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Climate Extremes, Soils and Topography, and Past and Present Land Use Shape Tree Cover in Central Anatolia (Türkiye)

Rafael E. Bernardi[1] | İsmail Bekar[2] | Mehmet Göktuğ Öztürk[3] | Çağatay Tavşanoğlu[3]

[1]Departamento de Ecología y Gestión Ambiental, CURE, Universidad de la República, Montevideo, Uruguay | [2]Chair of Ecoclimatology, School of Life Sciences, Technical University of Munich, Freising, Germany | [3]Division of Ecology, Department of Biology, Hacettepe University, Ankara, Türkiye

Correspondence: Rafael E. Bernardi (bernardirafael@gmail.com)

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ABSTRACT

Question: Central Anatolia is part of the Irano-Anatonian biodiversity hotspot, encompassing a diverse range of steppe grasslands, shrublands, and forests. Despite their high biodiversity and crucial ecosystem services, its ancient grass or subshrub-dominated steppe and forest-steppe vegetation is often neglected and, in many cases, considered as secondary vegetation resulting from extensive deforestation. However, the conditions that explain the distribution of the ecosystems in this semi-arid region remain poorly understood. Considering recent developments in the understanding of open ecosystems, we aim to understand what explains the distribution of tree cover in Central Anatolia.

Location: Central Anatolia, Türkiye.

Methods: We analyzed the influence of a comprehensive set of variables that shape tree cover distribution obtained from remote sensing and global and local databases. We used regression models to model tree presence and cover, considering the effects of climate, soils, topography, land use, and disturbances.

Results: Tree presence and cover were limited by poor and sodic-saline soils and limited by climate factors, including temperature and precipitation extremes. Trees were more prevalent in mountainous regions and in topographic conditions that enhance local resource availability and provide protection from disturbances and land-use impacts. Trees were also limited by agriculture and livestock density, although their presence increased in the proximity of human settlements.

Conclusions: Our findings indicate that environmental determinants, including climate, soils, topography, and disturbance regimes, shape tree cover in Central Anatolia, questioning the common belief that low tree cover is mainly due to extensive deforestation by humans. Our results have implications for the management and conservation of these ecosystems, particularly with respect to climate change, which could further exacerbate existing constraints on tree growth. Our findings can also inform the conservation efforts of ancient steppe grasslands and forests, as well as contribute to more resilient afforestation strategies.

1 | Introduction

The steppes of Central Anatolia are part of the Irano-Anatonian biodiversity hotspot (Eken, Evans, et al. 2005), and are composed of unique steppe vegetation and forest-steppes. They have a dominant grass layer with different degrees of tree and shrub cover, including isolated trees and open woodlands (Kürschner and Parolly 2012). Sparse forests of black pines (*Pinus nigra*), junipers (*Juniperus* spp.), and oaks (*Quercus* spp.) are found on the Central Anatolian plateau and particularly in the highlands (Ambarlı et al. 2016). The grasslands of Central Anatolia harbor rich biodiversity, including numerous endemic and narrowly distributed plant taxa (Eken, Evans, et al. 2005; Kurt et al. 2006). Unfortunately, many of these biodiversity-rich areas in Central Anatolia do not have protection status (Ambarlı et al. 2016; Eken et al. 2016; Şekercioğlu et al. 2011). This increase the vulnerability of these habitats to land-use pressures and management decisions that overlook their ecological determinants, such as climate and edapho-topographic conditions. Approximately 50% of Central Anatolian grasslands have already been converted to agriculture (Fırıncıoğlu et al. 2007; Kürschner and Parolly 2012). Recent research has highlighted the relevance of old-growth grasslands, enriching our understanding of these ecosystems (Bond 2016; Bond 2019; Parr et al. 2014; Veldman, Buisson, et al. 2015; Veldman, Overbeck, et al. 2015). These open ecosystems have high biodiversity and provide local and global benefits to people, including supporting livestock production, carbon sequestration, water and soil conservation (Bernardi, de Jonge, and Holmgren 2016; Ding and Eldridge 2021; Kühne et al. 2022; Singh et al. 2021). However, they are often undervalued and neglected (Bond 2016; Overbeck et al. 2007; Parr et al. 2014; Veldman, Overbeck, et al. 2015). Several characteristics observed in the grasslands and mixed systems of the steppes and forest-steppes of Central Anatolia align with the features of old-growth grasslands (Bond 2019; Veldman, Buisson, et al. 2015). This includes unique species assemblages absent in secondary grasslands, high diversity in the herbaceous layer including small-scale species richness, persistent bud banks, high clonal growth and resprouting ability (Tavşanoğlu and Bernardi 2024). Furthermore, there is paleoecological evidence suggesting that grass-dominated habitats and grassland–woodland systems were present millions of years ago in Central Anatolia (Akgün et al. 2007; Griffith et al. 2017), and steppe vegetation has persisted in Central Anatolia during the Holocene, at least since the last glacial maximum (Şenkul et al. 2018; Turner et al. 2010). Climatic changes during the Holocene have driven vegetation shifts in Central Anatolia from open steppe habitats to open woodlands and vice versa (Oybak-Dönmez et al. 2021). However, the Central Anatolian steppe is often considered as secondary vegetation resulting from deforestation for agriculture or the loss of its primary vegetation due to centuries of grazing (Kurt et al. 2006; Kürschner and Parolly 2012). This perception of steppes as secondary vegetation is widespread in many Eurasian countries (Erdős et al. 2019) and globally (Veldman, Buisson, et al. 2015). These conceptions often guide afforestation initiatives aiming to substitute existing grasslands with planted forests and pose a challenge to conserving grasslands or mixed tree-grass systems (Stevens et al. 2022). This is the case of the Central Anatolian steppes, under extensive afforestation efforts (Ayan et al. 2021; Çalişkan and Boydak 2017), which are one of the major threats on biodiversity (Ambarlı et al. 2016).

Despite the ecological importance of these ecosystems and their current threats, the determinants of their distribution in Central Anatolia remain poorly understood (Asouti and Kabukcu 2014). An extensive analysis of the factors that explain the distribution of tree cover of the Central Anatolian steppe and forest-steppe is urgently required for better conservation and management. This is particularly challenging because of the complex interplay of climate and human activities over millennia in this semi-arid region. Central Anatolia is one of the cradles of civilization, where humans have shaped vegetation for thousands of years and, in turn, human activities have been shaped by these ecosystems (Akça and Kapur 2014).

