

Unveiling the Ecological Niche: Long-Term Dynamics of Abandoned vs. Forested Landscapes and the Path to Species-Specific Forest Restoration

Nikolaos Oikonomakis

noikonoa@for.auth.gr

Aristotle University of Thessaloniki

Petros Ganatsas

Aristotle University of Thessaloniki

Marianthi Tsakalimi

Aristotle University of Thessaloniki

Research Article

Keywords: Forest species niche, landscape metrics, MaxEnt models, field abandonment, forest species dynamics

Posted Date: October 7th, 2025

DOI: <https://doi.org/10.21203/rs.3.rs-7216029/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License. [Read Full License](#)

Additional Declarations: No competing interests reported.

Abstract

This study investigates the long-term dynamics of forest expansion in abandoned and reforested landscapes, focusing on the ecological requirements of dominant forest species. Over a 79-year period (1945–2024), forest cover increased from 59.36–92.13% in Rhodope Mountain Range National Park-RMRNP, driven by the colonization of non-forested areas, particularly grasslands. The study examined expansion patterns of different Forest Types (FT), with key factors influencing colonization identified through bioclimatic and environmental models. Species such as *Quercus* spp., *Fagus sylvatica*, and *Pinus sylvestris* exhibited clear preferences for specific temperature ranges and elevation. The presence of parental forest stands and proximity to waterways also significantly influenced species distribution. Notably, *Quercus* species showed a positive correlation with increasing temperatures (BIO11) and low elevations (200–800 m. asl), while *Picea abies* expanded in higher altitudes and away from waterways, highlighting species sensitivity in waterlogged conditions. Specific species, such as *Betula pendula* and *Ostrya carpinifolia*, exhibited distinct ecological preferences for certain environmental conditions, with varying responses to ecological factors. Landscape metrics indicated a reduction in fragmentation and an increase in forest continuity, suggesting successful forest expansion. These findings underscore the importance of ecological niches in shaping forest recovery and offer insights into sustainable forest management practices.

1 Introduction

Ecoscientists now know that most of the world's vegetation in the future will consist of plant communities of secondary ecological succession; and humans will coexist with forests of secondary ecological succession that will fully utilize and depend on them (Guariguata and Ostertag 2001; Kennard 2002; Kubota et al. 2005; Oikonomakis and Ganatsas 2020). Knowledge of the homeostatic recovery possibilities of an ecosystem under the constant pressure of anthropogenic activities and subsequent abandonment is very important and enlightens ecology scientists and environmental managers (biologists - foresters, etc.) about the behavior of these natural ecosystems and their recovery potential (Bazzaz and Sipe 1987; Kelly and Harwell 1990; Benayas et al. 2007; Navarro and Pereira 2015; Wang et al. 2023; Ambs et al. 2024; Lloret et al. 2024). The study of these natural - semi-natural ecosystems contributes to their better understanding and equips future forest managers with knowledge that will contribute to their wiser management. Forest management for ecosystem services (conservation, timber production, habitat for rare animal and plant species, drinking water production, pollution control, CO₂ storage, etc.) can be done with a focus on one or more of them (McIntosh 1995; Buttoud 2002; Glück 2002; Baskent et al. 2008; Martynova et al. 2021).

The research area (Rhodope Mountain Range National Park-RMRNP) is part of the zone (Green Belt) in which anthropogenic activities were banned after World War II. For about 40 years, until 1989, natural ecosystems were able to develop almost unaffected by anthropogenic interventions since the establishment of this strict no-go zone (Terry et al. 2006; Riecken et al. 2010). In fact, it has been shown much earlier that this zone has preserved natural ecosystems and the development of highly beneficial habitats for biodiversity and has served as a refuge for protected animal and plant species. Therefore, it represents a characteristic landscape for the study of ecological succession of forests.

Land abandonment causes two different consequences for biodiversity (Plieninger et al. 2014). The positive consequences are associated with an increase in the abundance of various flora and fauna species. For example, several studies have concluded that the “passive landscape restoration” (Bowen et al. 2007) or “rewilding” (Navarro and Pereira 2015) benefits several bird and large mammal populations. Conversely, the negative consequences might be the loss of habitat for some species that depend on open areas between forested areas, the reduction of habitat patchiness, the exclusion of competitors, the invasion of non-native plants and the increase of forest fires (Benayas et al. 2007).

In the study area, there have been observed both positive and negative effects of land abandonment on flora and fauna in the study area. Increasing the area of forest ecosystems has led to improved forest health, increased canopy closure and expansion of forests onto abandoned pasture and agricultural land (Oikonomakis and Ganatsas 2012, 2020; Hinkov et al. 2019). The negative consequences concern some fauna species that live and move in semi-natural areas. The lack of open spaces (meadows) has resulted in the wild ungulates - red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and chamois (*Rupicapra rupicapra*) - using roads (Jensen 2018) and small gaps (Kuijper et al. 2009) for movement and feeding. This is related to the presence and abundance of carnivores such as brown bear (*Ursus arctos*), wolf (*Canis lupus*) and golden jackal (*Canis aureus*). The lack of open spaces also has consequences for large birds of prey, as it is difficult to find food (Pedrini and Sergio 2001; Regos et al. 2016; Grande et al. 2018; Sarasola et al. 2018). However, there are no detailed studies for fauna (including invertebrates, amphibians, reptiles, etc.) to determine how secondary successional forests affect the populations of these species (Bowen et al. 2007). For flora species, the negative consequences may be the invasion of non-native plants and the risk of forest fires, which must be considered. Both risks have not been reported for the area.

Landscape ecology is a branch of ecology which focuses on the patterns, processes and interactions of ecosystems at different spatial scales (Risser 1987; Turner 2005; Turner and Gardner 2015). Due to its utility for spatial analysis and environmental management, it also overlaps with geography, environmental science and conservation biology (Wu et al. 2007; Skidmore et al. 2011). As there are forest fragmentation phenomena in this research that have been attenuated over the years, there is a need to measure and assess them quantitatively and spatially. As a result, FRAGSTATS software (McGarigal 1995; Uuemaa et al. 2009; Kupfer 2012; Cardille and Turner 2017) developed by McGarigal and Marks (1994), was used to quantitatively assess changes in landscape fragmentation and forest continuity, providing insights into the ongoing ecological processes. Indeed, there have been radical changes in land cover in recent years, a real transformation of the landscape. To this end, Landscape Metrics (LMs) were used to estimate the overall landscape change, and LMs at the class level were used to estimate the behavior of the classes that were the main forest types in the study area (Neel et al. 2004).

The forest species of the area, which are the subject of scientific interest in the present study, have demonstrated specific behaviors regarding their spread in non-forest areas after their abandonment by livestock populations. To evaluate those behaviors, the maximum entropy (MaxEnt) method was used. This method is widely used in ecological niche modeling (ENM) as it can predict the distribution of species based on presence-only data (Warren et al. 2011; Raghavan et al. 2012; Mafuwe et al. 2022). The inclusion of presence-absence data, where information is available, can significantly improve accuracy. Although the MaxEnt model is not designed to use absence data (Phillips et al. 2006a; Guillera-Arroita et al. 2014), presence-absence data enable MaxEnt to distinguish between regions where a species cannot survive and those where it may have been overlooked. This leads to refined, accurate predictions of species' suitable habitats, especially in complex environments such as forests where microhabitats play a crucial role (Chetan et al. 2014; Yousaf et al. 2022). Studies using presence-absence data often have higher precision in predicting species distribution under climate change scenarios, as they provide more accurate predictions of habitat suitability, better model validation, reduced bias, and a better understanding of environmental constraints (Merow et al. 2013; Syfert et al. 2013; Fois et al. 2018; Warren et al. 2020).

In this study, the MaxEnt method was used for each of the major forest types (FTs) of the area to define their ecological "niche". Sampling was common for all forest species studied, so it was easier to obtain more absence data which were used when modeling each species separately. The ecological niche of the main forest species of the area can be described as follows for each species as follows:

Quercus species like *Q. petraea*, *Q. frainetto*, *Q. cerris* and *Q. pubescens* cover most of the study area, serve as key middle-succession species, covering large areas in mixed forests and playing an essential role in forest dynamics. Their ability to coexist with beech, pine, and hornbeam species ensures structural diversity and ecosystem stability. Understanding their ecological requirements helps in forest conservation, climate adaptation, and sustainable management (Caliskan et al. 2025; Fortini et al. 2025; Quaranta et al. 2025; Tesei et al. 2025).

Fagus sylvatica (the second most common species of the study area) plays a significant role in European forest ecosystems, offering shade tolerance, biodiversity support, and carbon sequestration. However, its ecological niche is under increasing pressure from climate change, competition with other species, and insect infestations (Liepiņš and Bleive 2025).

Pinus sylvestris (also common in the study area) is a pioneer species, playing a crucial role in ecosystem development, afforestation, and land restoration. Its ability to thrive in harsh environments and facilitate the establishment of other species makes it vital for early-stage forest succession. However, climate change and competition from late-successional species may limit its range in the future (Przybylski et al. 2025).

Picea abies is primarily a late-successional species due to its shade tolerance and ability to dominate mature forests. However, it can also function as a pioneer species in specific ecological contexts, particularly in boreal and Scandinavian landscapes following disturbances. This dual role allows it to thrive across various ecosystems (Caudullo et al. 2016).

Carpinus orientalis occupies a broad ecological niche, particularly in dry, rocky, and semi-arid environments. It contributes to soil stability, enhances biodiversity in degraded habitats, and competes with various species in mixed forest systems. Its resilience to climatic fluctuations makes it a valuable species in forest restoration and conservation efforts (Cărăbuș and Șofletea 2014; Varol et al. 2022).

Pinus nigra plays a vital role in ecological restoration, particularly in arid and degraded landscapes. Its adaptability, soil stabilization and improvement properties make it an essential species for reforestation efforts worldwide (Vacek et al. 2023).

Ostrya carpinifolia is a resilient species with a broad ecological niche, thriving in warm, rocky, and calcareous environments. Its role in stabilizing soils, contributing to biodiversity, and serving as an intermediate successional species makes it important for conservation and forest management (Pasta et al. 2016).

The Betula pendula is a highly adaptable species, occupying a broad ecological niche from boreal forests to degraded lands. It plays a crucial role in ecological restoration, soil stabilization, and afforestation while supporting biodiversity. Its rapid growth and resilience make it an excellent species for climate adaptation strategies (Vakkari 2009; Beck et al. 2016a).

The aim of the study is to investigate the long-term development of secondary ecological succession and forest expansion within the RMRNP with the help of cartographic data - satellite data and aerial photographs. The extent of the forest and its spatial patterns at landscape and class level (forest types/ecological succession trends) through time was thoroughly analyzed.

