Chestnut Ecology in the Caucasus

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Declaration of originality and confirmation of Conformance

As the author of this doctoral thesis, I confirm that this compilation is my original work and does not include materials from other authors that have already been published, accepted for publication, or submitted for a degree, unless properly cited.

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Vasil Metreveli

30.05.2025

აბსტრაქტი

დისერტაცია ეხება წაბლის (*Castanea sativa* Miller) ეკოლოგიიის შესწავლას კავკასიაში და სწავლობს გარემო ფაცტორებს, რომლებიც განსაზღვრავს წაბლის გავრცელებას, ზრდას და მდგომარეობას კავკასიის ეკორეგიონში. კვლევა ეფუძნება დეტალურ საველე მონაცემებს და აჩვენებს, რომ ჰაბიტატის ზუსტი მოდელები, რომლებიც მიღებულია ბუნებრივი წაბლის პოპულაციებდან აღებული მონაცემებით, ეფექტურად პროგნოზირებენ სახეობის გავრცელებას მთელს მის არეალში. რაც გარკვეულად ეწინააღმდეგება აქამდე გავრცელებულ მოსაზრებას, რომ ზუსტი მოდელირებისათვის აუცილებელია ფართომასშტაბიანი კონტინენტური მონაცემები. კვლევის მიხედვით, წაბლისთვის ოპტიმალური კლიმატური პირობებია მინიმუმ 500-დან 1000 მმ-მდე წლიური ნალექების რაოდენობა, 15-დან 30°C-მდე ტემპერატურა ყველაზე თბილ კვარტალში და -15°C-ზე მეტი ტემპერატურა ზამთარში. ჰაბიტატის ვარგისიანოვბა მნიშვნელოვნად მცირდება მშრალ, ცივ ან ჭარბად ტენიან პირობებში. სხვა და სხვა კლიმატური მონაცემების შედარებითმა ანალიზმა აჩვენა, რომ CHELSA v2.1 უკეთესად პროგნოზირებს წაბლის გავრცელებას, ვიდრე WorldClim v2.1-ი. განსაკუთრებით მთიან რეგიონებში. ეს გამოწვეულია იმით, რომ CHELSA v2.1 უკეთ ითვალისწინებს ტოპოგრაფიული ცვალებადობას. ბუნებრივი ტყეებში მოპოვებული მონაცემების გამოყენება ამცირებს მიკერძოებას, რომელიც დაკავშირებულია წარსულში ადამიანის მიერ გამოწვეულ ზემოქმედებასთან წაბლის გავრცელებაზე. მოდელების GBIF მონაცემებთით ვალიდაციამ კიდევ ოფრო გააუმჯობესა მათი ფართო გამოყენების საიმედოობა. დენდროქრონოლოგიურმა ანალიზმა ასევე დაადგინა ძირითადი გარემოს ფაქტორები, რომლებიც მოქმედებენ წაბლის ზრდაზე. ხეების ასაკი, ყველაზე ცივი თვის მინიმალური ტემპერატურა, ნალექების რაოდენობა ყველაზე მშრალ კვარტალში, ნიადაგის აზოტის შემცველობა და ნიადაგის მჟავიანობა (Ph) მნიშვნელოვნად მოქმედებენ წაბლის ყოველწლიურ შემატებაზე/ზრდაზე. კვლევამ ასევე გამოავლინა გარემოს ფაქტორები, რომლებიც მოქმედებენ წაბლის კიბოსაგან (*Cryphonectria parasitica*) გამოწვეულ სიგამხმრის სიმძიმეზე. კერძოდ, ჭარბი ნალექები, მაღალი ტემპერატურა და ხშირი ქვეტყე მნიშვნელოვნად ზრდის სიგამხმრეს. დისერტაციის შედეგები ხაზს უსვამს

პარამეტრული ეკოლოგიური მოდელების საჭიროებას და იძლვა მნიშვნელოვან ინფორმაციას წაბლის კონსერვაციისა და მართვის მეთოდებისთვის. რათა მომავალში წაბლის პოპულაციებს შენარჩუნდეს მედეგობა გარემოს ცვლილებების პირობებში.

საკვანძო სიტყვები: *Castanea sativa*; კავკასია; ჰაბიტატის ვარგისიანობა; პოტენციური გავრცელება; მაქსიმალური ენტროპიის მოდელი; ჰაბიტატის შერჩევის ინდექსი; დენდროქრონოლოგია; ზოგადი ადიტიური მოდელი (GAM); კლიმატის ცვლილება; ხეების ზრდის დინამიკა; კავკასიის რეგიონი; წაბლი; წაბლის სიგამხმრე; კლიმატი; მოდელირება; დეფოლიაციის სიმძიმე.

Summary

This dissertation examines the ecological parameters affecting the distribution, growth, and health of the Sweet Chestnut (*Castanea sativa* Miller) within the Caucasus ecoregion. The research utilises high-quality, region-specific data to show that accurate habitat suitability models derived from natural *Ca. sativa* populations in the Caucasus effectively predict the species' wider distribution in Europe and Asia Minor, thereby contesting earlier beliefs that extensive continental-scale data are necessary. Ideal climatic requirements for *Ca. sativa* cultivation include yearly precipitation of 500 to 1000 mm, temperatures in the warmest quarter between 15 and 30°C, and winter temperatures exceeding –15°C. Suitability markedly diminishes in very arid, frigid, or wet circumstances. Comparative assessments of climate datasets indicated that CHELSA v2.1 exhibited more prediction accuracy than WorldClim, especially in mountainous regions, owing to its improved depiction of topographic variance. Employing data only from natural stands reduces biases associated with previous human-induced range expansions, leading to strong and ecologically significant models. Validation against independent GBIF occurrence data further substantiated the models' dependability and extensive applicability. The scientists also identified key environmental factors influencing *Ca. sativa* growth by dendrochronological analysis. Tree age, minimum winter temperatures, precipitation in the driest quarter, soil nitrogen concentrations, and soil pH substantially affected yearly growth patterns, with younger trees showing increased growth rates. In addition, the research investigated the environmental factors influencing the severity of Chestnut blight (*Cryphonectria parasitica*), revealing complex relationships among precipitation, temperature, slope gradient, and understory vegetation density. Excessive precipitation, elevated temperatures, and thick understory vegetation markedly increased defoliation severity. These results highlight the need for precisely parameterised ecological models and provide significant insights for conservation and management methods to maintain robust *Ca. sativa* populations amid environmental changes.

Key words: Castanea sativa; Caucasus; habitat suitability; potential distribution; maximum entropy model; habitat electivity index; Dendrochronology; Generalized additive model (GAM); Climate change; Tree growth dynamics; Caucasus region; Chestnut; Chestnut blight; Climate; Modeling; Defoliation Severity;

Zusammenfassung

Diese Dissertation untersucht die ökologischen Faktoren, die die Verbreitung, das Wachstum und die Gesundheit der Edelkastanie (*Castanea sativa* Miller) in der Kaukasus-Ökoregion beeinflussen. Mithilfe hochwertiger, regionsspezifischer Daten zeigt die Studie, dass präzise Habitatmodelle, basierend auf natürlichen Kastanienbeständen im Kaukasus, die weitere Verbreitung der Art in Europa und Kleinasien zuverlässig vorhersagen können. Dies widerspricht der bisherigen Annahme, dass umfangreiche kontinentale Datensätze unverzichtbar seien. Optimale Umweltbedingungen für das Kastanienwachstum umfassen einen jährlichen Niederschlag zwischen 500 und 1000 mm, Temperaturen im heißesten Quartal zwischen 15 und 30 °C sowie Wintertemperaturen über –15 °C. Die Eignung nimmt unter extrem trockenen, kalten oder feuchten Bedingungen deutlich ab. Vergleichende Analysen verschiedener Klimadatensätze zeigten, dass CHELSA v2.1 eine höhere Vorhersagegenauigkeit als WorldClim bietet, insbesondere in gebirgigen Regionen, aufgrund einer verbesserten Darstellung der topographischen Variabilität. Die Verwendung von Daten ausschließlich aus natürlichen Beständen reduzierte Verzerrungen, die durch historische menschliche Ausbreitungen entstanden sind, und führte zu robusten und ökologisch relevanten Modellen. Die Validierung mit unabhängigen GBIF-Daten bestätigte zudem die Zuverlässigkeit und breite Anwendbarkeit der Modelle. Darüber hinaus identifizierte die Studie durch dendrochronologische Analysen entscheidende Umweltfaktoren, die das Wachstum der Kastanien beeinflussen. Faktoren wie Baumalter, minimale Wintertemperaturen, Niederschlag während des trockensten Quartals, Stickstoffgehalt und pH-Wert des Bodens beeinflussten die jährlichen Wachstumsmuster signifikant, wobei jüngere Bäume höhere Wachstumsraten aufwiesen. Die Studie untersuchte ebenfalls Umweltfaktoren, die die Schwere des Kastanienrindenkrebses (Cryphonectria parasitica) bestimmen. Komplexe Interaktionen zwischen Niederschlag, Temperatur, Hangneigung und Unterwuchsdichte wurden festgestellt. Übermäßiger Niederschlag, erhöhte Temperaturen und dichter Unterwuchs führten zu einer deutlich stärkeren Entlaubung. Zusammenfassend unterstreichen diese Ergebnisse die Bedeutung präzise parametrisierter ökologischer Modelle und bieten wertvolle Erkenntnisse für die Erhaltungs- und

Managementstrategien, um widerstandsfähige Kastanienbestände angesichts von Umweltveränderungen zu bewahren.

Schlüsselwörter: Edelkastanie; Kaukasus Habitateignung; potenzielle Verbreitung; Maximum-Entropie-Modell; Habitat-Elektivitätsindex; Dendrochronologie; Generalisierte additive Modelle (GAM); Klimawandel; Baumwachstumsdynamik; Kaukasus-Region; Kastanie; Kastanienrindenkrebs; Klima; Modellierung; Schweregrad der Entlaubung;

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List of abbreviations

MODIS	Moderate Resolution Imaging Spectroradiometer
GBIF	Global Biodiversity Information Facility
SDM	Species Distribution Model
AUC	Area under the curve
HEI	Habitat Electivity Index
CHELSA	Climatologies at High Resolution for the Earth's Land Surface Areas
SRTM	Shuttle Radar Topography Mission
BIOCLIM	Bioclimatic Variables (climate-related predictors used in modeling)
UNDP	United Nations Development Program
CNF	Caucasus Nature Fund
LGM	Last Glacial Maximum
GAM	Generalized Additive Model
AIC	Akaike Information Criterion
MSE	Mean Squared Error
SSP126	Shared Socioeconomic Pathway 1–2.6 (low emission scenario)
SSP370	Shared Socioeconomic Pathway 3–7.0 (intermediate emission scenario)
SSP585	Shared Socioeconomic Pathway 5–8.5 (high emission scenario)
BIO1–BIO19	Bioclimatic Variables from CHELSA
CMIP6	Coupled Model Intercomparison Project Phase 6
ISIMIP3b	Inter-Sectoral Impact Model Intercomparison Project Phase 3b
GFDL-ESM4	Geophysical Fluid Dynamics Laboratory Earth System Model v4
DEM	Digital Elevation Model
TPI	Topographic Position Index
TRI	Topographic Ruggedness Index
CEC	Cation Exchange Capacity
DBH	Diameter at Breast Height

REML	Restricted Maximum Likelihood
Cr. parasitica	Cryphonectria parasitica, the fungus causing Chestnut blight
Ca. sativa	*Castanea sativa* (Sweet Chestnut)
GAM	Generalized Additive Model
REML	Restricted Maximum Likelihood
AIC	Akaike Information Criterion
R	Statistical computing software (R Core Team, 2023)
CHELSA	Climatologies at High Resolution for the Earth's Land Surface Areas
"ocat"	Ordered categorical family (used in GAMs for ordinal response variables)
SD	Standard Deviation (used in descriptive statistics)

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Table 8 – AIC and Kendall rank correlation coefficient of the top 5 defoliation models

Appendix Table A1. Concurvity of model terms from the Generalized Additive Model and between each term and the rest of the model

1. General Introduction

Forests cover a significant part of the Earth's ice-free terrestrial area, despite the major conversion of forestland to agricultural and urban use. Forested areas, in tandem with wood products, generate freshwater from mountain watersheds, purify the air of several contaminants, provide habitats for wildlife and domestic grazing animals, and present leisure opportunities. Humans' influence on the forest ecosystem affects the species composition, tree coverage, age, and density of plants. The demand for forest products has prompted several problems, such as the introduction of nonnative and invasive species. All these lead the local species to extinction (Waring and Running, 2007). Recent experimental and theoretical studies indicate that species extinction leads to declines in productivity, nutrient retention, resistance to invasion, and other critical processes necessary for ecosystem functioning (Smith and Knapp, 2003). In addition, climate change has been identified as a key factor influencing forest ecosystems. (Triviño et al., 2023). The factors above enhance the interest of academics, managers, and policymakers in analysing forest ecosystems, examining associated pests that threaten indigenous forests and fauna and studying the ecology of tree species (McDowell et al., 2020; Millar and Stephenson, 2015; Nikinmaa et al., 2020).

"Species ecology" means an analysis of a certain species' interactions with its environment, including both biotic (living) and abiotic (non-living) elements. It studies the species' habitat, niche, distribution range, physiology and adaptations, species interaction and competition, and response to disturbance. Ecology covers three levels: the individual organism, the population (which includes individuals of the same species), and the community (comprising many species populations). At the organism and population levels, ecology studies the influence of the environment on species and vice versa (Begon and Townsend, 2021). To study the impact of the environment on species, it is crucial to understand species distribution, development (growth) and response to disturbance. Especially for the plant species, because they are less mobile compared to most animals. As immobile organisms, plants must adjust to environmental fluctuations through physiological and morphological modifications rather than behavioral mobility (Lambers et al., 2008). Therefore, they are more vulnerable to rapid environmental

changes than mobile animal species (Jump and Peñuelas, 2005). However, it is comparatively easier to study the plant response to the environmental factors than mobile animal species (Franklin and Miller, 2009). The abovementioned components and their interplay are mostly examined using ecological modelling.

Ecological Modelling is an empirical approach that correlates species' field observations with environmental predictor variables, applying a mixture of statistically or theoretically obtained response curves that most accurately represent the ecological needs of the species (Guisan and Thuiller, 2005) The models primarily depend on proven methodological principles, alongside biogeographical, ecological, and evolutionary theories for understanding the species' ecology (Guisan et al., 2017). In parallel to the development of computational technologies, Ecological modelling has become an essential instrument for analyzing complex interactions and predicting ecosystem reactions to external disturbances. Species distribution models (SDMs), growth models, and disease impact models assist researchers and managers in comprehending and predicting ecological alterations, especially in forest environments, for the different tree species in different regions (Franklin and Miller, 2009; Guisan et al., 2017).

Among the interesting tree species used in ecological research, the Sweet Chestnut (*Castanea sativa* Miller) is particularly significant for its unique ecological and economic values. *Ca. sativa* is a significant component of Caucasian and European forests. It is a relict deciduous tree species from the Fagaceae family, and is the only natural representative of the genus *Castanea* throughout Europe and the Caucasus (Conedera et al., 2024).

Ca. sativa often achieves heights of 20–35 meters and has substantial ecological and economic importance throughout its distribution area. It can appear in monospecific stands or within mixed forests, often combined with Fagus orientalis (beech), Carpinus betulus or Carpinus caucasica (hornbeam), and various oak (Quercus) species. In such contexts, it often appears as a subdominant or submissive element (Nakhutsrishvili, 2013). As a light-demanding plant, *Ca. sativa* needs significant light exposure during its first growing phases but demonstrates shade tolerance in subsequent life stages (Dolukhanov, 2010).

Ca. sativa grows in temperate areas characterised by moderate to high annual precipitation (500–2700 mm) and a mean annual temperature between 8°C and 15°C (Conedera et al., 2024). It may tolerate short frost occurrences down to –25°C and, with protective snow cover in the northern Caucasus, survive winter extremes as low as –35°C [2,10,11]. *Ca. sativa* often thrives at altitudes ranging from 100 to 1800 meters above sea level, preferring sandy to clay loam soils characterised by deep profiles and substantial water retention. While it often eschews calcareous soils, instances on limestone have been recorded in the Caucasus (Conedera et al., 2024; Dolukhanov, 2010; Nakhutsrishvili, 2013). Water and thermal stress, particularly in summer, may markedly impede photosynthesis and heighten susceptibility to pests and diseases (Conedera et al., 2021; Mahdi Najafpour, 2012).

Ca. sativa is distributed in Southern and Central Europe, parts of North Africa (notably Morocco), Northwest Europe (including England and Belgium), and Western Asia, encompassing northeastern Türkiye, Syria, and the Caucasus region (Georgia, Armenia, Azerbaijan, southern Russia, and northern Iran). Palynological and archaeological evidence suggest that *Ca. sativa* migrated to Europe from the Caucasus around 9,000 years ago, with two notable episodes of artificial expansion happening at 5,000 and 2,000 years ago, the latter coinciding with Roman agricultural dispersion. In regions like Great Britain, the species, formerly considered introduced, now expands naturally due to climate warming (Broadmeadow et al., 2005; Krebs et al., 2004a), however, its range expansion is increasingly constrained by increased summer droughts in southern Europe (Conedera et al., 2024).

Increased temperatures and modified precipitation patterns substantially influence the growth, distribution, and health of *Ca. sativa*, presenting considerable challenges to its populations and affecting their physiology and phenology (Beridze et al., 2023b). Changed temperatures may lead to a reduction in growth rate, impeding seed production and natural regeneration (REF). Furthermore, drought stress and increased evapotranspiration may diminish growth rates and increase trees' vulnerability to pests and diseases (Solla et al., 2024; Vlachou et al., 2024).

Among biotic hazards, Chestnut blight, induced by the fungus *Cryphonectria parasitica* (Murrill) M.E.Barr, is the most significant problem. The disease, first identified in 1904 in New York on C. dentata (Rigling and Prospero, 2018), certainly originated in East Asia and has subsequently destroyed *Ca. sativa* populations worldwide (Anagnostakis, 1987). The fungus infects plants via bark injuries, colonising cambial tissues, obstructing water and nutrient flow, and often resulting in death. American chestnut is very vulnerable, while *C. sativa* also shows significant sensitivity, in contrast to co-evolved Asian species like *Castanea mollissima* Blume and *Castanea crenata* Siebold & Zucc. which have high resilience. The pathogen was first identified in the Caucasus in 1938 and has since inflicted significant harm (Prospero et al., 2013). Notwithstanding the moderating influence of hypovirulent fungal strains (Heiniger and Rigling, 1994; Milgroom and Cortesi, 2004), the illness persists in its rapid spread. By 2010, more than 40% of Georgia's *Ca. sativa* forests (106,000 hectares) had been significantly affected by blight (Beridze and Dering, 2021; Tavadze et al., 2013), resulting in cascading ecological consequences such as biodiversity loss, disruption of nutrient cycling, and a decline in forest productivity (Baser and Bozoglu, 2020).

Historically, many people in Europe and the Caucasus ecoregion have found *Ca. sativa* to be a highly significant commercial species. *Ca. sativa* have been brought to various areas of the globe because of their economic significance. In the economics of European and Caucasian nations, fruits and timber play significant roles. People have been actively using *Ca. sativa* wood for agricultural and silvicultural reasons as well as for home construction. The fruits may be consumed raw, boiled, or fried; they have also been used to manufacture flour. Famous for its coppice use, *Ca. sativa* was the conventional way of stand renewal to quickly generate wood. Many *Ca. stands* in the Caucasus ecoregion were coppice stands used to provide fuel (Badenes and Byrne, 2012; Dolukhanov, 2010). Demand for *Ca. sativa* in Europe and the Caucasus ecoregion remains strong, driving increasingly rigorous management efforts to boost wood and nut goods (Venanzi et al., 2016).

The Caucasus ecoregion is situated between the Black Sea and the Caspian Sea, spanning 1300 km. Located between 36° and 51° E longitude and 36° and 47° N latitude, the region covers

580,000 km² and includes several prominent features, such as the North Caucasus Plain, the Greater Caucasus Range, the Lesser Caucasus, and the Highland of South Caucasus, which encompasses parts of Asia Minor (Tielidze and Wheate, 2018). The area serves as a notable Pleistocene refugium (Krebs et al., 2004; Tarkhnishvili et al., 2012). It is one of the 35 biodiversity hotspots globally (Zachos, 2011) and has a diverse flora including over 6,500 species of vascular plants, many of which are endemic (Zazanashvili et al., 2009). The Caucasus ecoregion has a diverse native tree flora of 153 species (Akhalkatsi, 2019). The predominant tree species are *Fagus orientalis* Lipsky, *Carpinus betulus* L., *Picea orientalis* (L.), and *Abies nordmanniana* (Steven) Spach (Tarkhnishvili, 2014). Forests mostly exist in mesic climates. The largest expanse of wooded regions is situated in the southern and eastern Black Sea coastline, northwest of the Greater Caucasus, and next to the southern Caspian Sea coast (Akhalkatsi, 2019).

The industrialisation era altered the species composition and structure of forests globally, especially in some regions of Europe. Primary forests were eliminated, and the majority of the continent's forests were cultivated. Simultaneously, native species were not given priority during reforestation efforts. Due to their significant economic worth, many species were imported from other continents. Numerous imported species that effectively adapted to the new environment were naturalised and widespread (Newbigin, 1928). Therefore, it isn't easy to study the true natural responses of the species to the environmental factors (Krebs et al., 2004b). Conversely, the forests in the Caucasus ecoregion have seen less influence. Despite substantial industrial cutting operations occurring in the 20th century (1930 to 1950), the subsequent period (1950 to 1990), the forests were mostly maintained for defensive and recreational purposes (Akhalkatsi, 2015). Furthermore, some forested regions in the Caucasus are still considered primary due to the challenging topography of the area. Consequently, the primary populations of *Ca. sativa* remain observable and evaluable (Beridze et al., 2023b). The Caucasus is a region where natural populations of *Ca. sativa*, with a lengthy evolutionary history, continues to exist (Prospero et al., 2013). Consequently, the examination of the conditions for the existence of *Ca. sativa* in the Caucasus ecoregion offers a valuable chance to identify an appropriate natural habitat throughout the species' distribution.

This research constitutes the doctoral dissertation about the ecology of *Ca. sativa* in the Caucasus region. This thesis clearly examines its ecological niche, distribution, and growth dynamics in light of the aforementioned obstacles, historical context, and information deficiencies, under present and anticipated climatic circumstances. In addition to the examination of environmental factors associated with Chestnut blight (*Cr. parasitica*).

1.1 Objectives

The study specifically aims to investigate:

1) Potential Distribution and Suitable Habitat for Chestnut (*Castanea sativa*)
2) Environmental covariates of Chestnut blight (*Cryphonectria parasitica*) in Georgia (Caucasus)
3) On the relationship between environment and growth of Sweet Chestnut (*Castanea sativa*) in the Caucasus

2. Chapter I

Potential Distribution and Suitable Habitat for Chestnut (*Castanea sativa*)

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Potential Distribution and Suitable Habitat for Chestnut (*Castanea sativa*)

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Abstract: Chestnut, *Castanea sativa* Miller (Fagales: Fagaceae), is an ecologically and economically important tree species of the forest ecosystem in Southern Europe, North-Western Europe, Western Asia, North Africa, and the Caucasus. The distributional range of chestnut in Europe has been highly modified by humans since ancient times. Biotic and abiotic factors have dramatically changed its distribution. Historic anthropogenic range expansion makes it difficult to identify habitat requirements for natural stands of chestnut. In the Caucasus, natural stands of chestnut survived in glacial forest refugia and landscapes that have been difficult for humans to colonize. To identify the species reliable habitat requirements, we estimated the relationship between climatic variables and 620 occurrence locations of natural chestnut stands from the Caucasus and validated the model using GBIF data from outside the Caucasus. We found that our best model is reasonably accurate and the data from the Caucasus characterize chestnut stands throughout the species range well.

Keywords: *Castanea sativa*; Caucasus; habitat suitability; potential distribution; maximum entropy model; habitat electivity index

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Picture 1. Cover image of the published article representing Chapter 1

2.1 Introduction

Understanding the ecological niche of *Ca. sativa* is necessary for its conservation and management. Species Distribution Models (SDMs) are essential instruments for identifying appropriate habitats and significant environmental factors (Franklin and Miller, 2009). Numerous studies have modelled *Ca. sativa* distribution in the Caucasus and Europe. The research by Conedera et al. (2024) indicated that its present European distribution encompasses over 2.5 million hectares, mostly in Italy, France, Spain, Portugal, and Switzerland. Their model also indicates the most favorable climatic conditions for the distribution. However, the work underscores the lack of data from the Caucasus ecoregion, as a critical area for examining the ecology and distribution of *Ca. sativa*.

Beridze et al. (2023b) show that their Species Distribution Models (SDMs) identified the Caucasus (Colchis Lowland, eastern Pontic Mountains, and Hyrcanian woods) as significant refugia during the Last Glacial Maximum (LGM). The existing model indicates that populations are limited to the Hyrcanian highlands. During the Early Holocene, favourable environments significantly expanded eastward, though. The SDM results were well correlated with ancient pollen data, indicating the historical existence and proliferation of *Ca. sativa* as projected by the models.

Another work by Beridze et al. (2023a) shows that temperature mostly influences the genetic diversity pattern in C. sativa, as shown by a considerable isolation-by-environment model. He asserts that climate change may substantially alter the distribution and genetic diversity of *Ca. sativa* in the future, resulting in habitat loss, particularly on the unique eastern edge of the species' distribution in Azerbaijan.

These studies illustrate significant efforts in examining the geographical distribution of *Ca. sativa*, along with other aspects. All of these underscore the significance of comprehensive samples, the need for further analysis, and the improvement of distribution models (Beridze et al., 2023b, 2023a; Conedera et al., 2024). Nonetheless, several challenges must be considered during the modelling of species distribution or ecological niches. Including designs for data collection, model selection, and predictor contribution (Araújo and Guisan, 2006), geographical scale (the

scope of the investigation and extrapolation region), among others (Xie et al., 2022). The models derived from local-scale data often fail to elucidate the worldwide distribution of species, and conversely (Jones et al., 2010). In addition, modelling widespread species such as *C. sativa* poses difficulties. Diverse regional scales, disparate climatic information, and methodological discrepancies can provide contradictory results (Araújo and Guisan, 2006; Soria-Auza et al., 2010). Furthermore, previous models for Europe and the Caucasus have been limited by limited data availability in native ecosystems (Beridze et al., 2023b; Conedera et al., 2024).

In the first chapter, we attempted to address these issues. The primary hypothesis of the first chapter hypothesised that *Ca. sativa* distribution model of the Caucasus is reliable in explaining the species' global range. Simultaneously with this theory, we tried to answer additional questions such as:

1. What are the suitable habitats and potential distribution areas for chestnut (*Castanea sativa*) within the Caucasus region?

The first question seeks to examine both ecological and biogeographical concerns. It aims to ascertain the precise environmental conditions, such as temperature and precipitation of different seasons, that delineate the ecological niche of *Ca. sativa* within its native habitats of the Caucasus ecoregion. Furthermore, the task reveals the areas where these favorable circumstances now exist, including the regions highly affected by human agriculture.

2. Can a distribution model developed using data from the Caucasus reliably predict the global range of *Castanea sativa*?

The second question aims to investigate the adaptability and resilience of ecological models across various geographical scales. This examines whether habitat suitability trends seen in the species' original and relatively primary range—the Caucasus—can be extended to its wider spread. This entails evaluating whether ecological niche models, developed using high-quality local data, can accurately represent the species' environmental envelope on a global scale.

3. Which climate dataset, CHELSA v2.1 or WorldClim v2.1, performs better for accurately modeling the distribution of chestnut (*Castanea sativa*)?

The third question implies analyses of the disparities in geographic resolution, data-generating techniques, and ecological authenticity of two commonly used datasets. Also assessing the effectiveness of each dataset in representing the bioclimatic variables pertinent to *Ca. sativa* ecology, including precipitation seasonality and temperature extremes, especially in intricate mountainous areas such as the Caucasus. The question implies assessment of the model performance and prediction accuracy to determine which dataset yields more ecologically significant and spatially precise habitat suitability maps.

2.2 Materials and Methods

2.2.1 Study Area

The study area represents the distribution range of the *Ca. sativa*, located between –16° and 72° E longitude and 26° and 77° N latitude. It covers the whole distribution range (Figure 2).

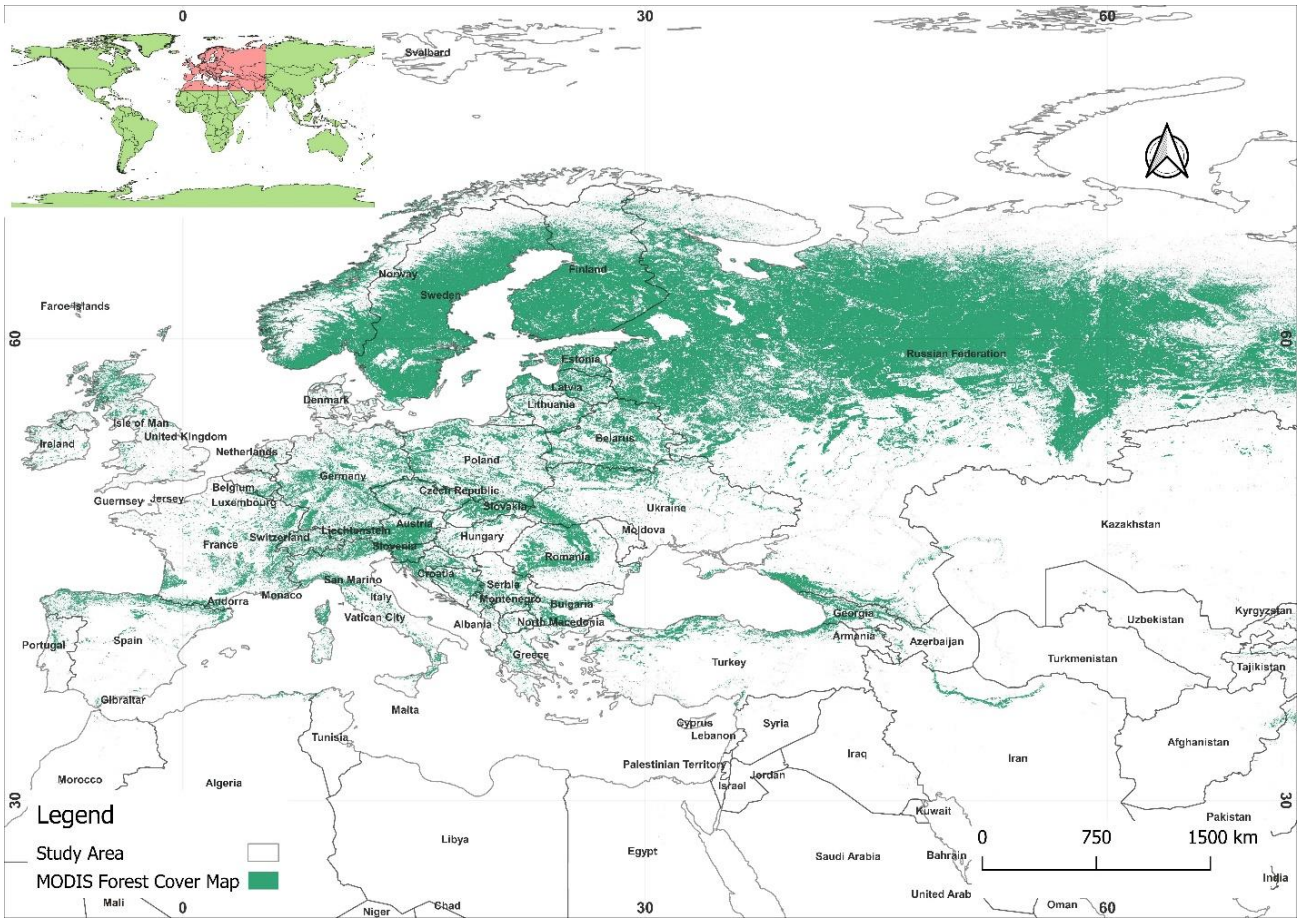

Figure 1. Map of the study area. The green color represents the forest cover from the Moderate Resolution Imaging Spectroradiometer (MODIS).

Modeling the species global range using the data from its natural habitat is a common tactic used for invasive species (Thuiller et al., 2005). However, given that it is challenging to distinguish between natural and anthropogenic *Ca. sativa* stands in Europe (Conedera et al., 2024), we decided to sample the Caucasus ecoregion rather than the entire study zone because it is a less impacted area compared with the other territories of the *Ca. sativa* distribution range (*Akhalkatsi*, 2015).

By employing this technique, we hope to eliminate the bias in the data caused by human intervention.

The ecoregion is located between 36° and 51° E longitude and 36° and 47° N latitude and is located between the Black Sea (oceanic nature) and the Caspian Sea. it represents the important Pleistocene refugia (Krebs et al., 2004; Tarkhnishvili et al., 2012). It covers an area of 580,000 km² and is composed of several prominent elements, including the North Caucasus Plain (below sea level); the Greater Caucasus Range, which is 1300 km in length from northwest to southeast between the Black Sea and Caspian Sea (highest peak 5642 m); the Lesser Caucasus 100 km to the south (from the Black Sea coast and Colchic lowlands to 4500 m); and the Highland of South Caucasus, which covers parts of Asia Minor (highest peak 5165 m) (Tarkhnishvili et al., 2012; Tielidze and Wheate, 2018) (Figure 3).

The Caucasus is one of the 35 biodiversity hotspots in the world (Mittermeier et al., 2011) and it has a very rich flora with over 6500 species of vascular plants, many of which are endemic species (Zazanashvili and Mallon, 2009). Forests are spread mostly in mesic climates. The biggest part of the forested areas is located close to the southern and eastern Black Sea coast, northwest of the Greater Caucasus, and along the southern coast of the Caspian Sea. The Caucasus region has rich native tree flora with 153 tree species (Akhalkatsi, 2019). The most dominant tree species are beech, hornbeam, chestnut, spruce, and fir (Tarkhnishvili, 2014).

2.2.2 Occurrence Data of Ca. sativa

The fieldwork was conducted from 2018 to 2022. The stratified random sampling method was used for planning 166 sample plots in Türkiye and Georgia. The geographical locations were predetermined by the random stratified sampling method, using forest inventory maps (Forest Management Plans from 1990 to the present period) (Aoyama, 1954). The *Ca. sativa* stands were polygonised from the maps and sampled using the pre-GPS points (sample plots) (Hayek and Buzas, 2010). The locations in the field were found and recorded using a GPS Garmin Montana 64s device. The coordinates of the single *Ca. sativa* tree in the stand were also considered occurrences and were used in the analyses.

The Ministry of Environmental Protection and Agriculture of Georgia provided 647 presence sample plots, sampled using the random systematic method (Iachan, 1982), from the first national forest inventory data in the country (collected in 2019–2021). The sample plots that were close to 1 km apart from the other occurrence spots were removed. In the end, 330 of the 647 locations were applied. An additional 30 occurrences were derived from herbarium specimens deposited in the Institute of Botany at Ilia State University, taken from 1960 until the present day. Four coordinates from Azerbaijan were provided by our colleague Berika Beridze in 2018. More than 30 randomly sampled records were provided by the United Nations Development Program (UNDP), among the project "Expansion and Improved Management Effectiveness of the Adjara Region's Protected Areas (00088000) /2015". Another 60 randomly sampled coordinates were provided by the Caucasus Nature Fund (CNF), collected from the project— "Technical assistance to conduct monitoring of the state of Sweet Chestnut and Chestnut Blight in Mtirala and Kintrishi Protected Areas in Georgia" (CNF/2021/TAGA-GEO-141).

In the end, 620 *Ca. sativa* presence samples were collected in Georgia, Türkiye, and Azerbaijan. To reduce spatial autocorrelation in the species distribution modeling, we used locations with a minimum of 1 × 1 km distance between them, because we applied the climate raster layers with a spatial resolution of 1 km cells (Dormann et al., 2007; Veloz, 2009) (Figure 3).