Recent advances in grassland dynamics across continents have improved our knowledge of the distribution of forests, savannas, and grasslands in various tropical and temperate regions. Traditionally, tree cover has been attributed primarily to climate, with early naturalists noting the strong correlation between precipitation, temperature, and biome types (Pausas and Bond 2019). Whittaker (1970) set the early framework to understand the climatic factors (mean precipitation and temperature) that are largely behind the distribution of vegetation, and it is worth noting that he described a climate range where different ecosystems are possible due to fire, soils, or other reasons. Analyses of global remote sensing tree cover data have framed the underdetermination of vegetation in relation to climate as alternative vegetation or biome states (Sankaran et al. 2005; Hirota et al. 2011; Staver et al. 2011; de Dantas et al. 2016; Bond 2019) and proposed strong feedbacks between grasses and fire or herbivory as the main mechanism involved. Large open ecosystems in tropical and subtropical regions can be maintained by feedback mechanisms between disturbances, such as fire and herbivore consumption, and grasses. These feedbacks can maintain grasslands as alternative states even in regions with sufficient precipitation to support closed-canopy forests. In temperate regions, these feedbacks can also sustain open states within the same environmental conditions and are thought to operate in several biomes (Ratajczak et al. 2014; Erdős et al. 2022; Stritih et al. 2023). For example, in other grassy biomes, domestic herbivores have replaced the herbivory of the Pleistocene megafauna as the dominant disturbance regime (Bernardi, Holmgren, et al. 2016). Feedback mechanisms operating may also depend on particular conditions of each region: for example, the effect of fire may be less relevant for arid or semi-arid ecosystems, where livestock can have a stronger role in limiting tree cover (Staal et al. 2018).

Several works have analyzed the factors associated with tree cover and presence in open and mixed ecosystems, to understand what explains woody vegetation and the distribution of ecosystem types across different biomes and regions (Sankaran et al. 2005; Aleman et al. 2017; Pletcher et al. 2022; Biancari et al. 2024). Human-induced global and local change affecting life-supporting ecosystems makes it crucial to examine the vegetation distribution in understudied regions such as the Central Anatolian steppes and the factors that determine it, including the role of wildfire patterns and domestic herbivory as disturbance regimes that shape and maintain open ecosystems (Tavşanoğlu 2017; Bahar and Tavşanoğlu 2024). Understanding the distribution of local vegetation and their potential changes requires taking into account large-scale factors that may operate at the biome level, such as climate and feedback dynamics with disturbance regimes, and how these factors can interact with the local features that determine natural resource availability. For example, topographic features can determine water availability and soil fertility. These conditions can directly and indirectly influence land use and disturbance regimes and mediate the effects of climate (Paganeli and Batalha 2022; Berazategui et al. 2023). These interactions can favor different alternative vegetation states sharply defined at local or subregional scales (Staal et al. 2018; Erdős et al. 2022). These concepts have direct relevance to the Anatolian steppes, challenging existing assumptions and current management strategies that include extensive afforestation efforts.

In this study, we evaluated environmental and human-related factors that the literature suggests influence tree cover. We included climate, topography, soils, land-use dynamics, human activity, and disturbance regimes to examine how they shape vegetation patterns in Central Anatolia. Given the region's semiarid climate and long history of human use, we hypothesized that climatic constraints, local resources, and human pressures are the main determinants of tree presence and cover. Moreover, understanding these constraints is necessary to inform current management and afforestation strategies. Using variables derived from global and local datasets, we developed and compared multiple candidate models to identify which factors best explain tree-cover distribution in the region. Finally, we discuss how these findings can inform the management and conservation of Central Anatolian ecosystems.

2 | Methodology

2.1 | Study Region

Our study region was defined using two WWF Ecoregions (Olson et al. 2001): "Central Anatolian Steppe and Woodlands" and "Central Anatolian Steppe" (Figure 1). These two ecoregions broadly correspond to Central Anatolia and occupy an area of 127.000 km^2. The region has a semi-arid cold climate according to the Koppen classification ("BSk") (Peel et al. 2007), that is, temperate regions with relatively high altitude, typically bordering a Mediterranean climate, with hot summers and cold and usually freezing winters. The mean annual precipitation in the region is ~430 mm (340–670 mm), with a dry season in July–September and the mean temperature is 10°C (5°C–12°C), with a minimum monthly temperature around January and a maximum in August (Fick and Hijmans 2017). Extremely cold temperatures and drought periods are frequent. Steppes extend across a dry central plateau and in tectonic depressions, with sparse woodlands and shrubs. There are sparse forests of pine (*Pinus nigra*), junipers (*Juniperus* spp.), and oaks (*Quercus* spp.), particularly in mountainous regions. Intensive and extensive cattle and sheep livestock are widespread, and large areas have been converted to agriculture, mainly for cereal production. The region has very few protected areas.

2.2 | Data

We used 33 topographic, climatic, soil, disturbance, and anthropogenic variables from various sources, each with different data formats and resolutions (Table 1, Figure 2, Appendix S1). These variables are well known as determinants of tree presence or cover in different parts of the world and provide good proxies for factors that determine the distribution of ecosystems. For example, climate is a well-known determinant of vegetation types in many parts of the world (Whittaker 1970). In particular, precipitation is a determinant of tree cover, and seasonality is known to influence tree cover in the tropics

