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Exploring spatial and temporal resilience in socio-ecological systems: evidence from sacred forests in Epirus, Greece

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Abstract

1. Socio-ecological resilience is the capacity of a system to adapt to changing ecological and social disturbances. Its assessment is extremely important to integrate long-term management of ecological and social features of natural ecosystems. This is especially true for Sacred Natural Sites, such as sacred forests and groves, where it can reveal the influence of social processes in ecosystem recovery or degradation.

2. Using tree ages determined through dendrochronology and tree population size-class distributions collected in five sacred forests in Epirus (NW Greece), we explore spatial and temporal dynamics of resilience in a socio-ecological system, identifying which cultural and social elements characterize resilience in space and time.

3. Our main results show that over past centuries sacred forests in Epirus underwent periods of varying tree establishment rate, depending on the intensity of human activities and historical disturbance events.

4. We also identified strong evidence of the role of the social component (i.e., the church and associated cultural praxis) in determining the spatial extent of the forests' current recovery phase, and thus the overall resilience of the system.

5. *Policy implications.* Appreciation of the ways sacred forests' ecological resilience is linked to changing socio-cultural praxis over both temporal and spatial scales is crucial for guiding conservation and restoration strategies. We argue that greater attention should be paid to the role of the social component of socio-ecological systems and specifically for sacred natural sites that provide both a nucleus of established forest habitat and the conditions necessary for forest recovery and restoration.

Keywords

Dendrochronology; depopulation; Socio-ecological resilience; Sacred Natural sites; tree size-class distribution.

1. Introduction

Ecological resilience is the capacity of an ecosystem to retain its structure and functionality after being subjected to damage caused by disturbances, which alter one or more of its determining conditions (Gunderson, 2000). This concept is particularly useful to understand how complex ecosystems react to exogenous disturbances, such as climate change, other anthropogenic stresses, or natural disasters (Angeler & Allen, 2016; Reyer et al., 2015; Seidl et al., 2016). Over recent decades numerous studies have assessed spatial and temporal patterns of the ecological resilience of forest ecosystems worldwide, sometimes linked to advocacy for greater efforts to tackle climate change and human disturbances to ecosystems (Muñoz et al., 2021; Ratajczak et al., 2018; Seidl et al., 2016; Sterk et al., 2017; Willis et al., 2018). While human activities are often the cause of system perturbation, they can also play an important role as a component of the system (the so-called socio-ecological system, SES) and in its recovery (Berkes & Folke, 1998). This perspective is becoming more prominent in resilience studies and acknowledges the fact that systems with both ecological and social features need to be assessed and managed in an integrated and holistic way (Sterk et al., 2017). Socio-ecological resilience has been assessed in many recent studies (e.g., Kelly et al., 2015; Mngumi, 2021; Nikinmaa et al., 2023; Ruiz-Ballesteros, 2011), yet quantitative evidence on how the social component influences the temporal and spatial dimensions of ecological recovery in forest SES is still lacking.

Sacred Natural Sites (SNS) are a particular type of SES defined as “areas of land or water having special spiritual significance to peoples and communities” (Oviedo et al., 2005). SNS include mountains, rivers and lakes, forests, caves, and islands and they range in scale from single trees, ponds or rocks, to wooded groves or forests up to entire mountain ranges. They represent places of worship and memory and are not restricted to any given region or culture (Bhagwat & Rutte, 2006). SNS are an exemplar of systems with a strong, culturally-based social component that would be expected to have a major impact on their resilience. Assessing socio-ecological resilience in SNS is extremely relevant to shed light on the social processes that influence ecosystem recovery or degradation (e.g., traditional religious taboos; Marini Govigli et al., 2021), with implications for forest management and nature conservation.

Sacred forests and groves are SNS that have been recognized as providers of important benefits related to human-nature relationships (Wild & McLeod, 2008). These contributions to people's quality of life are even more important in a context where urban populations are reviving forest-based spiritual practices (Roux et al., 2022). Sacred forests in Europe and the Mediterranean region have been subject to a complex history of successive cycles of decline associated with socio-economic instability and the undermining of existing cultural values, followed by periods of recovery (Roux et al., 2022). While the role of sacred forests in preserving traditional knowledge and management practices (cultural contributions) and environmental resources (ecological contributions) have both been widely explored (e.g., Avtzis et al., 2018; Dudley et al., 2012; Sahle et al., 2021), there is little empirical evidence on the linkage between the two (e.g. Plieninger et al., 2022; Stara, 2022; Alivizatou, 2021), and specifically of the impact of cultural praxes and processes (e.g., traditional management, taboos and informal norms of forest conservation and management) on the socio-ecological resilience of sacred forests. This knowledge is crucial to predict how sacred forests will develop in the future and how conservation interventions can best be directed.