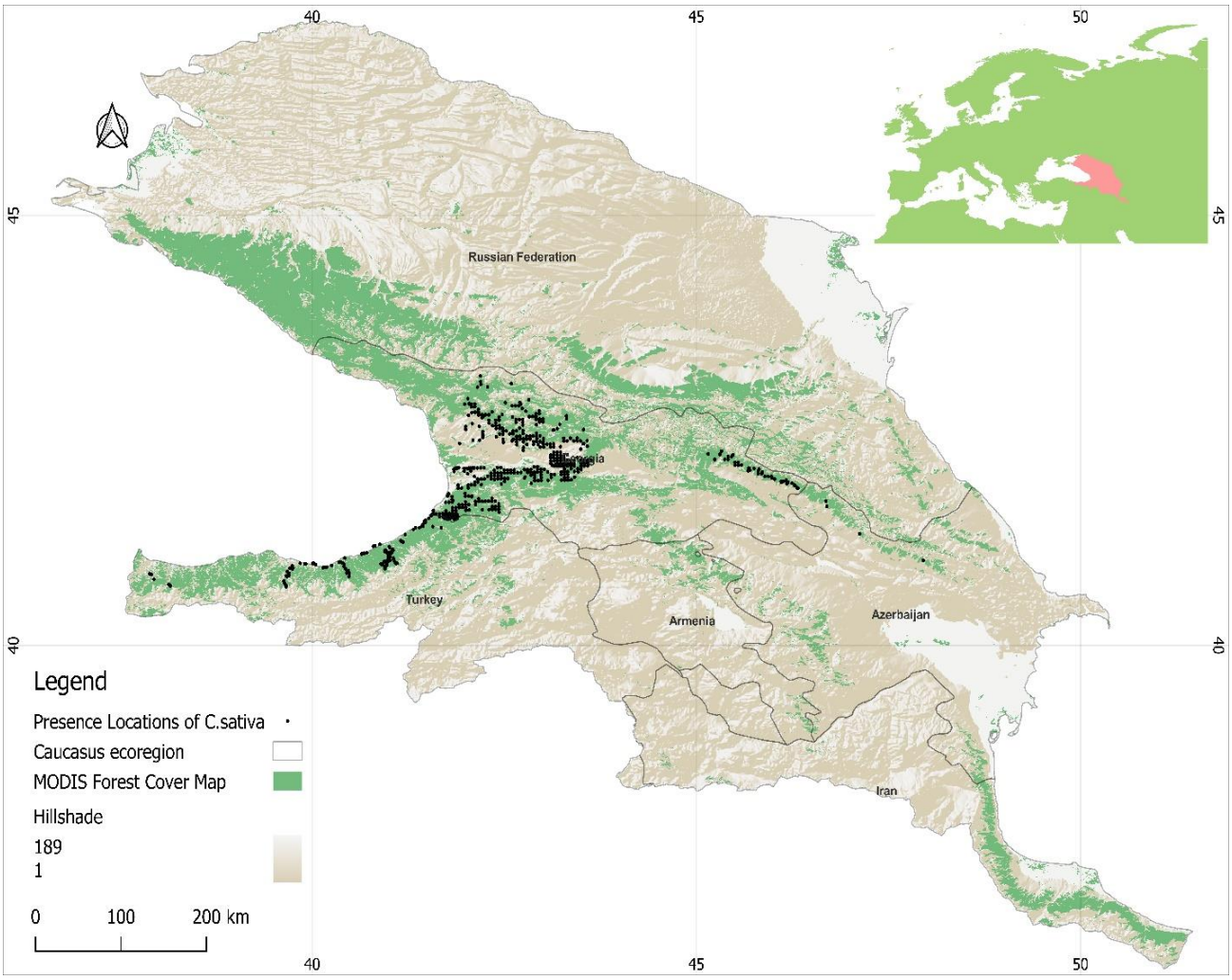

Figure 2. The map of the Caucasus ecoregion. The green color represents the forest cover of the Moderate Resolution Imaging Spectroradiometer (MODIS). The black points are the presence locations of *C. sativa* (620 locations).

We also used GBIF (Global Biodiversity Information Facility) data for Europe (downloaded from: https://doi.org/10.15468/dl.k6d6hn accessed on 25 February 2023) to check how the data from the Caucasus illustrates the favorable climate conditions for *C. sativa* in Europe (GBIF.Org User, 2023). The occurrences in parks, museums, botanical gardens, herbaria, and urban areas

were removed (Zizka et al., 2019). For cleaning the coordinates from the urban areas, we used a land cover map from MODIS (https://search.earthdata.nasa.gov/search accessed on 9 April 2018) (Friedl and Sulla-Menashe, 2019). The data were also cleaned of duplicate records and places with inaccurate geo-references (Maldonado et al., 2015). Finally, 37954 GBIF *Ca. sativa* presence records were used for validation of the *Ca. sativa* distribution in Europe (Appendix Figure A1).

2.2.3 Climatic Data

We used 1 km resolution present climate scenario raster layers of 19 bioclimatic variables from the CHELSA climatology data (CHELSA version 2.1, 30 s ~ 1 km^2, 1981–2010, downloaded from https://chelsa-climate.org, accessed on 3 February 2023) (Karger et al., 20017) and WorldClim climate data (World-Clim 2 version 2.1, 30 s ~ 1 km^2, 1970–2000, downloaded from http://www.worldclim.org/, accessed on 3 February 2023) (Fick and Hijmans, 2017) to compare the two different climate datasets (Table 1). The temperature variables of the CHELSA climatology data are multiplied by 10 (°C × 10) (Karger et al., 2017). The raster files from the climatic sources were cropped to the extent of the study area using the packages "rgdal" and "Raster" in R and were prepared for modeling (Bivand et al., 2022; Hijmans, 2023).

Table 1. Nineteen climate variables were used in the *Ca. sativa* distribution model.

Coded Bioclimatic Variables	Bioclimatic Variables
BIO1	Annual mean temperature
BIO2	Mean diurnal range (mean of monthly (maximum temperature – inimum temperature))
BIO3	Isothermally (BIO2/BIO7) (×100)
BIO4	Temperature seasonality (standard deviation ×100)
BIO5	Maximum temperature of warmest month
BIO6	Minimum temperature of coldest month
BIO7	Temperature annual range (BIO5–BIO6)
BIO8	Mean temperature of wettest quarter
BIO9	Mean temperature of driest quarter
BIO10	Mean temperature of warmest quarter
BIO11	Mean temperature of coldest quarter
BIO12	Annual precipitation
BIO13	Precipitation of wettest month
BIO14	Precipitation of driest month
BIO15	Precipitation seasonality (coefficient of variation)
BIO16	Precipitation of wettest quarter
BIO17	Precipitation of driest quarter
BIO18	Precipitation of warmest quarter
BIO19	Precipitation of coldest quarter

2.2.4 Modeling of Ca. sativa Suitable Habitats of Ca. sativa

To examine the pairwise correlations between predictor variables and to identify a source of error, the correlation matrices were built for both CHELSA and WorldClim climate variables using the "Hmisc" package in R (Appendix Figure A2 and Appendix Figure A3) (Frank, 2023). We used the predictors based on Pearson's correlation coefficient $r < 0.9$ (Schober et al., 2018). Using the "gtools" package in R, 119 uncorrelated variable combinations were created using both climate datasets (Warnes et al., 2015).

In addition to the uncorrelated variable combinations, we selected four additional groups of factors using CHELSA and WorldClim climate datasets (Table 2)—two variants using all of the variables and two others using the mechanistic predictor selection approach. In contrast with the correlative models, mechanistic species distribution models take into account how the environment affects the physiological performance of the species (Evans et al., 2015). The survival of *Ca. sativa* is connected to a combination of temperature and precipitation factors. For instance, *Ca. sativa* trees are very sensitive to summer droughts and a lack of precipitation during the hot months is vital to their survival (Conedera et al., 2021). Simultaneously, several studies concur that annual mean precipitation, as well as winter temperatures and precipitation, impact *Ca. sativa* distribution (Dolukhanov, 2010; Evans et al., 2015). Therefore, we created variable groups for both climate datasets based on this information.

To model the suitable habitats of *Ca. sativa* using the current climate, we used MaxEnt 3.4.1. It is a widely used algorithm for species distribution and ecological niche modeling, especially when only presence data are available (Phillips and Dudík, 2008). MaxEnt is well suited for presence-only data (Elith et al., 2006). In practice, it is not always easy to find the true absence coordinates because, in addition to human activities, herbivores and competition between tree species significantly alter species distribution (Vera et al., 2006). As a result, determining the threshold between true absence and absence data is difficult (Meier et al., 2010). Therefore, we sampled 10,000 background points (i.e., pseudo-absence points) inside the extent of the Caucasus ecoregion boundaries to study the distribution of environmental conditions in the study region (Phillips and Dudík, 2008; VanDerWal et al., 2009). A total of 48 models based on CHELSA

climate variables and 75 models based on WorldClim variables were created. The models were validated using 10-fold cross-validation and the mean area under the curve (AUC) of the receiver operating characteristic (ROC) curve (Bleyhl et al., 2019). The AUC (the area under the ROC curve) is believed to be one of the best options for estimating the appropriateness of a species environment, especially when background data are used (Merow et al., 2013).

Models were run with a maximum of 2500 iterations, quadratic and hinge features only, and default settings for convergence thresholds and regularization (Phillips and Dudík, 2008). Using the testing AUC, we selected 2 models out of 123 models, one from the CHELSA climate data and the other with WorldClim data. In addition, for each dataset, one model with all variables and one using a mechanistic approach was also selected. Finally, six models were chosen for the final inspection (Table 2).

Table 2. The models for the final inspection.

ID	Climate Data	Models	Variables
1	CHELSA V2.1	The model with all variables	All 19 BIO
2	CHELSA V2.1	Mechanistic model	BIO_19, BIO_18, BIO_12, BIO_11, BIO_10
3	CHELSA V2.1	The correlative model with the best AUC performances	BIO_19, BIO_18, BIO_16, BIO_15, BIO_11, BIO_10, BIO_09, BIO_08, BIO_07, BIO_06, BIO_04, BIO_03, BIO_02, BIO_01
4	Wordclim 2 V2.1	The model with all variables	All 19 BIO
5	Wordclim 2 V2.1	Mechanistic model	BIO_ 19, BIO_18, BIO_12, BIO_11, BIO_10
6	Wordclim 2 V2.1	The correlative model with the best AUC performances	BIO_19, BIO_18, BIO_17, BIO_15, BIO_13, BIO_09, BIO_08, BIO_06, BIO_04, BIO_03, BIO_02

2.2.5 Comparison of the Climate Datasets

To determine the best habitat suitability model of *Ca. sativa* for the Caucasus and Europe and to compare the performance of the WorldClim 2 and the CHELSA climate datasets, the presence coordinates of the GBIF (Global Biodiversity Information Facility) in Europe were used. Because of the large special bias of the GBIF data (Beck et al., 2014), the Habitat Electivity Indices (Jacob's Modified Electivity Index) were also calculated (Jacobs, 1974) in order to eliminate the influence of the tendentious coordinates during validation.

The habitat electivity index (HEI) is a regularly used technique for assessing species habitat preferences. It is used to compute the likelihood of the existence of a given organism in a specific habitat type based on the occurrences in that environment. The habitat selection of numerous species, including mammals, reptiles, amphibians, and birds, is often assessed using HEI. The index compares the preferences of various species for distinct environments by measuring the ratio of observed relative to anticipated abundances of a species in a given habitat. Furthermore, by quantifying the degree of selectivity for that environment, the index may be used to estimate the appropriateness and the quality of a habitat for a certain species. The index (HEI) is generated by subtracting two values: a species preference for a certain habitat and the likelihood of finding that habitat type in the environment.

The HEI formula is given as follows:

$$(P1 - P2)/[(P1 + P2) - (2 \times P1 \times P2)]$$

Where: P1 represents the abundance of the species in a specific habitat type (proportion of habitat used, the proportion of *Ca. sativa* occurrence points in the presence polygon) and P2 represents the availability of the habitat type in the environment (proportion of habitat available and proportion of the *Ca. sativa* presence polygon). The numerator (P1 – P2) reflects how favorable the environment is for the species, the denominator (P1 + P2) represents the entire amount of habitat accessible in the environment, and (2 * P1 * P2) represents the degree of connection between the P1 and P2 values (Jacobs, 1974). A higher degree of association would imply a

reduced overall availability of habitat, resulting in a smaller denominator and a higher index score. If $-1 < HEI < 0$, then the site is unsuitable. If $0 < HEI < 1$, then the location is valid. If $HEI = 0$, then the place is neither bad nor good (Lechowicz, 1982).

Two predictions (one from CHELSA and one from Wordclim 2) were chosen out of the six based on how well they fit the GBIF presence data from throughout Europe (with the highest HEI). To choose the best predictive model, the resulting models were mapped and the validity of the explanation of the ecological variables was determined through a comparison of the response curves. In addition, the binary maps were intersected to highlight the geographic disparity between the two climatic datasets. The binary maps were created using Maximum training sensitivity plus specificity threshold in Maxent (Hu and Jiang, 2010). To explain the discrepancies between the models, the variables were also intersected through cell-by-cell subtraction of CHELSA minus WorldClim (Bobrowski and Schickhoff, 2017).

2.3 Results

2.3.1 Comparison of the Models

The AUCs of the 10-fold cross-validation for models using both climate datasets were greater than 0.95 and barely differed between the WorldClim and CHELSA models. Following validation with GBIF data, the majority of WorldClim models had a higher Habitat Electivity Index (HEI) than CHELSA. On the other hand, the mechanistic models for both datasets showed the highest HEI (more than 0.93) (Table 3).

Table 3. HEI and AUC indices of the models.

ID	Climate Data	Models	AUC	HEI
1	CHELSA V2.1	The model with all variables	0.9634	–0.616084571
2	CHELSA V2.1	Mechanistic model	0.9535	0.932336488
3	CHELSA V2.1	The correlative model with the best AUC performances	0.9625	–0.382977772
4	Wordclim 2 V2.1	The model with all variables	0.9625	0.956727365
5	Wordclim 2 V2.1	Mechanistic model	0.9559	0.969826464
6	Wordclim 2 V2.1	The correlative model with the best AUC performances	0.9624	0.92322457

The models with BIO10 (mean temperature of warmest quarter), BIO11 (mean temperature of coldest quarter), BIO12 (annual precipitation), BIO18 (precipitation of warmest quarter), and BIO19 (precipitation of coldest quarter) variables for both climate data showed the highest performance. Nevertheless, the distribution pattern of *Ca. sativa* still differed highly between these two models and the HEI was not very different.

The cell-by-cell subtraction of CHELSA minus WorldClim indicates that the temperature and precipitation variable distributions were also different in these two models. For instance, the mean temperature of the warmest quarter (BIO 10) of CHELSA was nearly higher than the mean temperature of the warmest quarter of WorldClim everywhere. For CHELSA, the mean precipitation during the hottest quarter (BIO 18) was also greater in northern Europe and Hyrcanian forests, but lower in northern Africa. WorldClim in northern Europe had lower BIO 11 values than CHELSA, as well as in North Africa and the Hyrcanian region. The coldest quarter precipitation (BIO 19) was higher for WorldClim in northern Europe and North Africa, but lower

in the Hyrcanian regions. As for BIO 12, CHELSA was higher than WorldClim in the Hyrcanian mountains. It was, however, lower in northern Europe and Africa (Appendix Figure A4).

The results show that the WorldClim model predicted a wither distribution probability in the northwest of the European continent. The Faroe Islands, the southeast coast of Iceland, and north Norway are among the suitable locations for *Ca. sativa*, according to the WorldClim model. On the other hand, it did not show occurrence areas in the Hyrcanian forest of Azerbaijan and Iran, unlike CHELSA, which has a significant distribution in Hyrcanian woodlands, but a narrow distribution in northern Europe. Additionally, the CHELSA model did not illustrate any distribution across the continent of Africa, while the Wordclim model exhibited it (Appendix Figure A5).

Considering temperature-related factors (mean temperature of warmest quarter, mean temperature of coldest quarter) the WorldClim model was more difficult to explain. The BIO 11 curve of Wordclim did not display any distributional limits for high temperatures (higher than 10°) in contrast with CHELSA. Furthermore, the WorldClim BIO 10 curve did not indicate the presence of any lower distributional limits (Appendix Figure A6). As a result, we found a high suitability in locations where the forests could not exist (Appendix Figure A7). Therefore, for showing the final results, we selected the mechanistic model of CHELSA as it better revealed reliable suitable habitats for *Ca. sativa* in the Caucasus and Europe.

2.3.2 The Significance and Performance of the Variables

Jackknife of regularization training gain of the model shows the importance of variables. During the analyses, each variable was removed one at a time and a model was built using the variables that remained. Then, the test made a model with one variable at each stage. In addition, a model was also generated with all of the variables. The changes in the evaluation metric were recorded each time (AUC). Finally, we obtained the graph of individual environmental variable importance in the development of the MaxEnt model relative to all environmental variables (red bars), for each predictor variable alone (blue bars), and the drop in training gain when the variable was removed from the full model (green bars) (Phillips and Dudík, 2008). According to the Jackknife test, the warmest quarter precipitation (BIO18), the mean temperature of the warmest

quarter (BIO10), and the annual precipitation (BIO12) were most significant for the model of suitable habitats of *Ca. sativa* (Figure 4).

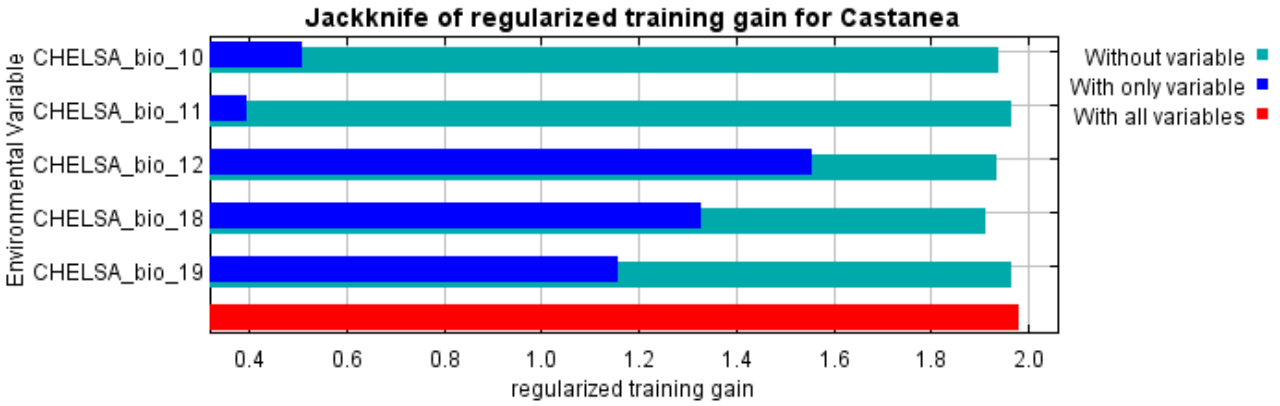

Figure 3. Importance of the environmental variables in the final (second) model.

The minimal annual precipitation (BIO 12) was 500 mm for the habitats of *Ca. sativa*, according to the habitat suitability model. As the precipitation increased from 500 mm to 1000 mm and eventually reached the plateau, the suitability of habitats rapidly increased. The likelihood of an occurrence likewise increased when the warmest quarter's precipitation (BIO 18) grew from 0 to 100. After that, it similarly became a plateau and then gradually declined. Simultaneously, the average temperature of the warmest quarter (BIO 10) for optimal suitability ranged from 15 to 30 degrees.

The extremely low winter temperature for the *Ca. sativa* was –18 degrees Celsius, while the optimal mean temperature of the coldest quarter (BIO 11) ranged between –15 and 5 degrees. The optimal range of precipitation for *Ca. sativa* in the coldest quarter (BIO 19) was 100 mm to 300 mm, after it reached a plateau. Meanwhile, the extreme minimum winter precipitation for *Ca. sativa* was 30 mm (Figure 5).

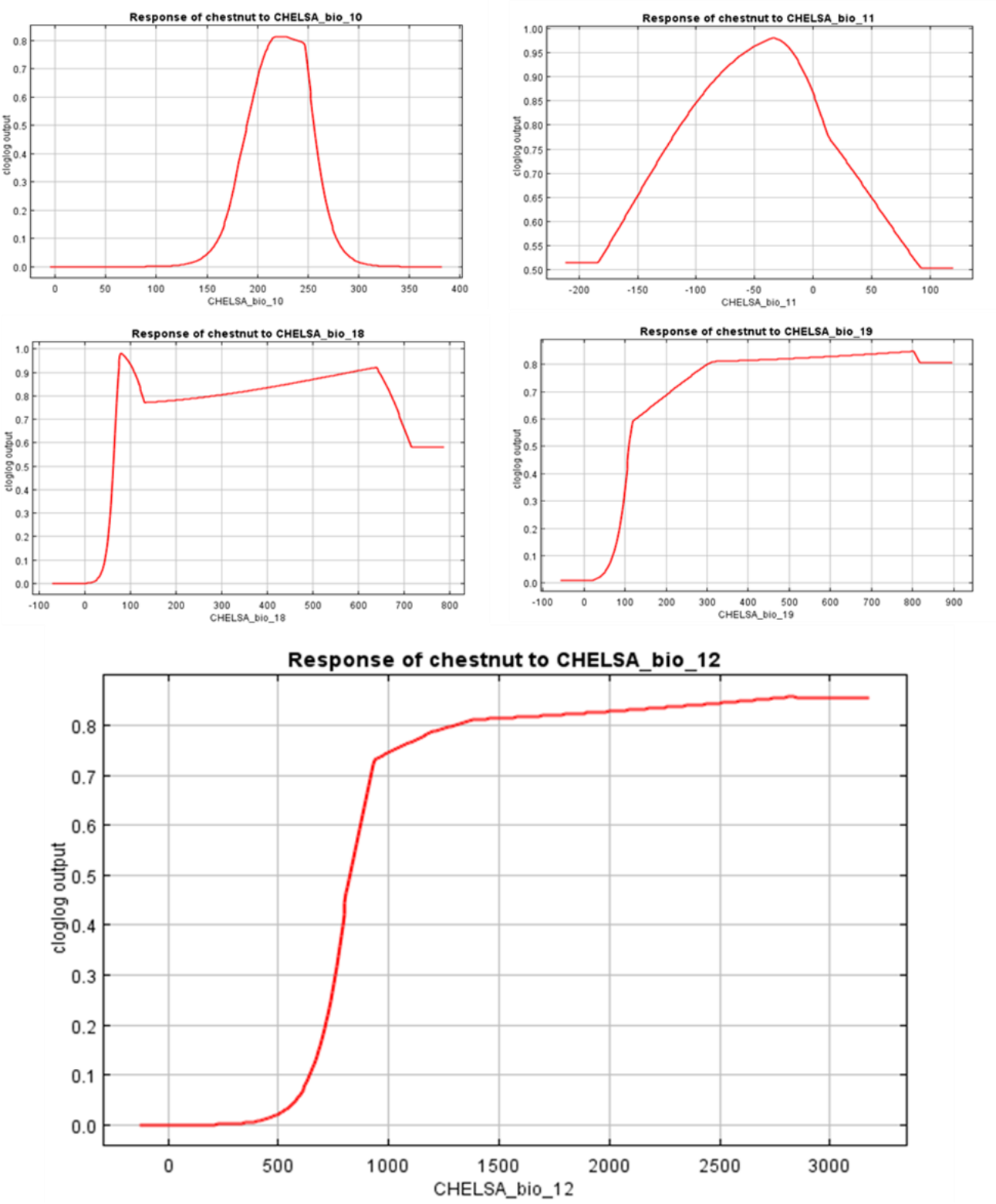

Figure 4. The response curves of the CHELSA climate variables affected by Maxent predictions.

2.3.3 Suitable Habitats Model in the Caucasus

According to the model, suitable habitats for *Ca. sativa* cover a significant part of the Caucasus. In glaciers and high mountain locations, as well as semi-desert and desert areas of Georgia, Azerbaijan, Dagestan, Armenia, Türkiye, and Iran, the distribution model predicted a zero probability of *Ca. sativa* occurrence. The mountains near the Lesser Caucasus' Black Sea shoreline were predicted to have the highest occurrence rate (>93%), as well as in the northwest part of Georgia (Svaneti and Abkhazia) of the Greater Caucasus (>93%). We obtained an interesting image in central Georgia (in the Katrly and Mtskheta-Mtianeti areas), where the likelihood of occurrence was lower (50%) than in the eastern Caucasus (>78%).

The likelihood of finding suitable *C. sativa* habitats was very high (87%) in the northwest Caucasus (Adyghe and Kabardino-Balkaria), where the habitats span a large area. A probability of 67% was found for the central part of the North Greater Caucasus (Ingushetia, North Ossetia). The possible distribution also covered forests in the eastern Greater Caucasus and the ecoregion southeast (Hyrcanian woods in Iran and Azerbaijan) with a likelihood of 74%–90%. The model performed poorly in the area of Azerbaijan's southwest and Armenia's southeast, as well as in the northern section of Armenia and the southern half of Georgia (Figure 6).

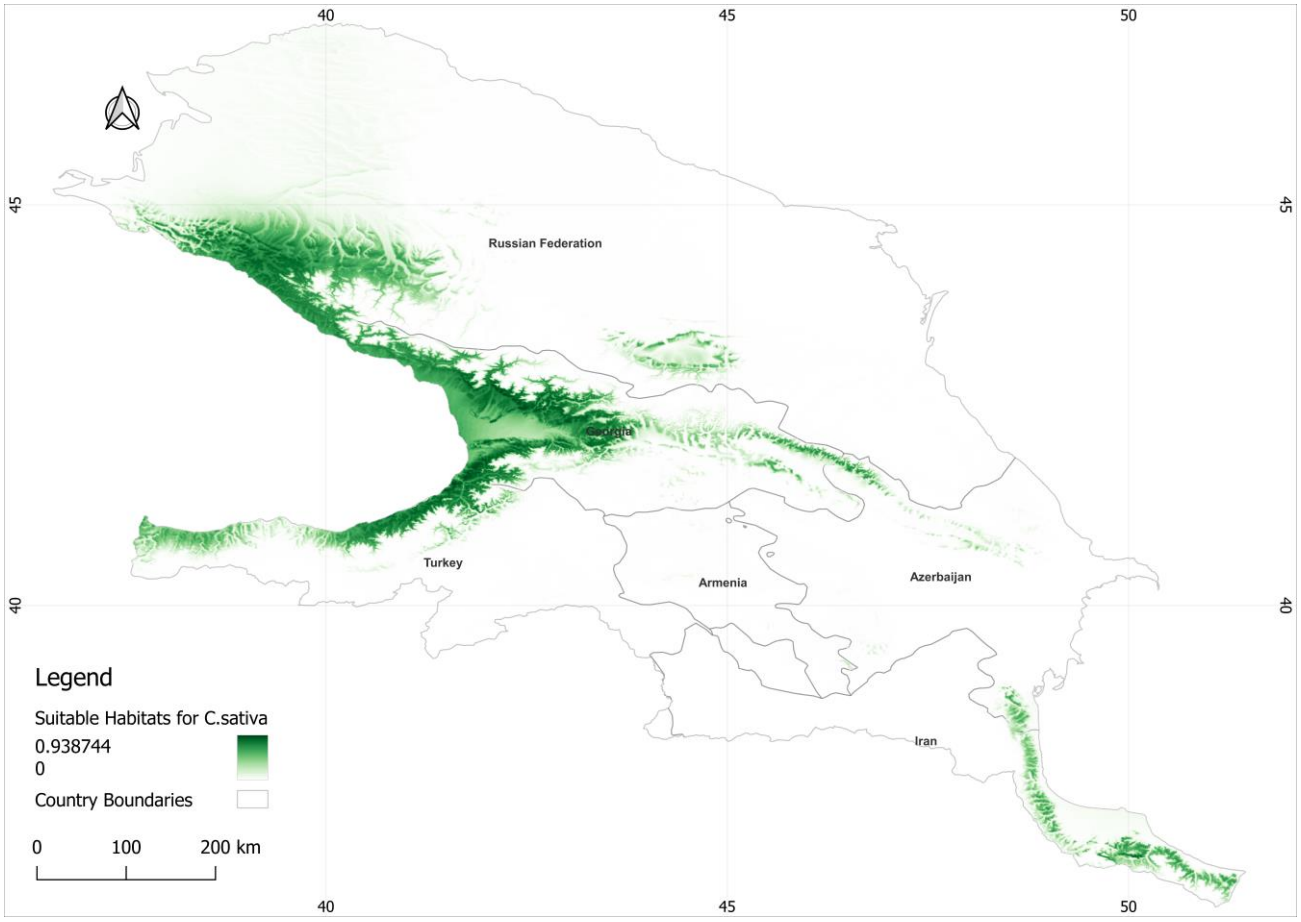

Figure 5. Representation of the Maxent model for suitable habitats for *Ca. sativa* in the Caucasus ecoregion. Darker colors show areas with more habitat suitability.

2.3.4 Suitable Habitats Model in Europe

According to the model, the current potentially suitable areas of *Ca. sativa* were estimated to be 3,758,621 km^2 in our study area. The suitable habitats of *Ca. sativa* were found to be distributed in Southern Europe (Portugal, Spain, Greece, Italy, and Türkiye), Central and Eastern Europe (Albania, Bosnia and Herzegovina, Croatia, Czech Republic, Hungary, Poland, Serbia, Slovakia, Slovenia, North Macedonia, Bulgaria, Georgia, Lithuania, Moldova, Romania, Ukraine, Armenia, Azerbaijan, and the Russian Federation), Northern Europe (Lithuania, Latvia, Estonia, Norway, and Denmark), Western Europe (France, Liechtenstein, Monaco, Switzerland, Belgium, Germany, Luxembourg, Netherlands, Austria, Montenegro, San Marino, and the United Kingdom), and Western Asia (Türkiye). However, Greece had the highest probability (>93%).

Furthermore, potentially suitable areas were detected in Central Asia (Kyrgyzstan) and Southern Asia (Iran, Afghanistan, and Pakistan). On the other hand, Latvia, Estonia, Denmark, Liechtenstein, Monaco, Belgium, Luxembourg, the Netherlands, the Czech Republic, Hungary, the United Kingdom, Poland, San Marino, Slovakia, Norway, Lithuania, Moldova, Armenia, and Kyrgyzstan had a relatively low probability (<50%) of *Ca. sativa* occurrence (Figure 7).

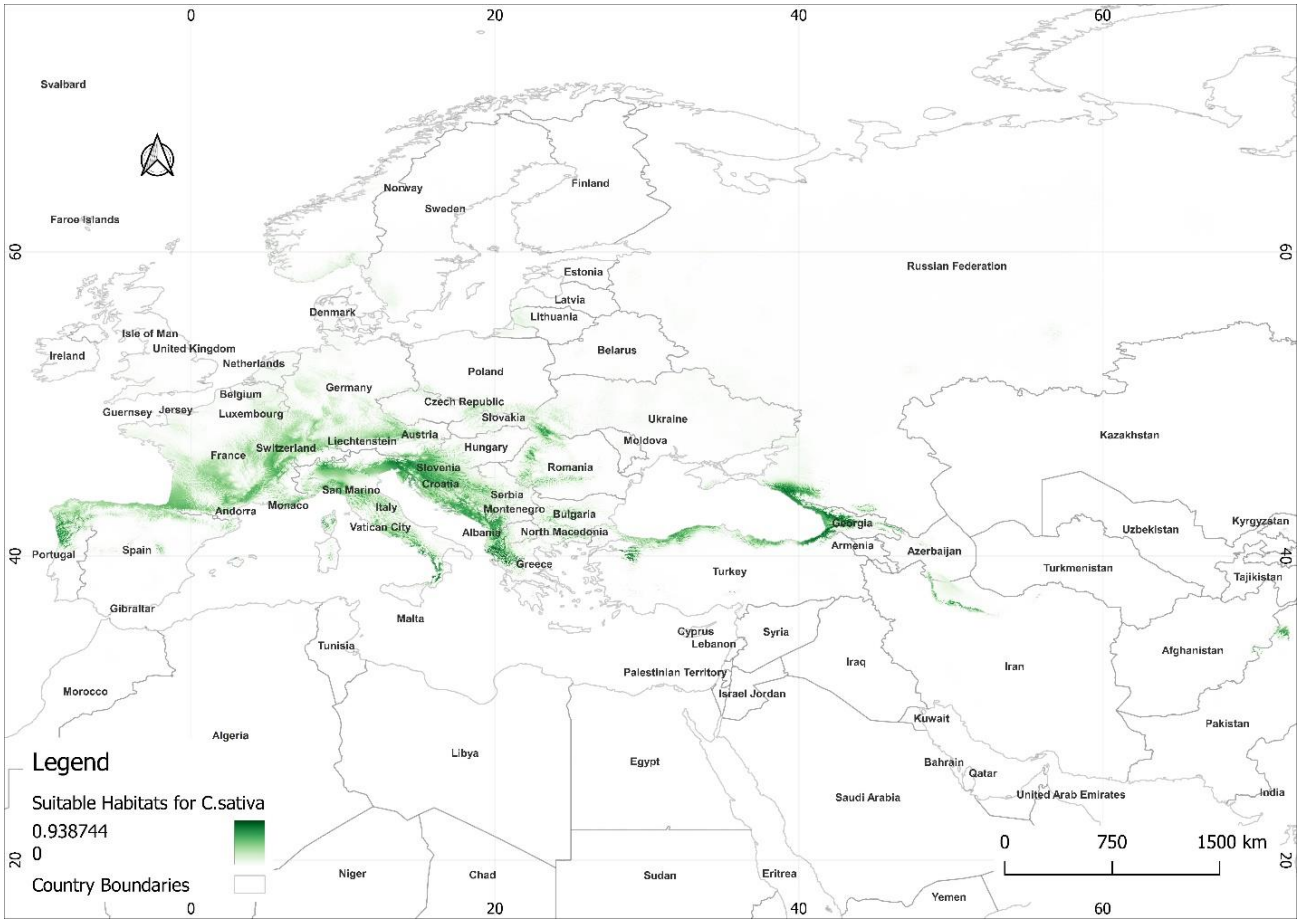

Figure 6. Representation of the Maxent model for habitat suitability of *Ca. sativa* in the species distribution range. Darker colors show areas with more habitat suitability.

2.4 Discussion

The evaluation of the model performance using various climatic datasets has not frequently been addressed in ecological niche modeling so far (Bobrowski and Schickhoff, 2017). In this work, climatic data from CHELSA and WorldClim are compared for the first time in the Caucasus to estimate the possible distribution of *Ca. sativa*.

The research demonstrated numerous interesting findings and approaches. (1) Evaluating and choosing the top climatic datasets first time for the Caucasus for developing a *Ca. sativa* distribution model. (2) Developing a valid, suitable habitat model on a local and global scale using data from the species' natural distribution range. (3) Validation of the model in the global range using Jacob's Modified Electivity Index (Jacobs, 1974), as the model evaluation using only AUC values based on presence-only GBIF data may show a contradictory result (Beck et al., 2014).

The special bias of the GBIF data can be substantially eliminated using habitat electivity indices (HEI), which are determined by the proportions of habitat used and the proportion of *Ca. sativa* occurrence points in the presence polygon (Jacobs, 1974). However, neither AUC nor other quality evaluation methods can always indicate model performances that are closely related to ecological knowledge (Hijmans, 2012).

2.4.1 Comparison of the Models

The mechanistic models with BIO 10 (mean temperature of the warmest quarter), BIO 11 (mean temperature of the coldest quarter), BIO 12 (annual precipitation), BIO 18 (precipitation of the warmest quarter), and BIO 19 (precipitation of the coldest quarter) variables showed the highest performance for both climate data. This demonstrates that mechanistic models are often more successful as the physiological characteristics of the species are taken into account (Evans et al., 2015).

Even though the best WorldClim and CHELSA models' habitat electivity indices (HEI) computed for validation with GBIF data were not very different, the intersection of their binary maps demonstrates the geographic discrepancy between them. The WorldClim model predicts a wither distribution probability in northern Europe. It does not, however, depict occurrence areas in the Hyrcanian woodland (Azerbaijan and Iran), unlike CHELSA, which has a wide range in the

Hyrcanian forests, but a small range in northern Europe. Furthermore, the CHELSA model does not show any suitability throughout the African continent, but the Wordclim model does (Appendix Figure A5). This should be due to differences in the data of the same variables in Wordclim and CHELSA (Bobrowski and Schickhoff, 2017). According to the cell-by-cell subtraction, Chelsea shows a dry and hot summer in North Africa compared with WorldClim. On the other hand, Hyrkan is less hot and wetter in summer and has a milder winter. At the same time, according to WorldClim, northern Europe has more annual precipitation but lower summer temperatures than CHELSA. Therefore, it is relatively dry according to CHELSA (Appendix Figure A4).

In addition, the Jackknife graph for the CHELSA climate datasets shows that precipitation of the warmest quarter (BIO 18), mean temperature of the warmest quarter (BIO 10), and annual precipitation (BIO 12) contribute the most to the distribution of *Ca. sativa* (Figure 4), in contrast with WorldClim where the temperature-related variables are ranked as the most important (Appendix Figure A8).

Based on the temperature-related factors (mean temperature of the warmest quarter and mean temperature of the coldest quarter), the WorldClim model is less reliable. Unlike CHELSA, the curve of the mean temperature of the coldest quarter of Wordclim does not depict any restrictions for distribution during high temperatures. In addition, the BIO 10 graph shows no lower limitations for the mean temperature of the warmest quarter for *Ca. sativa* distribution (Appendix Figure A6). As a result, the WorldClim indicates highly suitable areas in western Britain, northern Norway, the Faroe Islands, and Iceland (Appendix Figure A7), which are historically mostly covered by grasses and where only a few tree species can survive (Johansen, 1975).

As a consequence, we chose the CHELSEA mechanistic model as it indicates more reliable habitats for *Ca. sativa* in the Caucasus and Europe. This is most likely because CHELSA better explains the orographic effects, which improves habitat models, particularly in mountain locations (Karger et al., 2017). Many researchers, however, continue to use WorldClim data for species distribution modeling in the Caucasus and other mountain regions (Akobia et al., 2022),

with various approaches, species, time situations, locations, and datasets (Bobrowski and Schickhoff, 2017). As a result, before finalizing the models, data from various climatic sources should be checked in each scenario, as two different climate datasets allowed us to find the best possible habitat suitability model for *Ca. sativa*.

2.4.2 The Significance and Performance of Variables

The model predictors adequately describe the habitat requirements of the species. Our research shows that the minimal rainfall required for *Ca. sativa* is 500 mm. This is in agreement with the study of Nakhutsrisvili and Conedera (minimum 500–600 mm of rainfall) (Nakhutsrishvili, 2013, Conedera et al. 2024). The increase in the species habitat suitability with winter precipitation can be explained by snow coverage, which is also crucial for *Ca. sativa*, in addition to the temperature. This means that when the temperature is low, snow coverage is necessary for the survival of *Ca. sativa* seedlings and saplings.

The fact that snow cover is also important for *Ca. sativa*, in addition to temperature, could explain why the habitat appropriateness of the species increases with winter precipitation. This means that snow cover is essential for *Ca. sativa* seedlings and saplings to survive in cold climates (Gurney et al., 2011).

Furthermore, the figures reveal that the mean temperature of the hottest and coldest quarters, as well as winter and summer precipitation, have an important effect on *Ca. sativa* distribution. In general, we can tell that *Ca. sativa* prefers moderate climates. According to our model, a mean temperature of more than 30 degrees in the hottest quarter is stressful for *Ca. sativa*, most likely because it is an anisohydric species (Gomes-Laranjo et al., 2012).