The specific objectives of the research are the following:

- 1) The study of forest dynamics in the area using landscape ecology methods
- 2) Study the specific ecological characteristics, dynamics, and distribution patterns of each Forest Types (FT) within areas undergoing secondary ecological succession.
- 3) To test distribution models for each FT based on ground observations and to explain their behavior according to bibliography.

2 Materials and Methods

2.1 Description of the study area and land use history

The study area is mostly public land and is in the prefecture of Drama, Eastern Macedonia, Northern Greece on the Greek Bulgarian border. The area covers approximately 175006.16 hectares and lies between 61 and 2171 m a.s.l. It is located on the southern slopes of the RMRNP. The climate is a transition from sub-Mediterranean to Central European with a strongly humid continental character. The average annual temperature is 10.3 °C and the average annual precipitation is 875.3 mm throughout the year. In the northern regions, the area is dominated by Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and silver birch (*Betula pendula*) (Oikonomakis and Ganatsas 2012, 2020). Further south, the beech-spruce zone is dominated by beech (*Fagus sylvatica*), Macedonian spruce (*Abies borisii-regis*), black pine (*Pinus nigra*) and bog birch (*Betula pendula* Roth). The RMRNP is home to diverse wildlife, including species such as brown bear (*Ursus arctos*), grey wolf (*Canis lupus*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), chamois (*Rupicapra rupicapra ssp. balcanica*), wild boar (*Sus scrofa*), capercaillie (*Tetrao urogallus*), ptarmigan (*Bonasa bonasia*), golden eagle (*Aquila chrysaetos*), and many others. Seven sub-regions (GR1120003, GR1140001, GR1140002, GR1140003, GR1140004, GR1140008, GR1140009) of the RMRNP have been included in the Natura 2000 network of protected areas (two of them as Special Protection Areas and five as Special Areas of Conservation), two areas have been declared protected natural monuments, seven areas have been declared wildlife reserves, and three areas have been designated as biogenetic stocks by the European Council (Xofis et al. 2022). The RMRNP was declared a National Park in 2009 and is currently under the administration of the Management Body of Rhodope Mountain-Range National Park.

The area is a diverse mosaic of biotopes for different species of flora and fauna, with the forest species as the dominant element of the landscape forming the site conditions, affecting other species of flora and fauna. The type of orographic configuration of the area has resulted in the creation of different microclimatic conditions, and microenvironments. The combination of physiographic factors such as altitude, slope and exposure, as well as soil factors, bioclimatic factors and particular hydrographic conditions (streams, wet - dry soils, water reservoirs, etc.) creates all these microenvironments and different habitats that give rise to different types of flora and fauna. It is noteworthy that the capercaillie, a species with a narrow niche, forms a population in the RMRNP at the southernmost and lower latitudinal edge (Poirazidis et al. 2019). Forest species such as Scots pine, Norwegian spruce and silver birch also form populations at their "niche edge" (Oikonomakis and Ganatsas 2012, 2020).

The history of the site and land use have significantly influenced the vegetation patterns of the area. Before 1922, there were small settlements nearby inhabited by nomadic groups. Aerial photographs from 1945 show the traditional settlements. At that time, the landscape was characterized by extensive meadows and sparse remnants of forest. After 1946, the nomads left the region and a large part of the Central Rhodopes was declared a forbidden zone (Grigoriadis and Kmetova 2006). As a result, the scattered remnants of the parental forest gradually expanded and covered the entire area. Until 1960, the forests were managed by the Forestry Authority, which contributed to a greater expansion of the forest (Oikonomakis and Ganatsas 2020).

2.2 Data sources

The study of land cover change requires a large amount of data, its validation in the field and its continuous updating, as there are factors of variability, such as anthropogenic and natural factors that change the landscape over time (Verburg et al. 2011). Furthermore, it is important to combine and further process all this data to obtain the necessary information and advance scientific research. Considering the above statement, remote sensing (RS) in conjunction with geographic information systems (GIS) was used to study the land cover changes (Alqurashi and Kumar 2013). The data used as the main and supplementary data in this research were as follows:

- Ortho aerial photographs from 1945 and current (2015) RGB aerial photographs with a spatial resolution of 0.25 m, provided by the Greek cadastral service.
- Forest maps are prepared by the local forestry authority for the preparation of forest management plans with field measurements, which are updated every 10 years together with the forest management plans. The scale used was 1:20000. These analog maps were corrected using the high-resolution orthophotographs of the Greek cadastral service and a digital, up-to-date forest cover map was created.
- Digital elevation model (DEM) with a spatial resolution of 30 meters. The DEM was used to create class maps for elevation, aspect and slope.
- Historical climate data (19 bioclimatic variables) were downloaded from the world climatic data website: <http://www.worldclim.org> (accessed 27-9-2024). These variables are commonly used in ecological niche modeling (Hijmans et al. 2005; O'Donnell and Ignizio 2012; Fick and Hijmans 2017).
- Auxiliary data such as:
 1. CORINE 2000 (<http://geodata.gov.gr/dataset/corine-2000>),
 2. Natura 2000 outlines (<https://www.eea.europa.eu/data-and-maps/data/natura-11/natura-2000-spatial-data/natura-2000-shapefile-1>),
 3. Google maps (<https://www.google.gr/maps>)
 4. Ground observations of the area.
- Sentinel 2 mosaiced background using Sentinel 2 images which were acquired in summer with minimum cloud cover. Summer 2024 was used as a reference period.
- Spatial data of settlements and local municipalities from the Hellenic Statistical Authority (<https://www.statistics.gr/en/digital-cartographical-data>)
- 173 circular plots. All plots were established in the field in the period 2023-2024, their geographical coordinates were recorded and plotted on a map. In each plot, all tree species living in the forest that were recorded in the circular plot of 18 m in diameter (1017.36 m²).

All raster and vector datasets were transformed into the Hellenic Geodetic Reference System (HGRS '87).

2.3 Data processing and analysis

Orthoimages from 1945 were used to create land cover maps, which served as a base map for further spatial analysis. The Google Maps background was used as the current base map. A detailed photo interpretation (minimum mapping unit: 0.1 ha) was performed to classify the forest cover according to basic principles (Lillesand et al. 2015). The classification resulted in a four-class cover map, with the following classes: 1 - very sparse land cover (0%-25%), 2 - sparse land cover (26%-40%), 3 - medium land cover (41%-70%), 4 - dense land cover (71%-100%). The classification was performed with a semi-automatic digitizing method using 10 m. vertices.

Forest types were differentiated using the latest available Forest Service Forest maps. The dataset was corrected by any appropriate means, including photo interpretation and field observations, as well as other auxiliary data, such as the Sentinel 2 mosaic background, Land Use/Land Cover (LULC) maps from the CORINE 2000 dataset, and Google maps. The final vegetation cover maps included the following categories (Table 1):

Table 1. Forest types of the main forest species of the study area

Forest Type variable	Species dominating the forest type	Percentage of the study area (%)
FT 1	<i>Quercus spp.</i>	44.32
FT 2	<i>Fagus sylvatica</i>	21.20
FT 3	<i>Pinus sylvestris</i>	10.39
FT 4	<i>Picea abies</i>	5.20
FT 5	<i>Carpinus orientalis</i>	4.22
FT 6	<i>Pinus nigra</i>	2.66
FT 7	<i>Ostrya carpinifolia</i>	2.47
FT 8	<i>Betula pendula</i>	1.05

Other species expansion like *Quercus coccifera* (0.51%), *Populus nigra* (0.08%), *Pinus peuce* (0.04%) and *Abies borisii-regis* (0.02%) were not included in the analysis due to low percentage of land cover of the total area.

To measure land cover changes and the distribution of the forest types, a spatial analysis was performed. For all forest types, the distribution was spatially and quantitatively investigated in old forest stands (existed in 1945) and in new forest stands (established after 1945). Elevation, slope, aspect, bioclimatic variables and distance from parental forest stands were examined separately within the spatial database created with the appropriate GIS analysis, such as spatial overlay, reclassification, spatial query functions with either vector or raster layers (Oikonomakis and Ganatsas 2012, 2020).

Bioclimatic variables were tested for collinearity and correlations. Strong correlations among them can result in over-fitting models in species distribution modelling (Pradhan 2016). The variables were tested through multiple regression models and Variance Inflation Factors (VIF) were calculated. The cutoff value >10 was selected as in other studies (Shekede et al. 2018; Dong et al. 2020; Ncube et al. 2020). Variables with a typical variance inflation factor criterion of VIF >10 (Kim 2019) and a pairwise correlation of $r > 0.7$ were excluded in a stepwise procedure, excluding each time the one with the highest VIF, using the “usdm” package in R environment (Naimi et al. 2014).

As a result, only seven of them were selected: **BIO1, BIO2, BIO3, BIO7, BIO8, BIO11, BIO13** (Table 2). These variables can adequately delineate the tolerances of species in their climatic requirements.

Table 2. Bioclimatic variables used for the MaxEnt models

BIO1	Annual Mean Temp (°C)
BIO2	Mean diurnal range (°C)
BIO3	Isothermality
BIO7	Temp Annual Range (°C)
BIO8	Mean Temperature of Wettest Quarter (3-month interval) (°C)
BIO11	Mean Temperature of Coldest Quarter (3-month interval) (°C)
BIO13	Precipitation of Wettest Month (mm)

Boxplots were used as a data exploration method to gain further insights into the spatial distribution of forest species. The InterQuartile Range (IQR, Q1 – Q3), representing 50% of the distribution, was used as a robust scale measure (Larson 2006; Besseris 2019) to better understand the distribution of forest types in relation to each factor. The “Hmisc” library in R was used to calculate the Q1 and Q3 values weighted by the area of each FT. Using the `wtd.quantile()` function from the Hmisc library in R provides a statistically robust method of calculating quartiles that more accurately reflects the nuances of the data than simple quartiles. By incorporating area covering weights, it provides increased resilience to outliers, better accuracy for stratified data, and improved applicability for survey analysis (Kang and Lee 2005; Carrico et al. 2014).

All the variables were also converted to categorical ones, to cross-tabulate them with forest FTs and to estimate differentiations from expected values, performing the chi-square χ^2 test.

The following categories were selected:

- 1) Forest type categories as in Table 1,
- 2) Aspect: 1-North, 2-Northeast, 3-East, 4-Southeast, 5-South, 6-Southwest, 7-West and 8-Northwest.
- 3) Slope: 0–10%, 10–20%, 20–30%, 30–40%, 40–50%, 50–60%, 60–70%, 70–80% and > 80%,
- 4) Elevation: <800, 800-900, 900-1000, 1100-1200, 1200-1300, 1300-1400, 1400-1500, >=1500 m.

SPSS statistical package, version 29, was used also for statistical analysis.