In our study, we focus on a group of sacred forests located in Epirus (NW Greece) dating back to the 17th and 18th centuries. Assessing resilience in such a study setting is particularly novel because it provides us with the opportunity to examine the system's resilience from its inception (i.e. the inception of sanctity), a dimension that is often lost over time in most studies assessing the resilience of long-term spiritual SES. Our question is: *can we identify which cultural and social elements characterize sacred forest resilience in space and time?* Based on previous research conducted in Epirus, which reported the existence of strong cultural processes that persisted through time and their influence on the floristic composition and structure of local sacred forests (Marini Govigli et al., 2020), this study takes a further step hypothesising that:

- sacred forests in Epirus recovered ecologically during periods of reduced human disturbance, a change in the system's social component linked to regional changes in human population (temporal ecological resilience);
- the cultural locus of sacred forests (e.g., the church, where present) has a major influence on forest structure (spatial social resilience)

To test our first hypothesis, we used tree ages determined through dendrochronology and current tree population size-class distributions as indicators of forest dynamics, and its legacy in the current structure of the forests. To test the second hypothesis, we assessed the spatial relationship between a series of forest structure indicators and the locus of cultural practices. The presence of a few spaced, old trees located near a church (or icon stand or other religious structure) is typically identified as marking the cultural centre of the site itself (Aerts et al., 2016; Lagopoulos, 2002). We hypothesised a decline in tree stature and density with distance from the church, which may represent a dynamic equilibrium between the diminution of the strength of cultural taboos on tree cutting and livestock grazing, and a process of more recent forest expansion through natural colonization from the nucleus of protected forest adjacent to the church. Based on these insights, we explore patterns of temporal and spatial resilience across the studied sacred forests. Our results are valuable for forest conservation managers as they offer insights into the spatio-temporal responsiveness of spiritual SES to significant external societal changes.

2. Material and methods

2.1 Study area

The study area is in the north of the Epirus region (northwestern Greece), within the local administrative units of Zagori and Konitsa (Figure 1). In this area, recent studies have unveiled a large network of sacred forests (Avtzis et al., 2018; Govigli et al., 2020; Marini Govigli et al., 2021; Stara et al., 2016). These forests were established during the early period of the Ottoman occupation (15th-17th century) through a number of different forms of governance from strict religious regimes to community agreements resulting in overlapping and varied restrictions ranging from controlled use to strict prohibition of trespassing (Stara et al., 2016). Historical evidence indicates that the development of the sacred forests generally occurs concurrently with the foundation of the village.

While examples of sacred forests have been identified throughout the Mediterranean basin, they are often associated with monastic settlements (in the Northern part of the Mediterranean; Mallarach et al., 2012) and Muslim burial grounds (in the Southern Mediterranean basin; Jäckle et al., 2013). No Mediterranean areas have, so far, been shown to have such a diversity of ritual praxes as those identified in northwestern Greece. These sacred forests are therefore an excellent basis for revealing the relationship between forest structure and variation in cultural practices.

Based on previous ethnographic research, we selected five villages and a specific sacred forest associated with each to cover different vegetation types, elevations, and founding regimes, specifically religious dedication and excommunication (further described in the Supporting Information- S1). These were the sacred forests of: (i) Agios Nikolaos in Livadakia, belonging to the village of Vitsa (a broadleaved forest dominated by oak species); (ii) Kouri, village of Mazi (also broadleaved oak); (iii) Mereao, village of Palioseli (dominated by black pine); (iv) Agia Paraskevi, village of Vovoussa (comprising black pine and mixed broadleaf forest); and (v) Toufa, village of Greveniti (a broadleaved forest dominated by European beech).