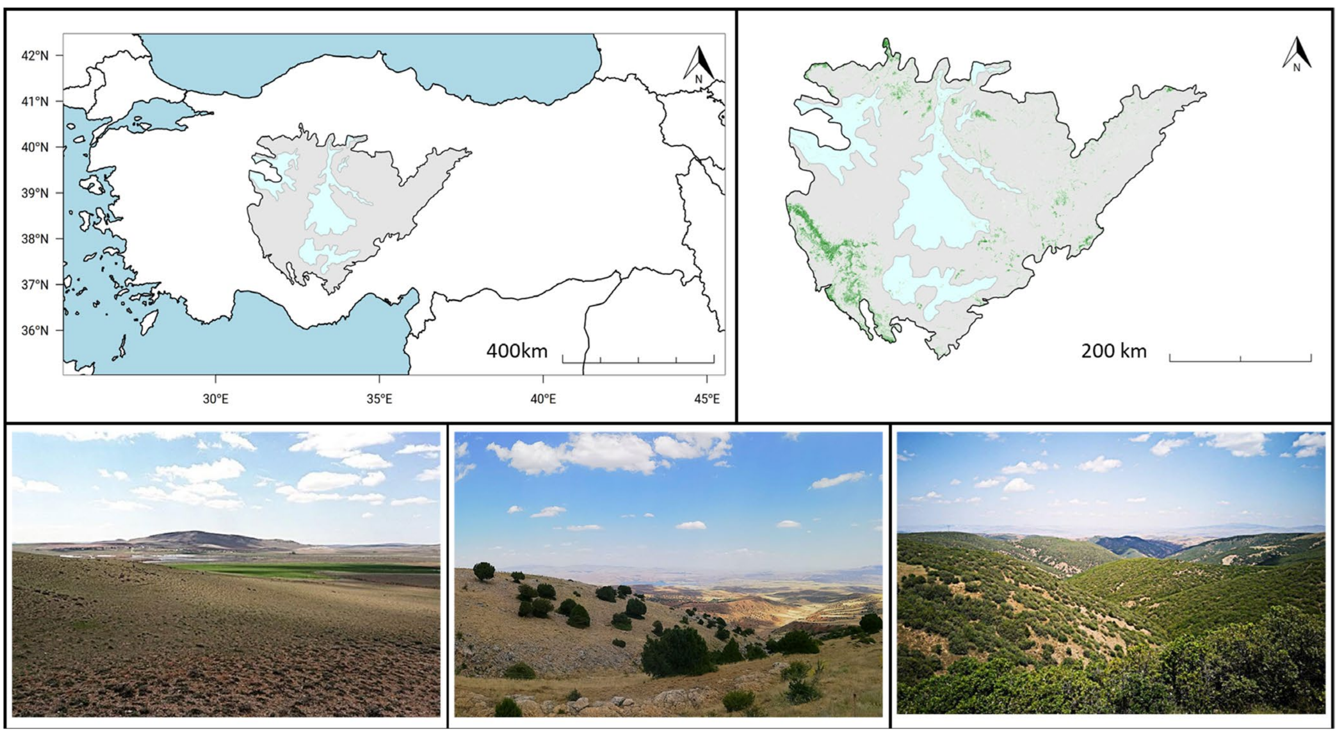

FIGURE 1 | Top: Map of Türkiye with region of study, and region of analysis, comprising the "Central Anatolia Steppe and Woodlands" Ecoregion (external contour, gray area) and the "Central Anatolia Steppe" subregion (internal contours, light-blue color). Bottom: Central Anatolian landscapes, from left to right: Steppe grassland (Konya), woodland-steppe vegetation and oak woodland (near Ankara).

TABLE 1 | Response and explanatory variables. Source data, source resolution, and units of environmental and anthropogenic variables used in the study.

Response variables	Name	Unit	Range	Mean	SD	Source resolution	Year	Source	References
Tree cover percentage	TC	%	0–87	2.14	8.18	100 m	2018	Corine Tree Cover	Copernicus Database
Tree presence	TP	—	0–1	0.13	0.34				

Independent variables	Name	Unit	Range	Mean	SD	Source resolution	Year	Source	References
Soil properties									
Soil organic carbon	C	dg kg^{-1}	22–73	42.91	6.72	250 m	2021	SoilGrid	(Poggio et al. 2021)
Cation exchange capacity	CEC	mmol(c) kg^{-1}	146–517	249.24	37.29				
Total nitrogen	N	cg/Kg	117–728	262.26	54.1				
Soil pH	pH	pH * 10	62.0–79.1	74.90	2.26				
Climate									
bio1: Annual mean temperature	T	°C	5.1–12.7	10.24	1.26	30 arc-second	1970–2000	Worldclim	(Fick and Hijmans 2017)
bio2: Mean diurnal range (Mean of monthly (max temp—min temp))	Day T Range	°C	10.3–15.2	12.59	0.91				
bio3:Isothermality (bio2/bio7) (*100)	Isothermality	Ratio	31.6–40.4	36.60	1.47				
bio4: Temperature seasonality (SD *100)	T Seasonality	°C	708–834	783.1	20.96				
bio5: Max Temperature of warmest month	Max. T	°C	19.5–29.7	26.27	1.59				
bio6: Minimum temperature of coldest month	Min. T	°C	−13.3 to −4.9	−8.80	1.45				
bio7: Temperature annual range (bio5-bio6)	T Range	°C	30.1–37.8	34.35	1.40				
bio8: Mean temperature of wettest quarter	T Wettest Q	°C	−2.0–12.3	5.80	3.81				
bio9: Mean temperature of driest quarter	T Driest Q	°C	13.8–21.9	19.39	1.30				
bio10: Mean temperature of warmest quarter	T Warmest Q	°C	13.9–22-5	19.66	1.41				
bio11: Mean temperature of coldest quarter	T Coldest Q	°C	−4.8-3.0	0.39	1.32				
bio12: Annual precipitation	P	mm	342–674	431.00	52.65				
bio13: Precipitation of wettest month	Max. P	mm	45.0–117.3	59.67	30.33				
bio14: Precipitation of driest month	Min. P	mm	1.0–20.8	7.18	2.80				

(Continues)

TABLE 1 | (Continued)

Independent variables	Name	Unit	Range	Mean	SD	Source resolution	Year	Source	References
bio15: Precipitation seasonality	P Seasonality	coef. variation	35.6–75.7	49.15	7.80				
bio16: Precipitation of wettest quarter	P Wettest Q	mm	124–309	161.70	30.33				
bio17: Precipitation of driest quarter	P Driest Q	mm	7.0–67.08	29.95	9.66				
bio18: Precipitation of warmest quarter	P Warmest Q	mm	15.4–94.4	46.88	13.11				
bio19: Precipitation of coldest quarter	P Coldest Q	mm	99–318	149.60	37.27				
Topography									
Altitude (DEM)	Altitude	m	388–3693	1182.34	284.66	25 m	2000	EU DEM	(Jarvis et al. 2008)
Slope	Slope	—	0–45.6	4.72	5.17				
Aspect	Aspect		−1-1	−0.14	0.69				
Multiscalar Topographic Position Index (MTPI)	Convexity	—	−142-249	0.14	16.6				
Basin area (log transformed)	Drainage	km^2	4.7–26.4	9.02	2.07				
Land use									
Road density	Roads	m^{-1}	0–2532	49.25	145.32	Vector Scale 1:100.000	2023	OSM	(OpenStreetMap contributors 2017) (accessed 2023)
Agricultural density	Crops	%	0–1	0.55	0.38	100 m	2018	Corine LC	Corine Land Cover (CLC) 2018
Disturbances									
Livestock density	Livestock	Livestock units km^{-2}	2.8–229.6	17.93	10.47	Admin. Units	2018	TURKSTAT	
Extensive livestock density	Ext. Livestock	Livestock units km^{-2}	1.2–90.9	9.23	4.64	Admin. Units	2018	TURKSTAT	
Fire occurrence	Fire	Burns	0–1	0.0037	0.06	250 m	2018	MODIS	MCD641

