 165 and 160 occurrence records.

Variable	165 records		160 records	
	Percent contribution	**Permutation importance**	**Percent contribution**	**Permutatio n importance**
Mean temperature of warmest quarter (BIO10)	70.4	36	64.8	53.9
Mean temperature of coldest quarter (BIO11)	11.1	46.2	21.6	29.1
Precipitation of warmest quarter (BIO18)	10.6	11.7	8.8	13.1
Precipitation of coldest quarter (BIO19)	7.9	6.1	4.9	3.9

Appendix 5. Figure: Results of the jackknife test of variable importance in the MaxEnt model for *Betula* spp.: (A) model calibrated with 165 occurrence records; (B) model calibrated with 160 occurrence records.



(A)



(B)

Appendix 6. Figure: Potential present-day distribution of *Betula* spp. in the Caucasus based on 160 occurrence records. Darker shades of green indicate higher predicted habitat suitability (probability of occurrence) derived from the MaxEnt model.