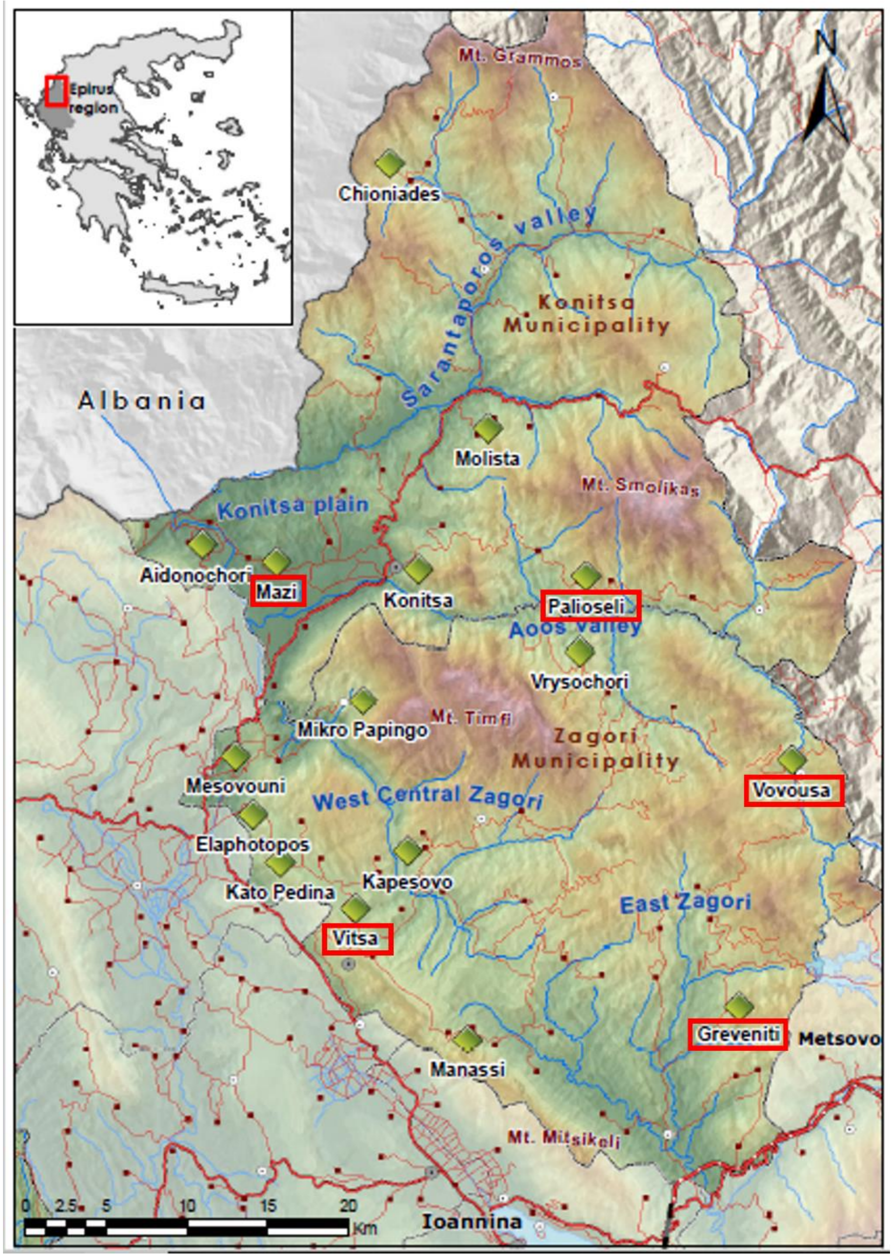


Figure 1. Location of the villages and associated sacred forests (indicated by red boxes) selected for this study in the Epirus region, Greece. Green diamonds indicate locations of other sacred forests where ethnographic research has been conducted. Adapted from Stara et al. (2016).