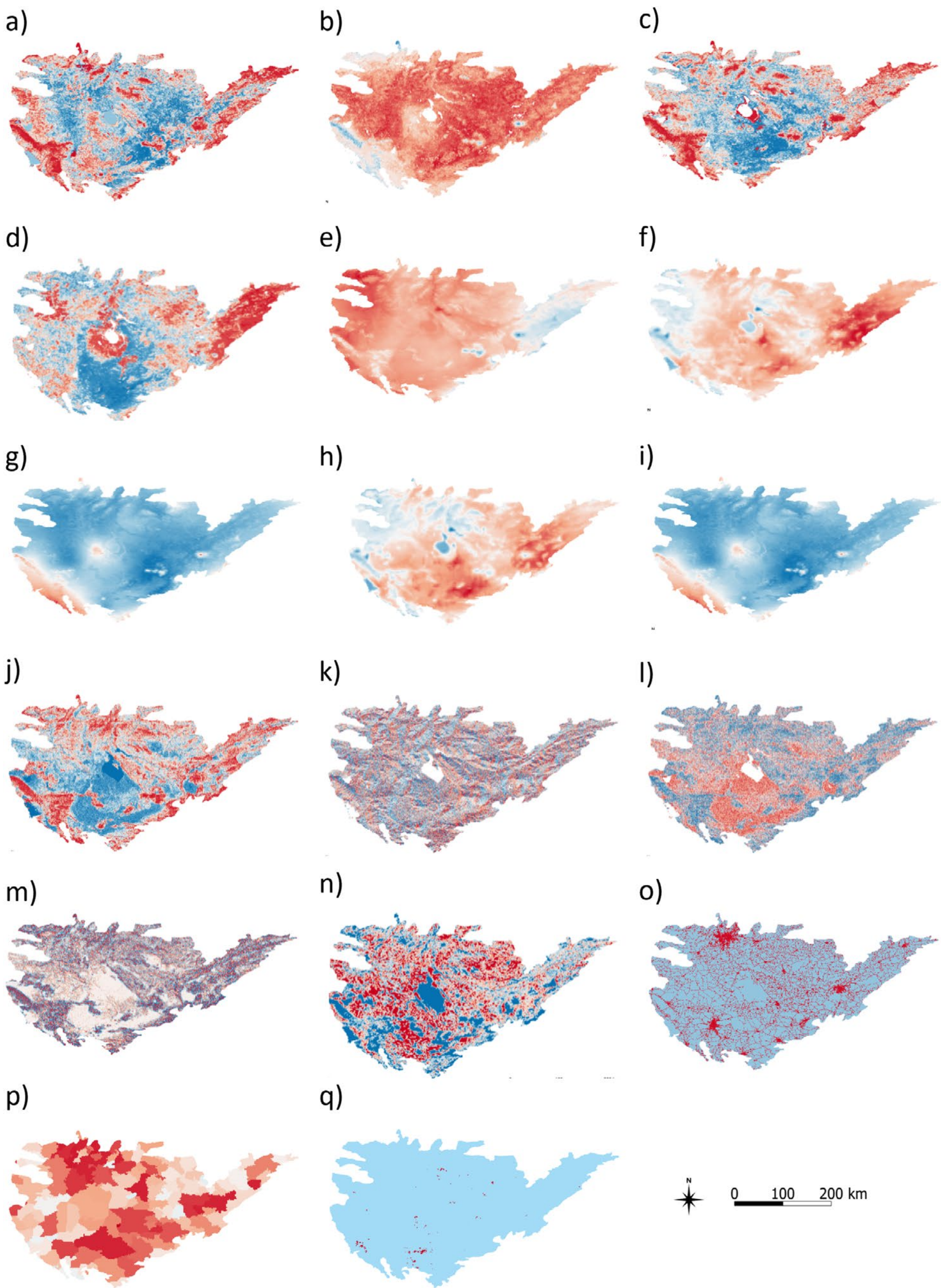

FIGURE 2 | Variables retained in the models of tree cover and presence. For graphic purposes, values were partitioned in percentiles, expressing higher values in red and lower values in blue. (a) N, (b) pH, (c) SOC, (d) CEC, (e) T Range, (f) Min. T, (g) Min. P, (h) Day T Range, (i) Isothermality, (j) Slope, (k) Aspect, (l) Drainage (m) Convexity, (n) Crops, (o)Roads, (p) Ext. Livestock, and (q) Fire.

(Holmgren et al. 2013; Xu et al. 2018). The availability of resources is also mediated by local conditions. Soils and topography affect the local distribution of tree formations; topography can determine landscape heterogeneity associated with hydrological flows, soil formation, and solar exposure (Berazategui et al. 2023). Land use reduces tree cover directly through land conversion to agriculture, and livestock can impede regeneration through browsing and trampling (Bond 2005; Staal et al. 2018; Bernardi, Buddeberg, et al. 2019). Human settlements are known to be associated with higher tree cover due to horticulture and agroforestry, gardens, fences, and the introduction of invasive species (McLean et al. 2017; Potgieter et al. 2017; Berazategui et al. 2023).

The response variable tree cover data was obtained from the Corine Tree Cover Density dataset (https://doi.org/10.2909/c7bf34ea-755c-4dbd-85b6-4efc5fd302a2) at a 100-m resolution, and all other data were resampled at this resolution. We used the, sp, terra and raster packages in R to process and resample data layers. We used bilinear interpolation for continuous data and nearest neighbor for discrete data. Smaller resolution rasters were aggregated to the 100 m Tree Cover raster. We assessed resampling quality through statistical comparison of rasters, particularly to avoid border effects. For climate data, we used 19 bioclimatic variables from WorldClim (Fick and Hijmans 2017). A set of topographic variables was included in the study; altitude was obtained from the

EU-DEM (Jarvis et al. 2008) and variables were aggregated at 100 m resolution. Slope and aspect were obtained with QGIS 3.22 using the GDAL function. The Aspect, which approximates the exposure of the terrain to the sun, was defined as the cardinal orientation of the terrain expressed as the cosine of the degree to the North in radians. We used the area flow of water runoff (log-transformed) determined by topography from the "Hydroinformatics at VT" github using the D8 Flow Accumulation equation at a 100 m resolution (Gannon 2023). The Topographic Wetness Index (TWI) (Alexander et al. 2016) and the Downslope TWI were evaluated, but we used the area flow ("Drainage") since the slope is included as an independent variable. We also included the relative position in the landscape or "Convexity" of the terrain, expressed as the Multiscalar Topographic Position Index (MTPI) (Conrad et al. 2015). Aspect and Convexity were obtained in the SAGA function of QGIS 3.22. Soil variables were obtained from the SoilGrids database at the surface level (Poggio et al. 2021). We used pH, CEC, total nitrogen (N), and soil organic carbon (SOC). We also modeled using the carbon–nitrogen (CN) ratio, a known predictor of plant growth, but did not obtain different results; therefore, we decided to keep the original variables. We evaluated the reliability of soil data in our models using uncertainty layers by comparing a subset of regions with low uncertainty with the overall data, and found no significant difference in the overall relationships between soil variables and tree cover.