2.3.1 Landscape Metrics (LMs)

A patch matrix model was utilized, providing an effective framework for analyzing the interactions between spatial patterns and ecological processes in both natural and human-altered landscapes (Ricketts 2001). If the grain sizes of the data vary, it is often necessary to resample the finer data to match the coarser grain. This process involves mapping the category of smaller cells to a single larger cell, as described by Turner and Gardner (2015).

For each forest type (FT), the following metrics were calculated using the FRAGSTATS program: Patch Density (PD), Edge Density (ED), Largest Patch Index (LPI), Aggregation Index (AI), Clumpiness Index (CLUMPY), Splitting Index (SPLIT), Shannon Diversity Index (SHDI), and Simpson's Diversity Index (SIDI). Rasters with a 10m spatial resolution were created for each forest type in 1945 and 2024. Forested areas that existed in both years were considered the same, while new forests (formed from abandoned fields and meadows after 1945) represented areas that altered the landscape by 2024. These metrics were calculated using an 8x8 cell neighborhood at both the class and landscape levels.

PD is expected to increase due to the expansion of new forests and the creation of new patches. However, it could also decrease if patches merge as the forest becomes more continuous. ED may show both increases and decreases, as it reflects patch consolidation but can also indicate a more fragmented or edge-dominated landscape in areas with new forests. Therefore, studying each forest type individually is important for understanding how they behave over time. LPI is expected to increase, as it indicates a growing dominance of one patch, suggesting forest expansion and reduced fragmentation. Both AI and CLUMPY measure the clustering of patches, a sign of forest expansion, while low SPLIT values indicate reduced fragmentation.

Finally, a high SHDI and SIDI (which are calculated for the entire landscape, not for individual classes) indicate greater diversity. This means the landscape is more complex, with a wider variety of land cover types that are more evenly distributed. Detailed descriptions and mathematical formulas for these metrics can be found in McGarigal (1995).

2.3.2 Bioclimatic niche

The bioclimatic niche for each forest type (FT) was defined using bioclimatic variables obtained from Bioclim (<http://www.worldclim.org>). The dataset, consisting of nineteen variables, was used to define the current climate at a local scale. It is based on long-term average data from 1971 to 2000 and represents the climate conditions of the study area (Hijmans et al., 2005).

2.3.3 Environmental niche

The environmental variables considered as potential predictors of forest type (FT) distribution included DEM-derived factors such as aspect, slope, and elevation, as well as the distance from old forest stands and waterways.

2.3.4 Statistical analysis

A three-step hierarchical approach was used to evaluate the primary factors influencing the distribution of each forest type (FT) using MaxEnt software. The first step involved defining a bioclimatic envelope (Čengić et al. 2020; Bandara et al. 2022), based solely on the bioclimatic factors mentioned earlier. Within this suitable bioclimatic envelope, the impact of environmental factors was then analyzed to identify the species' suitable habitat. The second step focused on the environmental envelope, using DEM-derived variables (aspect, slope, elevation), as well as the distance to old forests and waterways (Zhang et al. 2016; Kariminejad et al. 2019). The third step combined all variables, including the specific distances from the old parental clusters of each forest type. This final step allowed for the identification of

the most important factors influencing the distribution of each species. This step helped to understand how each factor behaves when all factors participate in the model for each FT (Amiri et al. 2020; Choi and Lee 2022).

This approach was designed to first highlight the role of bioclimatic parameters, which are crucial for determining species distribution, and then examine the environmental parameters within this envelope that influence both current and potential suitable areas for each FT. This method enables a more precise understanding of habitat suitability factors, which might otherwise be overlooked, and can contribute to the development of effective conservation management plans for each species. A more detailed analysis of the dataset, the area's geomorphology, and cross-checking the results with existing literature can lead to scientific conclusions about the spread potential of each FT.

MaxEnt is a versatile machine-learning method that estimates the probability of distribution of a target species (a statistical model of maximum entropy, closest to uniform) based on data constraints. It uses presence-only data in relation to explanatory variables. MaxEnt has been shown to provide reliable results with small sample sizes (Pearson et al. 2007) and is widely used to explore the current and/or potential distribution of species (Abdelaal et al. 2019). The method works iteratively, generating multiple probability distributions across the grid. It starts with a uniform distribution over the study area, and as each feature and its weight are updated, the model's accuracy improves, progressively favoring suitable areas (Phillips et al. 2006b). In this study the samples were as representative as possible from all regions of the study area. An effort was made to maintain a distance between samples about 2km. At the most cases this was possible, but it was not achieved only where access was difficult due to terrain and road network (Figure 1a, 1b).

3 Results and discussion

3.1 Land cover changes during the period 1945–2024 and forest tree colonization pattern for new-forested areas

The forest expansion during the last 79 years was phenomenal as observed in sub-regions (Oikonomakis and Ganatsas, 2020, 2012). In 1945, the non-forest area was extended to 40.64% of the total area studied, and the forests covered only 59.36%. In 2024, after the gradual colonization of forest species, the area was found to be covered by forest by 92.13%, while only a very low percentage (7.87%) thereof remained as forest openings (Table 3, Fig. 1a, 1b).

These very few areas that remained uncovered by forests are either remote areas (remained grasslands) or rocky areas which do not favor tree establishment, or the remained agricultural areas mainly in southern sites of the area where there are some mountainous villages. Specifically, the area includes 45 small settlements (mountainous villages) within the boundaries of the study area and 15 local communities with a local population of approximately 4800 people, according to Hellenic Statistical Authority.

Photointerpretation of the available images showed that some areas have not been reached yet and remain as forest openings, as the direction of the expansion indicates. Rocky areas are also photo-interpreted in small areas. Forest species colonized almost all the existing non-forested areas (grasslands), which were found to cover 57346.41 ha or 32.77% of the total area (Table 3, Fig. 1a, 1b).

Table 3
Land cover area in studied years and land cover changes

FOREST TYPES	1945		2024		Gains/Losses	
	Area (Ha)	%	Area (Ha)	%	Area (Ha)	%
<i>Abies borisii-regis</i>	11.59	0.01	26.74	0.02	15.15	0.01
<i>Betula pendula</i>	739.35	0.42	1829.84	1.05	1090.49	0.62
<i>Carpinus orientalis</i>	4480.67	2.56	7377.80	4.22	2897.13	1.66
<i>Fagus silvatica</i>	27699.42	15.83	37088.46	21.20	9389.05	5.37
<i>Ostrya carpinifolia</i>	2511.42	1.44	4329.12	2.47	1817.71	1.04
<i>Picea abies</i>	3822.35	2.18	9105.02	5.20	5282.67	3.02
<i>Pinus nigra</i>	3491.04	2.00	4653.84	2.66	1162.80	0.66
<i>Pinus peuce</i>	10.60	0.01	62.74	0.04	52.13	0.03
<i>Pinus silverstis</i>	5348.51	3.06	18160.65	10.38	12812.14	7.32
<i>Populus nigra</i>	96.25	0.06	131.77	0.08	35.52	0.02
<i>Quercus coccifera</i>	349.47	0.20	905.48	0.52	556.01	0.32
<i>Quercus spp.</i>	55314.35	31.61	77549.97	44.32	22235.61	12.71
Meadows	71110.26	40.64	13763.85	7.87	-57346.41	-32.77
Total	174985.28	100.00	174985.28	100.00		

3.2 Types of new forests and trends of forest succession

3.2.1 Physiographic differences between old and new forests and ecological requirements – patterns of the forest expansion

The patterns of the forest expansion were analyzed using environmental factors that arise from the orographic formation of the specific landscape (aspect, slope, elevation). Utilizing this analysis, useful information can be derived about the conditions under which each forest species in the region thrives best.

The Aspect categories are approximately equally distributed in the study area. The forested area in 1945 was also approximately equally distributed in the different aspect categories (Fig. 2 - left). On the contrary, in the newly shaped forests area (the area in which the forests expanded after 1945), S, SE and SW aspects are the more abundant (Fig. 2 - right). The geographical distribution analysis focused on the preference of each species to certain aspect categories, comparatively with the available ones. A chi-test was applied to compare the observed values with the expected values and the results showed that only the distribution of FT8 (*Betula pendula*) is statistically different from the expected distribution in both years (1945 and 2024). *B. pendula* showed a greater distribution on NW, W and North slopes in 1945, while in 2024 expanded more in West, SW and South facing slopes. This was also a result in Oikonomakis and Ganatsas (2020). Moreover, FT7 (*Ostrya carpinifolia*) showed a significant difference from the expected distribution of the Aspect in 1945, occurring mainly in East and SE aspect slopes. This preference remained in 2024 but the difference from expected values was not statistically significant. All the other FTs also show trends, but not statistically significant, which means that the Aspect is not the determining factor influencing these FTs' expansion.

In terms of altitude, FT1 (*Quercus spp.*) expanded almost to the same range in 2024 (Q1: 532 – Q3: 808 m.) as in 1945 (Q1: 521 – Q3: 833 m). All other FTs were slightly distributed in higher altitudes, except FT4 (*Picea abies*). FT4, unlike other FTs, changed its distribution and its newly formed forests have a mean altitude (mean: 1171.1 m, Q1: 744.9 - Q3: 1511.1 m) generally lower than old forests in 1945 (mean: 1375.8 m, Q1: 1369.5 - Q3: 1546.702 m). In other words, spruce forests expanded significantly to lower altitudes than those found in 1945, occupying a considerably larger altitudinal range (Fig. 3).

Regarding land slope as a factor, it is observed that all forest types established new forests in areas with lower slope inclinations (Fig. 4). This observation can be attributed to the fact that these areas were historically utilized by humans, either for agriculture or pasture. As a result, once these areas were abandoned, they became available for recolonization by forest species.

3.2.2 Landscape Metrics (LMs)

The results of the 6 LMs calculated in this study provide an insight into the spatial patterning of the changing landscape. Several results of calculations of the LM provide useful information for the specific area and the expansion of the forest in it, but also for the expansion of each forest type with a dominant forest species. Class Metrics (LM for each class – FT) were calculated to separate the behavior of each FT into the landscape of the study area (Table 4).

PD and ED are not the most important metrics, but they provide useful information in understanding fragmentation trends, particularly if patches are merging and reducing overall patchiness (PD) or edge effects (ED). More specifically, in this study, most forest types show reduced PD values, which indicates that patches are merging as the forest type expands and becomes more continuous. Only the FT4 (*Picea abies* forests) has increased PD values which can be explained by the numerous patches created in open areas, due to the following: a) *Picea abies* acts as pioneer species in the area and perhaps sparse trees existed in previously in open areas which contributed to this behavior. b) *Picea abies* is also a shade-tolerant species having the potential to create patches in previously forest stands dominating by other species (especially in *Pinus sylvestris* forests) (Oikonomakis and Ganatsas, 2012).