2.2 Tree size-class distributions

Tree size-class distribution is commonly used as an indicator of forest age structure and can be used to infer the disturbance history of the stand (e.g., Burkhart et al., 2012; Lai et al., 2013). Size-class distributions for each site were generated from data arising from a forest inventory performed in 2014-2015. This took the form of a systematic sampling design of 15 m x 15 m plots employed by fitting a square grid orientated to the site's cardinal directions. Within each plot, all trees with a diameter at breast height (i.e. at 1.3 m, dbh) ≥ 5 cm were identified and the dbh measured. A detailed description of the inventory procedures and variables is provided by Marini Govigli et al. (2020). The inventory recorded 135 plots in total across the five study sites. Size class distributions were obtained for the dominant tree taxon in each forest and an aggregation of the remaining taxa, using 5 cm dbh classes. The distributions were calculated based on numbers of individual stems, due to the presence of many multi-stemmed trees. The dominant tree taxa in each forest were identified in Marini Govigli et al. (2020): deciduous *Quercus* spp. in Vitsa and Mazi (*Quercus cerris, Quercus frainetto, Quercus pubescens,* and additionally *Quercus trojana* in Mazi), *Pinus nigra* in Vovoussa and Palioseli, and *Fagus sylvatica* in Greveniti.

2.3 Estimation of tree ages from cores

To investigate the temporal relationship between forest structure and changing cultural practices (temporal socio-ecological resilience), we used a combination of tree aging through dendrochronology and assessment of tree population size-class structures. Wood cores were extracted from trees of the dominant taxon in each forest at a stem height between 0.6 and 1 m. In the pine-dominated forests (Vovousa and Palioseli; trees cored in year 2015), the tree with the largest diameter in each plot was selected for coring, whereas in the oak- and beech-dominated forests (Vitsa, Mazi; year 2014 and Greveniti; year 2015) the second largest individual in each plot was selected, as a high proportion of the largest trees were found to have cavities in their centre. In such sites a second stage of sampling in 2015 added cores from an additional 86 individuals to fill in gaps in the diameter size range of cored trees (with dbh ≥ 5 cm). Only single-stemmed trees were selected for coring with one core taken per tree, to respect the sensitivity of the local communities to activities that may damage the trees in their sacred forests. This resulted in a total of 221 individual cores for the five study areas available for further analyses.

Coring was conducted following the procedure outlined in Phipps (1985). Cores were mounted dry and prepared by polishing them with progressively finer grades of sandpaper. Cores were then scanned at 1200 dpi, and the annual ring widths recorded using the tree ring dating software Coorecorder (Cybis Elektronik & Data, 2013b) and CDendro (Cybis Elektronik & Data, 2013a). Tree age was estimated by counting rings in the cores backwards from the first ring behind the bark to the pith. In this process, 16 cores were rejected, as rotten, damaged, or with rings that could not be distinguished. This reduced the available dataset to 205 cores (Supporting Information- S2). As the oldest deciduous oaks were often rotten in the middle and the angle of the core often did not intersect the oldest rings in the tree, not all the cores included the chronological centre of the tree (i.e., the pith). To avoid repeat coring of trees in such culturally sensitive sites, a methodology to estimate partial and incomplete cores was used. Models to estimate missing rings are widely used in the literature when using partial wood cores (e.g. Frelich & Graumlich, 1994; Norton et al., 1987). In this study, we followed the method of Rozas (2003) to estimate partial (visible arch of the inner rings) and incomplete (missing the inner arch and the pith) cores, which involved testing eight different methodologies to estimate missing rings. The estimation methods and their results are provided in the Supporting Information S3. Using the method which produced the smallest error, the ages of 89 partial and 54 incomplete cores were quantified (Supporting Information S4). Both linear and non-linear regression models were used to establish the relationship between tree age and dbh of the dominant taxon at each site. Model assumptions were tested and influential points showing a Cook's distance larger than 0.5 were carefully investigated. If such outliers corresponded to incomplete cores, then they were interpreted as error in the age estimation process and removed. Three error estimations of this kind were removed from the sample. The power law regression was selected for the estimation process as it maximized the average model fit (R^2) across the five sites.

Ages of all trees with stems ≥ 5 cm dbh of the dominant taxon at each site were predicted from the site-specific power law age-diameter regressions. This was used to transpose the size class distributions of the dominant taxon in each site to estimated age. These distributions were smoothed using non-parametric kernel density estimations (KDE). KDE is a non-parametric estimation that enables the fitting of a smooth curve (kernel density) to a set of observations, in this case the number of stems, allowing for the assessment of emerging patterns across tree class distributions. By placing the age-frequency KDE curves against historical village population data, we were able to assess whether drastic socio-economic changes in the region leading to significant rural depopulation resulted in recovery of the sacred forest systems characterised by a pulse of establishment of extant dominant trees. Human population data at village level were retrieved from available census data for the period 1868-2011[1].