2.4.3 Suitable Habitats Model

The other meaningful result of our study is that we developed a model of suitable habitats for *Ca. sativa* over all of the distribution ranges using data from the natural distribution areas of the species. Using this approach, we obtained a global model avoiding the spatial bias of the global data (Bowler et al., 2022), as, from the Last Glacial Maximum, the forests in the Caucasus have not changed as dramatically as in Europe (Dolukhanov, 2010).

Even though the predictive factors contributed differently to the model, our findings revealed that the species response to environmental conditions are complicated, and it is impossible to describe habitats using single particular variables (Bowler et al., 2022). Therefore, we have to discuss the temperatures and precipitations of the season together. We can observe from the analysis that precipitation factors are more relevant. However, temperature significantly restricts its dispersal in both the north and south.

Suitable habitats for *Ca. sativa* cover significant areas of the Caucasus and Europe. In the Caucasus, they are mostly found in Georgia, Azerbaijan, Armenia, the Russian Federation (Adyghe, Kabardino-Balkaria, Ingushetia, and North Ossetia), Iran, and Türkiye. Historically, the majority of these locations were appropriate for the cultivation of *Ca. sativa*. The genetic variety of the groups demonstrates that *Ca. sativa* naturally occurred in these places (Beridze et al., 2023), especially in the Hyrcanian highlands, which served as a south Caspian refugium (Gavashelishvili and Tarkhnishvili, 2016). *Ca. sativa* is now extinct in central Armenia and southern Türkiye (Beridze et al., 2023). Our model suggests a low suitability in those areas.

The distribution model correctly predicted the occurrence of *Ca. sativa* has been found with zero probability in glaciers and high mountain areas, as well as in semi-desert and desert areas. Our model also provides a reliable picture of distribution in Europe, where the suitable habitats of *Ca. sativa* occurs in Southern Europe, Central Europe, Eastern Europe, Northern Europe, Western Europe, and Türkiye. On the other hand, we found that the habitat suitability for *Ca. sativa* is very low in Northern Europe. This confirms the hypothesis that *Ca. sativa* was introduced there (Conedera et al., 2004). However, with the climate change scenarios, Great Britain and the northern parts of Europe are expected to become more suitable for *Ca. sativa* (Broadmeadow et al., 2005).

According to our model, suitable habitats for *Ca. sativa* were also detected in the Lesser Himalayas of Pakistan, Afghanistan, and Kyrgyzstan. Some studies confirm the occurrence of *Ca. sativa* in Pakistan. However, it is difficult to discuss whether it is natural or not in this part (Rahman et al., 2019). Our model also shows that there is very low habitat suitability for *Ca. sativa* in northern Africa. Even though they exist in the northern parts of the continent, they are

cultivated (Urbisz and Urbisz, 2007). One of the main factors, together with the climate for the distribution of the trees is competition (Howe and Estabrook, 1977). Therefore, with the highest probability, the whole suitable habitats of *Ca. sativa* are not covered by the chestnut trees, because of the high density of competitors. Shade-tolerant species as beech, spruce, and fir occupy large parts of the suitable habitats for *Ca. sativa* (Dolukhanov, 2010). The other factor is fruit availability, as they need to be dispersed (Howe and Estabrook, 1977). Due to these and other factors, the actual distribution area is comparably small.

2.5 Conclusions

Finally, we conclude that the suitable habitats model by CHELSA are less diffuse compared with WorldClim. It is in closer correspondence to the existing knowledge about the habitat suitability of *Ca. sativa*. The model predictions match the actual existing distribution range of *Ca. sativa* and correctly explain most of the natural global range of *Ca. sativa* (Conedera et al., 2024).

The weakness of our model is that we did not insert the soil parameters and proximity to glacial refugia into the model, whose inclusion substantially improves the current species distribution models (Tarkhnishvili et al., 2012). This is because sampling representativeness and the spatial resolution of the soil models are poor (Hengl et al., 2014) and the human-facilitated spread of *Ca. sativa* downplays the effect of proximity to the glacial refugia (Krebs et al., 2004).

However, we were still able to model the suitable reliable habitats in the Caucasus and Europe thanks to representative samples of *Ca. sativa* distribution from the part of the definite species natural range. In addition, testing climate datasets helped us to select the best climate datasets and improve our model. Therefore, we can say that *Ca. sativa* habitat suitability modeled from the data collected in the Caucasus is transferable and answers our research questions. This approach can be used to find suitable habitats for other chestnut species, as well as taxa of similar biogeographic histories.

3. Chapter II

On the relationship between environment and growth of sweet chestnut (*Castanea sativa*) in the Caucasus

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Current status: "Under Review"

3.1 Introduction

In addition to distribution modeling, this study examines the influence of temperature, soil, and terrain on *Ca. sativa* growth, using dendrochronological data. Prior tree ring studies have shown that the growth of C. sativa is significantly affected by environmental factors, especially precipitation and temperature extremes (Di Filippo et al., 2014). Precipitation in early spring fosters growth, whereas summer heat and dryness inhibit it. At lower elevations, water availability is essential for alleviating heat stress; nevertheless, excessive precipitation can lead to waterlogging and diminished development (Jarman et al., 2017). Edaphic variables, including soil pH, texture, and nutrient composition (particularly nitrogen and phosphorus), significantly influence growth (Cernusak et al., 2010; Conedera et al., 2021; Velizarova, 2015). However, dendrochronological analysis of *Ca. sativa* faces distinct difficulties due to development irregularities, including absent rings and ring shake (Romagnoli et al., 2004; Spina and Romagnoli, 2010). Cross-dating with co-occurring oak species is frequently essential for establishing reliable chronologies. Fortunately, the decay-resistant heartwood and dense sapwood structure of *Ca. sativa* contribute to the preservation of growth records (Jarman et al., 2017).

Due to the rapid progression of climate change, characterized by elevated temperatures, altered precipitation patterns, and heightened disturbance regimes (Comerford et al., 2013), there is an urgent need to comprehend and predict the growth responses of *Ca. sativa*. Predictions suggest diminished growth and regeneration in future warming scenarios, primarily attributed to heightened evapotranspiration and water stress (Beridze et al., 2023b; Solla et al., 2024; Vlachou et al., 2024).

The second chapter of the thesis presents the first integrative study of C. sativa growth in the Caucasus under both current and projected climate conditions. Specifically, we hypothesize that the growth of *Ca. sativa* is influenced by climatic, soil, and terrain. The research seeks to answer the following questions:

1. How do current climatic, terrain, and soil conditions influence annual ring growth of *Ca. sativa* in the Caucasus?

The first question of the second chapter examines how contemporary environmental factors namely climate, topography, and soil influence the annual ring growth of *Ca. sativa* in the Caucasus. This study examines the impact of temperature, precipitation, elevation, slope, and soil characteristics such as pH and nitrogen on annual tree growth. The emphasis is on determining which elements are most impactful and how their interactions influence tree growth. Comprehending these linkages elucidates the optimal growth circumstances for *Ca. sativa* trees.

2. How might these relationships alter the growth of *Ca. sativa* under future climate scenarios?

The second question of the second chapter investigates the potential changes in climate interactions, concerning the growth of *Ca. sativa* under prospective climate scenarios. It enquires if expected alterations in temperature and precipitation (e.g., under SSP126, SSP370, SSP585) would increase, reduce, or invert the influence these variables play on tree-ring growth. The goal is to comprehend how climate change may alter the growth patterns of species throughout the Caucasus. This involves using climate models to predict future circumstances and integrating them with growth models derived from existing data. This research is essential for projecting growth fluctuations or enhancements across various places.

3.2 Materials and Methods

3.2.1 Study area

Our study area encompasses the Caucasus ecoregion and lies between the Black Sea (oceanic) and the Caspian Sea, extending 1300 km (Figure 8). Situated between 36° and 51° E longitude and 36° and 47° N latitude, the region encompasses an area of 580,000 km² and consists of several notable features, including the North Caucasus Plain, the Greater Caucasus Range, the Lesser Caucasus and the Highland of South Caucasus, which includes portions of Asia Minor (Tielidze and Wheate, 2018). The region constitutes a significant Pleistocene refugium (Krebs et al., 2004; Tarkhnishvili et al., 2012).

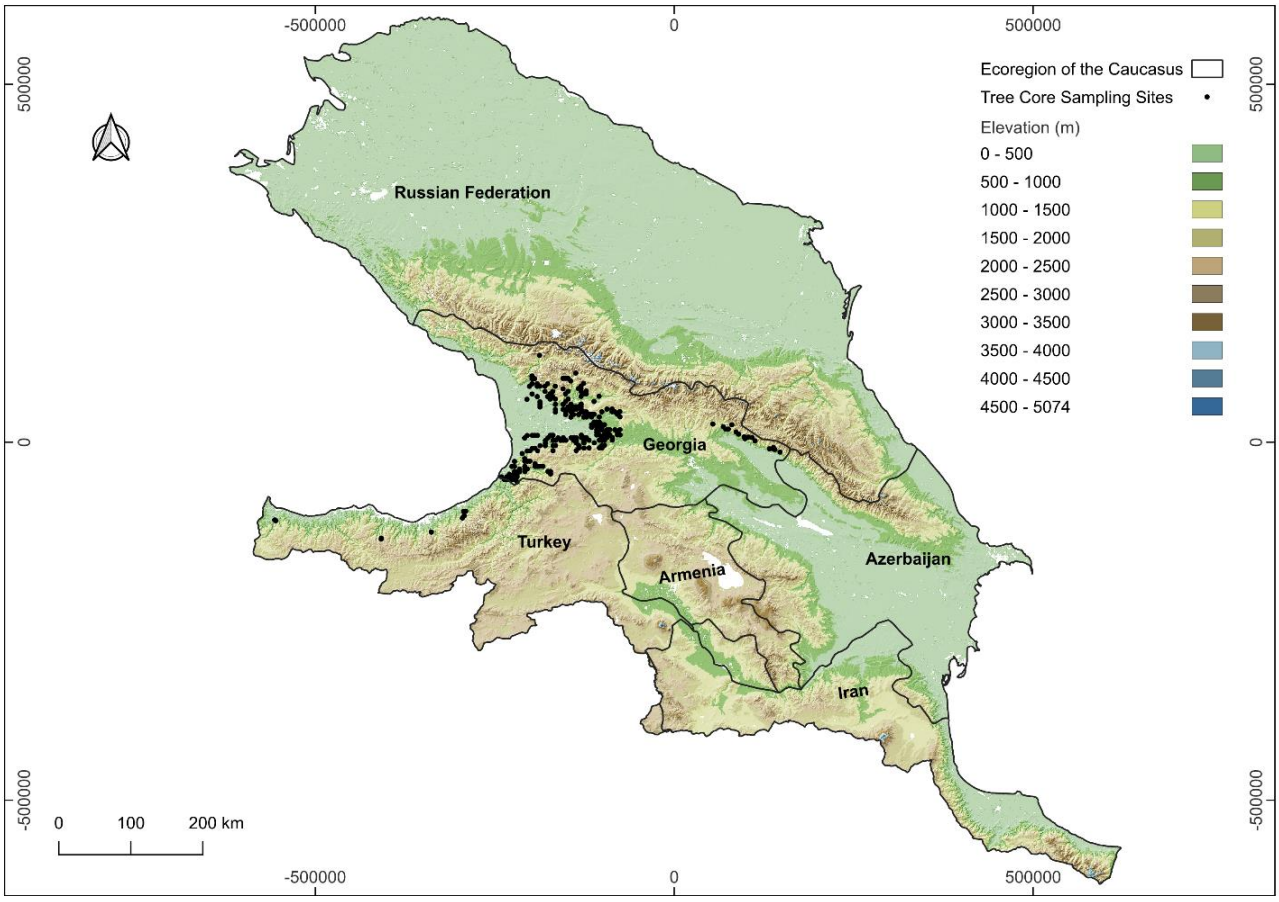

Figure 7. The map of the study area and *Ca. sativa* tree core sampling sites (n = 258).

3.2.2 Core samples

A sample of 200 tree cores from Georgia were obtained from Georgia's National Forest Inventory, done by the Ministry of Environmental Protection and Agriculture of Georgia between 2019 and 2021 (Ministry of Environmental Protection and Agriculture of Georgia, 2023). An additional 10 cores from Turkey and 48 from eastern Georgia were collected by VM for this study. Consequently, a total of 258 *Ca. sativa* trees, each representing a average size class in the plot, were cored using Haglöf 2-Thread increment borers (diameter 5 mm, length 40 cm) at a height of 1.3 meters (Diameter at Breast Height - DBH) from the ground.

The National Forest Inventory plots featured a multiple-layer concentric circular configuration with radii of 5, 10, and 15 meters (Ministry of Environmental Protection and Agriculture of Georgia, 2023). However, the plots taken by VM for this study utilized a single-layer circular design with a 12.6-meter radius. Wood core samples were collected at an elevation range of 112 to 1664 meters above sea level. The sampled trees exhibited a spatially well distributed pattern across a significant portion of the species' geographic range within Georgia. The sampled trees varied in diameter between 8-56 cm at DBH (Mean ± SD = 25 ± 10 cm). Each tree was optimally cored once from one side. The smallest minimum distance between sampled trees was 100 meters. Core samples were preserved in paper straws in the field for further investigation in the lab.

3.2.3 Processing core samples

Core samples were fixed to wooden mounting boards for further processing. The samples were smoothed using a WSL Core Microtome to improve the visibility of yearly rings (Gärtner and Nievergelt, 2010). For example, with ambiguous ring delineation post-smoothing, increasingly finer grades of sandpaper were used.

Samples were then scanned for ring-width measurement at a resolution of 1200 DPI. Annual ring measurements, increments, and calendar year assignments were ascertained using CooRecorder and Cdendro software (https://www.cybis.se/forfun/dendro/index.htm). This software enables ring measurements with an accuracy of 0.01 mm. Only fully formed last annual rings were measured, reflecting the year in which the tree finished its growth at the time of

sampling. Rings that were not fully developed, signifying incomplete growth during the sampling year, were omitted to guarantee measurement precision and comparability. This methodology reduced potential inaccuracies in annual ring-width analysis and guaranteed that only complete growth cycles were included in the dataset (Kvaratskhelia and Gavashelishvili, 2025). Subsequently, the width of the ring series was averaged for each core, and the data were processed for further analysis (Ortega Rodriguez et al., 2023).

3.2.4 Environmental Variables and Data Processing

This study incorporates different environmental variables to evaluate their influence on the growth dynamics of *Ca. sativa*. These include climatic, topographical, and soil characteristics. The age of the tree, a key factor influencing growth (Thomas, 2011), was also considered. The chosen variables provide insights into present conditions and possible future alterations under several climatic scenarios (Table 4).

We utilized 1 km resolution bioclimatic data (BIO1–BIO19) from CHELSA (1981–2010) and future climate predictions from the CMIP6 ISIMIP3b dataset (GFDL-ESM4, 2070–2100) under SSP126, SSP370, and SSP580 scenarios (CHELSA version 2.1, 30 s˜1 km2, downloaded from https://chelsa-climate.org, accessed on 4 March 2025) (Karger et al., 2017). Terrain characteristics at a resolution of 30m × 30m encompassed elevation, slope, aspect, surface roughness, the topographic ruggedness index (TRI), and the topographic position index (TPI) (Gupta and Dixit, 2024; Hayakawa et al., 2008). Soil parameters were sourced from ISRIC (250m × 250m resolution), which included soil texture, organic carbon, nitrogen, pH, coarse fragment volume, and cation exchange capacity (CEC) (Poggio et al., 2021).

All raster data were projected to the Albers Equal Area coordinate system for the Caucasus (Adams, 1927), resampled to a uniform resolution of 30m × 30m, and aligned with the DEM. The data were subsequently clipped and masked utilizing the Caucasus ecoregion shapefile, hence ensuring spatial consistency for ecological and geographical research.

Table 4. Environmental and soil variables

Category	Variable Name	Description
Age	Age	Age of the sampled tree in years
Climate	CHELSA Climate Variables V 2.1 (Current)	BIO 1–19 (Current Mean Temp, Precipitation, Seasonality, Extremes)
	CHELSA Climate Variables V 2.1 (Future)	BIO 1–19 (Future Mean Temp, Precipitation, Seasonality, Extremes) - CMIP6 ISIMIP3b – gfdl_esm4 (ssp126, ssp370, ssp580)
Topography	Elevation above sea level in (m)	Elevation Data Collected via the Shuttle Radar Topography Mission (SRTM)
	Surface Roughness	Variability in terrain elevation, calculated from SRTM DEM
	Topographic Ruggedness Index	Terrain heterogeneity based on elevation differences, from SRTM DEM
	Topographic Position Index	Indicates valley, mid-slope, or ridge; calculated from SRTM DEM
	Slope (0°–90°)	Terrain steepness, from SRTM DEM
	Aspect (0°–360°)	Slope direction, derived from SRTM DEM
Soil	Clay Content (%)	Averaged over depths: 0–5, 5–15, 15–30, 30–60, 60–100, 100–200 cm
	Silt Content (%)	Averaged over depths: 0–5, 5–15, 15–30, 30–60, 60–100, 100–200 cm
	Sand Content (%)	Averaged over depths: 0–5, 5–15, 15–30, 30–60, 60–100, 100–200 cm
	Organic Carbon (mg/kg)	Averaged over depths: 0–5, 5–15, 15–30, 30–60, 60–100, 100–200 cm
	Organic Carbon Density (kg C/m²)	Averaged over depths: 0–5, 5–15, 15–30, 30–60, 60–100, 100–200 cm
	Bulk Density of Fine Earth Fraction (kg/dm³)	Averaged over depths: 0–5, 5–15, 15–30, 30–60, 60–100, 100–200 cm
	Nitrogen Content (mg/kg)	Averaged over depths: 0–5, 5–15, 15–30, 30–60, 60–100, 100–200 cm
	Soil pH (H_2O)	Averaged over depths: 0–5, 5–15, 15–30, 30–60, 60–100, 100–200 cm
	Coarse Fragment Volume (cm³)	Averaged over depths: 0–5, 5–15, 15–30, 30–60, 60–100, 100–200 cm

3.2.5 Data analysis

To mitigate potential multicollinearity of the 34 independent variables considered in our study (Table 4) and to uncover potential sources of error, we created correlation matrices to analyze pairwise correlations among predictor variables (Schober et al., 2018). To reduce the dimensionality, environmental variables were partitioned into four distinct sets, ensuring that within each set, the Pearson's correlation coefficient between any two variables was below 0.75. Subsequently, 4,000 unique variable combinations were generated within each set using the 'gtools' package in the R statistical computing environment (Warnes et al., 2021).

We employed generalized additive models (GAMs) to examine the factors affecting the growth of *Ca. sativa*, focusing on the relationship between growth rate, tree age, and environmental variables (Table 4). Generalized Additive Models (GAMs) were selected for their capacity to capture non-linear and non-monotonic relationships and were run using the “mgcv” package (Wood, 2011; Wood et al., 2016) in R version 4.2.2 (R Core Team, 2016). Given that the dependent variable (average growth/width of the ring series of trees) was non-negative, continuous, and right-skewed, we employed the "Gamma" family with a log link function to address the variance that rises with the mean. Penalized thin plate regression splines were employed for expressing smooth terms, with smoothing parameters estimated using restricted maximum likelihood (REML) to guarantee robust estimation (Wood, 2011).

We examined all possible combinations of variables across the four sets, yielding 16,000 candidate models. We implemented a two-stage model evaluation strategy to achieve a balance between statistical robustness and ecological interpretability. We utilized 10-fold cross-validation, parallelized in R (Weston, 2022a, 2022b). We evaluate the predictive performance measured by Mean Squared Error (MSE) across all 16,000 candidate models, selecting only those models where all predictor terms were statistically significant ($p < 0.05$). This ensured both predictive accuracy and ecological interpretability. The final model was selected from this subset using the Akaike Information Criterion (AIC), which determines the most parsimonious model by balancing goodness of fit and model simplicity. The concurvity among model terms was also assessed to ensure model reliability (Chakrabarti and Ghosh, 2011).

The final model was employed to produce a spatial map of *Ca. sativa* growth. The growth map was subsequently compared to the species habitat suitability map of Metreveli et al. (2023). The growth raster was resampled to align with the spatial resolution and extent of the habitat suitability raster by bilinear interpolation. The two rasters were subsequently stacked and transformed into a data frame for pixel-wise analysis. A scatterplot was created to illustrate the correlation between habitat suitability and growth, and a linear regression model was applied to evaluate the statistical relationship. Pearson's correlation coefficient was computed to measure the strength of this association. To investigate spatial mismatches, both rasters were standardized (scaled from 0 to 1), and their difference was computed, giving a new raster that emphasizes locations where habitat suitability meets or falls low of growth predictions.

Future projections of the growth were developed using CHELSA climate data under the SSP126, SSP370, and SSP585 scenarios. To assess the significance and nature of the expected changes, the projected maps were clipped by the binary distribution map from Metreveli et al. (2023). Subsequently, paired statistical tests (t-tests and Wilcoxon) were performed between the maps, and summary statistics were calculated to assess differences in *Ca. sativa* growth among the SSP126, SSP370, and SSP585 scenarios. Predicted growth across scenarios was visualized through the boxplots. Spatial difference maps were created by subtracting current growth predictions from future estimates, and areas were classified into three categories: increase, decrease, or no change. These classified rasters were then stacked and mapped to highlight spatial patterns of growth variation under each climate scenario (Appendix Figure A9).

3.3 Results

3.3.1 Ca. sativa Growth Model

The six candidate models were chosen based on the Mean Squared Error (MSE) and with the significance tests. Among the candidate generalized additive models (GAMs), the best-performing model was identified by the lowest Akaike Information Criterion (AIC = 749.70). This model included Bio 06 (Minimum Temperature of the Coldest Month, °C), Bio 17 (Precipitation of the Driest Quarter, mm), Soil pH (H_2O), Nitrogen content (mg/kg), and Age (years) (Table 5).

Table 5. Mean Squared Error (MSE) and Akaike Information Criterion (AIC) of the top 6 models.

N	Model Variables	MSE	AIC
1.	**Bio 06** (Min Temp of Coldest Month, °C), **Bio 17** (Precipitation of Driest Quarter, mm), **Soil pH** (H_2O), **Nitrogen** (mg/kg), **Age** (years);	1.74	749.70
2.	**Bio 11** (Mean Temp of Coldest Quarter, °C), **Silt** (%), **Coarse Fragments** (cm^3), **Nitrogen** (mg/kg), **Age** (years);	1.77	752.17
3.	**Bio 01** (Annual Mean Temp, °C), **Nitrogen** (mg/kg), **Age** (years);	1.73	754.48
4.	**Bio 09** (Mean Temp of Driest Quarter, °C), **Coarse Fragments** (cm^3), **Age** (years);	1.73	755.27
5.	**Silt** (%), **Nitrogen** (mg/kg), **Age** (years);	1.74	756.61
6.	**Bio 01** (Annual Mean Temp, °C), **Coarse Fragments** (cm^3), **Age** (years);	1.79	758.20

The variables in the best model showed varying ranges and distributions. The sample of *Ca. sativa* trees had a skewed distribution towards lower mean increment values, with the majority of increments recorded below 5 mm. The ages of the examined trees varied from around 9 to 151 years, with the majority falling between 25 and 75 years, indicating a positively skewed distribution. Climatic conditions revealed that the sampled trees mostly inhabited areas where the lowest temperature of the coldest month ranged from roughly -7.5 °C to -1 °C and precipitation during the driest quarter generally fluctuated between 100 and 400 mm. Soil characteristics showed a unimodal distribution for pH, centered between 5 and 6.5. Nitrogen content typically varied from around 200 to 500 mg/kg (Figure 9).

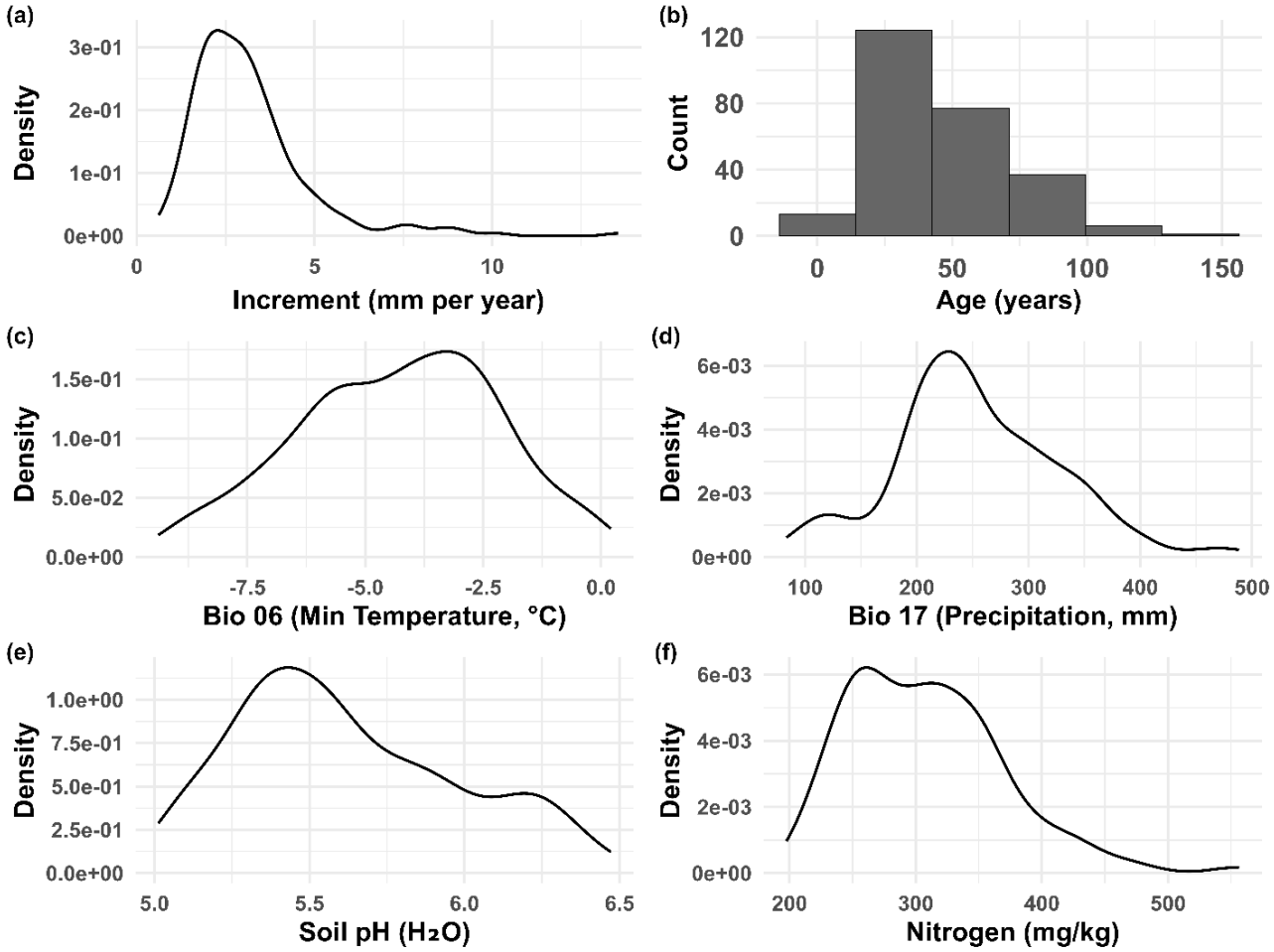

Figure 8. Density distributions of variables of the sampled *Ca. sativa* trees. These variables were used for modeling the *Ca. sativa* growth across the Caucasus ecoregion. See Table 4 for detailed descriptions of the predictors.

According to the evaluation of model term significance via the F-statistic and p-values, stand age (years) showed the most significant influence on *Ca. sativa* tree growth, whilst soil pH showed the smallest effect. Growth decreased markedly with increasing stand age, demonstrating a robust nonlinear relationship, particularly evident after around 50 years. Bio 17 (Precipitation of the Driest Quarter) had a negative linear relationship with growth, indicating that growth decreased when precipitation was higher than around 100 mm. Nitrogen content (mg/kg) and Bio 06 (Minimum Temperature of the Coldest Month, °C) demonstrated a significant positive linear relationship with growth, Soil pH had a negative relationship with growth, slightly declining at greater pH levels (Figure 10). The corresponding GAM had a reasonably high adjusted R^2 of 0.438, Model diagnostics indicated moderate concurvity between Soil pH and Nitrogen content (mg/kg), suggesting some redundancy in their effects. In contrast, Age and Bio 17 (Precipitation of the Driest Quarter) exhibited low concurvity, supporting their strong and independent contributions to the model (Appendix Figure A10).

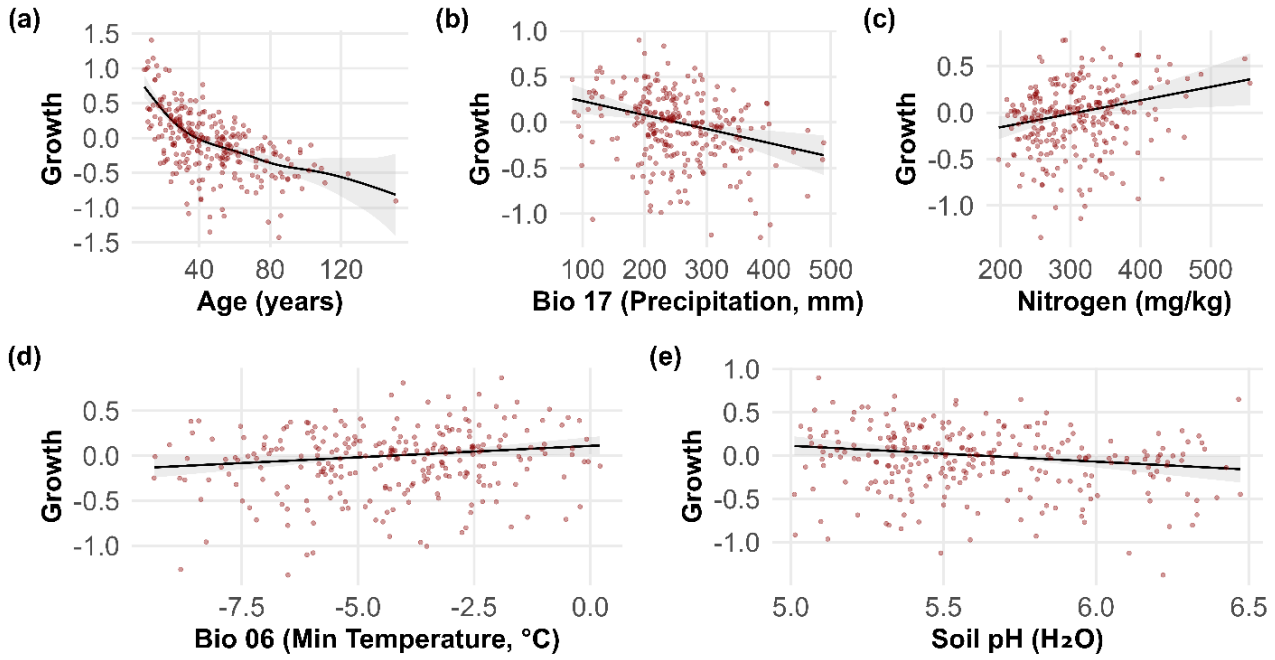

Figure 9. Partial residual plots from the best generalized additive model (GAM), showing the relationships between predictor variables and *Ca. sativa* tree growth in the Caucasus. Panels show effects of soil pH (H_2O), tree age (years), Bio06 (minimum temperature of the coldest month, °C), Bio17 (precipitation of driest quarter, mm), and nitrogen (mg/kg). Shaded areas represent 95 % Bayesian confidence intervals. See Table 4 for predictor descriptions.

The combined effects of the independent variables highlight the complexity and interrelation of age, climate, and soil factors in regulating *Ca. sativa* growth. Increment is greatest in younger stands (typically under 50 years) and decreases rapidly in older stands. Highest growth is achieved with moderately mild winter temperatures (Bio 06 from -4 to -2°C), reduced precipitation during the driest quarter (Bio 17 roughly 100-200 mm), elevated soil nitrogen levels (˜400-550 mg/kg), and strongly to moderately acidic soil pH (around 5.0–6.0). In contrast, growth significantly declines with longer stand ages, colder winter temperatures (Bio 6 < - 6°C), reduced nitrogen availability (< 300 mg/kg), excessive moisture (Bio 17 >200 mm), and near-neutral soil pH (> 6) (Figure 11).

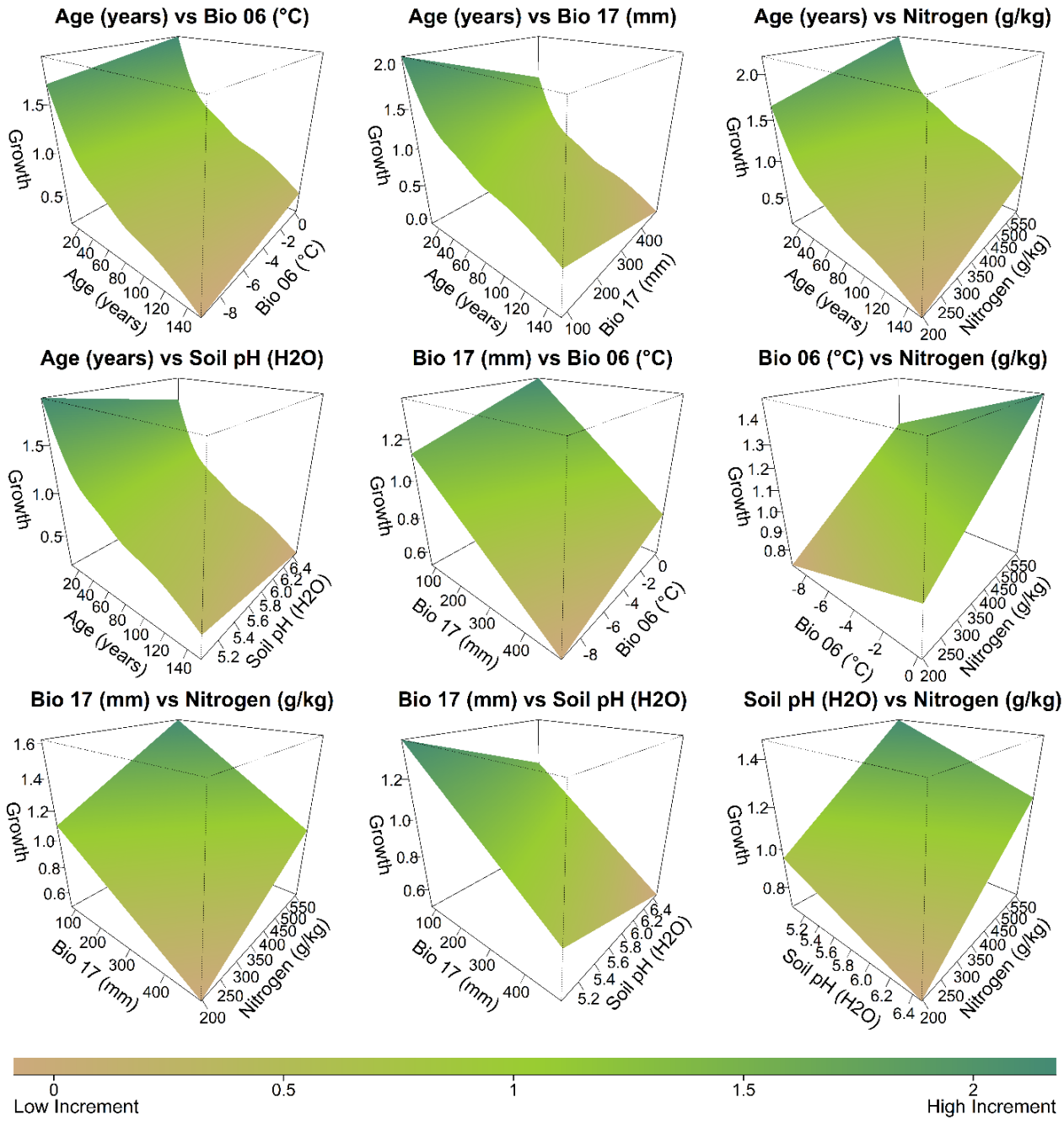

Figure 10. 3D plots showing the GAM-fitted relationships between pairs of predictor variables and *Ca. sativa* tree growth in the Caucasus. Each surface illustrates the combined effect of two predictors on the response variable. Growth increases from brown (low increment) to green (high increment). Axes represent observed data ranges. See Table 4 for detailed descriptions of predictor variables.

The modelled growth maps indicate that the best conditions for *Ca. sativa* growth are mostly located in the western segment of the Caucasus ecoregion (Figure 5). Significant growth increments over 3.5 mm are anticipated in the Kolkheti lowlands and along the Greater Caucasus mountain ranges, including substantial areas of western Georgia and extending into southern sections of the Russian Federation. Similarly, favorable conditions exist in the western portion of the Lesser Caucasus, particularly in southern Georgia and northwestern Turkey, indicative of beneficial climatic and soil conditions. In contrast, regions exhibiting smaller or negligible growth increments (1.6–2.0 mm/a) include central and southeastern Georgia, large areas of northeastern Azerbaijan, northern Iran, and Armenia. Moderate growth increments, reflecting intermediate ecological suitability, are seen in the south of the Russian Federation, eastern Georgia and southeastern Azerbaijan (Figure 12).