ED values were expected to decrease because this metric shows that patches are consolidating, which might suggest forest expansion. This happened in FT1, FT2, FT8 types but in other FTs the ED values had a slight increment indicating a more fragmented or edge-heavy landscape, which needs a careful explanation because the distribution taken account in calculations is only for the specific FT separate from other FTs which might exist between their patches. The creation of new forest patches is easy to happen in this area because there were isolated trees in the previous not forested areas (before 1945) and in other FTs also. These trees are usually the dominant species which create this specific FT formation. Isolated trees also usually are favored by nomadic livestock breeders for shade they provide to them and their livestock (Dyson-Hudson and Dyson-Hudson 1980; Caballero et al. 2009).

The rest of the metrics can provide more valuable information. For example, LPI increased in all FTs, which means that one patch is expanding in dominance, which suggests that the forest is growing and coalescing into a single large patch, reducing fragmentation.

AI and CLUMPY also increased for all FTs, indicating that the patches are clustering together, which is a sign of forest expansion. On the contrary, SPLIT values have been decreased for all FTs which indicates low fragmentation and leads also to the same conclusion of FTs expansion.

Table 4
Landscape Metrics for FTs as classes

Forest type	1945						2024					
	PD	LPI	ED	SPLIT	AI	CLUMPY	PD	LPI	ED	SPLIT	AI	CLUMPY
FT 1	0.65	5.81	31.22	122.50	97.53	0.96	0.34	16.80	28.97	21.93	98.36	0.97
FT 2	0.38	4.02	18.30	394.94	97.14	0.97	0.12	12.11	15.96	61.82	98.13	0.98
FT 3	0.93	0.32	8.08	58607.35	93.37	0.93	0.32	3.80	11.40	657.53	97.23	0.97
FT 4	0.80	0.35	5.81	50337.94	93.37	0.93	1.45	2.31	10.16	1832.80	95.10	0.95
FT 5	0.25	0.51	4.13	25135.08	96.09	0.96	0.13	0.64	5.58	12172.33	96.79	0.97
FT 6	0.24	0.52	4.22	21470.80	94.84	0.95	0.10	0.77	4.64	10120.08	95.75	0.96
FT 7	0.20	0.34	2.86	67563.48	95.20	0.95	0.09	0.49	3.81	21067.10	96.27	0.96
FT 8	0.04	0.07	1.03	683949.52	94.25	0.94	0.01	0.42	0.70	38137.91	98.56	0.99
*In red color are the values which indicate fragmentation (from year 1945 to year 2024) and in green the values which indicate defragmentation												

The same metrics were calculated for the whole landscape of the study area (Table 5). In this analysis, useful information and conclusions about the behavior of the forest can also be drawn. In contrast to Class Metrics (Landscape Metrics for each class), all these metrics showed improvement in the recent year which depicts the overall improvement of landscape. More specifically, PD and ED values decreased, which means that patches have been merged through years and edges have been decreased, leading to direct conclusions of forest expansion and defragmentation of the landscape. This was not obvious in classes where in some FTs, PD and ED values increased.

Table 5
Landscape Metrics for the whole landscape

YEAR	PD	LPI	ED	SPLIT	AI	SHDI	SIDI
1945	4.401	9.7673	59.4769	34.0236	97.0303	1.4852	0.707
2024	4.0717	16.7974	50.8067	15.5038	97.4691	1.6845	0.7357

LPI value also increased, meaning that the forest is growing and coalescing into a single large patch. Also, SPLIT values have been decreased and AI values increased showing that continuous patches were formed.

Finally, the increment of SHDI and SIDI, which both measure landscape diversity, reflect increased species richness and diversity and although not designed for forests, increment of those metrics can indicate changes in landscape composition which affect forests (Peng et al. 2010; Plexida et al. 2014; Sun et al. 2021).

3.2.3 Forest succession modeling using ground truth observations

3.2.3.1 Bioclimatic models

The Bioclimatic models performed as good as indicated by the AUC values (Table 6). Only 7 of the bioclimatic variables were incorporated to models (BIO1, BIO2, BIO3, BIO7, BIO8, BIO11, BIO13).

For FT1, the major determinant was the BIO11 (Mean Temperature of the Coldest Quarter - °C). The FT1 presence was increased as BIO11 values increasing until aprox. from - 1.5 °C to 3.5 °C. Ideally, BIO11 values should be above 0.5 °C. The BIO11 variable has the highest gain when used in isolation and it is also the variable that decreases the gain the most when it is omitted.

For FT2 also BIO11 is the determinant variable (has the highest gain when used and decreases the gain the most when it is omitted). In this case, there is a decrease in *Fagus sylvatica* abundance over 0 °C and it must not exceed 3 °C, due to the tolerance of the species to low temperatures and its non-resistance to high ones, or even due to the occupation of the habitat by more thermophilic species such as oak. Generally, BIO11 was the most important variable for all FTs, except FT6 and FT7.

The behavior of *Pinus nigra* FT, is explained because it has a broader heat tolerance range compared to many other *Pinus* species. On the contrary, the behavior of *Ostrya carpinifolia* FT7 is probably because the species is more water demanding than others in these locations.

Table 6
Bioclimatic MaxEnt models

Forest Type variable	Species dominating the forest type	AUC model values for bioclimatic niche	Variable with highest gain when used in isolation	Variable that decreases the gain the most when it is omitted
FT 1	<i>Quercus spp.</i>	0.685	BIO11	BIO11
FT 2	<i>Fagus sylvatica</i>	0.800	BIO11	BIO11
FT 3	<i>Pinus sylvestris</i>	0.727	BIO11	BIO11
FT 4	<i>Picea abies</i>	0.888	BIO11	BIO11
FT 5	<i>Carpinus orientalis</i>	0.767	BIO11	BIO11
FT 6	<i>Pinus nigra</i>	0.953	BIO7	BIO7
FT 7	<i>Ostrya carpinifolia</i>	0.804	BIO13	BIO13
FT 8	<i>Betula pendula</i>	0.834	BIO11	BIO11

3.2.3.2 Environmental models

The Environmental models performed as good as indicated by the AUC values (Table 7). For FT1 (Oak forests), the major determinant was the distance from older oak stands and the elevation. Oaks seems to increase with elevation increment but aprox. to 250 m., they reach a peak and then their abundance decreases to 1050 m. Further increment of the elevation values implies the reduction of their presence more rapidly. For FT2 (beech forests), the major determinant was also the distance from older beech stands and the elevation. Beech abundance increases with the elevation increment and, in the area, it does not meet the maximum altitude that will be the tipping point for altitude to act as an inhibitory factor in its spread. Similarly, beech forests in Europe, and especially at the southern part of its range

(Spain, Sicily) appear at altitudes higher than 1000 m and they can even be found at elevations of up to 2000 m (Durrant et al. 2016a). This happens because in these low latitude regions the beech can thrive easier at higher altitudes due to milder climatic conditions. Generally, Elevation seems to be the most important variable between the environmental variables to predict species expansion for broadleaf forest species and *P. abies*. On the contrary the expansion of the species *P. sylvestris*, *Quercus spp.*, *Ostrya carpinifolia* and *Betula pendula* expansion appear to be affected mostly by the distance from the parental stands, which is an important factor for all species.

Table 7
Environmental MaxEnt models

Forest Type variable	Species dominating the forest type	AUC model values for environmental niche	Variable with highest gain when used in isolation	Variable that decreases the gain the most when it is omitted
FT 1	<i>Quercus spp.</i>	0.694	Elevation	Elevation
FT 2	<i>Fagus sylvatica</i>	0.828	Elevation	Elevation
FT 3	<i>Pinus sylvestris</i>	0.735	Dist_ <i>P. sylvestris</i>	Dist_ <i>P. sylvestris</i>
FT 4	<i>Picea abies</i>	0.936	Dist_Waterways	Dist_Waterways
FT 5	<i>Carpinus orientalis</i>	0.768	Elevation	Elevation
FT 6	<i>Pinus nigra</i>	0.964	Aspect	Aspect
FT 7	<i>Ostrya carpinifolia</i>	0.840	Dist_ <i>Ostrya</i>	Dist_ <i>Ostrya</i>
FT 8	<i>Betula pendula</i>	0.875	Dist_ <i>Betula</i>	Elevation

3.2.3.3 MaxEnt models with all available parameters and response curves

The final MaxEnt models show the maximum AUC values since all parameters are used and, they give an insight into which variables are the most important when used in isolation or when omitted from all available variables (Table 8). The way each variable affects the presence of each FT can be further studied only in response curves.

Table 8
MaxEnt models with all available variables included.

Forest Type variable	Species dominating the forest type	AUC model values for niche	Variable with highest gain when used in isolation	Variable that decreases the gain the most when it is omitted
FT 1	<i>Quercus spp.</i>	0.703	Elevation	Dist_ <i>Quercus</i>
FT 2	<i>Fagus sylvatica</i>	0.832	Elevation	Aspect
FT 3	<i>Pinus sylvestris</i>	0.748	Dist_ <i>P. sylvestris</i>	Dist_ <i>P. sylvestris</i>
FT 4	<i>Picea abies</i>	0.932	BIO11	Dist_Waterways
FT 5	<i>Carpinus orientalis</i>	0.798	Elevation	BIO13
FT 6	<i>Pinus nigra</i>	0.976	BIO7	Aspect
FT 7	<i>Ostrya carpinifolia</i>	0.879	Dist_ <i>Ostrya</i>	Dist_ <i>Ostrya</i>
FT 8	<i>Betula pendula</i>	0.886	BIO11	BIO11

The response curves from each factor were analyzed to gain more thorough visions and deeper understanding of how each factor influenced the spread of each species.

For FT1 the most important bioclimatic variable was BIO11 (Mean Temperature of Coldest Quarter) and from environmental parameters the Elevation which was the determinant for its expansion. Both parameters have to do with the cold tolerance of those species. The reaction of *Quercus* species of the area to the average low quarter temperature seems to be positive with the increasing BIO11 value, reaching a maximum increase aprox. 2.5 °C and the altitudinal range seems to have negative result above 1000m (Fig. S1). These results are consistent with the literature which suggests that the optimal conditions for *Q. frainetto* are for winter temperatures 0–6 °C and elevation between 200 and 800 m. For *Q. pubescens* are 2–8 °C and 200-1500m, respectively, and for *Q. cerris* – 2–6 °C and 1000m. Finally, distance to parental stands seems to be the crucial factor showing a decline in probability of FT1 with the increase of distance.

For FT2 the most important bioclimatic variable was also BIO11 and from environmental parameters the elevation. The optimal value for BIO11 is near 0 °C and for Elevation values above 1100 m asl (Fig. S2). Neither of these parameters are acting restrictively because it can be found in Europe at low temperature locations to -5 °C (Durrant et al. 2016a). and altitudinal range of 500–1800 m. (Stupar and Čarni 2017), but both variables seem to have a strong influence of predicting the presence of the species. The Aspect variable seems to play also an important role decreasing the gain of modeling if omitted showing high preference to North and East slopes and low preference (cloglog < 0.5) to NE, SE and SW aspect slopes. Distance from parental stands seems to have also a crucial contribution since *Fagus sylvatica* (like oak species) is characterized by heavy seeds, low dispersal capacity about 20 m (Wagner et al. 2010), while it can regenerate well by resprouting.