2.4 Tree structural indicators

To investigate the spatial relationship between forest structure and the locus of cultural practices (spatial socio-ecological resilience), we ran a series of linear Pearson correlation tests between four structural indicators measured at the plot level and the plot's distance from the church building (for the three sacred forests with a central church building: Vitsa, Mazi, and Vovoussa). We utilized the church building and its precinct as the culturally-defined core of the system, based on anthropological and anecdotal evidence that identifies the church as the spiritual focal point around which the sacred forest develops. In folk religion, the church is personified as an epiphany (manifestation) of the deity (Stara et al., 2015), and villagers tend to be reluctant to interfere with the forest in its visual proximity. For instance, as expressed in an interview (Stara, 2012, page 61): "[Husband]: *Our field was downhill, close to the river but in view of the monastery, which belongs to the Virgin Mary. We never go to cut wood there. We went a few times, but my wife since then refuses to go.'* [Wife]: *'The field still belongs to us, not to the monastery, and it is located far away from it, but because of the view, I had the feeling that Virgin Mary was observing me. I cannot cut trees there' "* (Interview: 15/9/2006, Village Agios Minas). Furthermore, the largest trees in each sacred forest tend to be those situated closer to the church, frequently positioned next to the altar (typically in the eastern part of the building for Orthodox Christian churches).

The measured indicators are:

- the quadratic mean diameter (QMD, cm), conventionally used in forest ecology to measure the central tendency of a distribution, rather than the arithmetic mean. QMD gives more weight to larger trees within a plot (Curtis & Marshall, 2000);

[1] Official Greek statistics often do not match the real population living in villages, especially in rural areas. This is because many non-permanent residents prefer to register in their ancestral village rather than their usual residence elsewhere in Greece (Green, 2016). To overcome this issue, available datasets were verified using additional secondary sources, archive data, and ethnographic research. The final reconstructed population data are provided in Appendix 2.

- the Gini coefficient (GC), a 0-1 measure of inequality that is particularly useful to map tree size inequality and variability (Bourdier et al., 2016);
- the proportion of basal area larger than the QMD (BALM), an indicator that describes the skewness of the tree distribution curve (Valbuena et al., 2014);
- the total stem density (N, stems・ha^{-1}).

These indicators provide quantitative descriptions of forest structure in terms of tree diameter distribution (QMD), tree size variability (GC), skewness (BALM), and density (N) (Adnan et al., 2019). Forest structural indicators were calculated for all tree stems with dbh ≥5 cm by pooling the individual stem-level information obtained at plot-level and were computed separately for the dominant taxon in each forest (Section 2.2 and Supporting Information S5). We mapped and georeferenced the location of the churches and plots using ArcGIS (ESRI, 2020) spatial software. All statistical analyses were performed using the statistical language R (R Core Team, 2017).

3. Results

3.1 Tree size-class distributions

In all five sites the stem size class distributions of all species showed an overall steep, approximately exponential, decline in tree numbers with increasing size class (