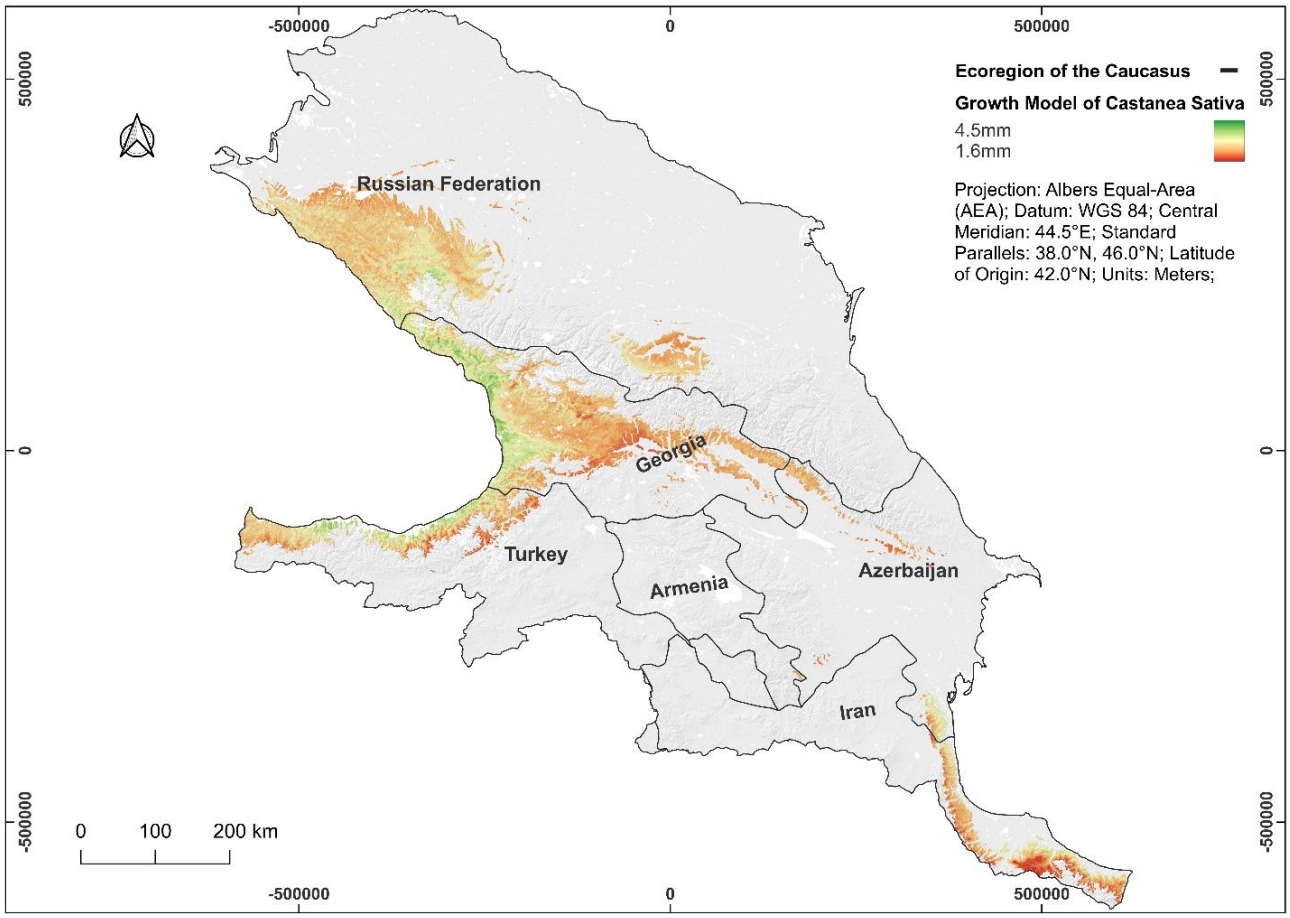

Figure 11. Modeled growth of *Ca. sativa* across the Caucasus Ecoregion at a resolution of 100x100 m. Growth predictions (mm/year), estimated using the best-fitting GAM, range from 1.6 mm (low, red) to 4.5 mm (high, green). Values are for visual interpretation and may not reflect local microsite variability. See Table 4 for details on model predictors.

3.3.2 Spatial patterns of Ca. sativa growth and habitat suitability

The analyzed spatial patterns of growth prediction and species habitat suitability indicated a moderate, positive, and highly significant correlation ($r = 0.30$, $p < 0.001$) and clear spatial heterogeneity. The model predicted that growth increases by approximately 0.47 mm for every 0.1-unit (on a standardized 0–1 scale) increase in habitat suitability, highlighting a meaningful, though modest, relationship (Appendix Figure A11). The majority of the area exhibited moderately positive differences, indicating that the habitat suitability model slightly overestimated the growth model in central regions. However, notable negative differences were evident along certain edges and peripheries (Figure 13).

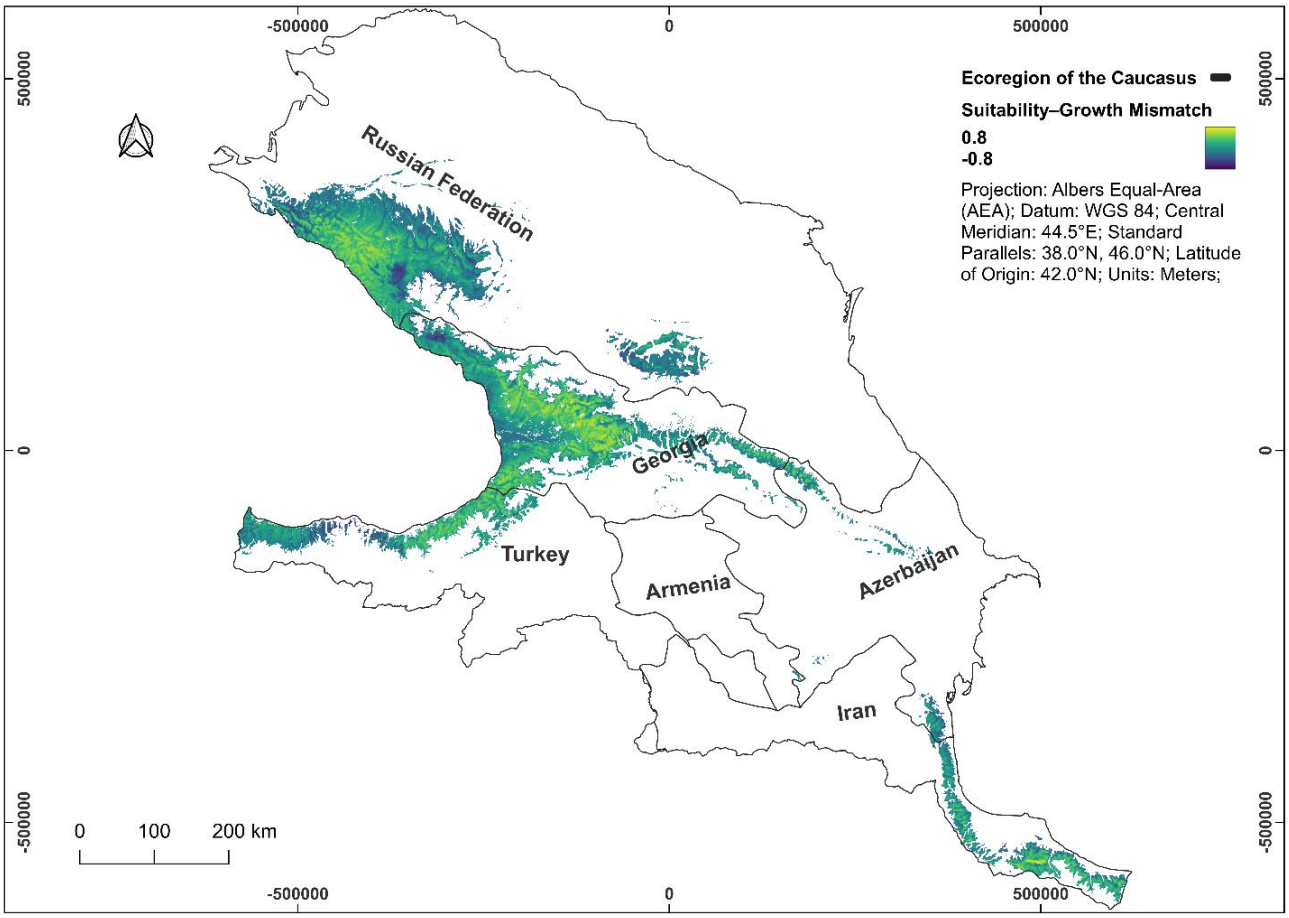

Figure 12. Spatial difference map between habitat suitability (distribution) and growth potential of *Ca. sativa* in the Caucasus Ecoregion. Values represent the standardized difference between the normalized habitat suitability model and the growth model, with positive values indicating areas more suitable for presence than for growth and negative values indicating the reverse. The color gradient shows the magnitude of difference, from –0.8 (growth > habitat suitability) to + 0.8 (habitat suitability > growth).

3.3.3 Projected Growth Under Climate Change Scenarios

The growth of *Ca. sativa* under current conditions and three future climatic scenarios (SSP126, SSP370, and SSP585) during the period 2071-2100 is undergoing major temporal changes. The average growth significantly decreased under SSP126 (mean difference = -0.34, $p < 2.2e-16$) and SSP370 (mean difference = -0.04, $p < 2.2e-16$), but a slight yet significant rise was seen under SSP585 (mean difference = 0.02, $p < 2.2e-16$). Wilcoxon signed-rank tests validate these findings, demonstrating very significant changes in growth across all prospective scenarios.

The boxplot visualization supports these statistical results, clearly demonstrating that SSP126 has the most significant negative effect relative to present conditions, whereas SSP585 reflects a little gain, and SSP370 maintains around current growth levels (Figure 14).

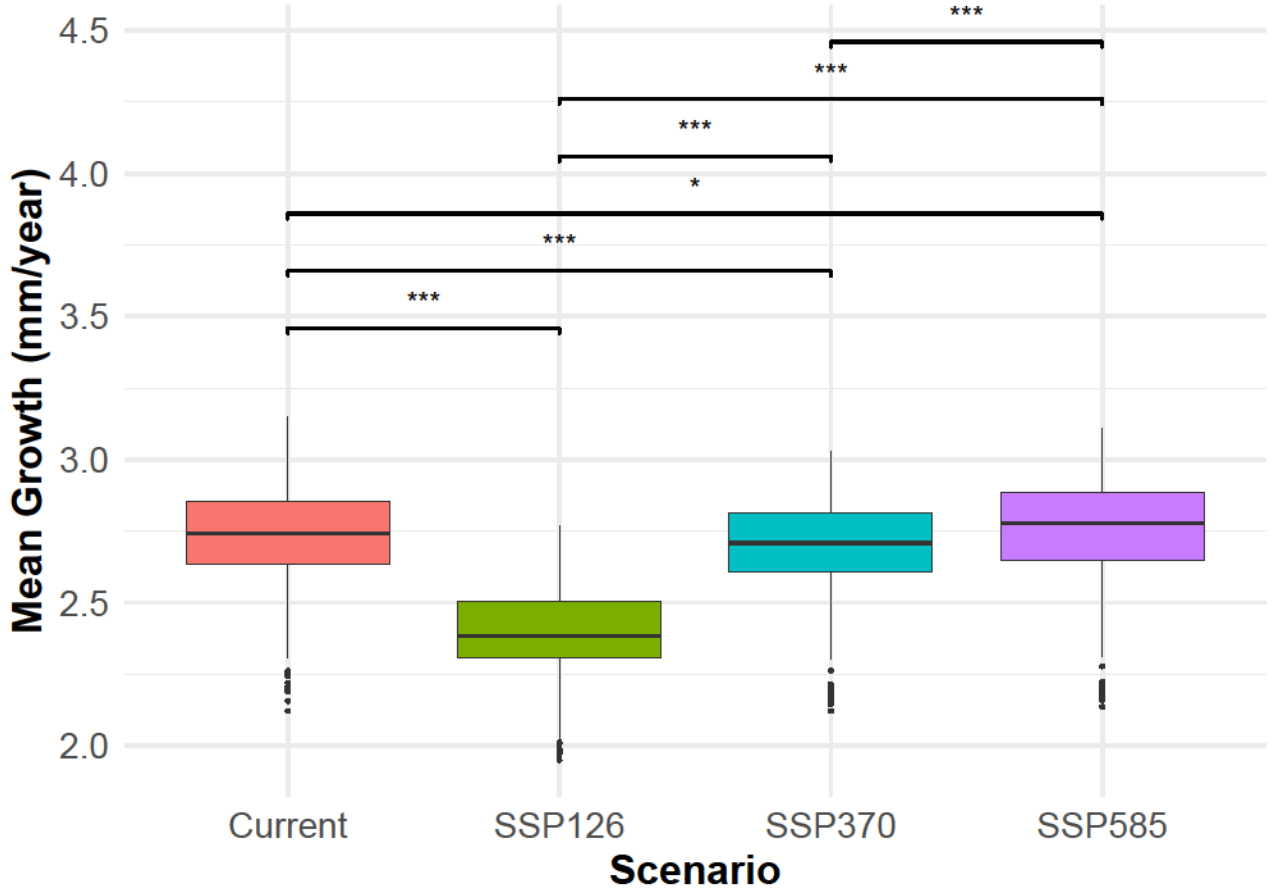

Figure 13. Boxplot comparison of predicted *Ca. sativa* growth under current climate and three future climate change scenarios (SSP126, SSP370, and SSP585). Growth predictions are based on GAM outputs. Asterisks indicate statistically significant pairwise differences between scenarios (**** = $p < 0.0001$). Growth is measured in mm/year. Color-coded boxplots correspond to scenarios shown in the legend.

The predicted maps depict major shifts in the geographical distribution of tree growth under several future climatic scenarios (2071–2100) in comparison to present conditions. In the low-emission scenario SSP126, the geographical distribution mostly mirrors current patterns, while the intensity of growth shows reduction, especially in formerly advantageous regions. The intermediate-emission scenario SSP370 indicates a geographical extension of optimum growth

conditions into central and southern regions, demonstrating improved suitability in some locations despite a general mild decline. Conversely, the high-emission scenario SSP585 demonstrates the most notable geographical alterations, characterized by a distinct northern and upper transition in growth suitability and increased growth in formerly marginal areas, indicating adaptive regional adjustments despite the overall stress seen in other locations (Figure 15).

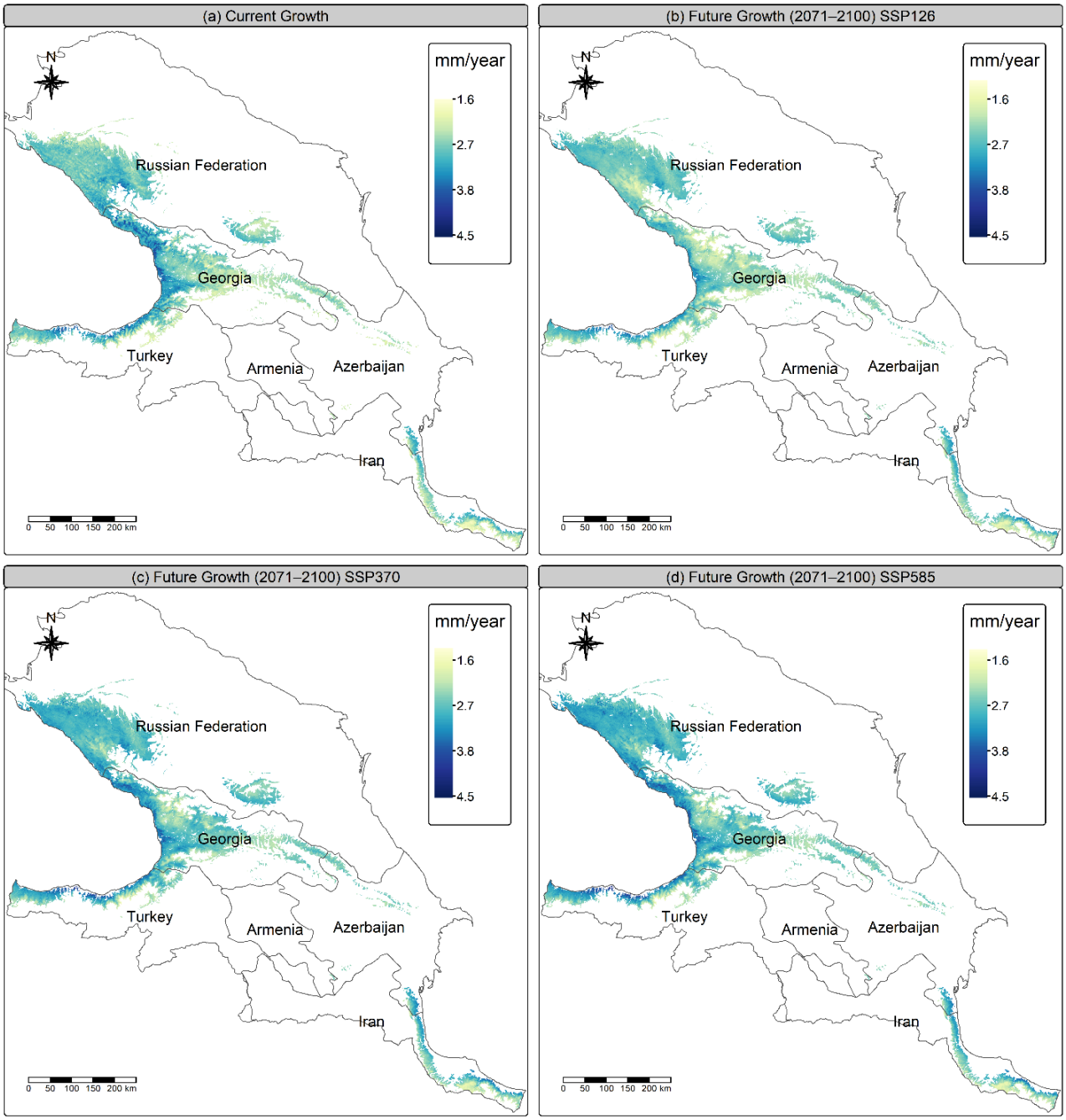

Figure 14. Predicted *Ca. sativa* growth under current and future climate scenarios across the Caucasus Ecoregion. (a) Current growth and future projections for the period 2071–2100 under (b) SSP126, (c) SSP370, and (d) SSP585 scenarios. Cell values represent GAM-predicted growth (mm/year). Maps are shown at 250 m resolution. The color scale indicates relative growth magnitude from low (1.6mm) to high (4.5mm).

3.4 Discussion

This study provides a comprehensive assessment of growth dynamics for *Ca. sativa* within the Caucasus region. Based on new dendroecological measurements of 258 wood cores, it clarifies the roles of climate, soil, age, and terrain-related variables by applying a Generalized Additive Model (GAM) framework on annual tree ring growth. The best model, selected based on the lowest Akaike Information Criterion (AIC), included the following predictors: minimum temperature of the coldest month, precipitation of the driest quarter, soil pH, nitrogen content, and tree age. These variables reflect a combination of climatic, edaphic, and biological factors, highlighting the multifactorial nature of tree growth.

3.4.1 Model of Ca. sativa growth

Generalized additive models revealed tree age as the primary factor affecting *Ca. sativa* growth, exhibiting a significant nonlinear negative relationship. Younger stands (typically under 50 years) demonstrated markedly greater growth increments compared to older stands, aligning with established physiological processes (Sillett et al., 2010). The decline associated with aging can be linked to reduced nutrient uptake efficiency, changes in carbon allocation favoring maintenance rather than growth, and hydraulic constraints typically seen in mature trees (Sillett et al., 2010).

Climatic factors were also essential in affecting growth. A positive correlation exists between the minimum temperature of the coldest month and tree growth. This finding is consistent with observations in other temperate tree species, indicating that winter and early spring warmth facilitates the earlier onset of physiological processes (Rashid et al., 2024). In contrast, increased precipitation in the driest quarter adversely affected growth. A combination of climate variables indicates that optimal growth occurs with moderately mild winter temperatures (Bio 06 ranging from -4 to -2°C) and less precipitation during the driest quarter (approximately 100-200 mm). The driest quarter for the Caucasus region has been calculated using data from local climate stations near our sample plots. The findings indicate that January, February, and March represent the driest months within the distribution zone of *Ca. sativa* in the Caucasus. Consequently, the driest quarter encompasses the precipitation recorded during these

specific months (Appendix Figure A12). Usually, late winter and early spring precipitation can induce stress in trees at any developmental stage, particularly under low-temperature conditions (Klisz et al., 2022). Particularly in early spring when they initiate active biological processes (Ziaco et al., 2016). *Ca. sativa* prefers predominantly sunny environments (Conedera et al., 2021). As a result, the snow melts during the daytime and infiltrates the soil. At night, temperatures drop significantly, resulting in ground frost that may adversely affect the roots (Reinmann et al., 2019). The results of the combined effect indicate that an increase in the temperature of the coldest month corresponds with a decrease in the influential effect of precipitation (Figure 11). This supports the assertion that a higher temperature in the coldest month, indicative of a mild winter, correlates with reduced freezing of soil water (Domisch et al., 2018).

The significance of Soil pH (H_2O) and Nitrogen content (mg/kg) in the model highlights their vital role in soil fertility and nutrient availability for tree growth, corroborating findings from other studies that demonstrate that optimal nutrient availability and acidity improve tree vitality and productivity (Andersson et al., 2000; Ouimet and Moore, 2015). The nitrogen concentration in the soil demonstrated a strong positive association with growth increments, underscoring nitrogen's essential function in tree biomass accumulation. Optimal development rates correlated with increased nitrogen concentrations (400-550 mg/kg), affirming nitrogen as a critical limiting resource in forest ecosystems (Ouimet and Moore, 2015). Conversely, soil pH had a comparatively lower but statistically significant negative impact on *Ca. sativa* growth, suggesting that an increase in soil pH (i.e., decreased acidity) correlates with a decline in growth. This trend indicates that *Ca. sativa* trees prefer more acidic soil conditions, often associated with lower pH values (Velizarova, 2015). The observed distribution of *Ca. sativa* (Figure 13) also indicates the species' adaptability to strongly and moderately acidic forest soils. These may enhance food availability and microbial interactions conducive to *Ca. sativa* physiology (Álvarez-Álvarez et al., 2025). The combined effects of Nitrogen and PH on the growth indicate that optimum development occurs at higher soil nitrogen concentrations (~400-550 mg/kg) and a strongly to moderately acidic soil pH (about 5.0–6.0).

The spatial model identified certain regional trends in *Ca. sativa* Potential for Growth with higher increments mostly found in the western Caucasus region, particularly in the Kolkheti plains and the areas along the Greater Caucasus mountains. These locations display favorable climate and soil conditions since they also represent the refugial habitats from the last glacial maximum (Tarkhnishvili et al., 2012; Gavashelishvili & Tarkhnishvili 2016). In contrast, areas with reduced growth potential, including central and southern Georgia, northeastern Azerbaijan, and northern Iran, indicate regional constraints associated with extreme climate, reduced soil acidity, and human-induced disruptions (Metreveli et al., 2023). Moderate growth increments, indicative of intermediate ecological suitability, are seen in southern Russia, eastern Georgia, and southeastern Azerbaijan, which also serve as refugial zones from the last glacial maximum (Tarkhnishvili et al., 2012).

3.4.2 Contrasting patterns of growth potential and species habitat suitability

The moderate yet significant correlation between modeled growth and species habitat suitability from Metreveli et al. (2023) gave ecological support for the model but highlighted noticeable geographic variation. Areas where the habitat suitability model overstated growth may indicate suboptimal soil conditions. The soil variables were excluded from that habitat suitability model. Simultaneously, regions with high suitability may be characterized by insufficient light, intense competition, or limited water availability for growth. Moreover, it is known that competition is more important than climate for tree growth (Gómez-Aparicio et al., 2011). Conversely, the overestimated growth in outlying places suggests that *Ca. sativa* has different physiological strategies that facilitate varying growth rates in areas of low suitability. Distinct climatic conditions might promote dispersal but are not conducive to growth (Serra-Diaz et al., 2013). The previous study on habitat suitability revealed that winter temperature and precipitation significantly influence *Ca. sativa* dispersion (Metreveli et al., 2023). In the initial stages of tree development, winter precipitation, particularly snow, has a substantial influence on *Ca. sativa* survival. (Suvanto et al., 2017). Nonetheless, it may provoke stress for growth (Domisch et al., 2018). Nevertheless, the inconsistency, the models exhibit a significant positive relationship (r=0.3), which might be considered sufficient. However, further investigation is needed to clarify

the distinct contributions of geographical scaling and temporal resolution in the divergence between these two methodologies (Serra-Diaz et al., 2013).

3.4.3 Projected Growth Under Climate Change Scenarios

Maps based on several future climatic scenarios (SSP126, SSP370, and SSP585) revealed considerable regional and temporal discrepancies in growth potential. Further study of the variables across several scenarios revealed that SSP370 to SSP585 indicates a higher warming level than SSP126 (Appendix Figure A13). Nonetheless, SSP126 has more precipitation compared to the Current SSP370 and SSP585 scenarios (Appendix Figure A14). This may serve as the primary elucidation of the growth alteration. Significant declines in growth were predicted in the low-emission scenario (SSP126), indicating that little warming combined with rising precipitation patterns intensifies current environmental stresses. The intermediate-emission scenario (SSP370) predicted rather steady growth conditions, suggesting a possible balance between rising temperatures and moisture availability. The high-emission scenario (SSP585) forecasted slight increases in average growth, accompanied by substantial northward and altitudinal changes in optimum growth conditions.

Subsequent evaluations of expected development variations illustrate alterations in projected *Ca. sativa* growth. In the lowest emissions scenario (SSP126), there is a distinct number of regions exhibiting a decline in growth, with only isolated areas of growth at the outer edges. The assessments for the remaining two scenarios (SSP370, SSP585) show very similar trends and regions of decline and increase. The geographical distribution changes markedly, exhibiting a major expansion of favorable growth zones toward the northern periphery and central areas, whereas large portions of the Kolkheti plain and southern parts persist in demonstrating reduced increments. These scenarios together indicate that climate change would likely result in significant regional changes in *Ca. sativa* growth suitability, with some peripheral places possibly gaining advantages while regions now exhibiting high growth rates face considerable decreases (Appendix Figure A9).

These findings are contrary to the distribution models proposed by Beridze et al. (2023). This indicates a significant reduction of appropriate habitat by the end of the century. Our analysis

suggests that the growth potential in many regions of the Caucasus remains largely steady or may even improve marginally, particularly under intermediate and high-emission scenarios (SSP370 and SSP585).

Finally, the growth and habitat suitability of *Ca. sativa* are mostly influenced by abiotic factors, but human involvement, artificial habitat alterations, and the impacts of pests and diseases are increasingly altering growth patterns, both now and in the future (Conedera et al., 2004; Connor, 2011; Metreveli et al., 2024). Additionally, integrating environmental data at different spatial resolutions (1 km², 30 m, and 250 m) may introduce scale mismatches, particularly in heterogeneous mountainous regions like the Caucasus, potentially affecting the precision and relevance of local growth predictions (Verburg et al., 2011). Therefore, the inclusion of biotic factors and the harmonization of data scales are critical for improving both current and future models.

3.5 Conclusion

Our study provides new perspectives on the determinants growth of Sweet chestnut (*Ca. sativa*) within the ecologically diverse Caucasus region based on new dendroecological measurements and generalized additive modelling. Our results highlight the interrelated influence of climate, soil chemistry, and tree age on growth. Specifically, our models identified age, minimum temperature of coldest month, precipitation in the driest quarter, soil nitrogen, and acidity as key determinants of *Ca. sativa* growth. Spatial investigation indicated that favorable growth circumstances are primarily found in western mountainous areas and the lowlands, whereas central and southeastern regions have restricted growth potential. Future climatic scenarios (2071–2100) forecast geographically heterogeneous responses, characterized by growth reductions under low emissions (SSP126), stability under intermediate conditions (SSP370), and marginal enhancements under high-emission scenarios (SSP585), accompanied by significant altitudinal and latitudinal shifts. These findings emphasize the necessity of accounting for local-scale environmental interactions and recommend the incorporation of dendrochronological growth evaluations into comprehensive ecological forecasting models to improve adaptive forest management strategies in the context of climate change.

4. Chapter III

Environmental covariates of Chestnut blight (*Cryphonectria parasitica*) in Georgia (Caucasus)

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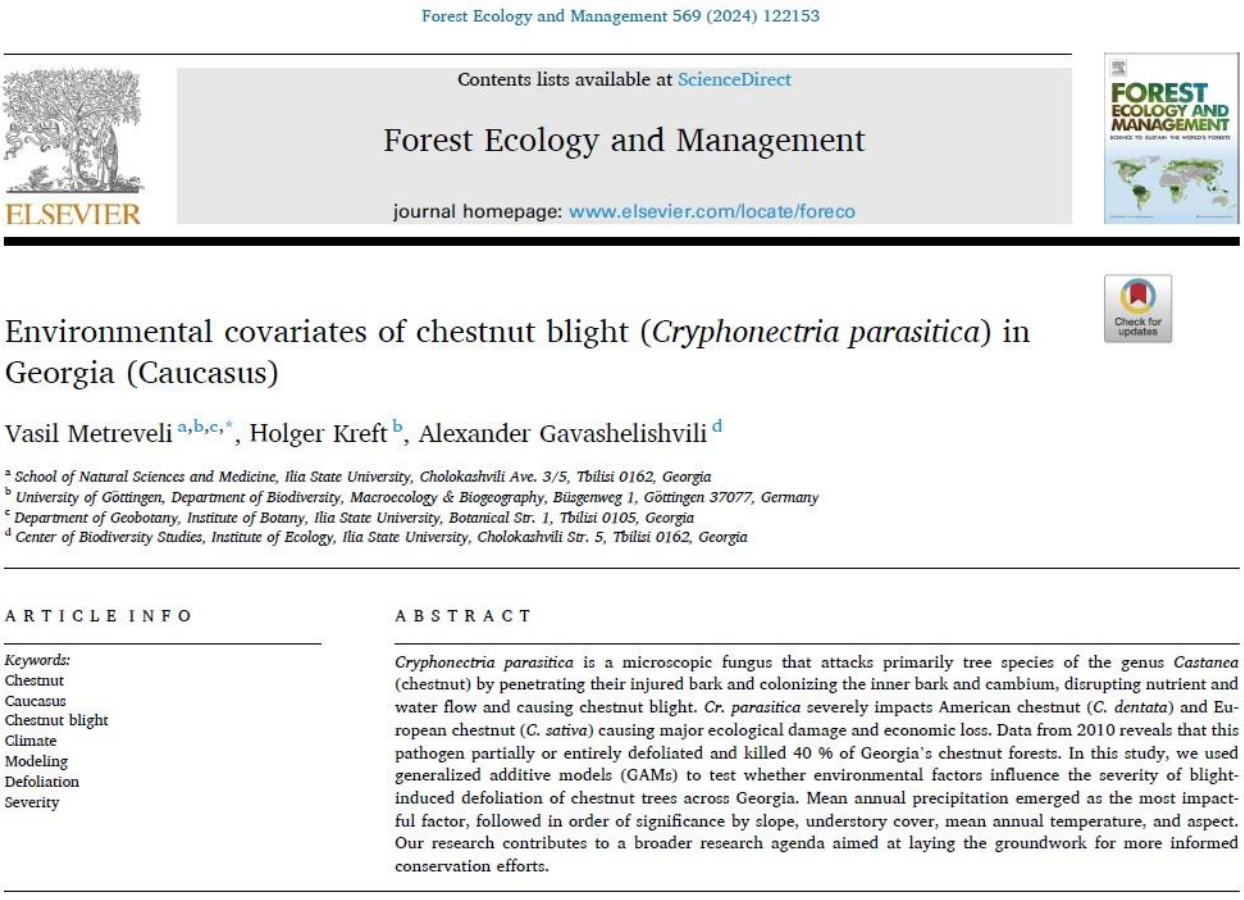

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Environmental covariates of chestnut blight (*Cryphonectria parasitica*) in Georgia (Caucasus)

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ABSTRACT

Cryphonectria parasitica is a microscopic fungus that attacks primarily tree species of the genus *Castanea* (chestnut) by penetrating their injured bark and colonizing the inner bark and cambium, disrupting nutrient and water flow and causing chestnut blight. *Cr. parasitica* severely impacts American chestnut (*C. dentata*) and European chestnut (*C. sativa*) causing major ecological damage and economic loss. Data from 2010 reveals that this pathogen partially or entirely defoliated and killed 40 % of Georgia's chestnut forests. In this study, we used generalized additive models (GAMs) to test whether environmental factors influence the severity of blight-induced defoliation of chestnut trees across Georgia. Mean annual precipitation emerged as the most impactful factor, followed in order of significance by slope, understory cover, mean annual temperature, and aspect. Our research contributes to a broader research agenda aimed at laying the groundwork for more informed conservation efforts.

Picture 2. Cover image of the published article representing Chapter 3

4.1 Introduction

The third chapter of this thesis examines the environmental factors affecting the severity of Chestnut blight (*Cryphonectria parasitica* (Murrill) M.E.Barr). The interaction between *Cr. parasitica, Ca. sativa* and environmental factors are a central concern in modern forest pathology and ecology. The disease significantly diminished the biological niche of *Castanea dentata* (Marsh.) Borkh (American chestnut), limiting it to disturbed, arid environments where it primarily survives as root sprouts instead of mature trees (Burke, 2012). This illustrates the disease's ability to alter forest structure and species interactions. Similarly, *Ca. sativa* in the Caucasus may be vulnerable to site-specific pressures that shape disease outcomes.

Considering the significant impacts of *Cr. parasitica*, many positive signals provide optimism. Studies show that environmental and biological elements may affect infection intensity (Heiniger and Rigling, 1994; Risteski et al., 2013), suggesting the possibility of impact mitigation under specific conditions. The regional variety in defoliation intensity indicates that temperature, geography, soil conditions, and forest structure may either mitigate or intensify the development of diseases (Beridze and Dering, 2021; Tavadze et al., 2013). Certain places may inherently resist blight due to local microclimates or soil characteristics. These findings emphasise the necessity to investigate not just the pathogen and host but also their interaction with the wider environment.

Environmental stresses, especially climate-related factors, markedly affect the severity of *Cr. parasitica*. Water stress, resulting from drought or variable moisture levels, is significantly linked to heightened defoliation and death in *Ca. sativa* (Waldboth and Oberhuber, 2009). Insufficient and excessive precipitation may harm tree health—droughts reduce trees' resilience, whereas extra moisture can promote fungus reproduction and disease spread. Likewise, increased temperatures, particularly throughout the growing season, have been associated with more severe infections due to heightened fungal activity (Van Drunen et al., 2018). These tendencies are particularly alarming in light of anticipated climate change scenarios, which forecast warmer and possibly drier conditions in numerous *Ca. sativa* cultivation areas.

Topographic and soil attributes influence disease dynamics by affecting microclimatic conditions. The gradient and direction of slopes impact solar exposure, drainage, and humidity, all of which affect host-pathogen interactions. Although higher slopes are commonly believed to diminish infection risk through improved drainage (Tindall et al., 2004), certain studies indicate that blight may still be more widespread based on aspect and local microclimates (Van Drunen et al., 2018). Soils with adequate drainage generally promote healthier trees; yet, they may paradoxically elevate disease risk when coupled with elevated heat and moisture levels (Brewer, 1995; Van Drunen et al., 2018). These findings underscore the intricate interaction of several environmental factors and the necessity for comprehensive, location-specific evaluation when determining disease susceptibility and formulating conservation strategies.

In light of this complexity, researchers are currently concentrating on multifactorial studies that incorporate tree-level features, site conditions, and climate variables to enhance the understanding of disease severity patterns. The third chapter of this study hypothesizes that the intensity of defoliation induced by Chestnut blight results from a complicated interaction between environmental conditions and tree attributes, particularly age. It posits that many environmental factors, such as precipitation, temperature, slope, understory cover, and aspect, interact with one another and with the tree's age to influence the degree of damage inflicted by the blight.

The study explicitly examines how geography, climate, and land cover attributes affect defoliation intensity in Georgian *Ca. sativa* stands. Chapter three aims to answer the following questions:

1. Does high precipitation on shallow slopes worsen disease outcomes?

The first question of the third chapter is to examine how the interplay between two environmental factors, precipitation and slope, affects the intensity of Chestnut blight (*Cryphonectria parasitica (Murrill) M.E.Barr*) in *Ca. sativa* trees. This inquiry examines the synergistic impacts of climate and terrain on disease dynamics, rather than evaluating each aspect independently.

2. Does a denser understory buffer the trees or increase pathogen spread?

The second question investigates the role of understory vegetation in influencing Chestnut blight severity. It addresses whether a thick layer of shrubs beneath the forest canopy provides a protective microclimate that helps trees resist infection (e.g., by stabilizing humidity or shielding bark from harsh weather), or instead creates favorable conditions for the pathogen by increasing moisture retention, reducing airflow, and promoting fungal spore survival and dispersal.

3. Does tree age make them more resilient or more vulnerable?

The inquiry examines the impact of *Ca. sativa* tree age on their susceptibility to Chestnut blight (Cryphonectria parasitica (Murrill) M.E.Barr). This examines whether mature trees, possessing enhanced defences and thicker bark, exhibit greater resilience to infection, or if a decline in vigour and physiological function makes them more susceptible to disease. This question also addresses the physiological and structural modifications linked to tree ageing and their potential impact on interactions with pathogens.

4.2 Materials and methods

Severity data of *Ca. sativa* trees were obtained from Georgia's 2019–2021 National Forest Inventory (source: The National Forest Agency of Georgia). Of this data set, 345 individual *Ca. sativa* trees had been aged using increment borers (Haglöf 2-Thread) in 345 sample plots. These trees were geographically almost evenly spread across most of the species distribution range in Georgia and were measured in circular sample plots (Figure 17).