For FT3, the most important bioclimatic factor was also BIO11 and from the environmental factors the distance from old *Pinus sylvestris* stands. It appears to be unaffected by most factors examined in the specific study area, so the distance from the old stands plays the most important role in its expansion. *P. sylvestris* is a light-demanding pioneer species and can colonize recently disturbed sites if competition and grazing pressure are low (Mátyás et al. 2004). Consequently, the species is the most suitable for the area as there were many abandoned fields to colonize. Additionally, due to its huge range it can coexist with most of the boreal species of Europe and Asia such as oaks, birch, beech, spruce, fir and other pines (Durrant et al. 2016b). The same behavior is displayed by the species in the study area, providing that the most typical boreal species exist there. The response to BIO11 of the species is an increase of abundance above - 2 °C and a decrease above its maximum (about - 0,5 °C). Its abundance also decreases smoothly with the increase of distance from the old *P. sylvestris* stands (Fig. S3).

For FT4, the most important bioclimatic factor was also BIO11, and the most important environmental factor was the distance to waterways. Optimum BIO11 values are about - 2.5 to -1 °C and its abundance increases as the distance from waterways increases (Fig. S4). *Picea abies* is known to be sensitive to summer drought or waterlogged conditions (Caudullo et al. 2016) and this is mainly due to its seedling's sensitivity to drought (Vlahakis 2023). This is possibly the reason why distance to waterways plays an important role as an environmental factor for species expansion in the area. In this case, it shows a negative correlation with distance to waterways possibly due to sensitivity of young seedlings or the competition of more water-demanding species.

For FT5, the most important bioclimatic factor was again BIO11, and the most important environmental factor was elevation. When all factors were examined together with a maxent model, BIO13 was the variable that decreases the gain the most when it is omitted. Abundance of *Carpinus orientalis* increases with the increasing BIO11 value reaching its maximum in 3.5 °C, increasing with the increment of BIO13 reaching its maximum around 70 mm/month, and it usually colonizes low elevated areas about 200–800 m. asl (Fig. S5). *Carpinus orientalis*, as it is more thermophilous species (Varol et al. 2022) reaches its maximum when minimum temperatures (BIO11) are about 3.5 °C (1.5 -4 °C) and altitudes about 200–800 m. a.s.l. *Carpinus orientalis* is also a xerophilous species (Varol et al. 2022) and this is maybe the reason why BIO13 is an important variable to its expansion. Although its biggest concentration is in areas where monthly precipitation is near 70 mm., which is reasonable for a broadleaf forest species, it also maintains a good concentration in lower rainfall areas.

For FT6, the most important bioclimatic factor was BIO7, and the most important environmental factor was Aspect. *Pinus nigra* populations were found in very wide temperature annual ranges (> 30 °C) and in southern slopes (4 = SE and 5 = South) (Fig. S6). *Pinus nigra* is known for its adaptability to a wide range of climatic conditions, including both warmer and drier environments. This resilience allows it to grow in regions with hot summers, unlike some other pine species that are more restricted to cooler or temperate zones (e.g. *Pinus sylvestris*). However, its heat tolerance is still less than that of species specifically adapted to very hot climates, such as some Mediterranean pines like *P. halepensis* and *P. brutia* (Ivetić et al. 2021). Also, this behavior may have to do with the fact that this species has been used in this area for reforestation to sites selected by the Forest Service with adverse site conditions to other forest species.

For FT7, the most important bioclimatic factor was BIO13, and the most important environmental factor was distance from parental stands. The optimal value for BIO13 is between 60–70 mm/month which shows a preference to humid areas. It also exhibits proximity dependence on parent stands, but it exists sparsely in remote areas too (Fig. S7). *Ostrya carpinifolia* is a stenohydric plant, meaning it maintains consistent transpiration and osmotic pressure even under moderate drought stress. It can colonize windy, sunny slopes but thrives in rainy or humid areas, such as deep ravines and canyons, where air humidity is high. It grows better in semi-shaded or sunny and humid sites. This explains why in the northernmost part of its range this species behaves as a light-demanding pioneer that prefers sunny and warm places, while in the southernmost countries it grows better in semi-shaded and more humid sites (Korkut and Guller 2008; Pasta et al. 2016).

The species *Betula pendula* (FT8) is a cold tolerating species showing its optimal BIO11 values around 0 °C (-1, 1 °C). This is obvious with the altitudinal specialization that it exhibits, showing its larger expansion at higher altitudes of the area (800–1800 m. asl.). An important variable for its expansion is also the distance from parental forest stands, as it is dependent on the proximity to them (Fig. S8). However, it is also observed in lower concentrations in large distances from parental forest stands, because it is light-demanding forest species with extremely small (light) abundant seeds, thus, it thrives as pioneers during early stages of secondary vegetation succession (Beck et al. 2016b; Oikonomakis and Ganatsas 2020).

4 Conclusion

The results of this study, which utilized field data, remote sensing data and supplementary cartographic data using RS and GIS technologies, confirm previous reports that land abandonment in Europe's mountainous regions is leading to a significant increase in forest cover and a reduction in open habitats. This trend was mapped and measured using landscape metrics for the forest, but also for each of the area's important forest species, which occur in large numbers. This defragmentation improves habitat connectivity, which is crucial for the movement and genetic flow of forest-dwelling species, especially for large mammals, and contributes to the conservation of biodiversity overall. In addition, this ecological succession has positive effects on biodiversity, especially for large mammals, carbon sequestration, recreation and other ecosystem services.

For fauna species that depend on open habitats, however, a decline in populations is to be expected. While forest ecosystems benefit from less fragmentation, the loss of landscape heterogeneity due to the reduction of open habitats could lead to a decline in some fauna species. From the current study it is also obvious the difference in forest composition in the old forests, which are more mature and closer to climax stage. The newer forests are mostly covered by pioneer species (early successional stages) which are light demanding and quickly expanding such as *Betula pendula*, *Pinus sylvestris* and *Pinus nigra*, while the older forests are covered by later successional species such as *Fagus sylvatica*, *Picea abies*, *Carpinus orientalis* and *Ostrya carpinifolia*. *Quercus spp.* species which are met in the area can be considered as intermediate species which are placed in lower altitudes of the area (mostly 500–800 m. a.s.l.). *Picea abies* also behaves both as pioneer species and as late successional, since it can tolerate shade.

As a conclusion, a fragmented landscape favors light demanding and pioneer forest species, while a more compact landscape leads to a more stable forest composition near to climax stage. The metric of fragmentation suggests that a balanced mosaic of forests and open areas is necessary to support a variety of species. The homogenization of the landscape, driven by the uncontrolled expansion of forests, may lead to a loss of biodiversity for species that rely on different habitat structures. The overall impact of this trend, whether positive or negative, depends on conservation priorities and local socio-ecological factors.

Nevertheless, monitoring land-use change over time using time- and cost-efficient methods is crucial to achieve conservation goals set at the policy level. While the preservation of natural processes such as ecological succession is essential for maintaining the integrity of ecosystems, planning must also consider local specificities. Targeted political and land policy interventions are therefore required. While natural reforestation offers ecological benefits, it is also important to strike a balance between forest expansion and the preservation of some open habitats. Spatially explicit planning based on landscape metrics should guide efforts to conserve both forest ecosystems and open habitats to prevent biodiversity loss.

As regards forest species, it is crucial to use scientific knowledge of their requirements, to manipulate them more efficiently and make more precise silvicultural interventions. The forest management must consider future projections of forest vegetation composition and the best achievement of the desired future forest, that will meet all those conditions contemplated by the research, combining all known forest ecosystem services and forest products with the appropriate hierarchy.

Declarations

Author Contribution

N.O. wrote the main manuscript and prepared all figures and tables. P.G. and M.T. supervised and reviewed the manuscript.

Data Availability

Ortho aerial photographs from 1945 and current (2015) provided by the Greek cadastral service (<https://maps.gov.gr/gis/map/>). Digital elevation model (DEM) with a spatial resolution of 30 meters (<https://dwtkns.com/srtm30m/>). Historical climate data

(<http://www.worldclim.org>)Natura 2000 outlines (<https://www.eea.europa.eu/data-and-maps/data/natura-11/natura-2000-spatial-data/natura-2000-shapefile-1>)Google maps (<https://www.google.gr/maps>)Sentinel 2 images (<https://browser.dataspace.copernicus.eu>)Spatial data of settlements and local municipalities from the Hellenic Statistical Authority (<https://www.statistics.gr/en/digital-cartographical-data>)