Livestock data were obtained from the Turkish Statistical Institute (TURKSTAT) for 2018. All livestock data were converted to standardized Livestock Units (LU) according to the Turkish Pasture Regulation. A LU is equivalent to one dairy cow of cultural breed, and equivalents are defined for other cattle types, sheep, and goats (Official Gazette of the Republic of Türkiye 1998). We divided livestock into intensive and extensive production according to the breeds, which are closely associated with feeding sources. Imported breeds were classified as intensive (and considered to largely be fed with ration), while native breeds were considered extensive (mostly grass-fed) (Yilmaz et al. 2012). Livestock density of each cell was obtained by dividing the LU of the smallest data unit (administrative division) by its area. The fire data for the year 2018 was obtained from the MODIS product MCD641, which provides monthly burnt area data. Given the large amount of agricultural fields in the region, we assessed excluding fires that occurred on agricultural fields from the fire data using the land cover layer (Bekar and Tavşanoğlu 2017).

Agricultural density was derived from the 100-m raster Corine Land Cover (2018), as the proportion of the cells in a 1-km buffer (excluding the center cell) classified as agriculture, using the *focal* function in the *terra* package in R (version 1.7–29) (Hijmans 2020). We used road density as a proxy for human settlements using the OpenStreetMap (OSM) road layer available (2023). We used the *osmextract* package in R to extract OSM data (Gilardi and Lovelace 2023) and the *Line Density* function in QGIS.

Although our analysis focuses on natural forests, there are no comprehensive data on forest plantations in Türkiye. In order to mask forest plantations and exclude them from our analysis, we assessed global databases such as the WRI Global Forest Watch by visually identifying approximately 100 points of plantations to assess their accuracy, but these were not in general included in the database. Therefore, we assessed the reliability of the database used, considering available plantation data from the General Directorate of Forestry in Türkiye for 14 Forest Management Units located in Konya and Karaman provinces in Central Anatolia, which corresponds to nearly 30% of our study region. Regions with afforestation plans were below 1% of the Forest Management Units total area, and samples with tree presence within plantations represented approximately 1% of the total samples with forest presence. Statistical analysis of tree cover values with and without plantations showed no differences (Welsh test $p = 0.77$). In addition, excluding plantations did not yield different results in the model assessments. Therefore, we decided to use the complete Corine tree cover dataset for better consistency.

2.3 | Data Analysis

Due to the prevalence of excess zeros in the tree cover data (Appendix S2), we used two different modeling approaches to assess the influence of various factors on tree cover within our study area. We utilized a generalized linear model (GLM) with binomial error distribution for tree presence (TP) Equations (1) and (2), and a GLM with Gaussian distribution to examine tree cover (TC) values Equations (2) and (3). Both models included a linear term and a stochastic component. In the stochastic components, the probability of tree presence Equation (1) was given by a binomial error distribution (a Bernoulli distribution for presence–absence data), and TC Equation (2) was a function of the expected mean percentage of TC for observation i (μi), and the variance of the error term (σ2) (assumed constant, or homoscedastic). The linear term included the regression intercept and coefficients (β0...βk), and the explanatory variables (X1i...Xki) for observation i.

$$p(TP)i \sim Bernoulli(p(TP)i) \tag{1}$$

$$p(TP)i = \frac{e^{\beta_0 + \beta_1 X_{1i} + \cdots + \beta_k X_{ki}}}{1 + e^{\beta_0 + \beta_1 X_{1i} + \cdots + \beta_k X_{ki}}} \tag{2}$$

$$TC \sim N\left(\mu_i, \sigma_2\right) \tag{3}$$

$$E(TC)i = = \beta_0 + \beta_1 X_{1i} + \cdots + \beta_k X_{ki} \tag{4}$$

For this, we extracted a random sample of 0.02% of the Corine 100 m × 100 m cells, resulting in a total of 160.349 points using the *set.seed* function in R. We modeled tree presence and absence using all points, converting TC data into binary values (1 and 0), and modeled TC using only the points with tree presence. This strategy mitigated potential biases and overdispersion caused by the excessive zeros in the dataset. Although a zero-inflated model is an alternative method for handling data with excess zeros, we opted against it due to its complexity and shortcomings in interpreting results compared to traditional models.

We applied an arc-sin of the square root transformation (Hirota et al. 2011) to the TC data to approximate normality and homoscedasticity. We first modeled each variable separately to understand it individual contributions to the variability in tree presence and cover data (Appendix S3). For each analysis, we started with a null model, followed by fitting a model that included the variable as a fixed factor. The significance of incorporating the fixed factor was then evaluated. In assessing the explanatory power of each variable on tree presence and cover, our focus was on the percentage of explained deviance/variance rather than *p* values. We adopted this approach because nearly all models yielded significant results ($p < 0.0001$ in most cases), regardless of the small effect sizes, which can be attributed to the large number of cells in our datasets. Consequently, the explanatory power of each variable was determined using the explained deviance and variance extracted from the model outputs. Additionally, we used diagnostic residual plots to ensure that the residuals were unbiased and homoscedastic. We assessed the spatial autocorrelation of TC by calculating Moran's I for each model, using the *spdep* package in R (Pebesma and Bivand 2023).

To identify the best explanatory model for presence/absence and tree cover data, we implemented a stepwise selection. Initially, we assessed the correlation among variables using the Pearson correlation coefficient to detect and remove autocorrelated variables (Appendix S4). This analysis reduced the number of variables considered for inclusion in the final model from 33 to 17. The stepwise procedure commenced based on the outcomes of separate variable models, prioritizing the inclusion of variables with the highest explanatory power (i.e., explained deviance or variance) or those resulting in the lowest Akaike information criterion (AIC). In subsequent stages, we incrementally introduced the best explanatory variable into the models and evaluated these models based on AIC and the explained deviance or variance, until the addition of any additional variable did not significantly enhance the model's explanatory power.

We performed all analyses in the R environment (version 4.1.2) (R Core Team 2021) and used the *corrplot* package (Wei and Simko 2021) to create a correlation matrix and its visualization.

3 | Results

The final models (Table 1, Figure 3, Appendix S5) explained 28% of the deviance for tree presence and 33% for tree cover. Both models were highly congruent in the variables included. These models point to a strong influence of soil properties, climate, topography, and land use on tree presence and cover. The explanatory power of the models increased to 31% and 34%, respectively, when a quadratic function for elevation was added (Appendix S6), accounting for the unimodal effect of height on TC. We kept the models with the original linear variables for simplicity.