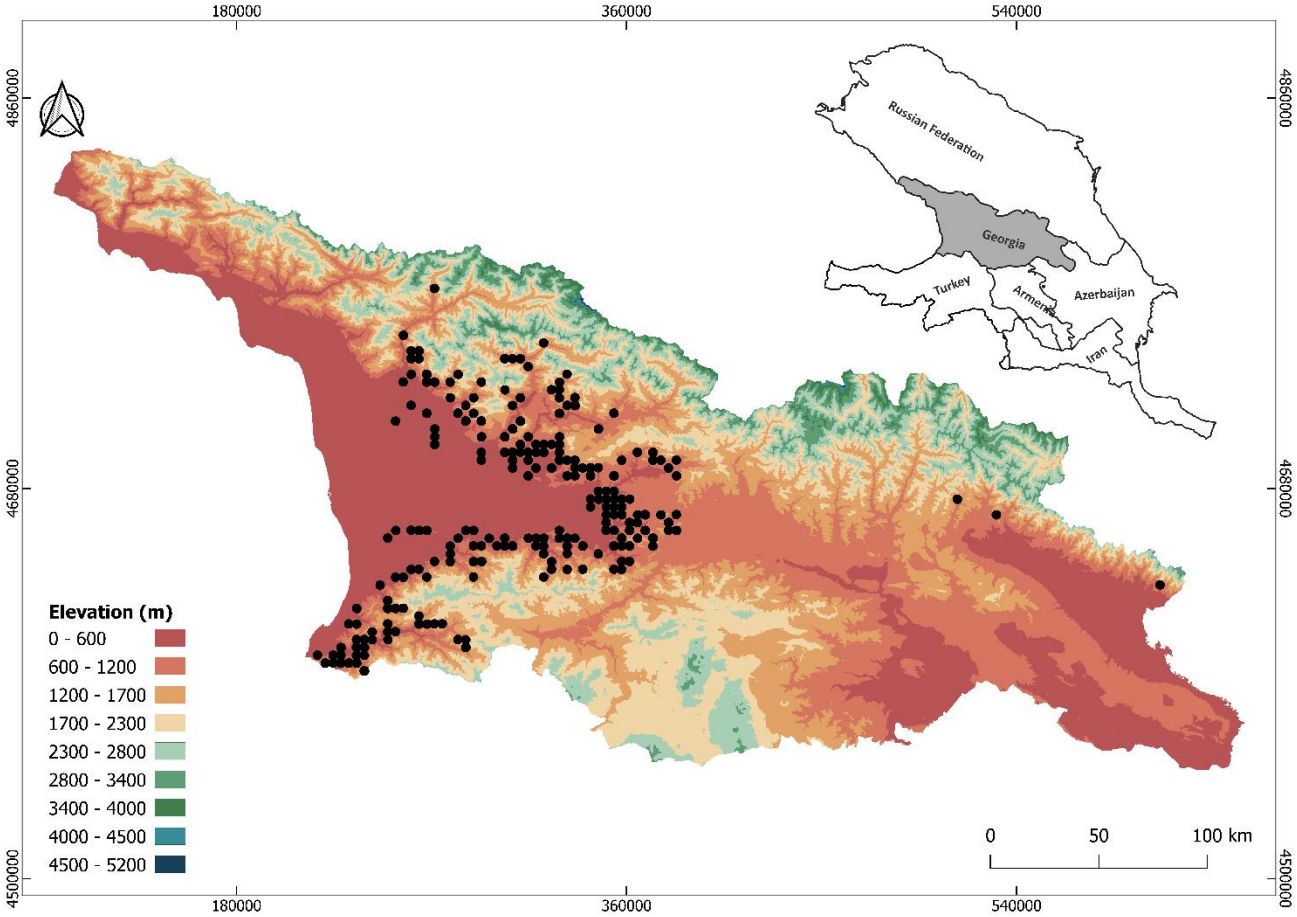


Figure 15. Sampling locations of *Ca. sativa* trees in Georgia (n = 345).

The sample plots were represented by multiple circular layers with predetermined radii, specifically 5, 10, and 15 m. Where, the understory cover, DBH (diameter on the breast height-130 cm), Height, the severity of *C. sativa* trees were assessed based on their diameter class and evaluated within a designated radius range of 5, 10, and 15 m, respectively. (Ministry of Environmental Protection and Agriculture of Georgia, 2023), (Appendix Figure A15).

The severity of the blight-induced defoliation had been visually evaluated by experts in the field during the initial inventory. Applying a thorough assessment of defoliation is important for determining the cause of a tree's health issues, such as disease, insects, or other factors (Dobbertin and Brang, 2001). All trees that were partly defoliated had canker and other signs of the blight. Thus, all defoliation was attributed to *Cr. parasitica* (Tavadze *et al.*, 2013).

The severity of the blight-induced damage was assessed using four levels of defoliation in the field: 0-25%, 25-50%, 50-75% and >75% (Lakatos *et al.*, 2014). Dead trees were excluded from the analysis due to the uncertain cause of death. The basal areas of all tree species, *C. sativa* trees and stumps were calculated for each sample plot. To identify which variables were associated with blight-induced defoliation, we used generalized additive models (GAMs) to relate the severity of blight-induced defoliation of *Ca. sativa* trees to age and environmental variables (**Table 6**). We used GAMs because they can reveal non-linear and non-monotonic relationships. GAMs were implemented using the "mgcv" package (Wood, 2011), (Wood *et al.*, 2016) in R version 4.2.2. (R Core Team, 2016). GAMs were fitted using the ordered categorical ("ocat") family with an identity link function because the dependent variable was ordinal (i.e. 4 levels of *Ca. sativa* tree damage). In this procedure, the observed categories were coded as 1, 2, 3, 4. The "ocat" family provides the output following a logistic distribution. The "ocat" output is a response latent variable, which estimates thresholds that mark the transitions between levels of the ordered categorical response. The first threshold was set to -1, and additional thresholds were estimated for the boundaries between the other categories. The probability that the output variable falls inside specific cut points indicates the likelihood that the ordered categorical variable belongs to the relevant category. Penalized thin plate regression splines were used to represent all the smooth terms in the model. The smoothing parameter was estimated using the restricted maximum likelihood

(REML) estimation method, which is the most robust of the available GAM methods. (Wood, 2011).

We explored all possible combinations of explanatory variables to identify the best model. The combination of all 10 explanatory variables (**Table 6**) yielded a total of 1023 alternative models to choose from. The predictive power of all models was evaluated through a 10-fold cross-validation. The cross-validation of many models was handled through R's parallelization capabilities (Weston, 2022a), (Weston, 2022b). The best model was selected by Kendall's rank correlation (Tau-b) between the observed values of the defoliation severity and the ones calculated through cross-validation. We opted for cross-validation for model selection because this procedure without any a priori assumptions measures the predictive performance of a model by efficiently running model training and testing on the available data. To select the least biased model, additionally, we evaluated our models using the Akaike information criterion (AIC) and also checked concurvity between model terms and between each term and the rest of the model using the "mgcv" package. Concurvity is a generalization of collinearity, better suited for non-linear relationships.

Table 6. Variables used for modelling the defoliation severity caused by chestnut blight (*Cryphonectria parasitica*) in *C. sativa* trees across Georgia.

Variable	Description
Age	Age of a *Ca. sativa* tree (years) extracted from Georgia's 2019–2021 national forest inventory data (source: The National Forest Agency of Georgia)
Elevation	Elevation above sea level (m): SRTM 1 arc-second (~30 m) elevation raster (downloaded from http://earthexplorer.usgs.gov)
Slope	Slope (°) calculated from the SRTM 1 arc-second (~30 m) elevation raster
Aspect	Aspect (°) calculated from the SRTM 1 arc-second (~30 m) elevation

	raster
Mean annual temperature	Mean annual daily mean air temperatures averaged over 1 year (°C): CHELSA_bio1_1981.2010_V.2.1 downloaded from the CHELSA climatology data, a set of global climate layers with a spatial resolution of 1 km^2 (Karger *et al.*, 2017). This data set was used because it best explains the ecological niche of *Ca. sativa* across its entire range (Metreveli *et al.*, 2023).
Mean annual precipitation	Accumulated precipitation amount over 1 year (kg m^{-2}): CHELSA_bio12_1981.2010_V.2.1 downloaded from the CHELSA climatology data, a set of global climate layers with a spatial resolution of 1 km^2 (Karger *et al.*, 2017). This data set was used because it best explains the ecological niche of *Ca. sativa* across its entire range (Karger *et al.*, 2017).
Chestnut basal area	Basal area of *Ca. sativa* (m^2), measured in circular plots of 707 m^2, extracted from Georgia's 2019–2021 national forest inventory data (source: National Forest Agency of Georgia)
Stand basal area	Stand basal area (m^2), measured in circular plots of 707 m^2, extracted from Georgia's 2019–2021 national forest inventory data (source: Ministry of Environmental Protection and Agriculture of Georgia)
Stump basal area	stump basal area (m^2), measured in circular plots of 707 m^2, extracted from Georgia's 2019–2021 national forest inventory data (source: National Forest Agency of Georgia)
Understory cover	% of understory, measured in circular plots of 78.5 m^2, nested within the main forest inventory plots(?) extracted from Georgia's 2019–2021 national forest inventory data (source: National Forest Agency of Georgia)

4.3 Results

Our sample of *Ca. sativa* trees had a skewed distribution towards lower defoliation severity (Figure 18). The proportions of observations with defoliation severity of 0-25%, 25-50%, 50-75%, and >75% were 40.6%, 22.9%, 25.2%, and 11.3%, respectively. The sampled trees occurred in rugged and mesic terrain and ranged in age from 9 to 151 years (**Table 7**). The distribution of these trees across four aspect categories of 0-90, 90-180, 180-270, and 270-360 was not significantly different (Chi-squared = 4.322, p-value = 0.2288).

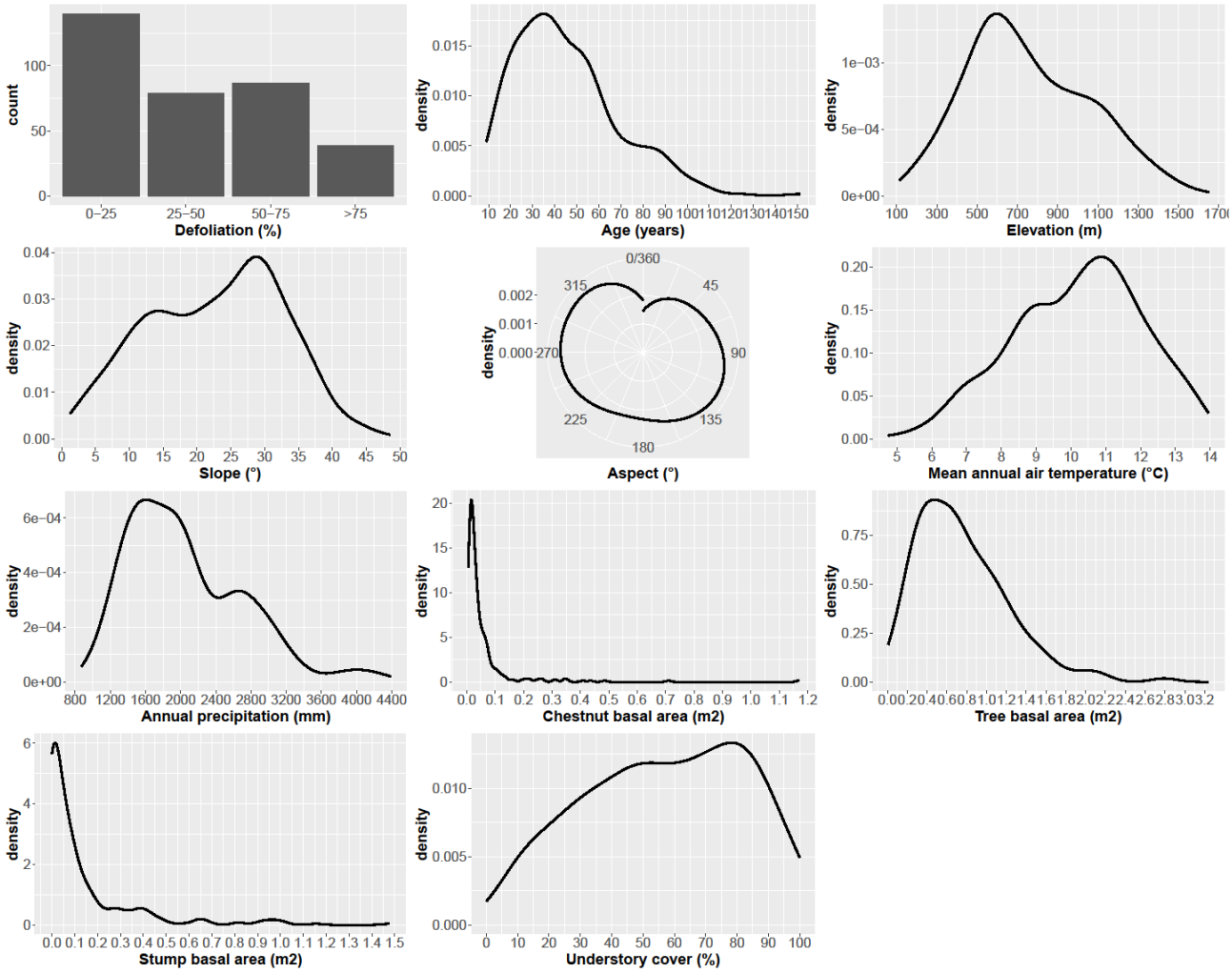


Figure 16. Kernel density distributions of variables of the sampled *Ca. sativa* trees. These variables were used for modeling the defoliation severity caused by chestnut blight (*Cryphonectria parasitica*) in *Ca. sativa* trees across Georgia.

Table 7. Summary statistics of the variables used for modeling the defoliation severity caused by chestnut blight (*Cryphonectria parasitica*) in sweet *Ca. sativa* trees across Georgia.

	Mean	Median	SD	Range
Tree age	45.1	40.00	23.4	9 - 151
Elevation	754.1	700.0	306.5	114 - 1651
Slope	22.7	23.7	10	1.2- 48.6
Mean annual temperature	10.2	10.5	1.8	4.8 - 13.1
Mean annual precipitation	2057.1	1942.6	671.3	869.8 - 4389.8
Chestnut basal area	0.05	0.03	0.1	0.006 - 1.2
Tree basal area	0.8	0.7	0.482	0.008 - 3.24
Stump basal area	0.13	0.05	0.3	0 - 1.48
Understory cover	56.8	60.00	25.6	0 - 100

Both the 10-fold cross-validation and AIC identified the same best GAM model, which included five predictor variables, namely, mean annual precipitation, slope, mean annual air temperature, and understory cover, aspect **(Table 8).**

Table 8. The AIC and Kendall rank correlation coefficient of the top 5 models.

N	Variables	Kendall rank correlation coefficient	AIC
1	slope, aspect, CHELSA_bio1, CHELSA_bio12, Understory_percent	0.327	822.1
2	Age, CHELSA_bio1, slope, aspect, CHELSA_bio12, Understory_percent	0.321	823.5
3	Age, slope, CHELSA_bio1, CHELSA_bio12, Understory_percent	0.316	824.9
4	elevation, slope, aspect, CHELSA_bio12, Understory_percent	0.31	826.1
5	slope, CHELSA_bio12, Understory_percent	0.309	827

According to model term significance measured through Chi-square (χ^2) and p-value as well as explained deviance, mean annual precipitation had the strongest influence on defoliation, while the aspect had the weakest. *Ca. sativa* trees on steeper slopes and with more understory cover had more defoliation (Figure 19). The defoliation severity map of the *Ca. sativa* can be seen in supplementary data (**Appendix Figure A16**). The relationship between defoliation and mean annual precipitation was more complex, with defoliation increasing as mean annual precipitation deviated from 2200 mm. This increase was steeper above this precipitation level than below it. Similarly, the response to mean annual temperature was non-linear, with defoliation increasing outside the range of 7-11°C (Figure 20). The increase was steeper above this temperature range.

The model predicted more defoliation on south-facing slopes, with a peak around 140°. At a precipitation amount close to 2200 mm, defoliation was the lowest and the other predictors had almost no impact (**Figure 20**). Even though, the Pearson correlation between slope and understory cover was negative (r=-0.141, p-value = 0.008922), they had similar effects on defoliation. This

model had negligible concurvity between model terms and between each term and the rest of the model (**Appendix Table A1**).

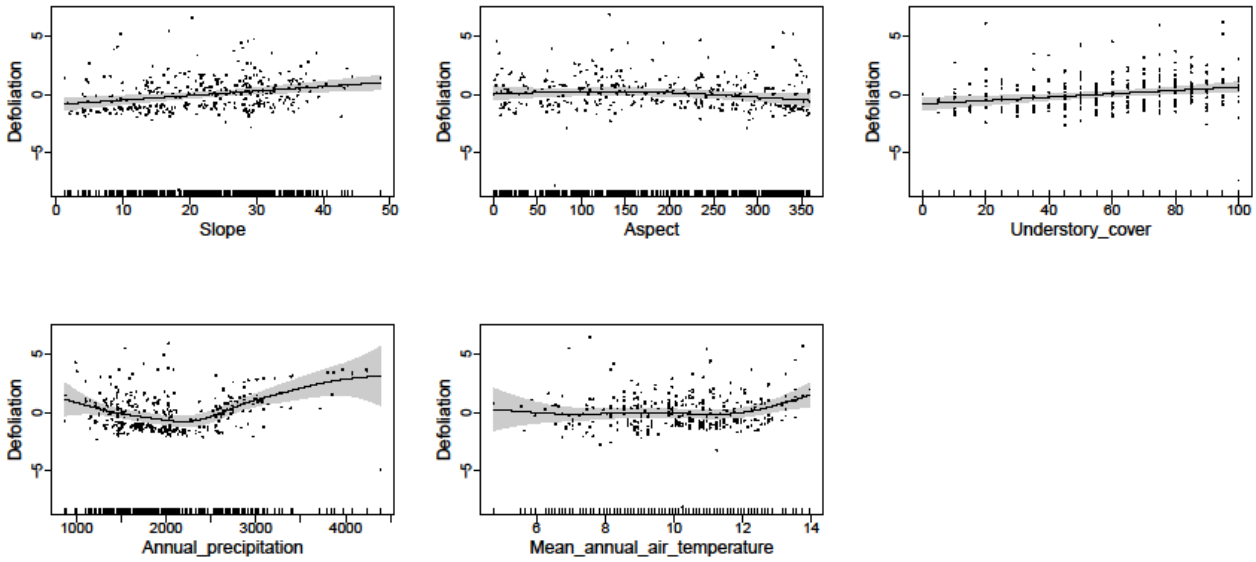
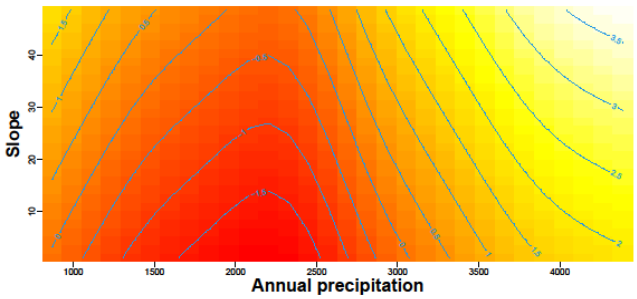
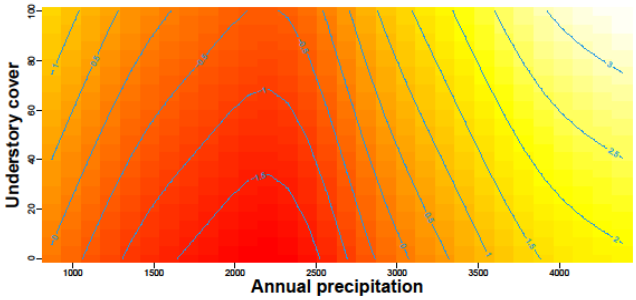
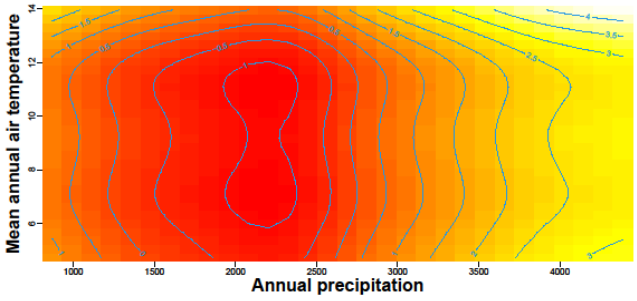
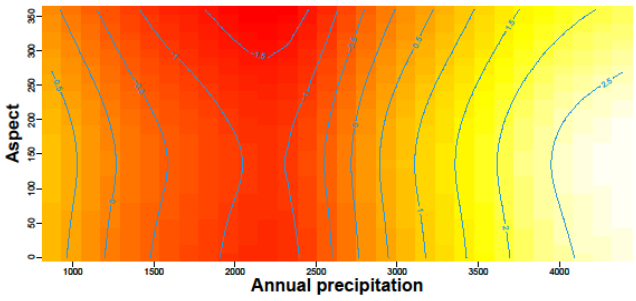


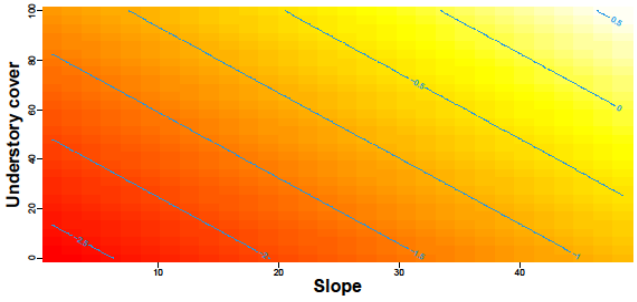
Figure 17. Partial residual plots, on the scale of the linear predictor, of the best generalized additive model (GAM) showing relationships between each predictor variable and the severity of blight-induced defoliation of *Ca. sativa* trees in Georgia (See Table 6 for the description of predictors). 95% Bayesian confidence intervals are shaded. Predictor distributions are shown on the x-axis. Observed data are plotted as points.

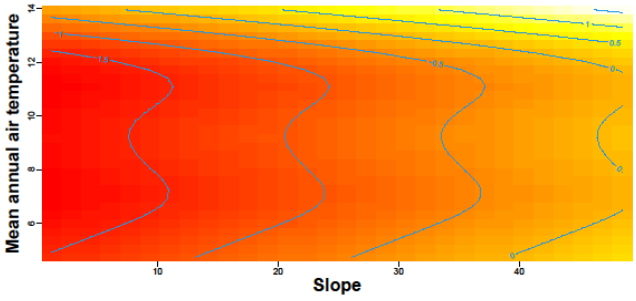

Slope
Annual precipitation

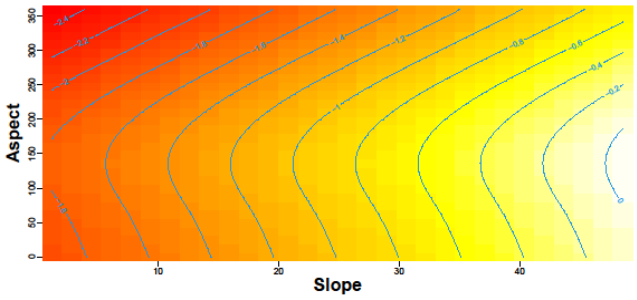

Understory cover
Annual precipitation

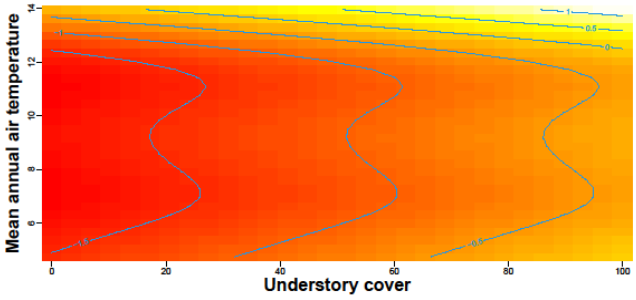

Mean annual air temperature
Annual precipitation

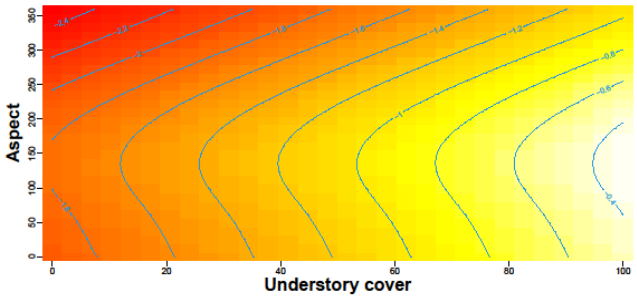

Aspect
Annual precipitation


Understory cover
Slope


Mean annual air temperature
Slope


Aspect
Slope


Mean annual air temperature
Understory cover


Aspect
Understory cover

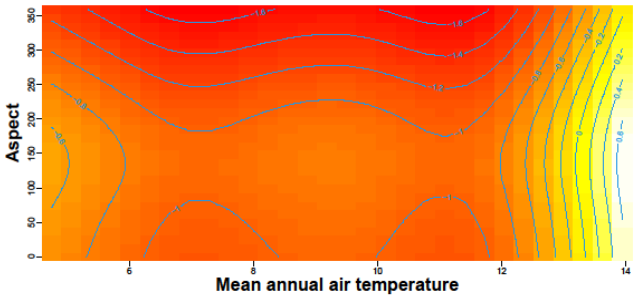

Aspect
Mean annual air temperature

Figure 18. Contoured 3D plots showing GAM-fitted relationships between pairs of predictors and the severity of blight-induced defoliation of *Ca. sativa* trees in Georgia (See Table 6 for the description of predictors). Defoliation increases from red to yellow.

4.4 Discussion

This study assessed for the first time in the Caucasus region the influence of the various environmental covariates, including precipitation, temperature, slope, understory cover, and aspect on the defoliation severity caused by chestnut blight. Our research shows that environmental conditions impact the disease severity of *Ca. sativa* trees caused by *Cr. parasitica* (chestnut blight fungus). Based on defoliation measurement from the national forest inventory, our GAM model analysis revealed that mean annual precipitation had the strongest effect on defoliation severity, while the aspect had the weakest. The defoliation severity for *Ca. sativa* trees was found to be higher in areas with steeper slopes and greater understory cover.

Observations with defoliation severity of no to mild infection were most frequent and were skewed towards lower defoliation severity. This may be the result of hypovirulence, which diminishes the pathogen's parasitic growth and sporulation capacity (Prospero et al., 2013). Alternatively, the majority of Georgian (Caucasian) *Ca. sativa* stands may have unfavorable environmental conditions to *Cr. Parasitica.* This study identified several key environmental factors that influence the severity of chestnut blight defoliation. Our most parsimonious model with the highest predictive power and negligible concurvity suggested that mean annual precipitation was the most important factor affecting blight-induced defoliation, followed in order of importance by slope, understory cover, mean annual temperature, and aspect. Defoliation in *Ca. sativa* trees increased with steeper slopes, more understory cover, and precipitation amounts away from 2200 mm. Similarly, to precipitation, the response to temperature was also non-linear, with increased defoliation outside the 7-11°C range. However, the rate of defoliation was steeper under higher precipitation and temperature conditions. The model predicted more defoliation on south-facing slopes. These findings suggested that environmental factors can influence blight-induced defoliation in *Ca. sativa* trees. This suggests that elevated precipitation and temperature made trees more affected by the infection. This is explained by *Cr. parasitica* being known for

thriving in warm, humid conditions (Anagnostakis, 1987). Consequently, *Ca. sativa* trees in warmer areas are more susceptible to the disease (Anagnostakis and Aylor 1984; Guérin and Robin 2003; Bolvanský 2014; Van Drunen, McCune and Husband 2018). At the same time, elevated precipitation levels can lead to increased splashing and water flow, which can help disperse fungal spores more effectively, potentially leading to wider infection. Also, if precipitation translates to consistently high humidity levels, it can create a more suitable environment for fungal growth and spore germination. Heavy precipitation or prolonged wet periods may stress trees, making them more susceptible to fungal infections like chestnut blight. Excessive precipitation can cause soil erosion, exposing tree roots and making them more vulnerable to infection. Conversely, dry conditions may hinder the movement of fungal spores, potentially slowing down the spread of the disease. However, drought may also stress trees, weakening their defences against fungal pathogens (Parker, Hill and Kuehnel 1993; Gao and Shain 1995; Waldboth and Oberhuber 2009. Both high and low temperatures may have similar impacts on infection severity.

Defoliation severity had a positive response to slope steepness in contrast to previous studies (Tindall *et al.*, 2004; Van Drunen *et al.* 2018). Steeper slopes may experience faster water drainage, leading to drier conditions that could limit fungal spore dispersal and growth. However, steeper slopes can also be more eroded and exposed to wind and sunlight, which can stress trees and make them more susceptible to infection.

Defoliation in *Ca. sativa* trees increased with more understory cover. This can be explained by better conditions for fungal development in such habitats. A dense understory can lead to higher humidity and lower temperatures near the ground, creating a more favorable environment for fungal growth and spore germination. Increased competition for water and nutrients from understory plants can stress the already vulnerable *Ca. sativa* trees, making them more susceptible to infection (Griffin et al., 1991). However, we also cannot rule out that the defoliation caused by Cr. parasitica has increased the understory cover.

In our study, *Ca. sativa* trees growing on south-facing slopes were more damaged by the blight. While the fungus can tolerate some direct sunlight, excessive exposure can be detrimental (Duque-Sarango, et. al., 2023). Sunlight can have opposing effects on *Cryphonectria parasitica*,

the fungus causing chestnut blight. While direct sunlight can indeed dry out the bark and hinder spore germination and growth, it can also create a warmer environment compared to ambient air throughout the day (Anagnostakis & Aylor 1984). This warmth potentially favors fungal growth, assuming sufficient moisture availability within the host during dry periods (Rankin 1914). This may explain more defoliation on south-facing slopes and further highlights the complex interplay between environmental factors and *Cr. parasitica*. Further research is necessary to elucidate the precise conditions under which sunlight benefits or hinders the pathogen, considering factors like bark moisture content, temperature thresholds, and specific sun exposure patterns.

Tree vulnerability to chestnut blight extends beyond simply its innate resistance. Rather, there appears to be a complex interplay between various environmental factors and their impact on both the host tree and *Cr. parasitica*. These factors can induce stress on each participant, creating conditions that either favor or hinder the progression of the disease.

This study focused on a specific geographic region and may not be directly applicable to other *Ca. sativa* populations with different environmental conditions. However, our previous study indicated that the ecological niche modeled for *C. sativa* in Georgia, the Caucasus represents that of *C. sativa* elsewhere (Metreveli *et al.*, 2023), and hence the relationship between blight-induced defoliation and the environment might be transferable beyond the Caucasus. Soil was not factored into this study and the age range of sampled trees was quite skewed, and further research is needed to understand how soil and age may affect defoliation patterns. While the model identified statistically significant relationships, further work is needed to elucidate the underlying mechanisms at play. Together, our study provides valuable insights into the environmental factors that influence chestnut blight defoliation. Understanding these factors is crucial for developing effective management strategies and predicting future disease outbreaks. Future research should focus on expanding the study area, incorporating a wider range of tree ages, exploring mechanistic linkages, and investigating the interactive effects of more environmental factors.

5. General Discussion

Each chapter enhances the expanding body of knowledge by investigating unique but connected ecological enquiries. All three studies showed significant patterns linking environmental gradients to the performance and resilience of *Ca. sativa* populations regarding disease severity, tree growth dynamics, and habitat suitability. The thesis also highlights the importance of the Caucasus ecoregion for understanding *Ca. sativa* ecology in light of current and future environmental issues.

The first chapter examines the general inquiry of the suitable environment and global distribution patterns of *Ca. sativa*. This indicates that modelling derived from natural occurrences in the Caucasus provides precise predictions of the species' niche over its entire distribution, including Europe and Asia Minor. This contradicts prior notions that distribution models need extensive continental-scale data and underscores the importance of high-quality, biologically representative data from refugial areas (Bowler et al., 2022; Elith and Leathwick, 2009).

The species prefers annual precipitation ranging from 500 to 1000 mm, with the hottest quarter temperatures between 15 to 30°C, and winter mean temperatures above –15°C. Suitability is optimal at moderate circumstances and decreases significantly in very dry, cold, or wet environments (Gurney et al., 2011; Mahdi Najafpour, 2012). These parameters provide a comprehensive framework for detecting susceptible or possibly resilient *Ca. sativa* populations.

In addition, the model comparison indicated that CHELSA v2.1 climate data produced more dependable predictions than WorldClim, owing to its superior control over topographic differences in mountainous regions such as the Caucasus (Karger et al., 2017; Maria and Udo, 2017). This knowledge is beneficial for future modelling attempts concerning additional montane or refugial tree species (Akobia et al., 2022).

The research addresses the issues associated with past human-induced range expansion and the difficulty in differentiating between natural and artificially formed stands in Europe (Mattioni et al., 2008). Using data from the natural areas, where *Ca. sativa* populations are mostly wild, the we mitigated this bias and generated more ecologically significant suitability maps (Prospero et al., 2013). The models demonstrated strong performance when validated against GBIF presence

data (Zizka et al., 2019), consequently confirming their generalisation. The work highlights that climate-driven habitat suitability models, when well parameterised, might be essential instruments in forest conservation strategy for *Ca. sativa* (Evans et al., 2015).

The second chapter offers a thorough assessment of the growth dynamics of *Ca. sativa* in the Caucasus by combining dendroecological measures (tree cores) with meteorological, relief, and soil data within a Generalised Additive Model (GAM) framework. The model found tree age, the lowest temperature of the coldest month, precipitation during the driest quarter, soil nitrogen concentration, and soil pH as key determinants of radial development. Juvenile trees (<50 years) demonstrated superior development, presumably attributable to physiological benefits associated with food absorption and carbon distribution (Sillett et al., 2010). Moderate winter temperatures correlated positively with growth (Rashid et al., 2024), but elevated precipitation in the driest quarter, especially from January to March, exerted a detrimental impact, possibly attributable to soil freezing and stress generated by late frost (Domisch et al., 2018; Ziaco et al., 2016). Moreover, elevated soil nitrogen concentrations (400–550 mg/kg) facilitated optimum development (Ouimet and Moore, 2015), although acidic soil conditions (pH 5.0–6.0) were favoured (Velizarova, 2015). Spatial patterns revealed rapid growth in the western Caucasus (e.g., Kolkheti plain), but central and southeastern parts exhibited diminished increments, likely attributable to less favorable soil and climatic circumstances (Metreveli et al., 2023; Tarkhnishvili et al., 2012).

A moderate yet notable relationship was identified between the growth model and an earlier established habitat suitability model from the first chapter. Nevertheless, significant geographic discrepancies indicate that the exclusion of soil factors in the habitat model likely resulted in overestimations in certain areas. Variations in light availability, competition, or water accessibility may also explain differences, as competition may occasionally exceed climate limitations on growth (Gómez-Aparicio et al., 2011). In contrast, the model's prediction of high growth in regions with lower habitat suitability indicates that C. sativa uses many physiological strategies to survive in unsuitable environments (Serra-Diaz et al., 2013). Winter precipitation, while beneficial for seedling vitality (Suvanto et al., 2017), can transform into a stressor during active growth phases (Domisch et al., 2018). Despite the moderate correlation

between the models (r = 0.3), this link establishes a basis for subsequent research to address scale-related or temporal differences between growth and distribution assumptions.

Future growth potential under climate change scenarios (SSP126, SSP370, SSP585) displayed divergent regional patterns. Under SSP126, increased precipitation combined with limited warming is anticipated to increase environmental stress, resulting in growth declines in numerous regions. In contrast, SSP370 and SSP585 predicted relatively stable or slightly elevated growth rates, accompanied by a northward and altitudinal shift in optimal growth zones. This contradicts previous studies projecting extensive habitat loss (Beridze et al., 2023b) and instead indicates that specific areas of the Caucasus may remain stable or potentially improve under future conditions. However, abiotic factors represent only a portion of the overall context. Human activities, land-use changes, pests, and diseases are progressively altering *Ca. sativa* growth patterns (Krebs et al., 2004b; Metreveli et al., 2023). Additionally, modelling accuracy is influenced by scale mismatches in environmental data (Verburg et al., 2011), particularly in topographically complex regions such as the Caucasus. However, Future projections can be enhanced by integrating biotic stressors and standardising spatial resolutions across datasets.

The third chapter examines the environmental factors influencing the severity of defoliation caused by *Cryphonectria parasitica* (Murrill) M.E.Barr (Chestnut blight). A Generalised Additive Model (GAM) determined that mean annual precipitation is the primary predictor, follow by slope, understory cover, mean annual temperature, and aspect. Defoliation severity intensified in locations with steeper slopes, denser understory, and precipitation amounts ranging from the ideal range (~2200 mm), as well as in temperatures exceeding 7–11°C. The findings indicate that warm and humid circumstances, which promote fungal proliferation and spore germination (Anagnostakis, 1987; Van Drunen et al., 2018), increase the vulnerability of trees to infection. Precipitation serves a dual function: excessive amounts facilitate spore dissemination and infection, whereas its deficiency impedes spread and exacerbates drought stress, hence further compromising tree health (Waldboth and Oberhuber, 2009).

The research additionally revealed heightened defoliation in trees situated on south-facing slopes and regions with extensive understory vegetation. South-facing slopes, although subjected

to increased sunshine that can make fungal spores dry, also maintain higher temperatures, which may favourably support the pathogen under sufficient moisture circumstances (Duque-Sarango et al., 2023). Thick understory vegetation can increase humidity and lower ground-level temperatures, fostering fungal growth and increasing tree stress due to competition for water and nutrients (Griffin et al., 1991). A feedback loop may develop where defoliation increases understory cover, hence increasing infection risk. The intricate interplay between environmental conditions and pathogen dynamics indicates a complex, multifactorial system that influences tree vulnerability beyond natural resistance characteristics.

This thesis integrates three interrelated research studies that improve our understanding of *Ca. sativa* ecology in the Caucasus through the examination of habitat suitability, growth dynamics, and vulnerability to disease across environmental gradients. Despite the Lack of studies, about the phylogenetic and diversity evaluation of various *Ca. sativa* stands, highlighting the necessity for additional research, this thesis establishes a basis for enhancing management and conservation measures for *Ca. sativa* populations.