References

1. Abdelaal M, Fois M, Fenu G, Bacchetta G (2019) Using MaxEnt modeling to predict the potential distribution of the endemic plant *Rosa arabica* Crép. in Egypt. *Ecol Inform* 50:68–75
2. Alqurashi A, Kumar L (2013) Investigating the use of remote sensing and GIS techniques to detect land use and land cover change: A review. *Advances in Remote Sensing*
3. Ambs D, Schmied G, Zlatanov T, et al (2024) Regeneration dynamics in mixed mountain forests at their natural geographical distribution range in the Western Rhodopes. *For Ecol Manage* 552:121550. <https://doi.org/10.1016/J.FORECO.2023.121550>
4. Amiri M, Tarkesh M, Jafari R, Jetschke G (2020) Bioclimatic variables from precipitation and temperature records vs. remote sensing-based bioclimatic variables: Which side can perform better in species distribution modeling? *Ecol Inform* 57:101060
5. Bandara APMJ, Madurapperuma BD, Edirisinghe G, et al (2022) Bioclimatic envelopes for two bat species from a tropical island: Insights on current and future distribution from ecological niche modeling. *Diversity (Basel)* 14:506
6. Baskent EZ, Keles S, Yolasigmaz HA (2008) Comparing multipurpose forest management with timber management, incorporating timber, carbon and oxygen values: A case study. *Scand J For Res* 23:105–120. <https://doi.org/10.1080/02827580701803536>
7. Bazzaz FA, Sipe TW (1987) Physiological Ecology, Disturbance, and Ecosystem Recovery. 203–227. https://doi.org/10.1007/978-3-642-71630-0_10
8. Beck P, Caudullo G, de Rigo D, Tinner W (2016a) *Betula pendula*, *Betula pubescens* and other birches in Europe: distribution, habitat, usage and threats
9. Beck P, Caudullo G, Rigo D de, Tinner W (2016b) *Betula pendula*, *Betula pubescens* and other birches in Europe: distribution, habitat, usage and threats. In J. San-Miguel-Ayanz, D. de Rigo, G. Caudullo, T. Houston Durrant, & A. Mauri (Eds.). Publication. In: *European Atlas of Forest Tree Species* (p. e010226)
10. Benayas JMR, Martins A, Nicolau JM, Schulz JJ (2007) Abandonment of agricultural land: An overview of drivers and consequences. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources* 2:. <https://doi.org/10.1079/PAVSNNR20072057>
11. Besseris GJ (2019) Evaluation of robust scale estimators for modified Weibull process capability indices and their bootstrap confidence intervals. *Comput Ind Eng* 128:135–149
12. Bowen ME, McAlpine CA, House APN, Smith GC (2007) Regrowth forests on abandoned agricultural land: A review of their habitat values for recovering forest fauna. *Biol Conserv* 140:273–296. <https://doi.org/10.1016/J.BIOCON.2007.08.012>
13. Buttoud G (2002) Multipurpose management of mountain forests: which approaches? *For Policy Econ* 4:83–87
14. Caballero R, Fernandez-Gonzalez F, Badia RP, et al (2009) Grazing systems and biodiversity in Mediterranean areas: Spain, Italy and Greece. *Pastos* 39:9–154
15. Caliskan S, Aslan V, Tandoğan M, et al (2025) Influence of gamma irradiation treatments on the germination, moisture, viability and radicle length of *Quercus frainetto* acorns. *Int J Radiat Biol* 1–10
16. Cărbăuş MC, Şofletea N (2014) European hornbeam (*Carpinus betulus* L.) and oriental hornbeam (*C. orientalis* Mill.): a review on origin, evolution, phytocoenology and genetics.
17. Cardille JA, Turner MG (2017) Understanding Landscape Metrics. *Learning Landscape Ecology* 45–63. https://doi.org/10.1007/978-1-4939-6374-4_4
18. Carrico C, Gennings C, Wheeler DC, Factor-Litvak P (2014) Characterization of Weighted Quantile Sum Regression for Highly Correlated Data in a Risk Analysis Setting. *J Agric Biol Environ Stat* 20:100. <https://doi.org/10.1007/S13253-014-0180-3>
19. Caudullo G, Tinner W, De Rigo D (2016) *Picea abies* in Europe: distribution, habitat, usage and threats
20. Čengić M, Rost J, Remenska D, et al (2020) On the importance of predictor choice, modelling technique, and number of pseudo-absences for bioclimatic envelope model performance. *Ecol Evol* 10:12307–12317
21. Chetan N, Praveen K, one GV-P, 2014 undefined (2014) Delineating ecological boundaries of Hanuman langur species complex in peninsular India using MaxEnt modeling approach. *journals.plos.org*N Chetan, KK Praveen, GK VasudevaPloS one, 2014•[journals.plos.org](https://doi.org/10.1371/journal.pone.0087804) 9:87804. <https://doi.org/10.1371/journal.pone.0087804>

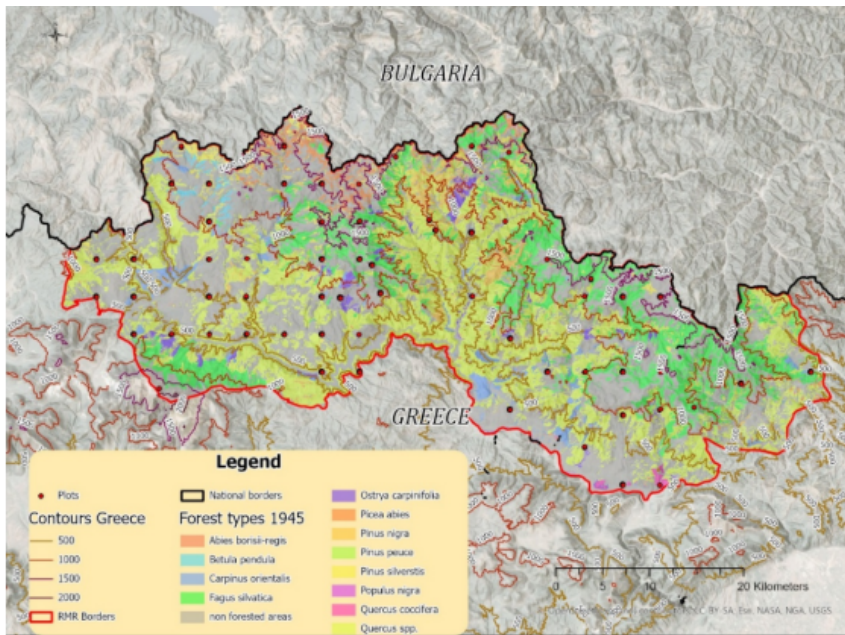
22. Choi J, Lee S (2022) Principal bioclimatic variables of ten dominant plant species in Korea wetland using the Maxent model. *Ecol Eng* 183:106729
23. Dong X, Ju T, Grenouillet G, et al (2020) Spatial pattern and determinants of global invasion risk of an invasive species, sharpbelly *Hemiculter leucisculus* (Basilevsky, 1855). *Science of The Total Environment* 711:134661
24. Durrant T, de Rigo D, Caudullo G (2016a) *Fagus sylvatica* in Europe: distribution, habitat, usage and threats
25. Durrant TH, Rigo D De, Caudullo G (2016b) *Pinus sylvestris* in Europe: distribution, habitat, usage and threats. *European Atlas of Forest Tree Species* 132–133
26. Dyson-Hudson R, Dyson-Hudson N (1980) Nomadic pastoralism. *Annu Rev Anthropol* 15–61
27. Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International journal of climatology* 37:4302–4315
28. Fois M, Cuenca-Lombraña A, Fenu G, Bacchetta G (2018) Using species distribution models at local scale to guide the search of poorly known species: Review, methodological issues and future directions. *Ecol Modell* 385:124–132
29. Fortini P, Proietti E, Stojnic S, et al (2025) First Results of a Geometric Morphometric Analysis of the Leaf Size and Shape Variation in *Quercus petraea* Across a Wide European Area. *Forests* 16:70
30. Glück P (2002) Property rights and multipurpose mountain forest management. *For Policy Econ* 4:125–134
31. Grande JM, Orozco-Valor PM, Liébana MS, Sarasola JH (2018) Birds of Prey in Agricultural Landscapes: The Role of Agriculture Expansion and Intensification. *Birds of Prey: Biology and conservation in the XXI century* 197–228. https://doi.org/10.1007/978-3-319-73745-4_9
32. Grigoriadis N, Kmetova E (2006) 14. Rhodope Mountains. *The Green Belt of Europe: From Vision to Reality* 137
33. Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. *For Ecol Manage* 148:185–206. [https://doi.org/10.1016/S0378-1127\(00\)00535-1](https://doi.org/10.1016/S0378-1127(00)00535-1)
34. Guillaera-Aroita G, ... JL-M in E, 2014 undefined (2014) Maxent is not a presence–absence method: a comment on Thibaud et al. *Wiley Online Library* 5:1192–1197. <https://doi.org/10.1111/2041-210X.12252>
35. Hijmans RJ, Cameron SE, Parra JL, et al (2005) VERY HIGH RESOLUTION INTERPOLATED CLIMATE SURFACES FOR GLOBAL LAND AREAS. *INTERNATIONAL JOURNAL OF CLIMATOLOGY Int J Climatol* 25:1965–1978. <https://doi.org/10.1002/joc.1276>
36. Hinkov G, Kachova V, Velichkov IV, Dinca L (2019) The Effect of Grazing on Old Oak Forests from Eastern Rhodopes Mountains, Bulgaria
37. Ivetić V, Tsakalidimi M, Ganatsas P, et al (2021) Freezing and heating tolerance of *Pinus nigra* seedlings from three south to North Balkan provenances. *Sustainability* 13:9290
38. Jensen AJ (2018) Crossing Corridors: Wildlife use of jumpouts and undercrossings along a highway with wildlife exclusion fencing
39. Kang SJ, Lee M (2005) Q-convergence with interquartile ranges. *J Econ Dyn Control* 29:1785–1806. <https://doi.org/10.1016/J.JEDC.2004.10.004>
40. Kariminejad N, Hosseinalizadeh M, Pourghasemi HR, et al (2019) Evaluation of factors affecting gully headcut location using summary statistics and the maximum entropy model: Golestan Province, NE Iran. *Science of the Total Environment* 677:281–298
41. Kelly JR, Harwell MA (1990) Indicators of ecosystem recovery. *Environ Manage* 14:527–545. <https://doi.org/10.1007/BF02394708/METRICS>
42. Kennard DK (2002) Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia. *J Trop Ecol* 18:53–66. <https://doi.org/10.1017/S0266467402002031>
43. Kim JH (2019) Multicollinearity and misleading statistical results. *Korean J Anesthesiol* 72:558–569
44. Korkut S, Guller B (2008) Physical and mechanical properties of European Hophornbeam (*Ostrya carpinifolia* Scop.) wood. *Bioresour Technol* 99:4780–4785
45. Kubota Y, Katsuda K, Kikuzawa K (2005) Secondary succession and effects of clear-logging on diversity in the subtropical forests on Okinawa Island, southern Japan. *Biodivers Conserv* 14:879–901. <https://doi.org/10.1007/s10531-004-0657-4>
46. Kuijper DPJ, Cromsigt JPGM, Churski M, et al (2009) Do ungulates preferentially feed in forest gaps in European temperate forest? *For Ecol Manage* 258:1528–1535. <https://doi.org/10.1016/J.FORECO.2009.07.010>
47. Kupfer JA (2012) Landscape ecology and biogeography: Rethinking landscape metrics in a post-FRAGSTATS landscape. *Prog Phys Geogr* 36:400–420. <https://doi.org/10.1177/0309133312439594>
48. Larson MG (2006) Descriptive statistics and graphical displays. *Circulation* 114:76–81