Soil properties were primary determinants of TC. Tree presence and cover were positively associated with total nitrogen, soil organic carbon, and acidic soils and negatively associated with the cation exchange capacity ($p < 0.0001$).

Trees also showed strong associations with climatic variables; particularly with temperature extremes (both diurnal and annual) and precipitation. Tree presence and cover were positively associated with the minimum monthly temperature ($p < 0.0001$). Tree presence was associated with minimum

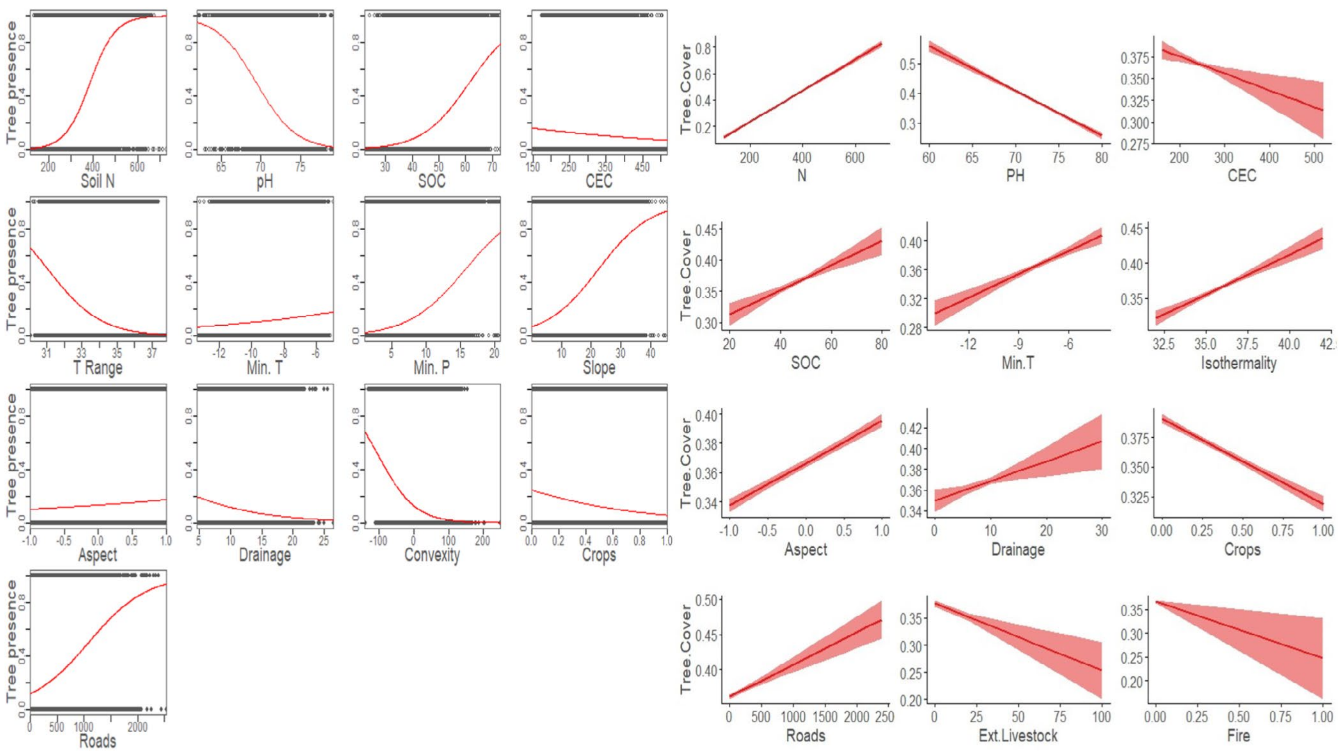

FIGURE 3 | Partial plots of variables retained in selected GLM models. Left: Tree presence versus explanatory variables, binomial distribution. Right: Tree cover (transformed) versus explanatory variables.

monthly precipitation ($p < 0.0001$) and with the annual temperature range ($p < 0.0001$). Tree cover was associated with isothermality ($p < 0.0001$), an indicator of daily versus annual range, which was highly correlated with day temperature range, but we used it as it did not correlate with other variables (like pH). The annual and diurnal (i.e., the mean difference between the maximum and minimum monthly temperatures) temperature ranges were also highly correlated (Pearson Corr. $= 0.89$); and minimum precipitation and temperature, seasonality and diurnal and temperature ranges tended to have high overall correlations (Appendix S4), highlighting the overall effect of interaction of extreme conditions.

Tree cover and presence were also associated with topographic traits; tree presence increased in steeper slopes ($p < 0.0001$), and both tree presence and cover increased in southern slopes (Aspect) ($p < 0.0001$), in more concave terrain (tree presence $p < 0.0001$, tree cover $p = 0.01$); and with higher water availability due to larger drainage area (tree presence $p < 0.0001$, tree cover $p = 0.02$).

Land use was also a determinant of tree presence and cover. Both decreased in areas with higher agricultural densities ($p < 0.0001$) and increased in areas with higher human presence (i.e., higher road density) ($p < 0.0001$). Tree cover decreased in areas with higher extensive livestock densities and more frequent fire occurrence ($p < 0.0001$). Values of spatial autocorrelation were low for tree presence (Moran's I $= 0.27$, $p < 0.0001$) and cover (Moran's I $= 0.22$, $p < 0.0001$).

Regarding the individual contribution of the variables considered, an analysis of the variables with higher explanatory power revealed high consistency in both models regarding the effect of soils, climate, topography, and land-use variables when considered independently. Those with higher predictive power (using an arbitrary threshold of 5%) included pH, total nitrogen, and soil organic carbon. Regarding the climatic variables, tree presence and cover were negatively associated with the mean annual and diurnal temperature range. Tree presence and cover also decreased with temperature seasonality and increased with mean annual precipitation. The slope was the main individual topographic variable with a positive association with tree presence and cover. Finally, crop density in the surrounding region was negatively associated with both tree presence and cover.