6. Outlook and Recommendations

This PhD dissertation offers extensive insights into the ecology of the Sweet Chestnut (*Ca. sativa*) in the Caucasus ecoregion, focusing on habitat suitability, growth dynamics especially in the context of climate change and the effects of environmental factors on its defoliation severity. Despite comprehensive research, numerous areas persist as promising for future investigation to improve comprehension, conservation, and management of this ecologically and economically vital species.

6.1 Future Research Directions

Plant Diversity in the different stands of Ca. sativa

Subsequent studies should concentrate on investigating plant species composition and genetic diversity within *Ca. sativa* populations. Comparative tests among different populations can help to understund the correlations between genetic diversity, species composition, and environmental factors. These studies are essential for comprehending the ecological dynamics of *Ca. sativa* forests and guiding conservation measures.

- ***Genetic Studies***

This study found essential climatic and edaphic parameters influencing *Ca. sativa* distribution, defoliation severity and growth; nonetheless, genetic diversity among populations across several environmental gradients remains little explored. Future research, including genomic methods, will be important for comprehending adaptations and resilience mechanisms in populations of *Ca. sativa,* particularly in the context of climate change scenarios.

- ***Calculating the Defoliation severity by Remote Sensing***

Calculating the defoliation severity with advanced remote sensing methods can significantly improve spatial modeling of chestnut blight (*Phriphonectria parasitica*) impact of *Ca. sativa* forests. Future research should leverage high-resolution satellite imagery and lidar data to monitor *Ca. sativa* stands, assess forest health, and detect early signs of stress and defoliation on a broader scale.

- ***Blue Intensity Dendrochronology Studies***

Employing the Blue Intensity technique for analysing *Ca. sativa* growth is advisable to address the constraints of conventional Tree-Ring Width assessments. Analysing latewood blue intensity in connection to climatic conditions could provide more accurate insights into *Ca. sativa* growth responses and enhance the understanding of environmental stressors impacting *Ca. sativa* growth.

- ***Competition Studies with Other Tree Species***

Subsequent research should examine the competitive dynamics between *Ca. sativa* and various tree species. These studies should assess the impact of competition on the distribution, growth, and defoliation severity of *Ca. sativa*, as well as how competition intensity may vary under different future climate scenarios. Comprehending these connections can significantly improve the management of *Ca. sativa* forests and their resilience to environmental changes.

6.2 Recommendations

- ***Adaptive Management***

Due to the sensitivity of *Ca. sativa* distribution and growth to climatic extremes, such as drought and temperature anomalies, it is essential to design and apply adaptive management strategies that incorporate climate resilience. Recommended practices include assisted migration, selective breeding for drought resistance, and the preservation of genetic variety.

- ***Sustainable Forest Practices, Blight Management and Monitoring***

Ca. sativa forests require management approaches that balance ecological sustainability and economic productivity. Recommendations include low-impact harvesting methods, regeneration practices that promote genetic diversity, and integrated management to mitigate the impacts of chestnut blight (*Cryphonectria parasitica*). At the same time Intensified monitoring and research into biological control measures for chestnut blight are advisable.

- ***Policy and Regional Cooperation***

Successful conservation of *Ca. sativa* forests requires regional collaboration among the nations of the Caucasus ecoregion. Policymakers must prioritise the establishment of transboundary ecological corridors and protected regions, promoting collaborating research and conservation measures.

- ***Raising public awareness and involvement in the management***

Increasing the involvement of communities in the conservation and sustainable management of *Ca. sativa* forests are crucial. Programs highlighting the ecological significance of *Ca. sativa* forests, sustainable management strategies, and the effects of climate change should be established to enhance public knowledge and involvement.

7. Conclusion

This thesis represents an extensive and multi-dimensional evaluation of the ecological determinants influencing the distribution, growth, and susceptibility to disease of *Ca. sativa* Miller (Sweet Chestnut) in the Caucasus. The study illustrates that climate variables, specifically temperature and precipitation, alongside soil chemistry and tree age, are critical factors influencing *Ca. sativa* performance, achieved through the integration of habitat suitability modelling, dendroecological growth analysis, and disease severity evaluation. The CHELSA-based habitat suitability model demonstrated superior accuracy and ecological realism compared to WorldClim, closely correlating with the established global distribution of *Ca. sativa*; nonetheless, limitations persist due to the omission of soil factors and proximity to glacial refugia. Growth models suggest that optimal conditions predominantly exist in the western Caucasus, however future projections under various climatic scenarios demonstrate regionally diverse responses, with possible stability or enhancement under intermediate and high-emission scenarios. The severity of disease induced by *Cryphonectria parasitica* (Murrill) M.E.Barr was associated with complex link between environmental stressors and pathogen behaviour. Although the findings are regionally concentrated, research validates the applicability of results beyond the Caucasus, rendering them pertinent to wider *Ca. sativa* conservation initiatives. In order to improve the models, establishing a foundation for several future research fields and management strategies is necessary. Future research can enhance ecological resilience and sustainability by focussing on genetic diversity, species composition, advanced dendrochronological techniques, competition studies, long-term monitoring, ecological modelling, and integrated remote sensing methods. Simultaneously, adaptive management, sustainable forestry methods, enhanced disease management, regional collaboration, and community involvement will guarantee that *Ca. sativa* forests persist as resilient and viable ecosystems amid shifting climatic conditions.

Contribution of the doctoral candidate to the publications

This section provides an overview of the doctorate candidate's contributions to the two published and one submitted papers that comprise the cumulative dissertation.

First Chapter / Published Article:

Potential Distribution and Suitable Habitat for Chestnut (*Castanea sativa*)

Vasil Metreveli [1,2,3,*], Holger Kreft [2], Ilia Akobia [4], Zurab Janiashvili [5], Zaza Nonashvili [5], Lasha Dzadzamia [1], Zurab Javakhishvili [1] and Alexander Gavashelishvili [6]

Forests 2023, 14, 2076.

https://doi.org/10.3390/f14102076

Doctoral Candidate's Contribution:

- Writing – review and editing,
- Writing – original draft,
- Visualization,
- Validation,
- Software,
- Resources,
- Project administration,
- Methodology,
- Investigation,
- Formal analysis,
- Data curation,
- Conceptualization.

Second Chapter / Submitted Article:

On the relationship between environment and growth of sweet chestnut (*Castanea sativa*) in the Caucasus

Vasil Metreveli [a,b,c*], Holger Kreft [b,d,e], Zurab Javakhishvili [a], Sandro Mdivani [a], Giorgi Chikorashvili [f], Ilia Akobia[a,g], Alexander Gavashelishvili [h]

Dendrochronologia 2025, 15, DENDRO-D-25-00080

Doctoral Candidate's Contribution:

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- Formal analysis,
- Data curation,
- Conceptualization.

Third Chapter / Published Article:

Environmental covariates of chestnut blight (Cryphonectria parasitica) in Georgia (Caucasus)

Vasil Metreveli [a,b,c,*], Holger Kreft [b], Alexander Gavashelishvili [d]

Forest Ecology and Management 569 (2024) 122153.

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- ☐ Investigation,
- ☐ Formal analysis,
- ☐ Data curation,
- ☐ Conceptualization.

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Potential Distribution and Suitable Habitat for Chestnut (*Castanea sativa*)

Vasil Metreveli [1,2,3,*], Holger Kreft [2], Ilia Akobia [4], Zurab Janiashvili [5], Zaza Nonashvili [5], Lasha Dzadzamia [1], Zurab Javakhishvili [1] and Alexander Gavashelishvili [6]

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On the relationship between environment and growth of sweet chestnut (*Castanea sativa*) in the Caucasus

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Environmental covariates of chestnut blight (*Cryphonectria parasitica*) in Georgia (Caucasus)

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8. References

Akhalkatsi, M. Forest Habitat Restoratio in Georgia, Caucaus Ecoregion; Mtsigobari: Tbilisi, GA, USA, 2015; ISBN 978-9941-450-68-6

Akhalkatsi, M. Pine Forest on Tree-Line Ecotone in the Mountain Kazbegi in the Georgia (South Cau-casus). Agri. Res. Technol. Open Access J. 2019, 21, 556149. https://doi.org/10.19080/ARTOAJ.2019.21.556149

Akobia, I., Janiashvili, Z., Metreveli, V., Zazanashvili, N., Batsatsashvili, K., Ugrekhelidze, K., 2022. Modelling the potential distribution of subalpine birches (Betula spp.) in the Caucasus. Community Ecol. 23, 209–218. https://doi.org/10.1007/s42974-022-00097-4

Adams, O.S., 1927. Tables for Albers projection (No. 378). US Government Printing Office.

Álvarez-Álvarez, P., Aviñoa-Arias, A., Díaz-Varela, E., López-Bao, J.V., Pérez-Girón, J.C., 2025. Impact of climate change over distribution and potential range of chestnut in the Iberian Peninsula. Front. For. Glob. Change 8, 1561027. https://doi.org/10.3389/ffgc.2025.1561027

Anagnostakis, S.L. American Chestnut Sprout Survival with Biological Control of the Chestnut-Blight Fungus Population. For. Ecol. Manag. 2001, 152, 225–233. https://doi.org/10.1016/S0378-1127(00)00605-8

Anagnostakis, S.L. and Aylor, D.E. (1984) The effect of temperature on growth of Endothia (Cryphonectria) parasitica in vitro and in vivo Mycologia, 76 (3), pp. 387-397. https://doi.org/10.1080/00275514.1984.12023857

Anagnostakis, S.L., 1987. Chestnut Blight: The Classical Problem of an Introduced Pathogen. Mycologia 79, 23–37. https://doi.org/10.1080/00275514.1987.12025367

Andersson, F.O., Ågren, G.I., Führer, E., 2000. Sustainable tree biomass production. For. Ecol. Manag. 132, 51–62. https://doi.org/10.1016/S0378-1127(00)00379-0

Aoyama, H. A Study of the Stratified Random Sampling. Ann. Inst. Stat. Math. 1954, 6, 1–36. https://doi.org/10.1007/BF02960514

Araújo, M.B., Guisan, A., 2006. Five (or so) challenges for species distribution modelling. J. Biogeogr. 33, 1677–1688. https://doi.org/10.1111/j.1365-2699.2006.01584.x

Badenes, M.L., Byrne, D.H., 2012. Fruit Breeding, Handbook of Plant Breeding. Springer US, Boston, MA. https://doi.org/10.1007/978-1-4419-0763-9

Bakuradze, G. Assessment of Above-Ground Carbon Stocks in the Forest Ecosystem of Georgia; Ilia State University: Tbilisi, GA, USA, 2023.

Baser, U., Bozoglu, M., 2020. Chestnut blight and technical efficiency in chestnut production: Case study of Aydin Province, Turkey. Sci. Hortic. 263, 109048. https://doi.org/10.1016/j.scienta.2019.109048

Beck, J.; Böller, M.; Erhardt, A.; Schwanghart, W. Spatial Bias in the GBIF Database and Its Effect on Modeling Species' Geographic Distributions. Ecol. Inform. 2014, 19, 10–15. https://doi.org/10.1016/j.ecoinf.2013.11.002

Begon, M., Townsend, C.R., 2021. Ecology: from individuals to ecosystems, Fifth edition. ed. Wiley, Hoboken Chichester.

Beridze, B., Dering, M., 2021. Problems and threats to the Caucasus forest ecosystems on the example of Castanea sativa. Kosmos 70, 19–26. https://doi.org/10.36921/kos.2021_2662

Beridze, B., Sękiewicz, K., Walas, Ł., Danelia, I., Farzaliyev, V., Kvartskhava, G., Szmyt, J., Dering, M., 2023a. Niche modelling suggests low feasibility of assisted gene flow for a Neogene relict tree, Castanea sativa Dendrobiology 90, 58–75. https://doi.org/10.12657/denbio.090.005

Beridze, B., Sękiewicz, K., Walas, Ł., Thomas, P.A., Danelia, I., Fazaliyev, V., Kvartskhava, G., Sós, J., Dering, M., 2023b. Biodiversity protection against anthropogenic climate change: Conservation prioritization of Castanea sativa in the South Caucasus based on genetic and ecological metrics. Ecol. Evol. 13, e10068. https://doi.org/10.1002/ece3.10068

Beridze, B., Sękiewicz, K., Walas, Ł., Thomas, P.A., Danelia, I., Kvartskhava, G., Farzaliyev, V., Bruch, A.A., Dering, M., 2023c. Evolutionary history of Castanea sativa in the Caucasus driven by Middle and Late Pleistocene paleoenvironmental changes. AoB PLANTS 15, plad059. https://doi.org/10.1093/aobpla/plad059

Beridze, B.; Dering, M. Problems and Threats to the Caucasus Forest Ecosystems on the Example of Castanea sativa. Kosmos 2021, 70, 19–26. https://doi.org/10.36921/kos.2021_2662

Bivand, R.; Keitt, T.; Rowlingson, B.; Pebesma, E.; Sumner, M.; Hijmans, R.; Rouault, E.; Maintainer, R.B. Package 'rgdal'. Bindings for the Geospatial Data Abstraction Library. 2022, p.172. Available online: https://cran.r-project.org/web/packages/rgdal/index.html (accessed on 15 May 2022).

Bleyhl, B.; Arakelyan, M.; Askerov, E.; Bluhm, H.; Gavashelishvili, A.; Ghasabian, M.; Ghoddousi, A.; Heidelberg, A.; Khorozyan, I.; Malkhasyan, A.; et al. Assessing Niche Overlap between Domestic and Threatened Wild Sheep to Identify Conservation Priority Areas. Divers. Distrib. 2019, 25, 129–141. https://doi.org/10.1111/ddi.12839

Bobrowski, M.; Schickhoff, U. Why Input Matters: Selection of Climate Data Sets for Modelling the Potential Distribution of a Treeline Species in the Himalayan Region. Ecol. Model. 2017, 359, 92–102. https://doi.org/10.1016/j.ecolmodel.2017.05.021

Bolvanský, M., Ostrovský, R., Kobza, M., Adamčíková, K., Pažitny, J., Juhásová, G. (2014) Spread of chestnut blight in Slovakia in relation to the site topography and climatic characteristics Acta Hortic., 1043, pp. 35-42. https://doi.org/10.17660/ActaHortic.2014.1043.3

Bowler, D.E., Callaghan, C.T., Bhandari, N., Henle, K., Benjamin Barth, M., Koppitz, C., Klenke, R., Winter, M., Jansen, F., Bruelheide, H., Bonn, A., 2022. Temporal trends in the spatial bias of species occurrence records. Ecography 2022, e06219. https://doi.org/10.1111/ecog.06219

Brewer, L.G., 1995. Ecology of Survival and Recovery from Blight in American Chestnut Trees (Castanea dentata (Marsh.) Borkh.) in Michigan. Bull. Torrey Bot. Club 122, 40. https://doi.org/10.2307/2996402

Broadmeadow, M.S.J., Ray, D., Samuel, C.J.A., 2005. Climate change and the future for broadleaved tree species in Britain. For. Int. J. For. Res. 78, 145–161. https://doi.org/10.1093/forestry/cpi014

Bunn, A.G., 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28, 251–258. https://doi.org/10.1016/j.dendro.2009.12.001

Burke, K.L., 2012. Niche contraction of American Chestnut in response to Chestnut blight. Can. J. For. Res. 42, 614–620. https://doi.org/10.1139/x2012-002

Cernusak, L.A., Winter, K. and Turner, B.L., 2010. Leaf nitrogen to phosphorus ratios of tropical trees: experimental assessment of physiological and environmental controls. New Phytologist, 185(3), pp.770-779. https://doi.org/10.1111/j.1469-8137.2009.03106.x

Chakrabarti, A., Ghosh, J.K., 2011. AIC, BIC and Recent Advances in Model Selection, in: Philosophy of Statistics. Elsevier, pp. 583–605. https://doi.org/10.1016/B978-0-444-51862-0.50018-6

Cienciala, E., Russ, R., Šantrůčková, H., Altman, J., Kopáček, J., Hůnová, I., Štěpánek, P., Oulehle, F., Tumajer, J., Ståhl, G., 2016. Discerning environmental factors affecting current tree growth in Central Europe. Sci. Total Environ. 573, 541–554. https://doi.org/10.1016/j.scitotenv.2016.08.115

Comerford, D.P., Schaberg, P.G., Templer, P.H., Socci, A.M., Campbell, J.L., Wallin, K.F., 2013. Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest. Oecologia 171, 261–269. https://doi.org/10.1007/s00442-012-2393-x

Conedera, M., Krebs, P., Gehring, E., Wunder, J., Hülsmann, L., Abegg, M., Maringer, J., 2021. How future-proof is Sweet chestnut (Castanea sativa) in a global change context? For. Ecol. Manag. 494, 119320. https://doi.org/10.1016/j.foreco.2021.119320

Conedera, M., Tinner, W., Krebs, P., de Rigo, Daniele, Caudullo, Giovanni, San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A., 2024. Castanea sativa in Europe: distribution, habitat, usage and threats. University of Bern. https://doi.org/10.7892/BORIS.80790

Conedera, M.; Krebs, P.; Gehring, E.; Wunder, J.; Hülsmann, L.; Abegg, M.; Maringer, J. How Future Proof Is Sweet Chestnut (Castanea sativa) in a Global Change Context. Forest Ecology and Management, 2021, 494, 119320. https://doi.org/10.1016/j.foreco.2021.119320

Conedera, M.; Manetti, M.C.; Giudici, F.; Amorini, E. Distribution and economic potential of the Sweet chestnut (Castanea sativa Mill.) in Europe. Ecmed 2004, 30, 179–193. https://doi.org/10.3406/ecmed.2004.1458

Connor, S.E., 2011. A promethean legacy: Late Quaternary vegetation history of Southern Georgia, the Caucasus. Louvain, Belgium: Peeters.

Di Filippo, A., Piovesan, G., Romagnoli, M., Helle, G., Gaertner, H., 2014. Proceedings of the DENDROSYMPOSIUM 2013 : May 8th - 11th, 2013 in Viterbo, Italy. Sci. Tech. Rep. 1405. https://doi.org/10.2312/GFZ.B103-14055

Dobbertin, M., Brang, P., 2001. Crown defoliation improves tree mortality models. For. Ecol. Manag. 141, 271–284. https://doi.org/10.1016/S0378-1127(00)00335-2

Dolukhanov, A., 2010. Forest Vegetation of Georgia. Tbilisi, Tbilisi, Georgia.

Domisch, T., Martz, F., Repo, T., Rautio, P., 2018. Winter survival of Scots pine seedlings under different snow conditions. Tree Physiol. 38, 602–616. https://doi.org/10.1093/treephys/tpx111

Dormann, C.F.; McPherson, J.M.; Araújo, M.B.; Bivand, R.; Bolliger, J.; Carl, G.; Davies, R.G.; Hirzel, A.; Jetz, W.; Daniel Kissling, W.; et al. Methods to Account for Spatial Autocorrelation in the Analysis of Species Distributional Data: A Review. Ecography 2007, 30, 609–628. https://doi.org/10.1111/j.2007.0906-7590.05171.x

Duque-Sarango, P., Delgado-Armijos, N., Romero-Martínez, L., Pinos-Vélez, V., 2023. Assessing the potential of ultraviolet irradiation for inactivating waterborne fungal spores: kinetics and photoreactivation studies. Front. Environ. Sci. 11, 1212807. https://doi.org/10.3389/fenvs.2023.1212807

Elith, J., Leathwick, J.R., 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Elith, J.; Graham, C.H.; Anderson, R.P.; Dudík, M.; Ferrier, S.; Guisan, A.; Hijmans, R.J.; Huettmann, F.; Leathwick, J.R.; Lehmann, A.; et al. Novel Methods Improve Prediction of Species' Distributions from Occurrence Data. Ecography 2006, 29, 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Evans, T.G., Diamond, S.E., Kelly, M.W., 2015. Mechanistic species distribution modelling as a link between physiology and conservation. Conserv. Physiol. 3, cov056. https://doi.org/10.1093/conphys/cov056

Fick, S.E.; Hijmans, R.J. WorldClim 2: New 1-km Spatial Resolution Climate Surfaces for Global Land Areas. Int. J. Climatol. 2017, 37, 4302–4315. https://doi.org/10.1002/joc.5086

Frank, E.H., Jr. Package 'Hmisc', The Comprehensive R Archive Network, 2023. Available online: https://hbiostat.org/R/Hmisc/ (accessed on 10 May 2022)

Franklin, J.; Miller, J.A. Mapping Species Distributions: Spatial Inference and Prediction; Ecology, bio-diversity and conservation; Cambridge University Press: Cambridge, UK; New York, NY, USA, 2009; ISBN 978-0-521-87635-3

Friedl, M. and Sulla-Menashe, D., MODIS/Terra+Aqua Land Cover Type Yearly L3 Global 500m SIN Grid MCD12Q1. NASA EOSDIS Land Processes Distributed Active Archive Center, South Dakota, USA, 2019. Available online: https://search.earthdata.nasa.gov/search (accessed on 20 May 2023)

Gao, S., Shain, L. (1995) Effects of water stress on chestnut blight Can. J. Forest Res., 25, pp. 1030-1035. https://doi.org/10.1139/x95-112

Gärtner, H., Nievergelt, D., 2010. The core-microtome: A new tool for surface preparation on cores and time series analysis of varying cell parameters. Dendrochronologia 28, 85–92. https://doi.org/10.1016/j.dendro.2009.09.002

Gavashelishvili, A.; Tarkhnishvili, D. Biomes and Human Distribution during the Last Ice Age: Biomes and Humans during the Ice Age. Glob. Ecol. Biogeogr. 2016, 25, 563–574. https://doi.org/10.1111/geb.12437

Gomes-Laranjo, J.; Dinis, L.-T.; Martins, L.; Portela, E.; Pinto, T.; Ciordia, M.; Feito, I.; Majada, J.; Peixoto, F.; Pereira, S.; et al. Characterization of Chestnut Behavior with Photosynthetic Traits. In Applied Photosynthesis; Najafpour, M., Ed.; InTech: London, UK, 2012; ISBN 978-953-51-0061-4

Gómez-Aparicio, L., García-Valdés, R., Ruíz-Benito, P., Zavala, M.A., 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests:

implications for forest management under global change: NEIGHBORHOOD MODELS AND TREE GROWTH DRIVERS. Glob. Change Biol. 17, 2400–2414. https://doi.org/10.1111/j.1365-2486.2011.02421.x

Griffin, G.J., Smith, H.C., Dietz, A., Elkins, J.R., 1991. Importance of hardwood competition to American chestnut survival, growth, and blight development in forest clearcuts. Can. J. Bot. 69, 1804–1809. https://doi.org/10.1139/b91-229

Guérin, L., Robin, C. (2003) Seasonal effect on infection and development of lesions caused by Cryphonectria parasitica in Castanea sativa. Forest Pathol., 33 (4), pp. 223-235 https://doi.org/10.1046/j.1439-0329.2003.00329.x

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. Habitat suitability and distribution models: with applications in R, Ecology, biodivesity and conservation. Cambridge university press, Cambridge, United Kingdom.

Gulisashvili, V. Chestnut in the Caucasus; Nature: Tbilisi, 1967.

Gupta, L., Dixit, J., 2024. Investigating the spatial distribution of flood inundation and landforms using topographic position index (TPI) and geomorphon-based automated landform classification methods. J. Earth Syst. Sci. 133, 126. https://doi.org/10.1007/s12040-024-02343-x

Gurney, K.M., Schaberg, P.G., Hawley, G.J., Shane, J.B., 2011. Inadequate Cold Tolerance as a Possible Limitation to American Chestnut Restoration in the Northeastern United States. Restor. Ecol. 19, 55–63. https://doi.org/10.1111/j.1526-100X.2009.00544.x

Hayakawa, Y.S., Oguchi, T., Lin, Z., 2008. Comparison of new and existing global digital elevation models: ASTER G-DEM and SRTM-3. Geophys. Res. Lett. 35, 2008GL035036. https://doi.org/10.1029/2008GL035036

Hayek, L.-A.C.; Buzas, M.A. Surveying Natural Populations: Quantitative Tools for Assessing Biodi-versity; Columbia University Press: New York, NY, USA, 2010; ISBN 978-0-231-14620-3

Heiniger, U., Rigling, D., 1994. Biological control of Chestnut blight in Europe. Annu. Rev. Phytopathol. 32, 581–599. https://doi.org/10.1146/annurev.py.32.090194.003053

Hengl, T.; De Jesus, J.M.; MacMillan, R.A.; Batjes, N.H.; Heuvelink, G.B.M.; Ribeiro, E.; Samuel-Rosa, A.; Kempen, B.; Leenaars, J.G.B.; Walsh, M.G.; et al. SoilGrids1km—Global Soil Information Based on Automated Mapping. PLoS ONE 2014, 9, e105992. https://doi.org/10.1371/journal.pone.0105992

Hijmans, R. Raster package in R, The Comprehensive R Archive Network, 2023. p.172. Available online: https://rspatial.org/raster (accessed on 8 February 2022).

Hijmans, R.J. Cross-Validation of Species Distribution Models: Removing Spatial Sorting Bias and Calibration with a Null Model. Ecology 2012, 93, 679–688. https://doi.org/10.1890/11-0826.1

Howe, H.F.; Estabrook, G.F. On Intraspecific Competition for Avian Dispersers in Tropical Trees. Am. Nat. 1977, 111, 817–832. https://doi.org/10.1086/283216

Hu, J.; Jiang, Z. Predicting the Potential Distribution of the Endangered Przewalski's Gazelle. J. Zool. 2010, 282, 54–63. https://doi.org/10.1111/j.1469-7998.2010.00715.x

Iachan, R. Systematic Sampling: A Critical Review. Int. Stat. Rev. Rev. Int. Stat. 1982, 50, 293. https://doi.org/10.2307/1402499

Jacobs, J. Quantitative Measurement of Food Selection: A Modification of the Forage Ratio and Ivlev's Electivity Index. Oecologia 1974, 14, 413–417. https://doi.org/10.1007/BF00384581

Jarman, R., Moir, A.K., Webb, J., Chambers, F.M., 2017. Sweet Chestnut (Castanea sativa) in Britain: its dendrochronological potential. Arboric. J. 39, 100–124. https://doi.org/10.1080/03071375.2017.1339478

Johansen, J. Pollen Diagrams From the Shetland and Faroe Islands. New Phytol. 1975, 75, 369–387. https://doi.org/10.1111/j.1469-8137.1975.tb01402.x

Jones, C.C., Acker, S.A., Halpern, C.B., 2010. Combining local- and large-scale models to predict the distributions of invasive plant species. Ecol. Appl. 20, 311–326. https://doi.org/10.1890/08-2261.1

Jump, A.S., Peñuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecol. Lett. 8, 1010–1020. https://doi.org/10.1111/j.1461-0248.2005.00796.x

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the earth's land surface areas. Sci. Data 4, 170122. https://doi.org/10.1038/sdata.2017.122

Keleş, S.Ö., Ünal, S., Akan, S., Karadeniz, M., 2024. Chestnut blight (Cryphonectria parasitica (Murr.) Barr) disease incidence and its effect on the morphological and anatomical features of Castanea sativa trees. For. Pathol. 54, e12843. https://doi.org/10.1111/efp.12843

Klisz, M., Jevšenak, J., Prokopuk, Y., Gil, W., Mohytych, V., Puchałka, R., 2022. Coping with Central European climate – xylem adjustment in seven non-native conifer tree species. Dendrobiology 88, 105–123. https://doi.org/10.12657/denbio.088.008

Konstantinidis, P., Tsiourlis, G., Xofis, P., Buckley, G.P., 2008. Taxonomy and ecology of Castanea sativa Mill. forests in Greece. Plant Ecol. 195, 235–256. https://doi.org/10.1007/s11258-007-9323-8

Krebs, P.; Conedera, M.; Pradella, M.; Torriani, D.; Felber, M.; Tinner, W. Quaternary Refugia of the Sweet Chestnut (Castanea sativa Mill.): An Extended Palynological Approach. Veget. Hist. Archaeobot. 2004, 13, 145–160. https://doi.org/10.1007/s00334-004-0041-z

Kurdadze, T. Influence of Competition on Beech Growth in Mtskheta-Mtianeti Region Based on Na-tional Forest Inventory Data; Ilia State University: Tbilisi, GA, USA, 2020.

Kvaratskhelia, R., Gavashelishvili, A., 2025. Common Yew (Taxus baccata) as a climate archive: Reconstructing 200 years of temperature change in Georgia (Caucasus). Dendrochronologia 89, 126285. https://doi.org/10.1016/j.dendro.2024.126285

Kvavadze, E. Identification of Anthropological Landscapes and Human Activity in Georgia in Correla-tion with Holocene Black Sea Level Fluctuations. Earth 2015, 4, 120. https://doi.org/10.11648/j.earth.s.2015040501.32

Lakatos, F., Mirtchev, S., Mehmeti, A., Shabanaj, H., 2014. Manual for visual assessment of forest crown condition (No. ISBN 978-92-5-108641-4). FAO.

Lambers, H., Chapin, F.S., Pons, T.L., 2008. Plant Physiological Ecology. Springer New York, New York, NY. https://doi.org/10.1007/978-0-387-78341-3

Lechowicz, M.J. The Sampling Characteristics of Electivity Indices. Oecologia 1982, 52, 22–30. https://doi.org/10.1007/BF00349007

Loo, J.A., 2009. Ecological impacts of non-indigenous invasive fungi as forest pathogens. Ecological impacts of non-native invertebrates and fungi on terrestrial ecosystems, pp.81-96. https://doi.org/10.1007/978-1-4020-9680-8_6

Luoto, M.; Virkkala, R.; Heikkinen, R.K. The Role of Land Cover in Bioclimatic Models Depends on Spatial Resolution. Glob. Ecol. Biogeogr. 2006, 16, 34–42. https://doi.org/10.1111/j.1466-822X.2006.00262.x

Mahdi Najafpour, M. (Ed.), 2012. Applied Photosynthesis. IntechOpen, Erscheinungsort nicht ermittelbar.

Maldonado, C.; Molina, C.I.; Zizka, A.; Persson, C.; Taylor, C.M.; Albán, J.; Chilquillo, E.; Rønsted, N.; Antonelli, A. Estimating Species Diversity and Distribution in the Era of B Ig D Ata: To What Extent Can We Trust Public Databases? Glob. Ecol. Biogeogr. 2015, 24, 973–984. https://doi.org/10.1111/geb.12326

Maria, B., Udo, S., 2017. Why input matters: Selection of climate data sets for modelling the potential distribution of a treeline species in the Himalayan region. Ecol. Model. 359, 92–102. https://doi.org/10.1016/j.ecolmodel.2017.05.021

Mattioni, C., Cherubini, M., Micheli, E., Villani, F., Bucci, G., 2008. Role of domestication in shaping Castanea sativa genetic variation in Europe. Tree Genet. Genomes 4, 563–574. https://doi.org/10.1007/s11295-008-0132-6

McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark, J.S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G.C., Jackson, R.B., Johnson, D.J., Kueppers, L., Lichstein, J.W., Ogle, K., Poulter, B., Pugh, T.A.M., Seidl, R., Turner, M.G., Uriarte, M., Walker, A.P., Xu, C., 2020. Pervasive shifts in forest dynamics in a changing world. Science 368, eaaz9463. https://doi.org/10.1126/science.aaz9463

Meier, E.S.; Kienast, F.; Pearman, P.B.; Svenning, J.-C.; Thuiller, W.; Araújo, M.B.; Guisan, A.; Zim-mermann, N.E. Biotic and Abiotic Variables Show Little Redundancy in Explaining Tree Species Dis-tributions. Ecography 2010, 33, 1038–1048. https://doi.org/10.1111/j.1600-0587.2010.06229.x

Merow, C.; Smith, M.J.; Silander, J.A. A Practical Guide to MaxEnt for Modeling Species' Distributions: What It Does, and Why Inputs and Settings Matter. Ecography 2013, 36, 1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x

Metreveli, V., Kreft, H., Akobia, I., Janiashvili, Z., Nonashvili, Z., Dzadzamia, L., Javakhishvili, Z., Gavashelishvili, A., 2023. Potential Distribution and Suitable Habitat for chestnut (Castanea sativa). Forests 14, 2076. https://doi.org/10.3390/f14102076

Metreveli, V., Kreft, H., Gavashelishvili, A., 2024. Environmental covariates of chestnut blight (Cryphonectria parasitica) in Georgia (Caucasus). For. Ecol. Manag. 569, 122153. https://doi.org/10.1016/j.foreco.2024.122153

Milgroom, M.G., Cortesi, P., 2004. Biological control of Chestnut blight with hypovirulence: A Critical Analysis. Annu. Rev. Phytopathol. 42, 311–338. https://doi.org/10.1146/annurev.phyto.42.040803.140325

Millar, C.I., Stephenson, N.L., 2015. Temperate forest health in an era of emerging megadisturbance. Science 349, 823–826. https://doi.org/10.1126/science.aaa9933

Ministry of Environmental Protection and Agriculture of Georgia, First national forest inventory in Georgia, Report, 2023, pp-122

Mittermeier, R.A.; Turner, W.R.; Larsen, F.W.; Brooks, T.M.; Gascon, C. Global Biodiversity Conser-vation: The Critical Role of Hotspots. In Biodiversity Hotspots; Zachos, F.E., Habel, J.C., Eds.; Springer: Berlin/Heidelberg, Germany, 2011; pp. 3–22, ISBN 978-3-642-20991-8

Nakhutsrishvili, G. The Vegetation of Georgia (South Caucasus); Springer: Berlin/Heidelberg, Germany, 2013; ISBN 978-3-642-29914-8. https://doi.org/10.1007/978-3-642-29915-5

Newbigin, M.I., 1928. Man, and the forest in Europe: the pre-industrial period. Empire Forestry Journal, 7(2) 209–224

Nie, X., genes involved in the resistance to Cryphonectria parasitica during early disease development in Chinese chestnut. BMC Zhao, S., Hao, Y., Gu, S., Zhang, Y., Qi, B., Xing, Y. and Qin, L., 2023. Transcriptome analysis reveals key Plant Biology, 23(1), p.79. https://doi.org/10.1186/s12870-023-04072-7

Nikinmaa, L., Lindner, M., Cantarello, E., Jump, A.S., Seidl, R., Winkel, G., Muys, B., 2020. Reviewing the Use of Resilience Concepts in Forest Sciences. Curr. For. Rep. 6, 61–80. https://doi.org/10.1007/s40725-020-00110-x

Occurrence data of Castanea sativa, Global Biodiversity Information Facility (GBIF), 2023. Available online: https://doi.org/10.15468/dl.k6d6hn (accessed on 25 February 2023).

Oosthoek, K.J. and Hölzl, R., 2018. Managing Northern Europe's Forests. Histories from the Age of Improvement to the Age of Ecology. berghahn New York–Oxford.

Ortega Rodriguez, D.R., Sánchez-Salguero, R., Hevia, A., Granato-Souza, D., Cintra, B.B.L., Hornink, B., Andreu-Hayles, L., Assis-Pereira, G., Roig, F.A., Tomazello-Filho, M., 2023. Climate variability of the southern Amazon inferred by a multi-proxy tree-ring approach using Cedrela fissilis Vell. Sci. Total Environ. 871, 162064. https://doi.org/10.1016/j.scitotenv.2023.162064

Ouimet, R., Moore, J.-D., 2015. Effects of fertilization and liming on tree growth, vitality and nutrient status in boreal balsam fir stands. For. Ecol. Manag. 345, 39–49. https://doi.org/10.1016/j.foreco.2015.02.032

Parker, G.G., Hill, S.M., Kuehnel, L.A. (1993) Decline of understory American chestnut (Castanea dentata) in a southern Appalachian forest. Can. J. Forest Res., 23, pp. 259-265. https://doi.org/10.1139/x93-035

Phillips, S.J.; Dudík, M. Modeling of Species Distributions with Maxent: New Extensions and a Com-prehensive Evaluation. Ecography 2008, 31, 161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

Poggio, L., De Sousa, L.M., Batjes, N.H., Heuvelink, G.B.M., Kempen, B., Ribeiro, E., Rossiter, D., 2021. SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. SOIL 7, 217–240. https://doi.org/10.5194/soil-7-217-2021

Prospero, S.; Lutz, A.; Tavadze, B.; Supatashvili, A.; Rigling, D. Discovery of a New Gene Pool and a High Genetic Diversity of the Chestnut Blight Fungus Cryphonectria Parasitica in Caucasian Georgia. Infect. Genet. Evol. 2013, 20, 131–139. https://doi.org/10.1016/j.meegid.2013.08.009

Quinn, J. Gatekhili Mountains, Gatekhili State: Fractured Alpine Forest Governance and Post-Soviet Development in the Republic of Georgia. Rga 2017. 105, 1–14. https://doi.org/10.4000/rga.3619

R Core Team (2023). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

R Core Team, 2016. The R Project for Statistical Computing.

Rahman, I.U.; Afzal, A.; Iqbal, Z.; Abd_Allah, E.F.; Alqarawi, A.A.; Calixto, E.S.; Ali, N.; Ijaz, F.; Kausar, R.; Alsubeie, M.S.; et al. Role of Multivariate Approaches in Floristic Diversity of Manoor Valley (Himalayan Region), Pakistan. Appl. Ecol. Env. Res. 2019, 17, 1475–1498. https://doi.org/10.15666/aeer/1702_14751498

Rankin, W. H. 1914. Field studies on the Endothia canker of chestnut in New York state. Phytopathology 4: 233-261.