49. Liepiņš K, Bleive A (2025) The Potential of European Beech (*Fagus sylvatica* L.) in the Hemiboreal Baltic Region: A Review. *Forests* 16:109
50. Lillesand TM, Kiefer RW, Chipman JW (2015) Remote Sensing and Image Interpretation. 704
51. Lloret F, Escudero A, Lloret J, Valladares F (2024) An ecological perspective for analysing rural depopulation and abandonment. *People and Nature* 6:490–506. <https://doi.org/10.1002/PAN3.10606>
52. Mafuwe K, Broadley S, Moyo S (2022) Use of maximum entropy (Maxent) niche modelling to predict the occurrence of threatened freshwater species in a biodiversity hotspot of Zimbabwe. *Afr J Ecol* 60:557–565. <https://doi.org/10.1111/AJE.12928>
53. Martynova M, Sultanova R, Khanov D, et al (2021) Forest management based on the principles of multifunctional forest use. Taylor & FrancisM Martynova, R Sultanova, D Khanov, E Talipov, R Sazgutdinova *Journal of Sustainable Forestry*, 2021•Taylor & Francis 40:32–46. <https://doi.org/10.1080/10549811.2020.1734025>
54. Mátyás C, Ackzell L, Samuel CJA (2004) EUFORGEN technical guidelines for genetic conservation and use for Scots pine (*Pinus sylvestris*). Bioversity International
55. McGarigal K (1995) FRAGSTATS: spatial pattern analysis program for quantifying landscape structure
56. McGarigal K, Marks BJ (1994) FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Version 2.0. Forest Science Department, Oregon State University, Corvallis 67:
57. McIntosh R (1995) The history and multi-purpose management of Kielder Forest. *For Ecol Manage* 79:1–11
58. Merow C, Smith MJ, Silander Jr JA (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36:1058–1069
59. Naimi B, Hamm NAS, Groen TA, et al (2014) Where is positional uncertainty a problem for species distribution modelling? *Ecography* 37:191–203. <https://doi.org/10.1111/J.1600-0587.2013.00205.X>
60. Navarro LM, Pereira HM (2015) Rewilding abandoned landscapes in Europe. *Rewilding European Landscapes* 3–23. https://doi.org/10.1007/978-3-319-12039-3_1
61. Ncube B, Shekede MD, Gwitira I, Dube T (2020) Spatial modelling the effects of climate change on the distribution of *Lantana camara* in Southern Zimbabwe. *Applied Geography* 117:102172
62. Neel MC, McGarigal K, Cushman SA (2004) Behavior of class-level landscape metrics across gradients of class aggregation and area. *Landsc Ecol* 19:435–455. <https://doi.org/10.1023/B:LAND.0000030521.19856.CB/METRICS>
63. O'Donnell MS, Ignizio DA (2012) Bioclimatic Predictors for Supporting Ecological Applications in the Conterminous United States. US Geological Survey Data Series 691 10
64. Oikonomakis N, Ganatsas P (2020) Secondary forest succession in silver birch (*Betula pendula* roth) and scots pine (*pinus sylvestris* l.) southern limits in europe, in a site of natura 2000 network – an ecogeographical approach. *For Syst* 29:1–16. <https://doi.org/10.5424/fs/2020292-15680>
65. Oikonomakis N, Ganatsas P (2012) Land cover changes and forest succession trends in a site of Natura 2000 network (Elatia forest), in northern Greece. *For Ecol Manage* 285:153–163. <https://doi.org/10.1016/j.foreco.2012.08.013>
66. Pasta S, de Rigo D, Caudullo G (2016) *Ostrya carpinifolia* in Europe: distribution, habitat, usage and threats. European Atlas of Forest Tree Species Publ Off EU, Luxembourg
67. Pearson RG, Raxworthy CJ, Nakamura M, Townsend Peterson A (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J Biogeogr* 34:102–117
68. Pedrini P, Sergio F (2001) Golden eagle *aquila chrysaetos* density and productivity in relation to land abandonment and forest expansion in the alps. *Bird Study* 48:194–199. <https://doi.org/10.1080/00063650109461218>
69. Peng J, Wang Y, Zhang Y, et al (2010) Evaluating the effectiveness of landscape metrics in quantifying spatial patterns. *Ecol Indic* 10:217–223
70. Phillips S, Anderson R, modelling RS-E, 2006 undefined (2006a) Maximum entropy modeling of species geographic distributions. Elsevier 190:231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
71. Phillips SJ, Anderson RP, Schapire RE (2006b) Maximum entropy modeling of species geographic distributions. *Ecol Modell* 190:231–259
72. Plexida SG, Sfougaris AI, Ispikoudis IP, Papanastasis VP (2014) Selecting landscape metrics as indicators of spatial heterogeneity—A comparison among Greek landscapes. *International Journal of Applied Earth Observation and Geoinformation* 26:26–35
73. Plieninger T, Hui C, Gaertner M, Huntsinger L (2014) The Impact of Land Abandonment on Species Richness and Abundance in the Mediterranean Basin: A Meta-Analysis. *PLoS One* 9:98355. <https://doi.org/10.1371/journal.pone.0098355>

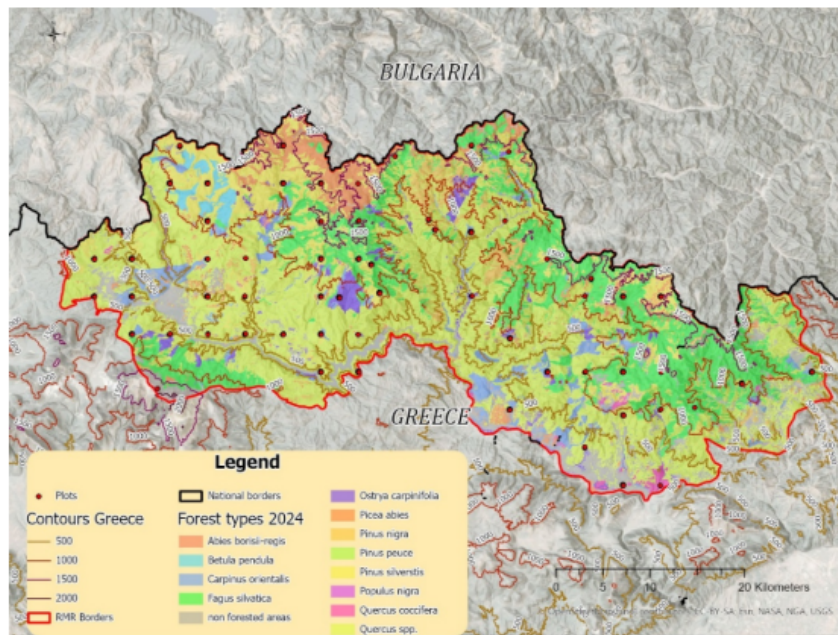
74. Poirazidis K, Bontzorlos V, Xofis P, et al (2019) Bioclimatic and environmental suitability models for capercaillie (*Tetrao urogallus*) conservation: Identification of optimal and marginal areas in Rodopi Mountain-Range National Park (Northern Greece). *Glob Ecol Conserv* 17:e00526
75. Pradhan P (2016) Strengthening MaxEnt modelling through screening of redundant explanatory bioclimatic variables with variance inflation factor analysis. *Researcher* 8:29–34
76. Przybylski P, Związek T, Kowalczyk J, Słowiński M (2025) Research perspectives on historical legacy of the Scots pine (*Pinus sylvestris* L.): Genes as the silent actor in the transformation of the Central European forests in the last 200 years. *Elementa: Science of the Anthropocene* 13:
77. Quaranta L, Di Marzio P, Fortini P (2025) *Quercus cerris* Leaf Functional Traits to Assess Urban Forest Health Status for Expeditious Analysis in a Mediterranean European Context. *Plants* 14:285
78. Raghavan R, Heath A, Acarology KL... and A, 2020 undefined (2012) Predicting the potential distribution of *Amblyomma americanum* (Acari: Ixodidae) infestation in New Zealand, using maximum entropy-based ecological niche. *Springer* 7:32202. <https://doi.org/10.1371/journal.pone.0032202>
79. Regos A, Domínguez J, Gil-Tena A, et al (2016) Rural abandoned landscapes and bird assemblages: winners and losers in the rewilding of a marginal mountain area (NW Spain). *Reg Environ Change* 16:199–211
80. Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. *Am Nat* 158:87–99
81. Riecken U, Ullrich K, Lang A (2010) 1 . A vision for the Green Belt in Europe. 3–10
82. Risser PG (1987) Landscape Ecology: State of the Art. 3–14. https://doi.org/10.1007/978-1-4612-4742-5_1
83. Sarasola JH, Grande JM, Negro JJ (2018) Birds of prey: Biology and conservation in the XXI century. *Birds of Prey: Biology and conservation in the XXI century* 1–522. <https://doi.org/10.1007/978-3-319-73745-4>
84. Shekede MD, Murwira A, Masocha M, Gwitira I (2018) Spatial distribution of *Vachellia karroo* in Zimbabwean savannas (southern Africa) under a changing climate. *Ecol Res* 33:1181–1191
85. Skidmore A, Franklin J, ... TD-... J of G, 2011 undefined (2011) Geospatial tools address emerging issues in spatial ecology: a review and commentary on the Special Issue. *Taylor & Francis* 25:337–365. <https://doi.org/10.1080/13658816.2011.554296>
86. Stupar V, Čarni A (2017) Ecological, floristic and functional analysis of zonal forest vegetation in Bosnia and Herzegovina. *Acta Bot Croat* 76:15–26. <https://doi.org/10.1515/botcro-2016-0041>
87. Sun H, Hu J, Wang J, et al (2021) Rspd: A novel remote sensing index of plant biodiversity combining spectral variation hypothesis and productivity hypothesis. *Remote Sens (Basel)* 13:3007
88. Syfert MM, Smith MJ, Coomes DA (2013) The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS One* 8:e55158
89. Terry A, Ullrich K, Riecken U (2006) The green belt of Europe: from vision to reality. IUCN, Gland, Switzerland and Cambridge, UK
90. Tesei G, Bonanomi G, D'Ottavio P, et al (2025) Under the Crown of Scattered Beech (*Fagus sylvatica*): Impact on Plant Community, Soil Resources, and Fungal Diversity. *Journal of Vegetation Science* 36:e70021
91. Turner MG (2005) Landscape ecology: What is the state of the science? *Annu Rev Ecol Evol Syst* 36:319–344. <https://doi.org/10.1146/ANNUREV.ECOLSYS.36.102003.152614/CITE/REFWORKS>
92. Turner MG, Gardner RH (2015) Introduction to Landscape Ecology and Scale. *Landscape Ecology in Theory and Practice* 1–32. https://doi.org/10.1007/978-1-4939-2794-4_1
93. Uuemaa E, Antrop M, Roosaare J, et al (2009) Landscape metrics and indices: an overview of their use in landscape research. *biblio.ugent.be* 3:1
94. Vacek Z, Cukor J, Vacek S, et al (2023) Role of black pine (*Pinus nigra* JF Arnold) in European forests modified by climate change. *Eur J For Res* 142:1239–1258
95. Vakkari P (2009) Silver birch (*Betula pendula*)
96. Varol T, Cetin M, Ozel HB, et al (2022) The effects of climate change scenarios on *Carpinus betulus* and *Carpinus orientalis* in Europe. *Water Air Soil Pollut* 233:45
97. Verburg PH, Neumann K, Nol L (2011) Challenges in using land use and land cover data for global change studies. *Glob Chang Biol* 17:974–989
98. Vlahakis WC (2023) Sensitivity of Norway Spruce (*Picea abies*) to inundation.
99. Wagner S, Collet C, Madsen P, et al (2010) Beech regeneration research: From ecological to silvicultural aspects. *For Ecol Manage* 259:2172–2182. <https://doi.org/10.1016/J.FORECO.2010.02.029>