From a geographical perspective, TC was notably lower in the Central Anatolian Steppe Ecoregion, and higher in certain areas of the Steppe and Woodlands Ecoregion. In the Central Anatolia Steppe Ecoregion, trees were only present in 5% of the sample cells (tree cover mean = 8%), and in the Steppe and Woodland Ecoregion, trees were present in approximately 15% of the cells (tree cover mean = 17%). This difference between ecoregions was consistent with the main topographic differences between the plateau that largely defines the Central Anatolia Steppe and the hillier terrain of the Steppe and Woodlands region (Figure 1), and was captured by the association of trees with slope and other topographic variables such as aspect and concavity. Alternative models, including a quadratic response to altitude, had a stronger explanatory power and a stronger association with slope. TC has a unimodal relationship with altitude (Appendix S7), increasing until approximately 1800 m, where tree presence dropped abruptly due to physiological limitations; almost no trees could be found above a tree line of 2000 m in the region. Hilly regions with intermediate altitudes and high slopes are in many cases also related to the agricultural frontier; that is, forests persist in regions where topographic and geologic conditions for agriculture become less suitable (Table 2, Figures 2 and 3). Temperature amplitudes are particularly high in the Central Steppe (Aksaray province and the eastern part of Konya province) and to the east of the study region (Kayseri and Sivas provinces), which has particularly lower minimum temperatures, and where tree cover is also very low.

4 | Discussion

We identified the environmental and land-use factors shaping tree cover in Central Anatolia; we discuss their effect and interactions and the implications in terms of the current distribution of ecosystem types, the resilience of this system in the face of climate or land-use changes, and to inform management and conservation decisions regarding afforestation of open ecosystems.

Tree cover in Central Anatolia was shaped by the interplay of climate, local conditions, land use, and disturbances (Table 2, Figure 3). In Central Anatolia, both soil properties and climate conditions appear as main determinants of tree cover, indicating that tree growth faces restrictions in a stressful environment constrained by soil properties and in extreme climate conditions.

Soil properties were strongly associated with tree presence and cover in Central Anatolia. Soil fertility was associated with higher tree cover, as expected, despite some trees showing high tolerance to nutrient-poor soils (Yildiz et al. 2018). Interestingly, in our study, trees appeared to be limited by alkaline soils with high CEC. These two variables are often correlated (Weil and Brady 2002), but in the Central Anatolian steppes, they are associated with saline-sodic soils (Akça and Kapur 2014; Korkanç and Korkanç 2016). Soil type is a major determinant of plant assemblages in the Central Anatolian steppes, with diverse bedrock and soil types shaping local plant diversity (Kurt et al. 2006; Kürschner and Parolly 2012). Areas of high conservation value are often linked to specific types of steppe vegetation that grow on unique soil substrates, such as marly, haline, and serpentine soils (Eken, Bozdoğan, et al. 2005). These soil-driven vegetations harbor numerous endemic species, most of which are highly specific to their soil types (Yıldırımlı 2012; Ghazanfar et al. 2014). Our findings highlight soil chemistry as a key limiting factor for tree cover, likely reflecting the diversity and prevalence of such specialized habitats in Central Anatolia. In addition to natural geological formations, human activities such as irrigation and overgrazing have historically contributed to soil degradation, resulting in saline conditions and reduced organic matter content (Akça and Kapur 2014; Korkanç and Korkanç 2016). These degraded soils may further constrain tree growth in some regions (Yildiz et al. 2017). Consequently, the combined effects of natural and anthropogenic factors driving poor soils emerge as a primary determinant of tree distribution in Central Anatolia. Despite this constraint, in some cases, positive feedbacks between forests and soil properties could improve poor soils in areas where forest expands or is planted, although results are uncertain and may have unintended consequences

TABLE 2 | Final Models. Tree Presence and Tree Cover models with coefficients and *p*-value of variables retained in final models. Positive and negative signs before each variable indicate the sign of the effect on tree presence and cover.

GLM Model Tree Presence		**$R^2 = 0.28$**	**LM Model Tree Cover (%)**		**$R^2 = 0.32$**
TP ~+ N−pH + SOC−CEC−T Range + Min. T + Min P+ Slope + Aspect + Drainage−Convexity−Crops + Roads			TC ~+ N−pH−CEC + SOC + Min. T + Isothermality + Aspect + Drainage−Convexity−Crops + Roads−Ext. Livestock−Fire		
Explanatory variables			**Explanatory variables**		
Variables	**Estimate**	***p***	**Variable**	**Estimate**	***p***
N	0.00775	< 0.0001	N	0.001189	< 0.0001
pH	−0.1220	< 0.0001	pH	−0.015060	< 0.0001
SOC	0.0705	< 0.0001	CEC	−0.000193	0.002
CEC	−0.0070	< 0.0001	SOC	0.001954	< 0.0001
Day T Range	−0.1730	< 0.0001	Min. T	0.010770	< 0.0001
Min. T	0.1290	< 0.0001	Isothermality	0.011420	< 0.0001
Min. P	0.0415	< 0.0001	Aspect	0.029020	< 0.0001
Convexity	−0.0166	< 0.0001	Drainage	0.001905	0.003
Slope	0.0538	< 0.0001	Crops	−0.072180	< 0.0001
Aspect	0.3280	< 0.0001	Roads	0.000046	< 0.0001
Drainage	0.0793	< 0.0001	Ext. Livestock	−0.001243	< 0.0001
Crops	−1.1800	< 0.0001	Fire	−0.119000	0.006
Roads	0.00240	< 0.0001			

by altering ecohydrological balances (Liu et al. 2022; Yıldız et al. 2022; Yang et al. 2024).

Climate plays a crucial role in limiting tree growth. In Central Anatolia, trees were strongly limited outside a "climatic envelope" of milder climate, involving temperature and precipitation and its combined effects. Interestingly, the annual and diurnal temperature ranges, which were negatively related to tree presence and tree cover, were the single climatic variables with the highest explanatory power when independently assessed. These results suggest that regions with the coldest and warmest extremes can expose trees to freezing and hydric stress. This is consistent with the limiting effect of the monthly minimum temperature and precipitation, and is broadly in line with the expected vegetation under the semi-arid conditions of Central Anatolia (Kenar and Kikvidze 2019), for example, as per the Whittaker climate map (1970, 167), and with recent phytogeographic analysis of the broader region. The region is a transitional area between contiguous regions with a particular climate, related in part to its topography. Its climate is characterized by low precipitation in summer, low minimum temperature in winter, and extreme daily and seasonal temperature variations (Djamali et al. 2012). These climatic factors can be considered to broadly align with the "Goldilocks principle" of higher abundance at intermediate climatic conditions (Mo et al. 2022; Ramiadantsoa and Turner 2023), and impose a constraint on tree growth that is not associated with local human land use or disturbance regimes, and depict a complex climatic landscape that should be thoroughly considered when analyzing management strategies, including afforestation plans. The importance of climatic limitation as an external constraint is a key consideration due to low resilience of forests under climatic extremes.