Rashid, M.H.U., Li, Y., Farooq, T.H., Ahmad, I., Nawaz, M.F., Sohail, M., Wu, P., 2024. Influence of Cambium Mechanism in Plantsin Relation to Different Environmental Stresses. Pol. J. Environ. Stud. 33, 503–514. https://doi.org/10.15244/pjoes/171578

Reinmann, A.B., Susser, J.R., Demaria, E.M.C., Templer, P.H., 2019. Declines in northern forest tree growth following snowpack decline and soil freezing. Glob. Change Biol. 25, 420–430. https://doi.org/10.1111/gcb.14420

Rigling, D., Prospero, S., 2018. Cryphonectria parasitica, the causal agent of chestnut blight: invasion history, population biology and disease control. Mol. Plant Pathol. 19, 7–20. https://doi.org/10.1111/mpp.12542

Risteski, M., Milev, M., Rigling, D., Milgroom, M.G., Bryner, S.F., Sotirovski, K., 2013. Distribution of Chestnut blight and diversity of Cryphonectria parasitica in chestnut forests in Bulgaria. For. Pathol. 43, 437–443. https://doi.org/10.1111/efp.12051

Romagnoli, M., Nocetti, M., Sarlatto, M., Evangelistella, L., 2004. Dendrochronological assessment of Chestnut (Castanea sativa) for dating purposes in Central Italy. Dendrochronologia 21, 117–130. https://doi.org/10.1078/1125.7865.00048

Schober, P., Boer, C., Schwarte, L.A., 2018. Correlation Coefficients: Appropriate Use and Interpretation. Anesth. Analg. 126, 1763–1768. https://doi.org/10.1213/ANE.0000000000002864

Serra-Diaz, J.M., Keenan, T.F., Ninyerola, M., Sabaté, S., Gracia, C., Lloret, F., 2013. Geographical patterns of congruence and incongruence between correlative species distribution models and a process-based ecophysiological growth model. J. Biogeogr. 40, 1928–1938. https://doi.org/10.1111/jbi.12142

Sillett, S.C., Van Pelt, R., Koch, G.W., Ambrose, A.R., Carroll, A.L., Antoine, M.E., Mifsud, B.M., 2010. Increasing wood production through old age in tall trees. For. Ecol. Manag. 259, 976–994. https://doi.org/10.1016/j.foreco.2009.12.003

Smith, M.D., Knapp, A.K., 2003. Dominant species maintain ecosystem function with non-random species loss. Ecol. Lett. 6, 509–517. https://doi.org/10.1046/j.1461-0248.2003.00454.x

Solla, A., Dorado, F.J., González, R., Giraldo-Chaves, L.B., Cubera, E., Rocha, G., Martín, C., Martín, E., Cuenca, B., Del Pozo, J.L., Pérez, F., Martín, M.Á., 2024. Chestnut trees (Castanea sativa Mill.) for climate change. Acta Hortic. 273–282. https://doi.org/10.17660/ActaHortic.2024.1400.32

Soria-Auza, R.W., Kessler, M., Bach, K., Barajas-Barbosa, P.M., Lehnert, M., Herzog, S.K., Böhner, J., 2010. Impact of the quality of climate models for modelling species occurrences in countries with poor climatic documentation: a case study from Bolivia. Ecol. Model. 221, 1221–1229. https://doi.org/10.1016/j.ecolmodel.2010.01.004

Spina, S., Romagnoli, M., 2010. Characterization of ring shake defect in Chestnut (Castanea sativa) wood in the Lazio Region (Italy). Forestry 83, 315–327. https://doi.org/10.1093/forestry/cpq014

Suvanto, S., Henttonen, H.M., Nöjd, P., Helama, S., Repo, T., Timonen, M., Mäkinen, H., 2017. Connecting potential frost damage events identified from meteorological records to radial growth variation in Norway spruce and Scots pine. Trees 31, 2023–2034. https://doi.org/10.1007/s00468-017-1590-y

Tarkhnishvili, D.; Gavashelishvili, A.; Mumladze, L. Palaeoclimatic Models Help to Understand Current Distribution of Caucasian Forest Species: Modeling West Asian Forest Refugia. Biol. J. Linn. Soc. 2012, 105, 231–248. https://doi.org/10.1111/j.1095-8312.2011.01788.x

Tarkhnishvili, D.N. Historical Biogeography of the Caucasus; Wildlife protection, destruction and extinction; Nova Publishers: New York, NY, USA, 2014; ISBN 978-1-63321-910-6

Tavadze, B., Supatashvili, A., Rigling, D., Sotirovski, K., Mamukashvili, T.I., Chitia, S. T, S.T., 2013. Pathological status of Chestnut stands in Georgia. Annals of Agrarian Science 11, 107–110

Thomas, S.C., 2011. Age-Related Changes in Tree Growth and Functional Biology: The Role of Reproduction, in: Meinzer, F.C., Lachenbruch, B., Dawson, T.E. (Eds.), Size- and Age-Related Changes in Tree Structure and Function, Tree Physiology. Springer Netherlands, Dordrecht, pp. 33–64. https://doi.org/10.1007/978-94-007-1242-3_2

Thuiller, W.; Richardson, D.M.; Pyšek, P.; Midgley, G.F.; Hughes, G.O.; Rouget, M. Niche-based Modelling as a Tool for Predicting the Risk of Alien Plant Invasions at a Global Scale. Glob. Chang. Biol. 2005, 11, 2234–2250. https://doi.org/10.1111/j.1365-2486.2005.001018.x

Tielidze, L.G., Wheate, R.D., 2018. The Greater Caucasus Glacier Inventory (Russia, Georgia and Azerbaijan). The Cryosphere 12, 81–94. https://doi.org/10.5194/tc-12-81-2018

Tindall, J.R., Gerrath, J.A., Melzer, M., McKendry, K., Husband, B.C., Boland, G.J., 2004. Ecological status of American chestnut (Castanea dentata) in its native range in Canada. Can. J. For. Res. 34, 2554–2563. https://doi.org/10.1139/x04-145

Triviño, M., Potterf, M., Tijerín, J., Ruiz-Benito, P., Burgas, D., Eyvindson, K., Blattert, C., Mönkkönen, M., Duflot, R., 2023. Enhancing Resilience of Boreal Forests Through Management Under Global Change: a Review. Curr. Landsc. Ecol. Rep. 8, 103–118. https://doi.org/10.1007/s40823-023-00088-9

Tugushi, L. Chestnut forests of Abkhazia and ways to improve them, Forest Institute of Tbilisi, PhD thesis, Ochamchire, 1965, 150, 33-37

Urbisz, A.; Urbisz, A. European Chestnut (Castanea sativa Mill.)-a Tree Naturalized on the Baltic Sea Coast? Pol. J. Ecol. 2007, 55, 175–179

Van Drunen, S.G., McCune, J.L., Husband, B.C., 2018. Distribution and environmental correlates of fungal infection and host tree health in the endangered American chestnut in Canada. For. Ecol. Manag. 427, 60–69. https://doi.org/10.1016/j.foreco.2018.05.051

VanDerWal, J.; Shoo, L.P.; Graham, C.; Williams, S.E. Selecting Pseudo-Absence Data for Presence Only Distribution Modeling: How Far Should You Stray from What You Know? Ecol. Model. 2009, 220, 589–594. https://doi.org/10.1016/j.ecolmodel.2008.11.010

Velizarova, E., 2015. Physico-Chemical and Morphological Properties of Soils in Chestnut (Castanea sativa Mill.) Habitats of Belasitsa Mountain. Silva Balcanica 60–70

Veloz, S.D. Spatially Autocorrelated Sampling Falsely Inflates Measures of Accuracy for Presence-Only Niche Models. J. Biogeogr. 2009, 36, 2290–2299. https://doi.org/10.1111/j.1365-2699.2009.02174.x

Venanzi, R.; Picchio, R.; Piovesan, G. Silvicultural and Logging Impact on Soil Characteristics in Chestnut (Castanea sativa Mill.) Mediterranean Coppice. Ecol. Eng. 2016, 92, 82–89. https://doi.org/10.1016/j.ecoleng.2016.03.034

Vera, F.W.M.; Bakker, E.S.; Olff, H. Large Herbivores: Missing Partners of Western European Light-demanding Tree and Shrub Species? In Large Herbivore Ecology, Ecosystem Dynamics and Con-servation; Danell, K., Bergström, R., Duncan, P., Pastor, J., Eds.; Cambridge University Press: Cam-bridge, UK, 2006; pp. 203–231, ISBN 978-0-521-83005-8

Verburg, P.H., Neumann, K., Nol, L., 2011. Challenges in using land use and land cover data for global change studies. Glob. Change Biol. 17, 974–989. https://doi.org/10.1111/j.1365-2486.2010.02307.x

Vettraino, A.M.; Morel, O.; Perlerou, C.; Robin, C.; Diamandis, S.; Vannini, A. Occurrence and Dis-tribution of Phytophthora Species in European Chestnut Stands, and Their Association

with Ink Disease and Crown Decline. Eur. J. Plant Pathol. 2005, 111, 169–180. https://doi.org/10.1007/s10658-004-1882-0

Vlachou, M., Kakavas, K., Birbilis, D., Chavenetidou, M., 2024. Dendrochronology and genetic diversity through climate change: A critical review of Sweet Chestnut. E3S Web Conf. 585, 03002. https://doi.org/10.1051/e3sconf/202458503002

Waldboth, M., Oberhuber, W., 2009. Synergistic effect of drought and Chestnut blight (Cryphonectria parasitica) on growth decline of European chestnut (Castanea sativa). For. Pathol. 39, 43–55. https://doi.org/10.1111/j.1439-0329.2008.00562.x

Waring, R.H., Running, S.W., 2007. Forest ecosystems: analysis at multiple scales, 3rd ed. ed. Elsevier/Academic Press, Amsterdam; Boston.

Warnes, G.R.; Bolker, B.; Lumley, T.; Warnes, M.G.R. Package ' Gtools', The Comprehensive R Archive Network, R Package version, 3(1), 2021. Available online: https://github.com/r-gregmisc/gtools (ac-cessed on 05 April 2022).

Weston, S., 2022a. doParallel: Foreach Parallel Adaptor for the "parallel" Package.

Weston, S., 2022b. foreach: Provides Foreach Looping Construct.

Wood, S.N., 2011. Fast Stable Restricted Maximum Likelihood and Marginal Likelihood Estimation of Semiparametric Generalized Linear Models. J. R. Stat. Soc. Ser. B Stat. Methodol. 73, 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

Wood, S.N., Pya, N., Säfken, B., 2016. Smoothing Parameter and Model Selection for General Smooth Models. J. Am. Stat. Assoc. 111, 1548–1563. https://doi.org/10.1080/01621459.2016.1180986

Xie, D.-J., Zhang, F.-X., Wang, C.-J., Wan, J.-Z., 2022. Integrating Different Scales into Species Distribution Models: A Case for Evaluating the Risk of Plant Invasion in Chinese Protected Areas under Climate Change. Appl. Sci. 12, 11108. https://doi.org/10.3390/app122111108

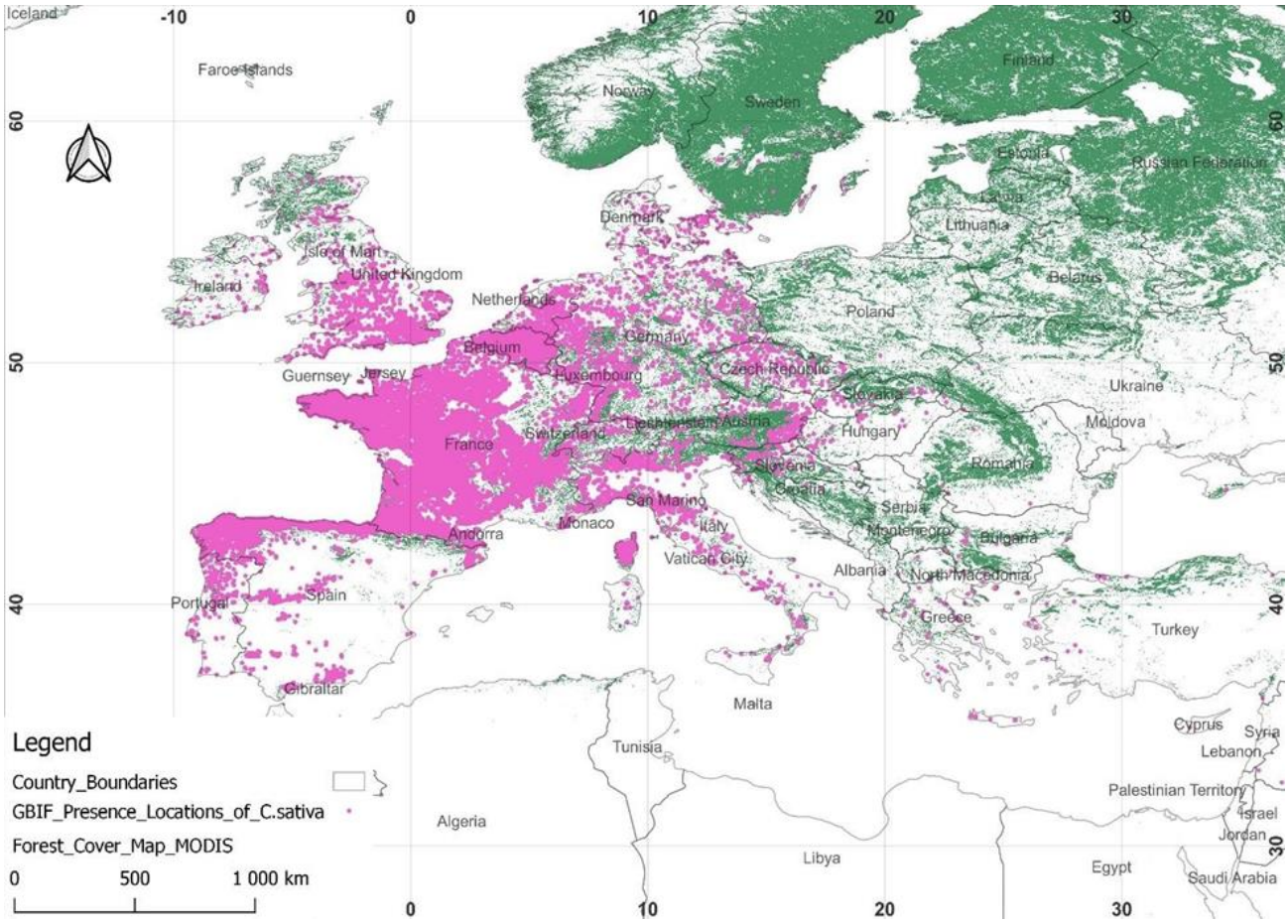
Zachos, F.E., 2011. Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas. Springer Berlin / Heidelberg, Berlin, Heidelberg

Zazanashvili, N.; Mallon, D. Status and Protection of Globally Threatened Species in the Caucasus; CEPF, WWF: Tbilisi, USA, 2009; Volume 232; ISBN 978-9941-0-2203-6

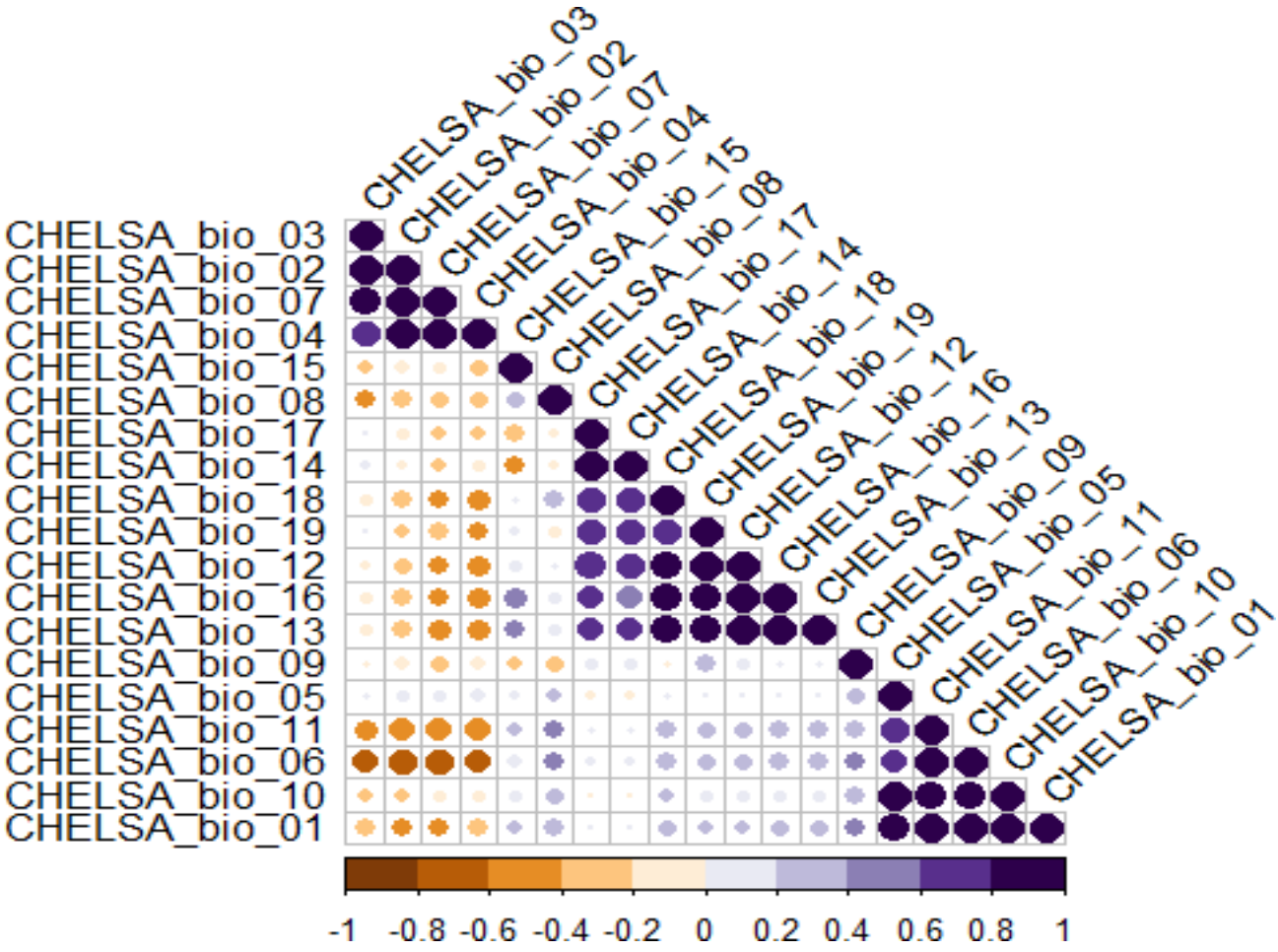
Ziaco, E., Biondi, F., Rossi, S., Deslauriers, A., 2016. Environmental drivers of cambial phenology in Great Basin bristlecone pine. Tree Physiol. 36, 818–831. https://doi.org/10.1093/treephys/tpw006

Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., Svantesson, S., Wengström, N., Zizka, V., Antonelli, A., 2019. COORDINATECLEANER: Standardized cleaning of occurrence records from biological collection databases. Methods Ecol. Evol. 10, 744–751. https://doi.org/10.1111/2041-210X.13152

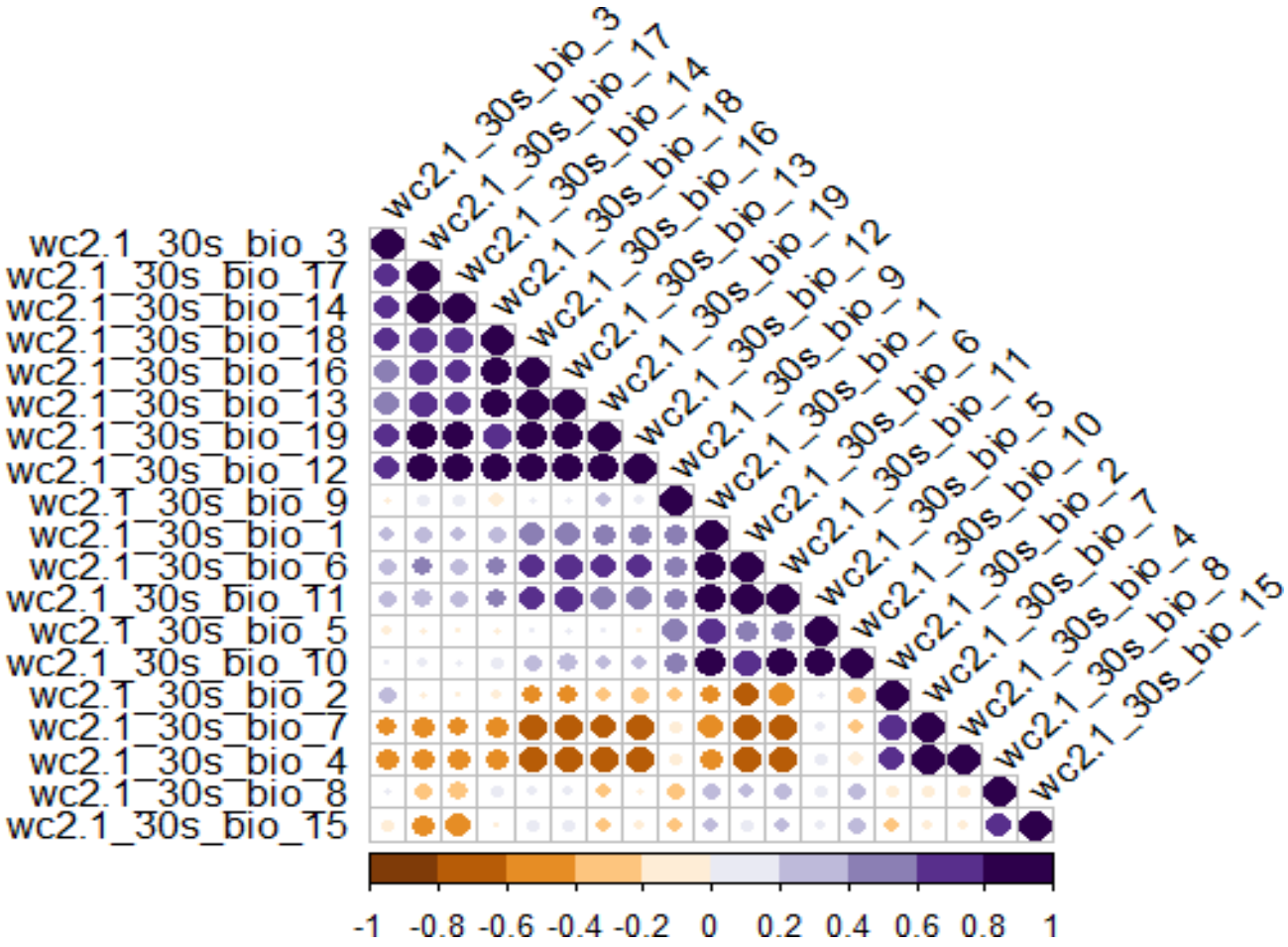
9. Appendices



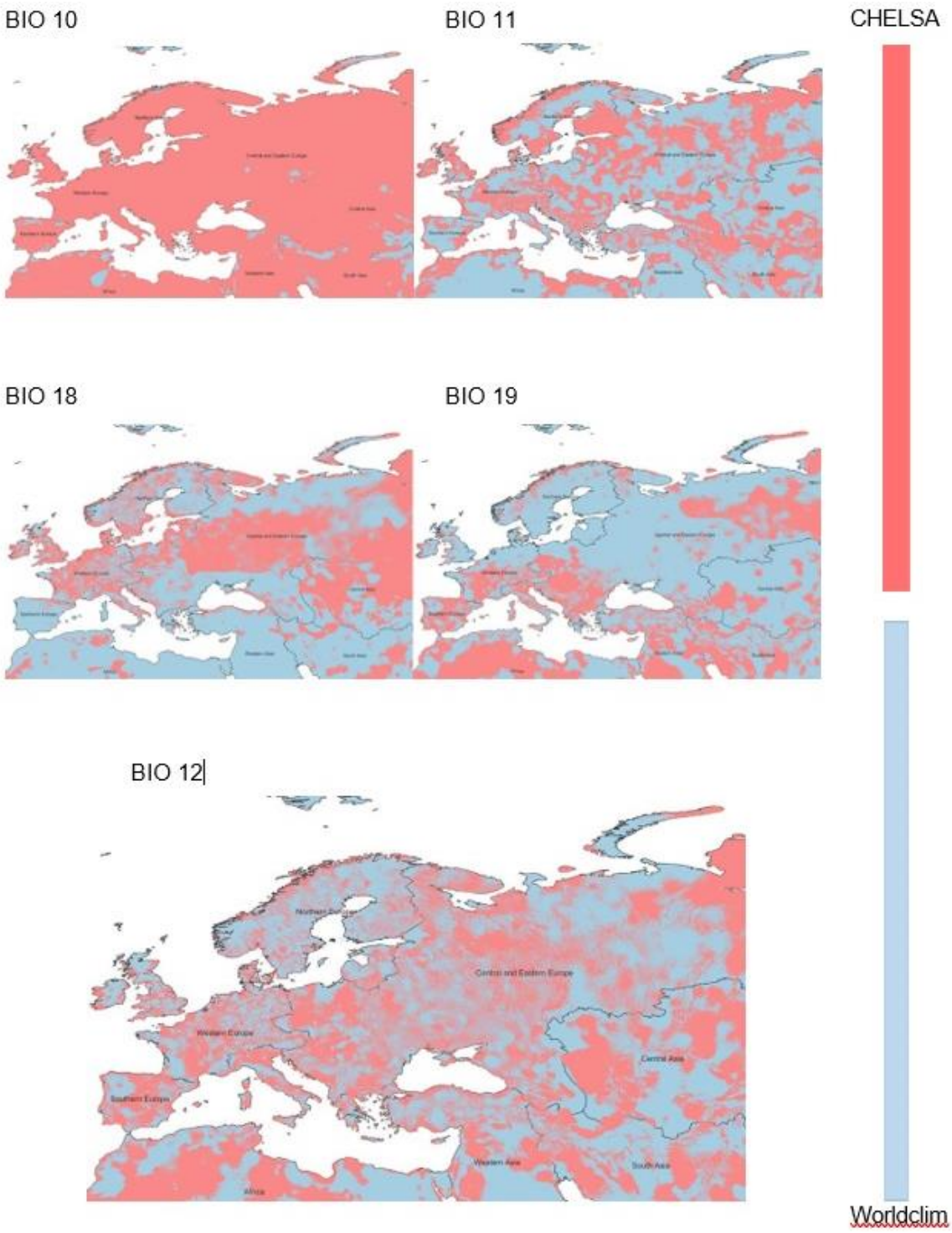
Appendix Figure A1. The map of the GBIF data distribution. The green color represents the forest cover of the Moderate Resolution Imaging Spectroradiometer (MODIS). The pink points are the presence locations of *Ca. sativa* (37954 occurrence points).



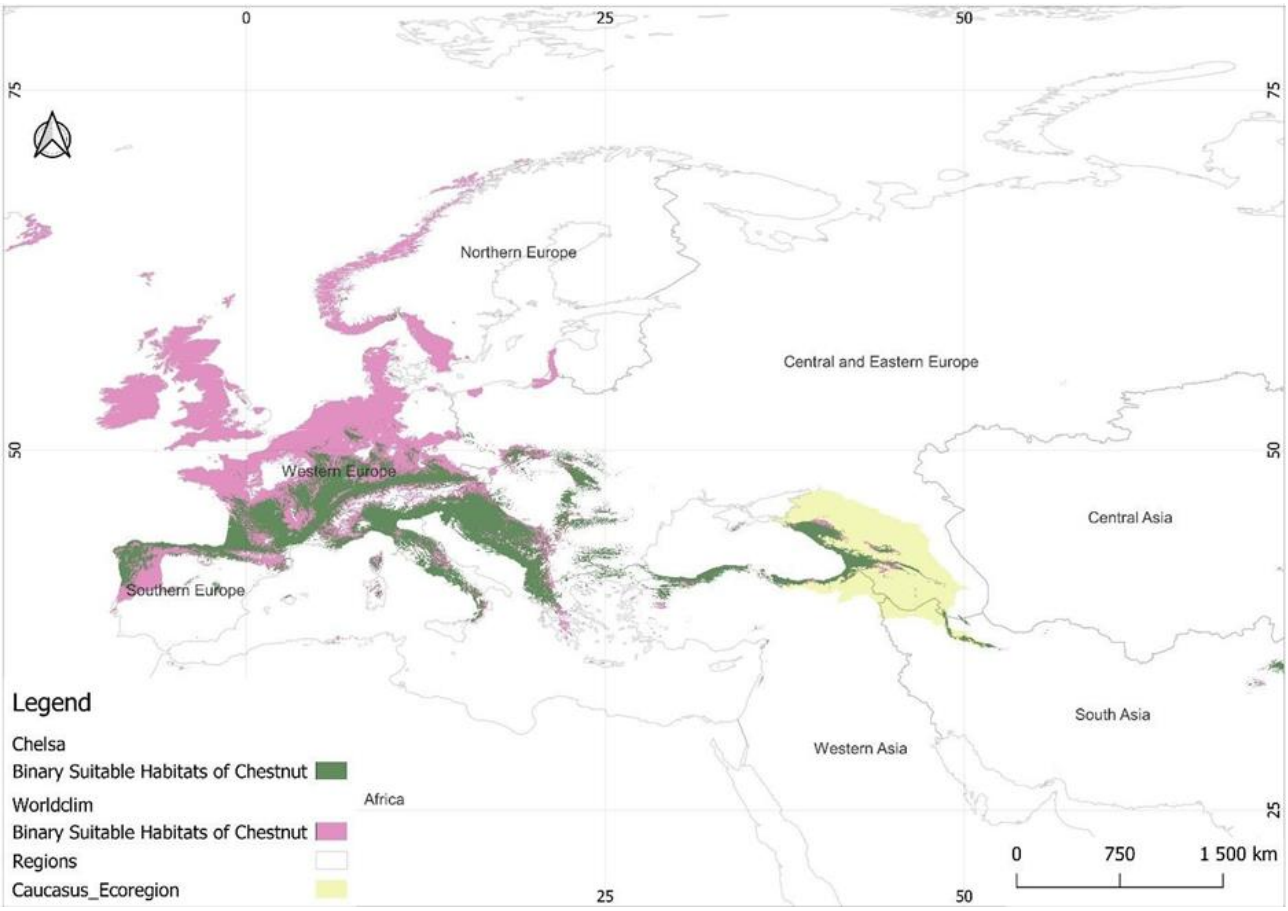
Appendix Figure A2. The figure represents the correlation matrix of CHELSA climate data variables. Positive correlations are illustrated in purple. The negative correlations are represented by the brown color. The correlation coefficients are equal to the size of the circle and the intensity of the color. The legend color on the bottom of the correlogram shows the correlation coefficients and comparable colors. Correlations with p-values greater than 0.05 are considered insignificant. Correlations that are not statistically significant are not displayed in the correlogram.



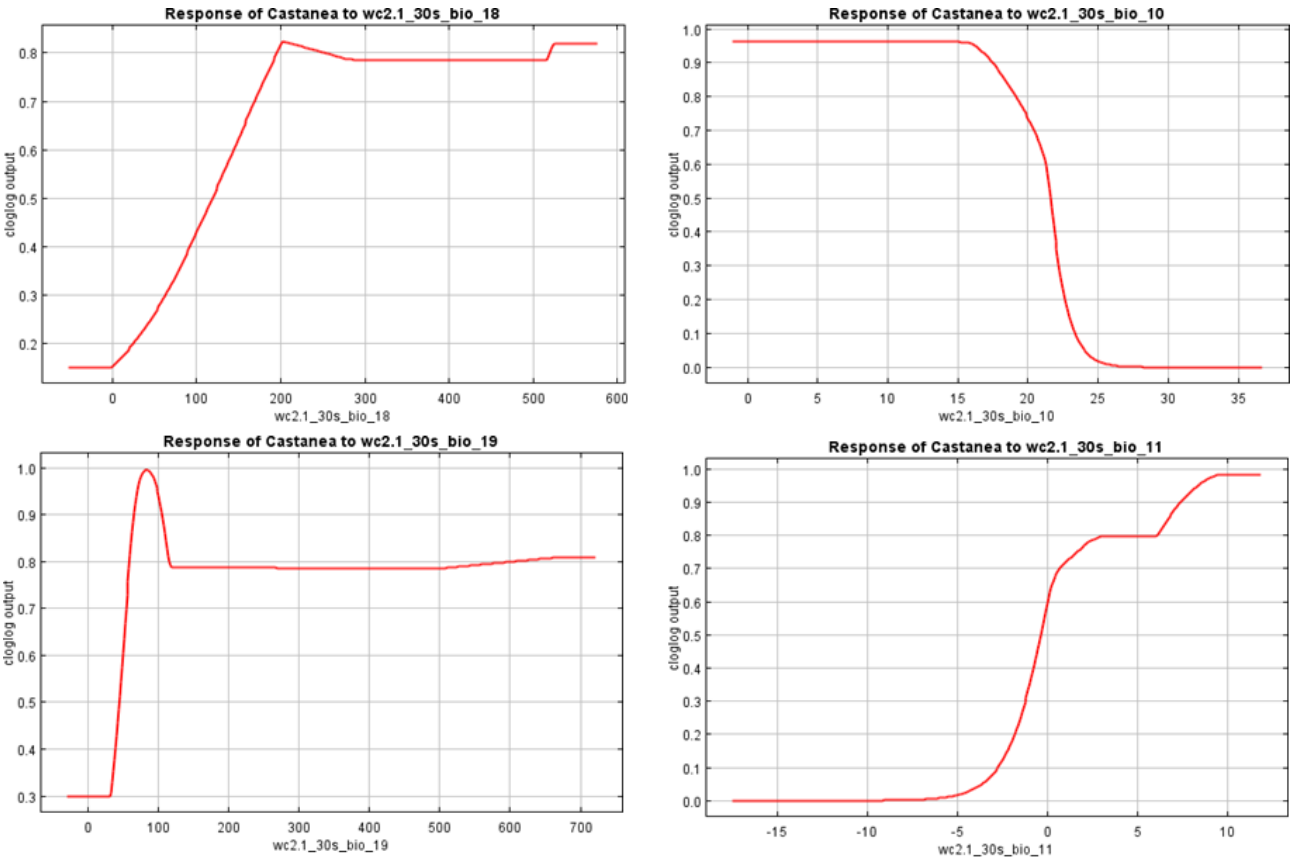
Appendix Figure A3. The figure represents the correlation matrix of WorldClim climate data variables. Positive correlations are illustrated in purple. The negative correlations are represented by the brown color. The correlation coefficients are equal to the size of the circle and the intensity of the color. The legend color on the bottom of the correlogram shows the correlation coefficients and comparable colors. Correlations with p-values greater than 0.05 are considered insignificant. Correlations that are not statistically significant are not displayed in the correlogram.

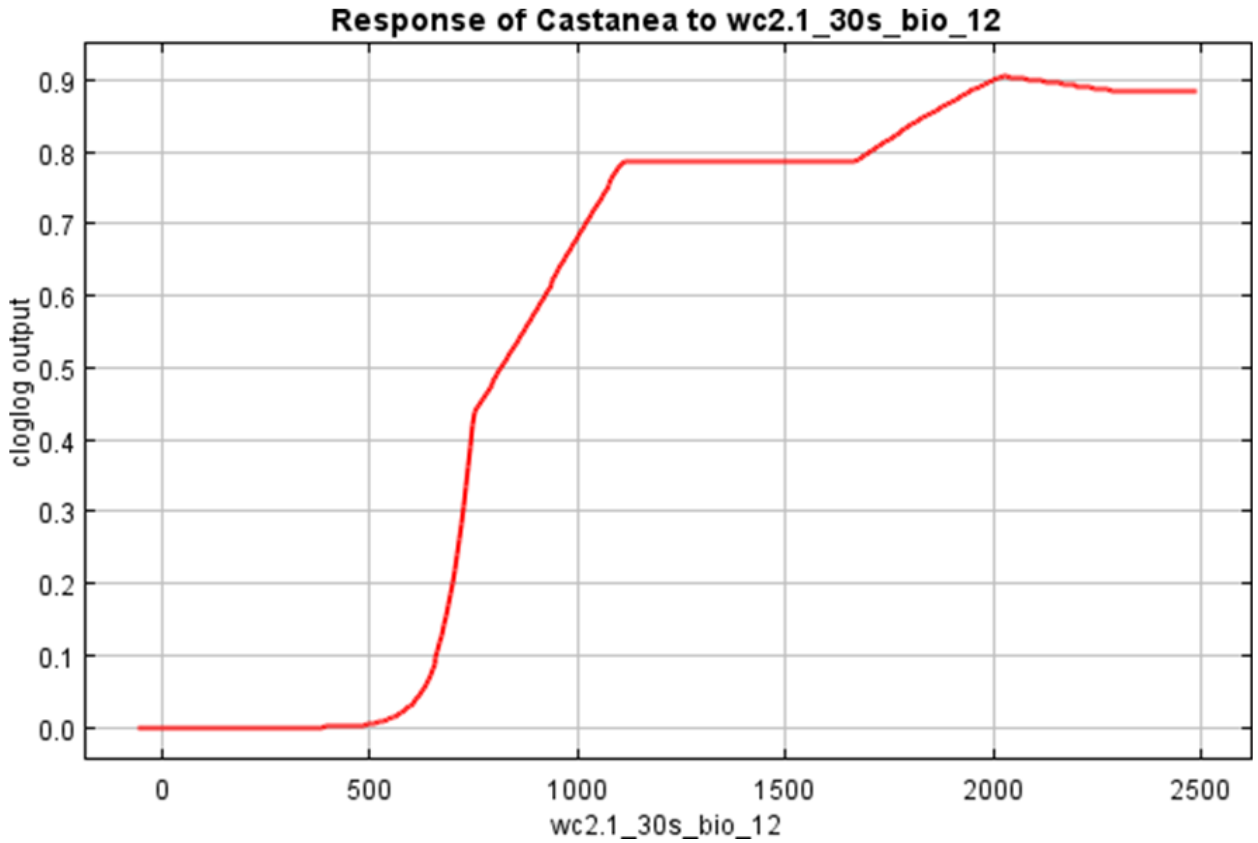


Appendix Figure A4. The figure represents the cell-by-cell subtraction of CHELSA minus WorldClim, showing the differences between the temperature and precipitation variables of these two climate models. The red areas represent the pixels or groups of the pixels where CHELSA values are higher than WorldClim pixel values. The blue areas represent the pixels where WorldClim shows higher values.