100. Wang X, Zhang Z, Zhang Q, et al (2023) Afforested and abandoned land ecosystems exhibit distinct soil microbial biomass stoichiometric homeostasis over chronosequence. *Land Degrad Dev* 34:5389–5400. <https://doi.org/10.1002/LDR.4852>
101. Warren D, applications SS-E, 2011 undefined (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Wiley Online Library* 21:335–342. <https://doi.org/10.1890/10-1171.1>
102. Warren DL, Matzke NJ, Iglesias TL (2020) Evaluating presence-only species distribution models with discrimination accuracy is uninformative for many applications. *J Biogeogr* 47:167–180
103. Wu J, Wang D, Bauer ME (2007) Assessing broadband vegetation indices and QuickBird data in estimating leaf area index of corn and potato canopies. *Field Crops Res* 102:33–42. <https://doi.org/10.1016/j.fcr.2007.01.003>
104. Xofis P, Spiliotis JA, Chatzigiovanakis S, Chrysomalidou AS (2022) Long-Term Monitoring of Vegetation Dynamics in the Rhodopi Mountain Range National Park-Greece. *Forests* 2022, 13, 377
105. Yousaf A, Hadi R, Khan N, et al (2022) Identification of suitable habitat for *Taxus wallichiana* and *Abies pindrow* in moist temperate forest using maxent modelling technique. *Saudi J Biol Sci* 29:103459. <https://doi.org/10.1016/J.SJBS.2022.103459>
106. Zhang L, Liu S, Sun P, et al (2016) Using DEM to predict *Abies faxoniana* and *Quercus aquifolioides* distributions in the upstream catchment basin of the Min River in southwest China. *Ecol Indic* 69:91–99

Figures



a



b

Figure 1

a. Land cover and forest types in the year 1945.

Non forested areas cover a large percentage of the total area

b. Land cover and forest types in the year 2024. Previously non forested areas have been covered mainly by oaks, beech and pines (mainly *P. sylvestris*)

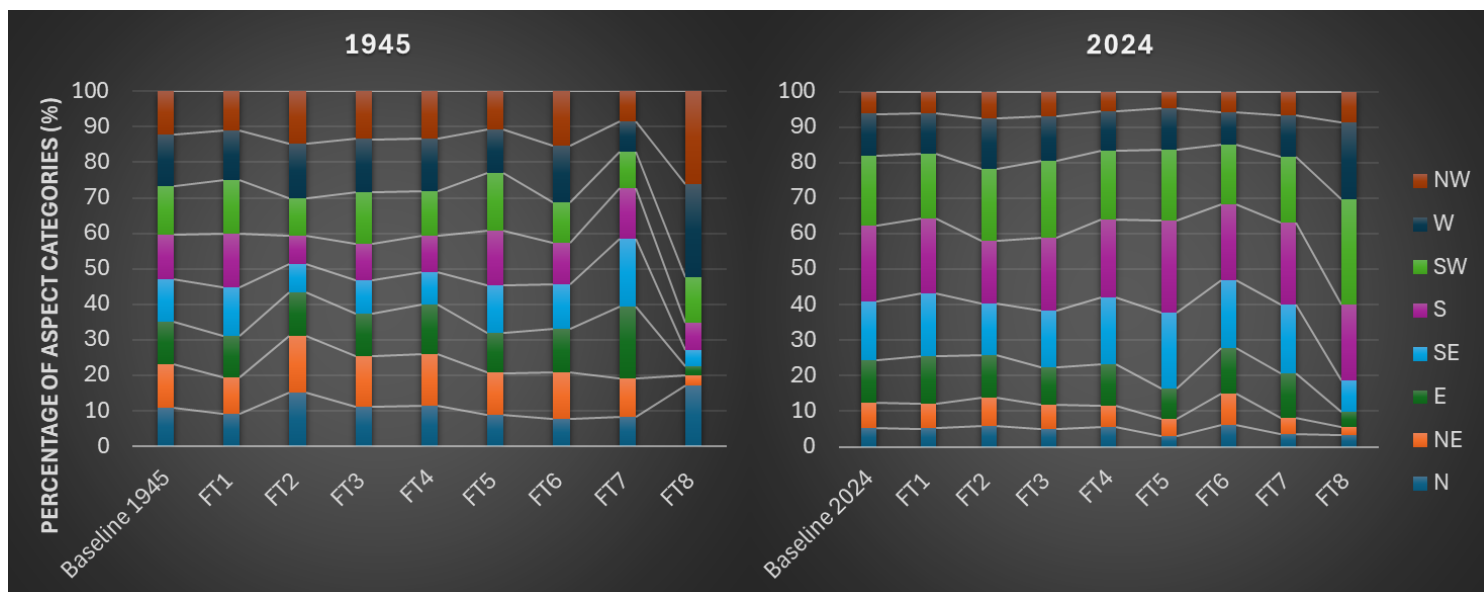


Figure 2

Distribution of aspect categories for baseline (1945 left and 2024 right) and for each FT in relation to baseline.

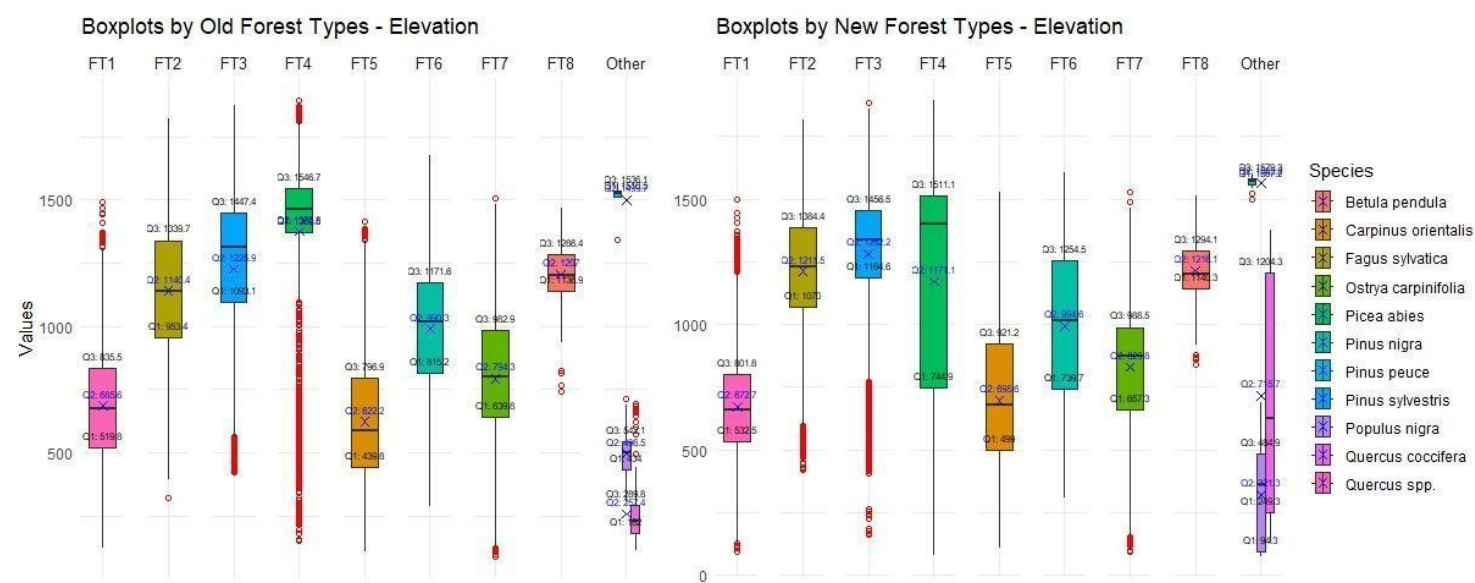


Figure 3

Boxplots of the expansion of forest types (dominant forest species) in relation to Elevation

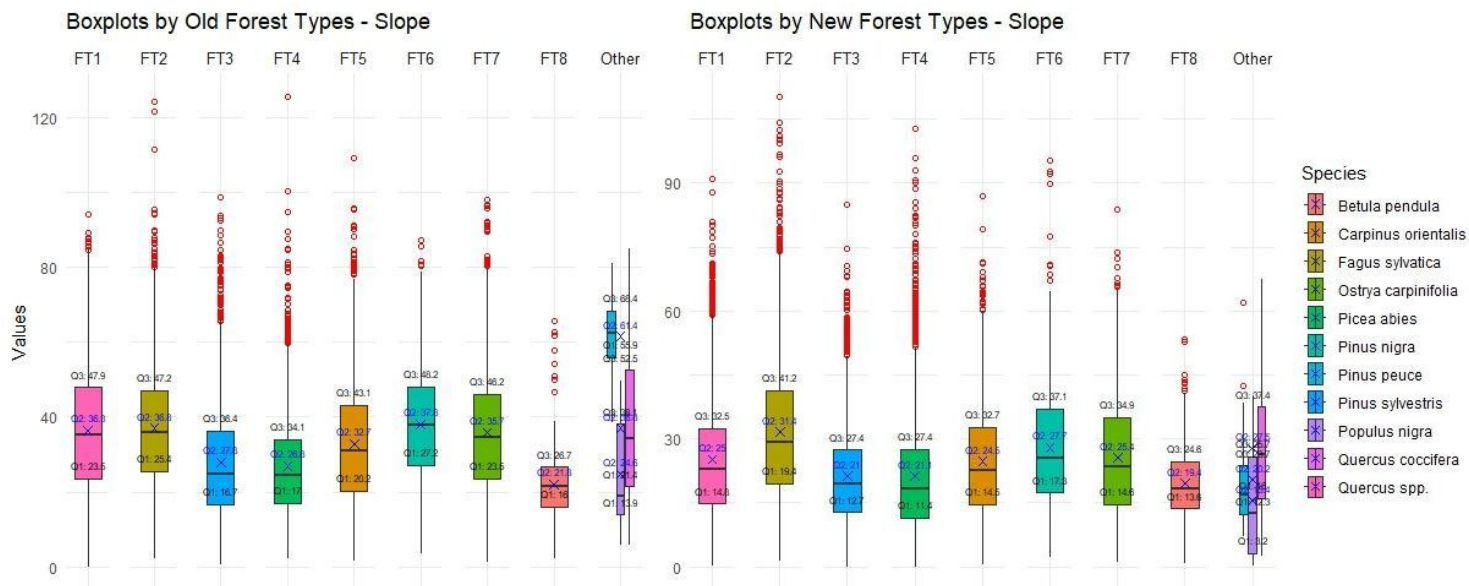


Figure 4

Boxplots of the expansion of forest types (dominant forest species) in relation to Slope

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Supplementarymaterial.docx](#)