Topography also appears to have an effect on trees, being favored in mountainous areas with steeper slopes, with higher solar radiation, and in local depressions with higher water runoff. These findings are consistent with analyses placing the forest relicts of Central Anatolia mainly in its mountains (Kahveci 2022), and have been found in other regions, where local elevation and rocky terrain can favor trees in several ways, as is the case in the more rugged areas of the Central Anatolian Steppe and Woodlands, which appear to have more favorable conditions for resilient forests. Trees will be more abundant at midaltitudes, since tree growth is generally limited above the tree line at approximately 2000 m (Appendix S7). Rugged terrain, outcrops, creeks and crevices, and depressions and drainages can generate microclimate niches, accumulate soil and water and, since they are less suitable for agriculture, provide protection against human land use and disturbances such as herbivory and fire (Müller et al. 2012; Gartzia et al. 2014; Brazeiro et al. 2018; Chytrý et al. 2022; Berazategui et al. 2023). In addition, sun irradiance can favor trees in southern-oriented slopes (Måren et al. 2015). Solar exposure has been found to be relevant to several species in the region (Kahveci 2023). Our work suggests that these local sites may act as pockets of resilience even under harsh overall climatic conditions.

Land use also influenced tree cover distribution. Agriculture had a negative effect associated with land conversion, while human presence showed a positive effect, a pattern observed elsewhere; humans tend to locally increase tree cover in the landscape due to afforestation and in uses such as green fences. Furthermore, woody invasive species tend to increase as they disperse from settlements to their surroundings (Potgieter et al. 2017; Berazategui et al. 2023).

We found a negative, although weak, effect of extensive livestock and fire, two well-known disturbances known to limit tree cover that have been found elsewhere. Livestock can be a primary determinant of tree cover, particularly in semi-arid regions where forests are less common (Staal et al. 2018; Bernardi, Staal, et al. 2019; Erdős et al. 2022). The negative effect of fire appears to be associated with agricultural practices, since fires not associated with agriculture were significantly less frequent and did not show any effect on tree cover in our model. Livestock is known to shape the plant community in the region (Fırıncıoğlu et al. 2007; Özüdoğru et al. 2021), with moderate livestock densities contributing to higher diversity (Bahar and Tavşanoğlu 2024), and despite being relatively weak, its effects in our model are notable, considering the coarse resolution at which livestock data are available. This suggests that more detailed livestock data might show a stronger and more direct limiting effect on tree distribution; and that management of livestock may be a key factor to conserve these ecosystems, particularly in mixed forest–grassland systems.

Our findings are consistent with previous analyses of tree species that highlighted the role of latitudinal climate gradients and altitude in shaping the woody composition in the region (Kenar and Kikvidze 2019), and the occurrence of the herbaceous steppes under drier conditions characteristic of Paleartic steppes (Wesche et al. 2016). Our work is also aligned with analyses for steppe arid and semi-arid regions of Eurasia (Chytrý et al. 2022; Erdős et al. 2022; Bede-Fazekas et al. 2023). In this context, considering a broader set of variables, including land use and disturbances in open landscapes that drive ecosystem changes, as well as local favorable conditions for trees (Török and Dengler 2018) can provide nuance and have direct implications for the conservation and management of these unique ecosystems.

These results can be understood by considering Central Anatolia as a region where forests, woodlands, shrublands, and grasslands can coexist as alternative biome states. This is supported both by paleoecological evidence and by the properties of Central Anatolia grasslands, such as high biodiversity, consistent with valuable old-growth ecosystems (Tavşanoğlu and Bernardi 2024). In this context, an interplay of broader climate patterns, the availability of resources mediated by local conditions, and disturbance regimes can determine suitable conditions for different ecosystem types, in line with the models proposed for temperate Asian regions (Erdős et al. 2022).

Our results suggest that forests in Central Anatolia result from the interplay of climate, soils, and topographic conditions. This challenging landscape may explain the current scarce forest cover. Although land conversion in agricultural areas, along with soil depletion, livestock, and fire regimes significantly limit tree cover, our findings indicate that ecological drivers play a larger role in determining tree cover than previously thought, questioning the common belief that extensive deforestation by humans is the primary cause of the lack of trees in Central Anatolia. Future management strategies should recognize that the scarce trees in the Central Anatolian steppes align with a mosaic of steppe and shrub vegetation, where particular soil and topographic conditions create suitable conditions for forests and tree formations.

5 | Conclusions

Our analysis indicates that landscapes of high resilience for forests are not widespread, but rather limited by stressful conditions due to oligotrophic or depleted soils and the extreme temperatures and hydric stress of Central Anatolia's sub-arid climate. Particular interactions between temperature and precipitation regimes determine a general limit to its capacity to support forests, setting a limitation in line with traditional considerations of early naturalists for semi-arid regions.

However, this strong constraint on tree growth can vary depending on local conditions, where more suitable resources and protection from disturbances and human land use—such as topographic features—can create regions of high resilience for forests. Disturbances like livestock and fire also appear to have an effect, albeit moderate, on the forest cover of Central Anatolia, possibly through feedback with herbaceous and shrub vegetation. These findings suggest a combination of factors explaining forest cover in Central Anatolia, with a higher presence of trees in the mountainous regions surrounding the Central Anatolian Steppes and in areas where climate and soils can generate more suitable conditions.

Historical deforestation can, within this context, also explain the scarcity of trees in some regions of Central Anatolia. Human land use had direct effects on tree cover in these regions due to deforestation and conversion to agriculture, and also by depleting soils throughout the centuries, resulting in current conditions of poor and acid soils, and removal of genetic material, wiping out ancient forests. However, assessing the extent of past forests and the impacts of past human activity must take into account the strong evidence characterizing Central Anatolia as an open system where forests and woodlands would coexist with ancient grasslands, which are highly resilient and particularly rich ecosystems (Tavşanoğlu and Bernardi 2024). These findings should be considered when designing afforestation plans in Central Anatolia. Because forests and grassy-dominated ecosystems can be considered alternative states in many regions with suitable conditions for forests, careful assessment of how the interplay of large scale and local factors generates resilient landscapes for forests in this matrix of grassy systems is needed to understand its future resilience, that is, the ability to persist when facing changes in climate or land use. Climate change could amplify current climate restrictions increasing the forests' vulnerability and the risk of fires and forest dieback. Mixed systems may be more adapted to the climate and soil constraints identified in this work and can persist under extensive livestock management. In this regard, our results can contribute to a better understanding of the ecosystems in Central Anatolia and to the management of this region for agriculture, afforestation, and conservation.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.18866288 Reference number: 18866288.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Descriptive statistics of explanatory variables. **Appendix S2:** Histogram of tree cover data. **Appendix S3:** Independent analysis of explanatory variables. **Appendix S4:** Analysis of correlations. **Appendix S5:** Stepwise selection. **Appendix S6:** Models with a quadratic altitude term. **Appendix S7:** Tree cover versus explanatory variables retained.