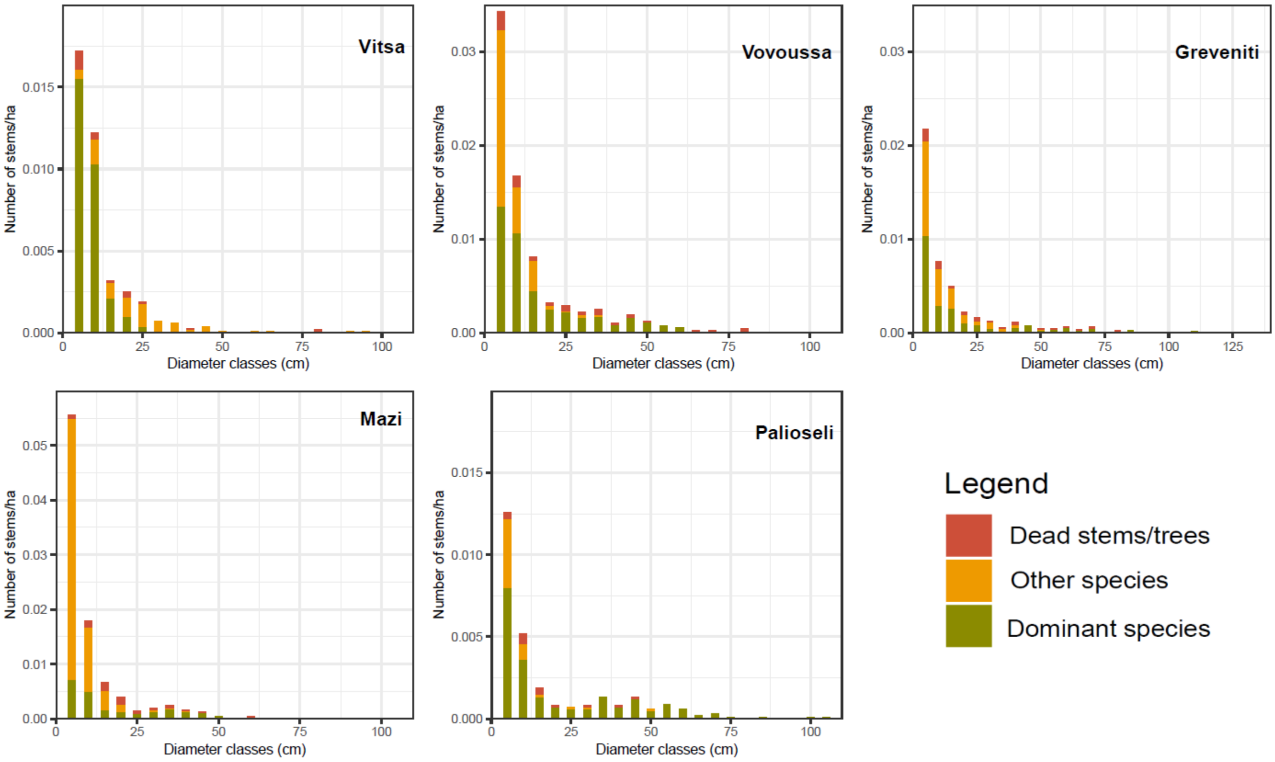


Figure 2). However, in the forests of Mazi and Palioseli there was clear evidence of bimodality in the distribution with a second peak in numbers in the 30-45 cm dbh range. When the distributions are restricted to the dominant taxon in each forest, clear evidence of a second peak, in medium size ranges (varying from ca. 20 to 70 cm dbh per site), is shown in all five sites (