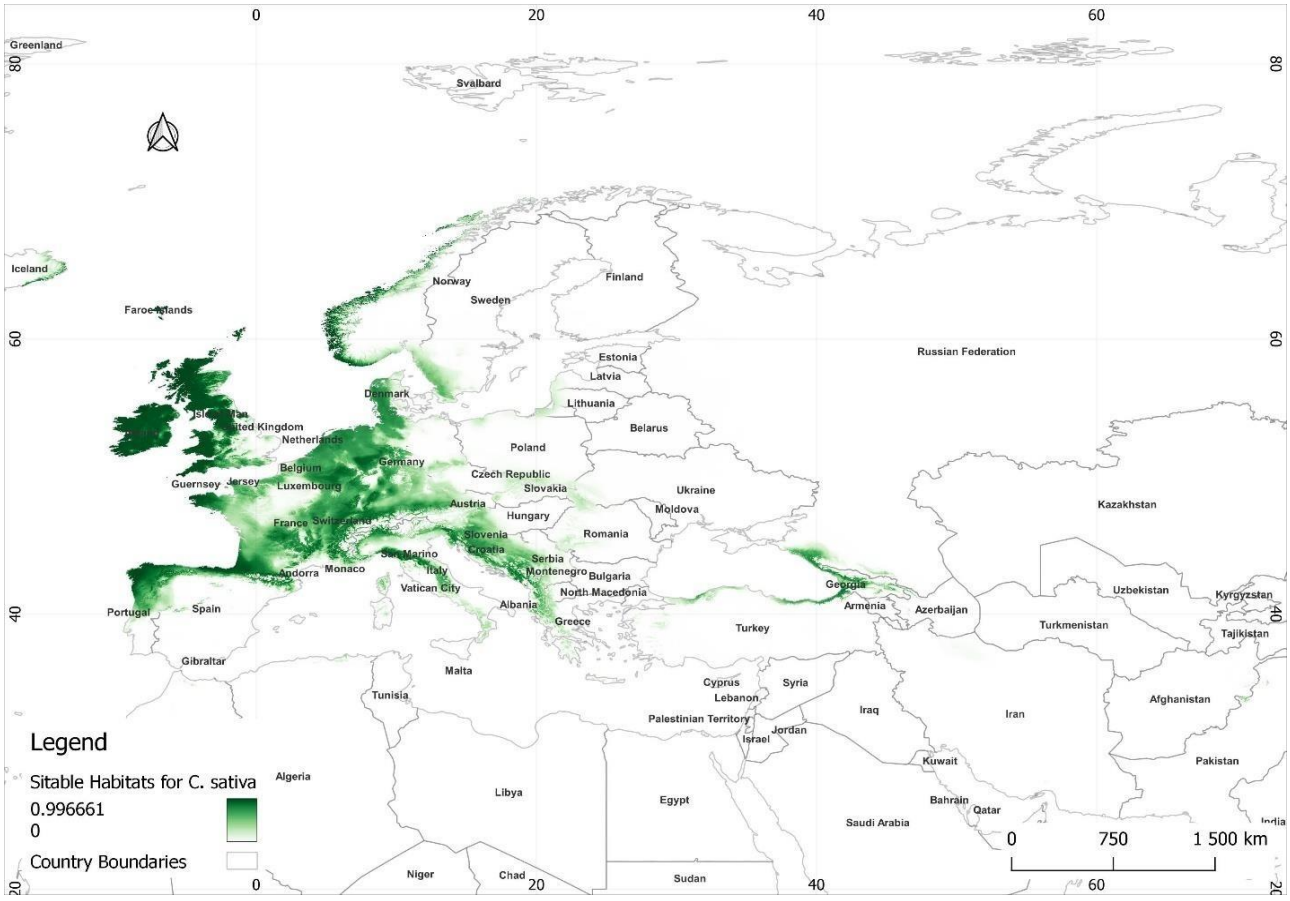


Appendix Figure A5. The Figure shows the differences between the *Ca. sativa* distribution models made by CHELSA and WorldClim climate data. The Green Area represents the model by CHELSA climate data, and the Pink color represents the model done by WorldClim.

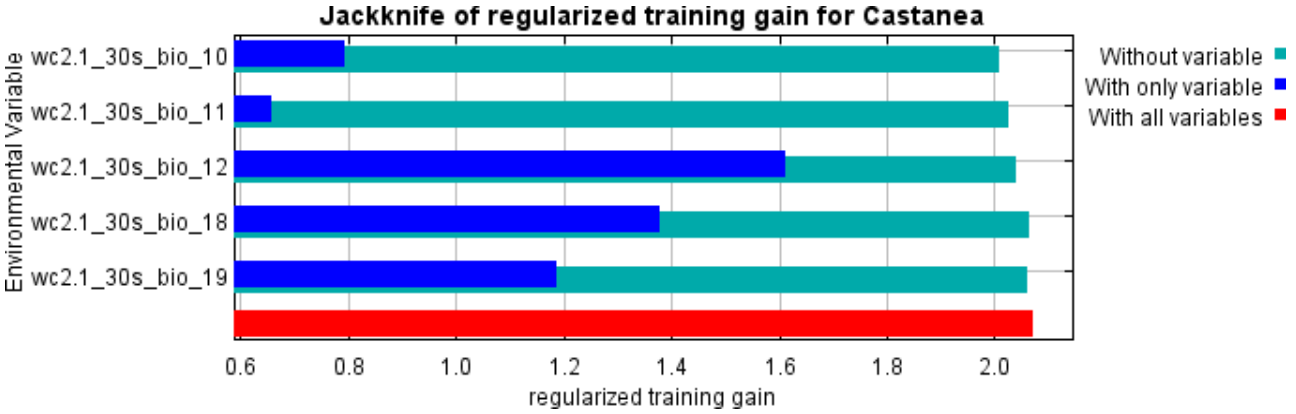




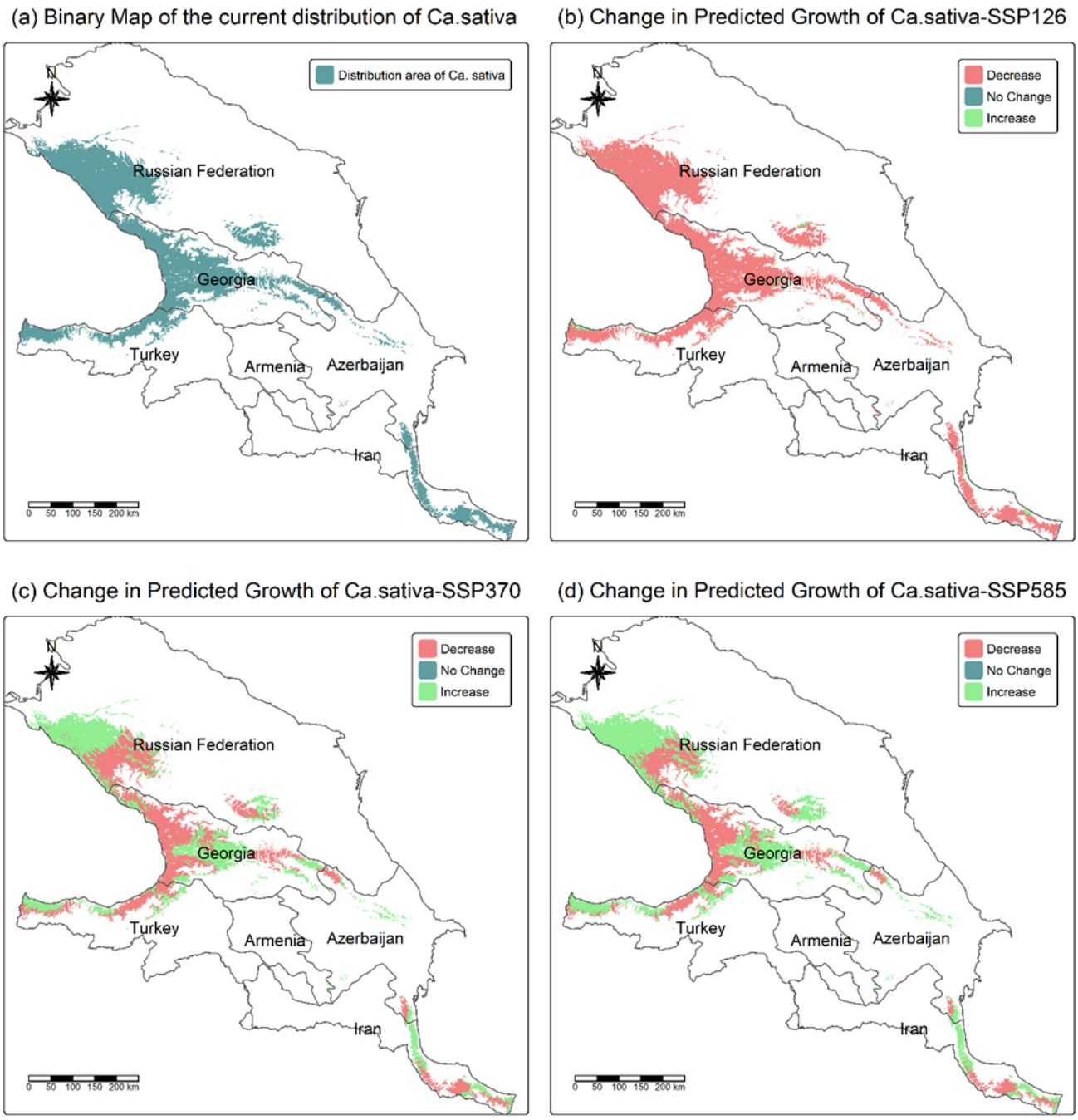
Appendix Figure A6. The response curves of the WorldClim climate variables.



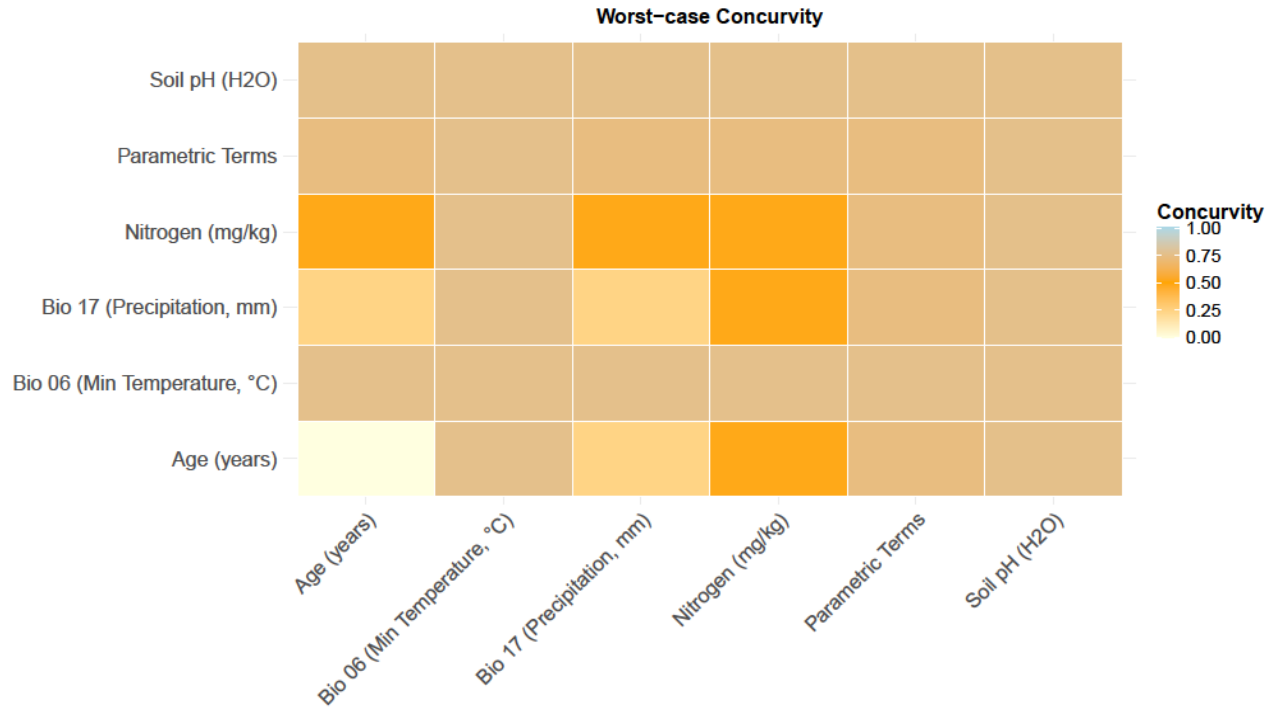
Appendix Figure A7. Representation of the Maxent model for habitat suitability of *Ca. sativa* in the species distribution range done by WorldClim 2 data. Warmer colors show areas with more habitat suitability.



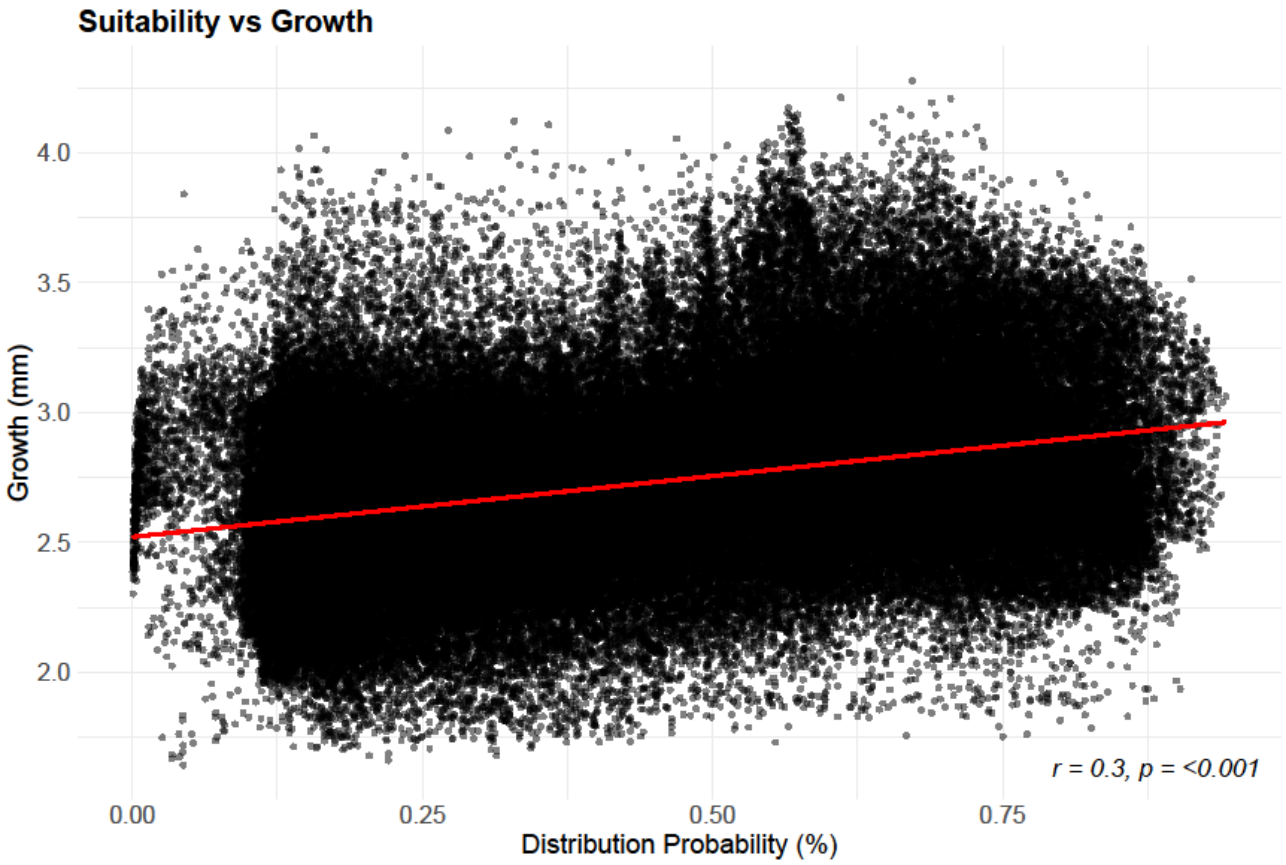
Appendix Figure A8. Contribution graph of the environmental variables in the Mechanistic model done by Worldclim Climate Data.



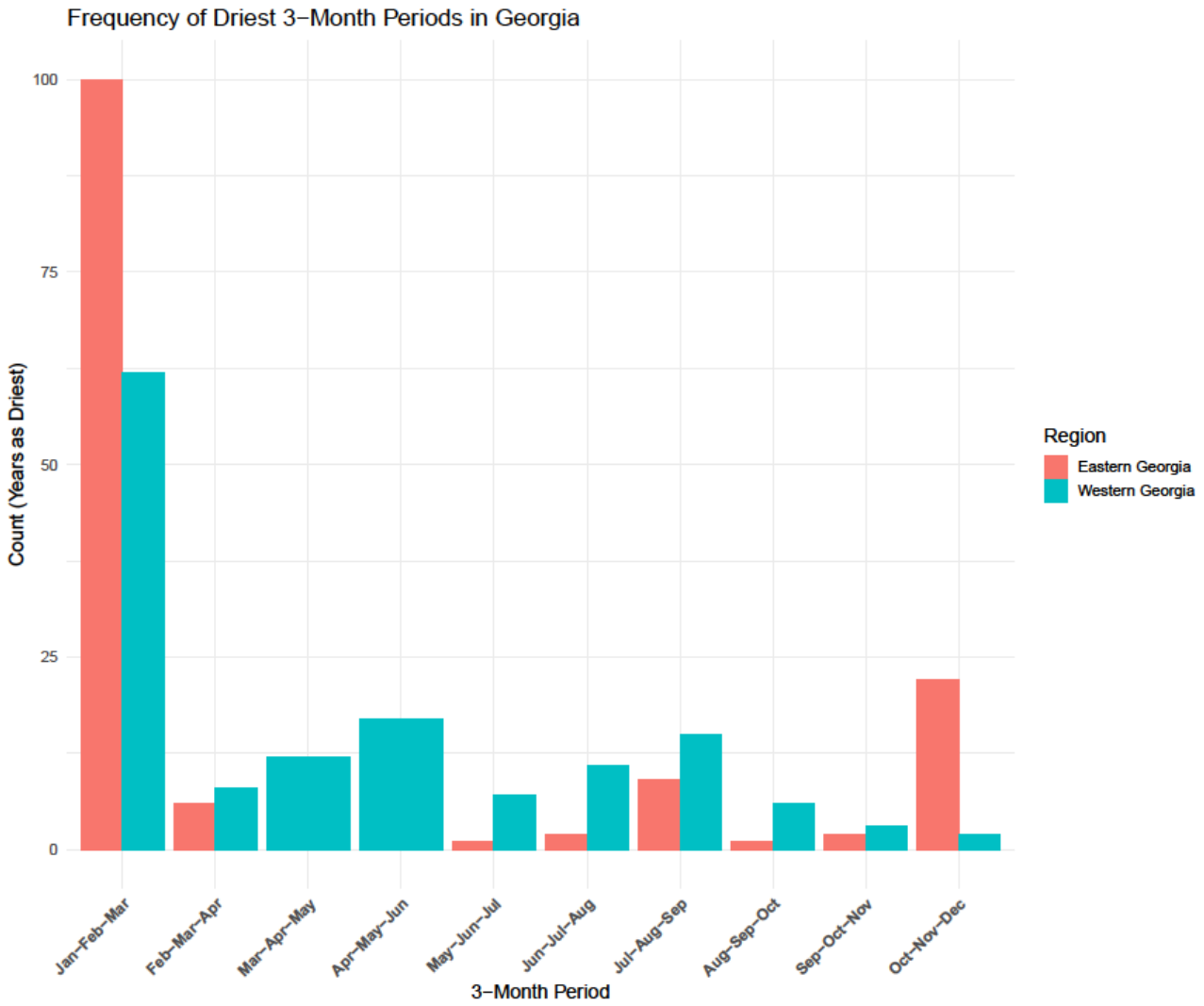
Appendix Figure A9. *Ca. sativa* Growth Prediction (Future vs. Current) in the Caucasus. Panel (a) shows the binary current distribution. In the existing distribution range of *Ca. sativa*, climatic scenarios SSP126, SSP370, and SSP585 affect expected growth. SSP126 reduces growth, especially in central and western locations, with limited peripheral expansion. While similar, SSP370 grows more in northern and marginal locations. SSP585 expects northern and periphery regions to expand, while the centre and southern regions to shrink.



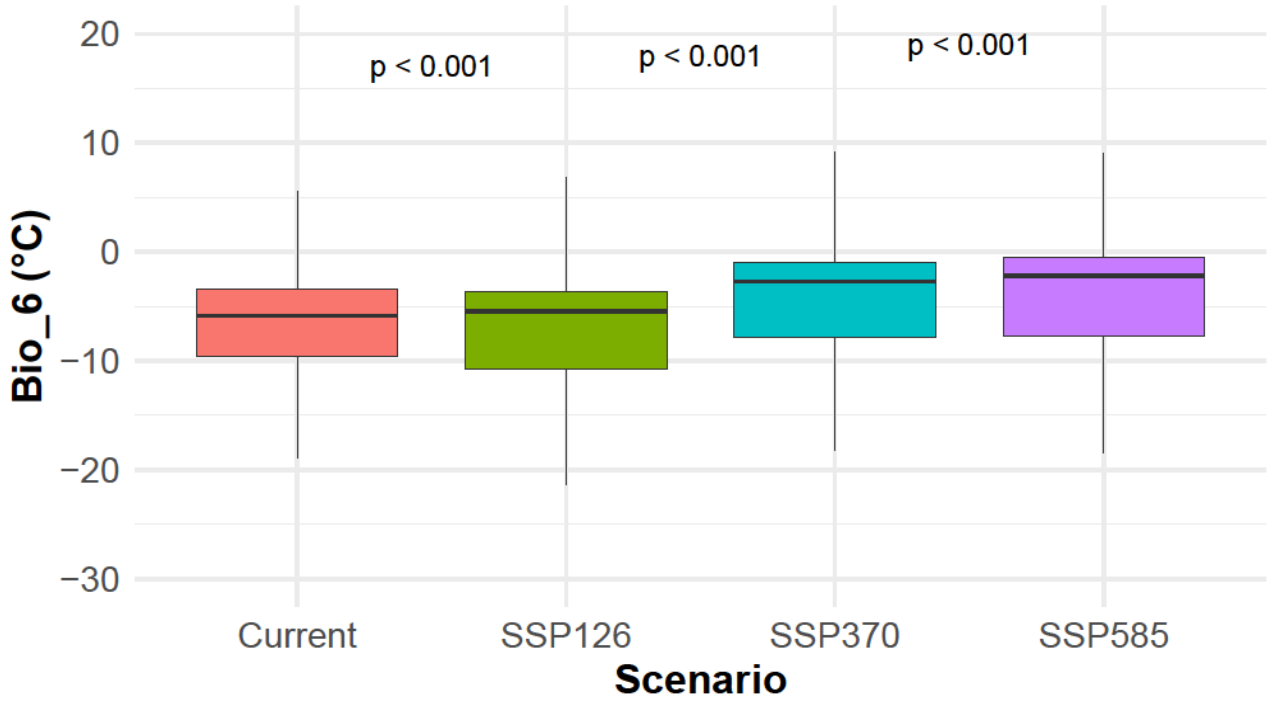
Appendix Figure A10. Diagnostics of concurvity for Generalized Additive Model (GAM) terms. Panels display worst-case concurvity values, indicating how much others can predict each term. Higher values indicate possible redundancy. Age and Bio 17 show minimal concurvity, however Nitrogen and Soil pH display elevated concurvity across estimations. This signifies moderate redundancy among certain predictors, especially soil factors.



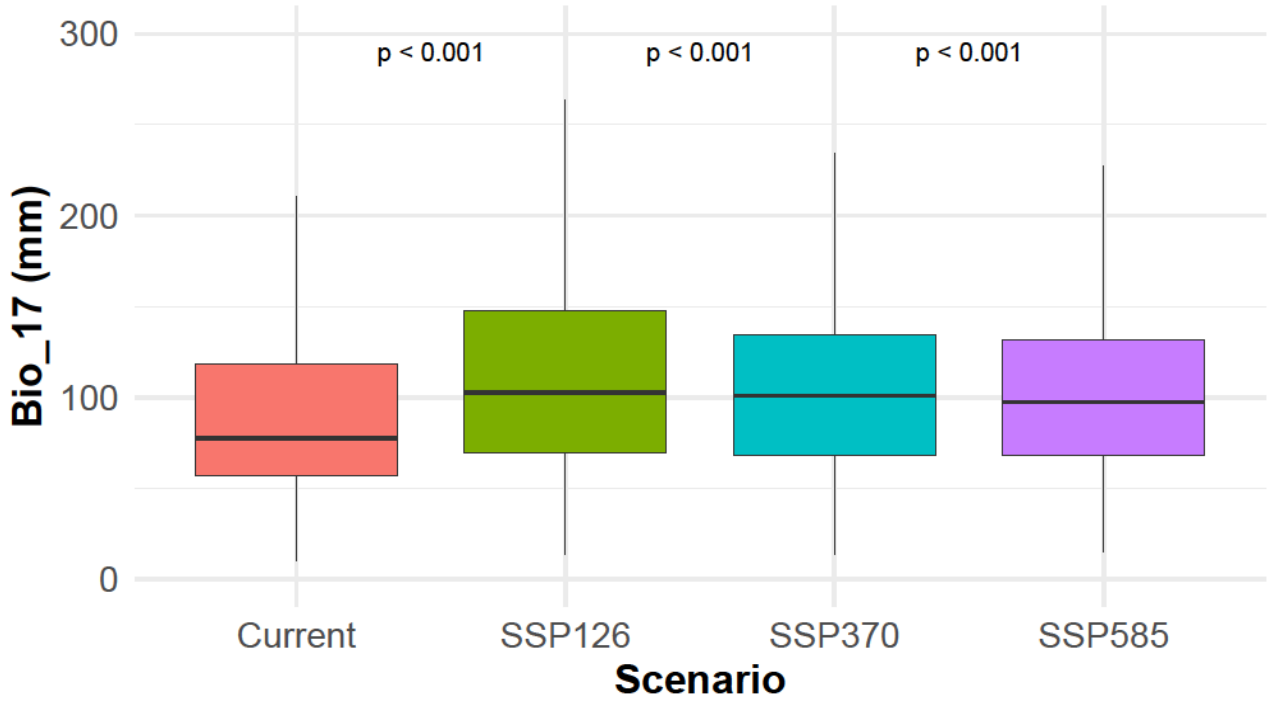
Appendix Figure A11. Relationship between habitat suitability and projected growth of *Ca. sativa* in the Caucasus. The figure illustrates the correlation between habitat suitability (distribution probability, %) and anticipated growth (mm) of *Ca. sativa*. Each point represents a pixel value derived from spatial models. The red line represents a linear regression fit ($r = 0.19$, $p < 0.001$), signifying a weak yet statistically significant positive connection. This suggests that areas with higher predicted suitability only moderately correspond to greater potential growth.



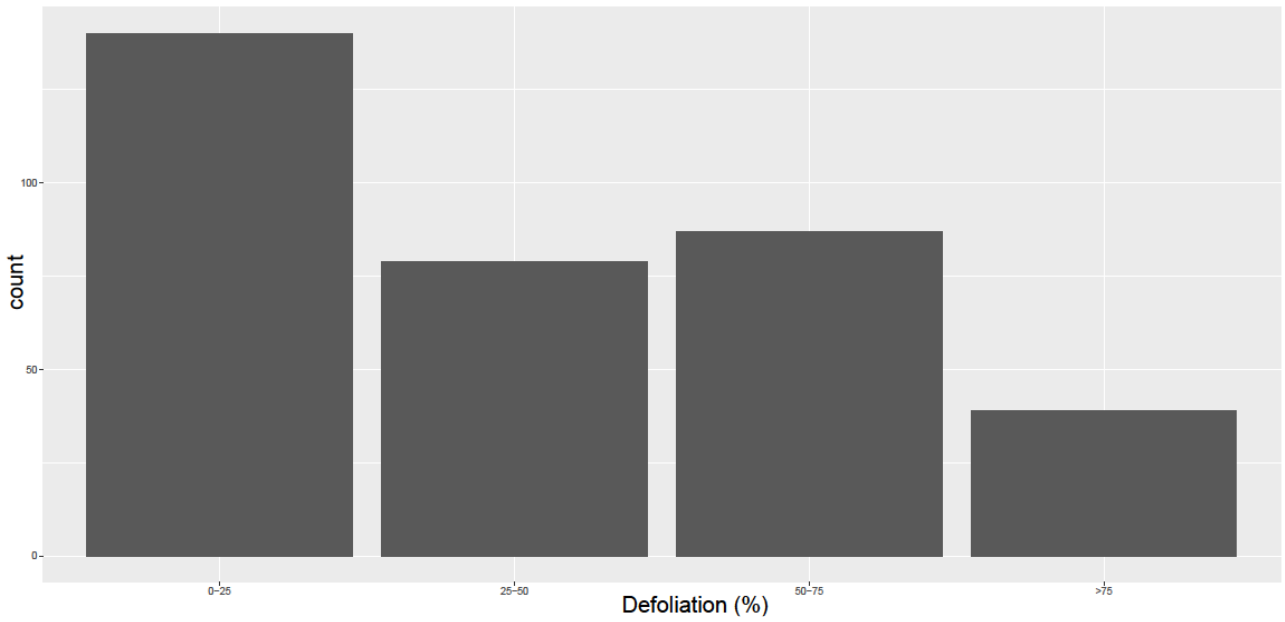
Appendix Figure A12. Frequency of the driest three-month intervals (rolling quarters) in Western and Eastern Georgia. Each bar represents the number of years in which a given 3-month rolling window (e.g., Jan–Feb–Mar, Feb–Mar–Apr) was classified as the driest quarter, determined by median monthly precipitation among meteorological stations in each region. The data indicate that period from January to March was the most frequently driest quarter in both regions, particularly in Eastern Georgia, suggesting consistently low precipitation during late winter. These results reflect distinct seasonal precipitation patterns across the western humid and eastern continental climatic zones of the Georgian Caucasus.



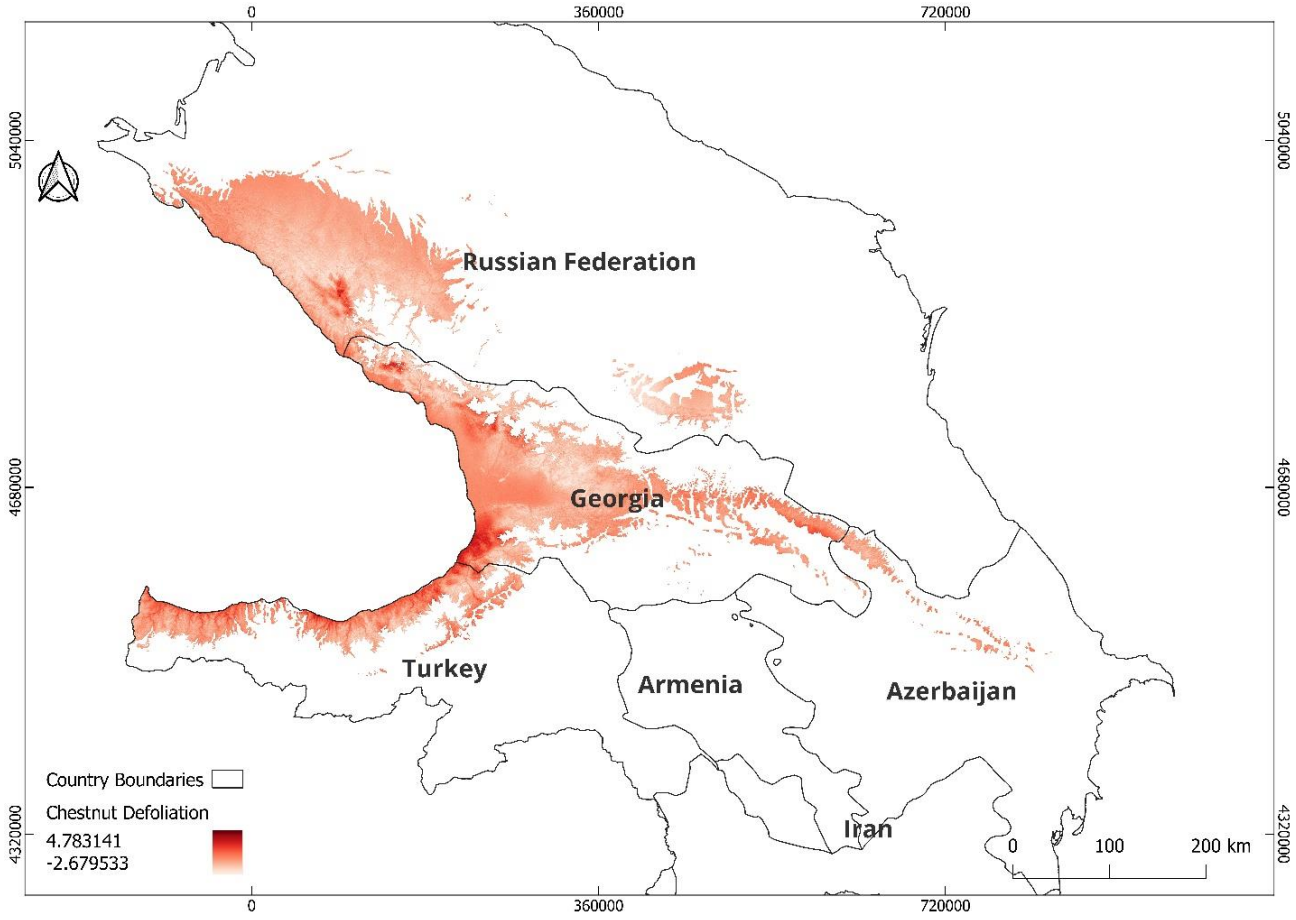
Appendix Figure A13. Boxplot of Bio_6 (Minimum Temperature of Coldest Month, °C) for present and future climatic scenarios (SSP126, SSP370, SSP585). The image illustrates the distribution of Bio_6 values derived from CHELSA climate data for the present time and three prospective SSP scenarios. A statistically significant increase in Bio_6 values is seen in all future scenarios relative to the current environment (Wilcoxon test, $p < 0.001$). SSP126 is seeing little growth. This signifies a persistent warming trend in the coldest month, with the median temperature steadily rising from the present to SSP585.



Appendix Figure A14. Boxplot of Bio_17 (Precipitation during the Driest Quarter, mm) for present and future climatic scenarios (SSP126, SSP370, SSP585). The figure illustrates the distribution of Bio_17 values obtained from CHELSA climate data for both present and future scenarios. All future projections indicate a statistically significant increase in precipitation during the driest quarter relative to the present climate (Wilcoxon test, $p < 0.001$). This suggests a probable transition to more humid circumstances during the driest period of the year. The SSP126 scenario shows the most significant anticipated rise in Bio_17, followed by SSP370 and SSP585.



Appendix Figure A15. Distribution of the severity of defoliation caused by Chestnut blight in 345 forest plots in Georgia.



Appendix Figure A16. Map of the defoliation severity of *Ca. sativa*.

Appendix Table A1. Concurvity of model terms from Generalized Additive Model and between each term and the rest of the model

measure	para	s(slope)	s(aspect)	s(Mean annual air temperature)	s(Annual precipitation)	s(Understory cover)
worst	1.84E-21	0.262	0.317	0.347	0.352	0.271
observed	1.84E-21	0.224	0.141	0.279	0.242	0.225
estimate	1.84E-21	0.203	0.173	0.244	0.200	0.215

worst	para	s.slope	s.aspect	s.Mean annual air temperature	s.Annual precipitation	s.Understory cover
para	1	1.29E-25	1.45E-25	2.19E-27	8.65E-25	1.63E-21
s.slope	1.28E-25	1	0.110	0.107	0.136	0.083
s.aspect	1.45E-25	0.110	1	0.128	0.102	0.127
s.Mean annual air temperature	2.20E-27	0.107	0.128	1	0.216	0.156
s.Annual precipitation	8.73E-25	0.136	0.102	0.216	1	0.096
s.Understory cover	1.63E-21	0.083	0.127	0.156	0.096	1

observed	para	s.slope	s.aspect	s.Mean annual air temperature	s.Annual precipitation	s.Understory cover
para	1	2.04E-33	1.15E-31	1.16E-31	1.19E-28	1.81E-33
s.slope	1.28E-25	1	0.041	0.024	0.109	0.062
s.aspect	1.45E-25	0.019	1	0.022	0.068	0.040
s.Mean annual air temperature	2.20E-27	0.038	0.031	1	0.076	0.048

s.Annual precipitation	8.73E-25	0.096	0.062	0.154	1	0.056
s.Understory cover	1.63E-21	0.044	0.038	0.080	0.042	1

estimate	para	s.slope	s.aspect	s.Mean annual air temperature	s.Annual precipitation	s.Understory cover
para	1	1.92E-28	2.60E-28	3.87E-30	3.11E-27	6.19E-24
s.slope	1.28E-25	1	0.046	0.027	0.061	0.059
s.aspect	1.45E-25	0.024	1	0.028	0.032	0.039
s.Mean annual air temperature	2.20E-27	0.041	0.022	1	0.086	0.045
s.Annual precipitation	8.73E-25	0.082	0.074	0.119	1	0.055
s.Understory cover	1.63E-21	0.035	0.052	0.072	0.025	1