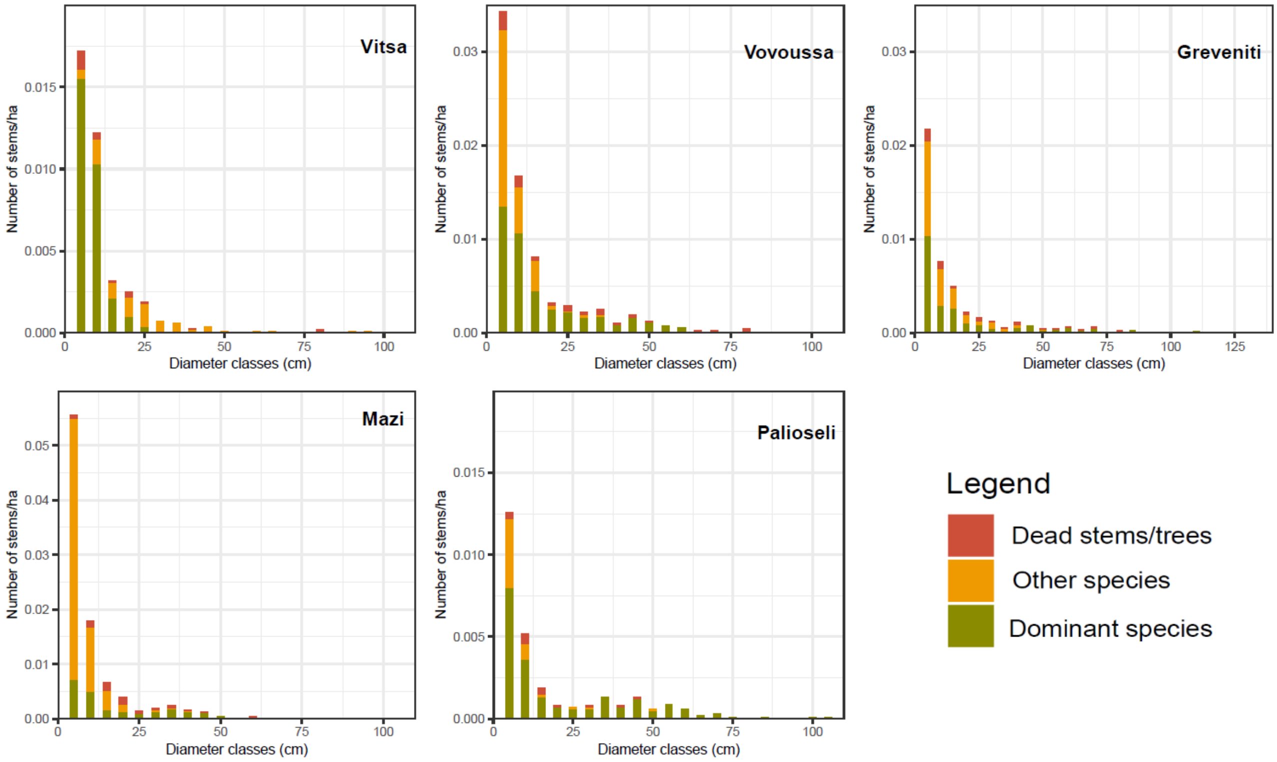


Figure **2** and Supporting information S6).

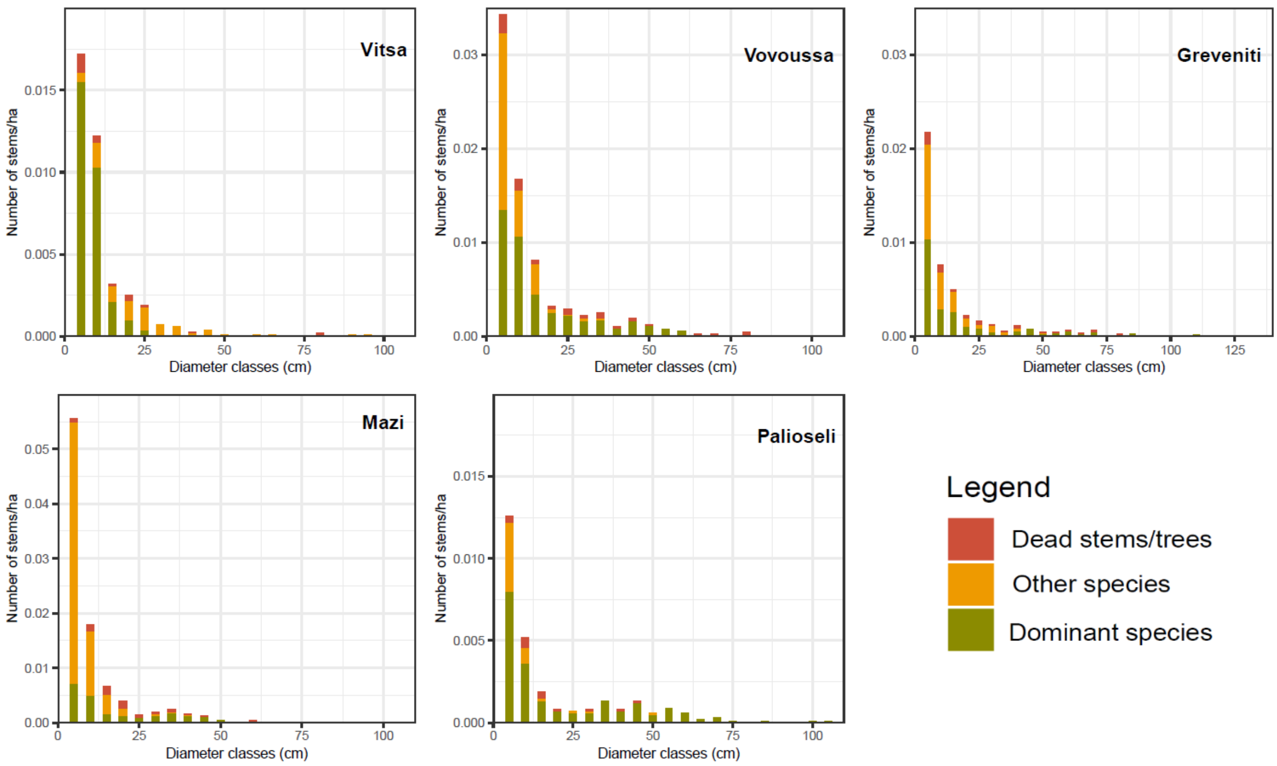


Figure 2. Tree stem diameter size-class distributions in the five study forests distinguishing between the

dominant taxon in each site, other tree taxa and dead trees/stems. Size classes are defined in 5 cm dbh classes by the lower interval limit.

3.2 Tree age and human population trends

The median age (50th percentile) of all the trees from which wood cores were taken lay within a range of 88-148 years before the sample year (2014 or 2015), with the third quartile (75th percentile) being greater than 140 years for every site's age distribution (Supporting information S7). Amongst all sampled trees, the oldest *Quercus* spp. tree was located at Vitsa and dated to the year 1671, the oldest *P. nigra* (dated 1621) was at Vovoussa and the oldest *F. sylvatica* (dated 1817) was at Greveniti. The oldest tree cored in Mazi was dated 1773 (a 241 years old *Quercus* spp. at the sampling date), while the oldest tree in Palioseli was dated 1765 (a 250 years old *P. nigra* at the sampling date).

As expected, there was a significant positive relationship between dbh and age of the cored trees with model coefficients of determination (R^2) all above 0.5 (Figure 3).

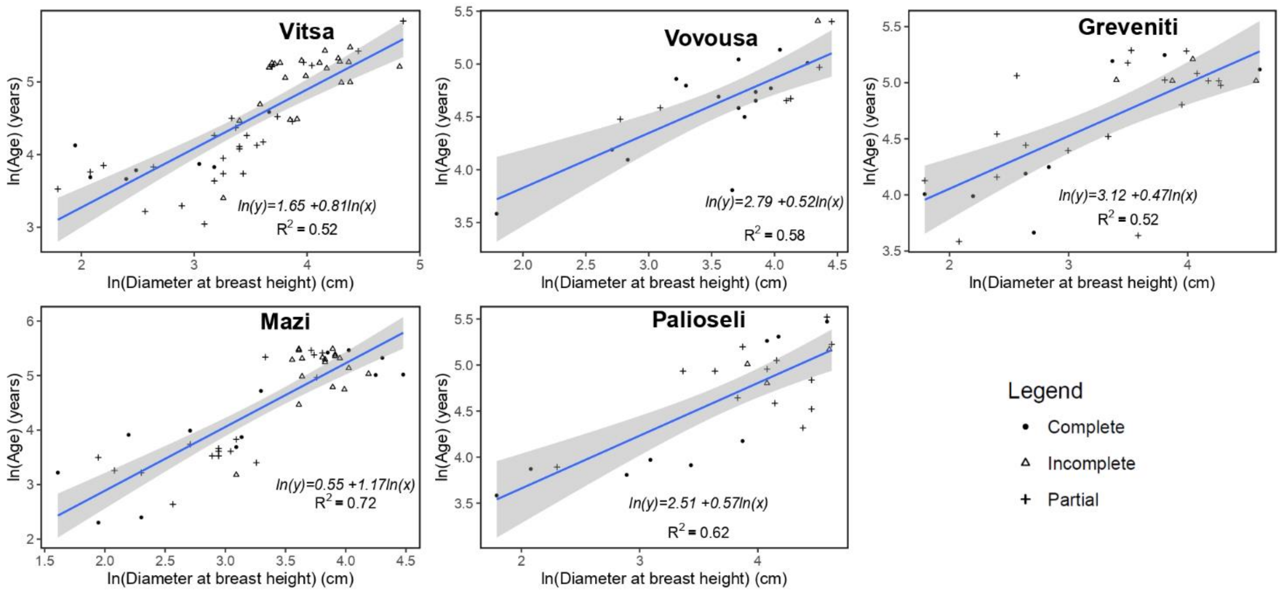


Figure 3. Age-diameter at breast height (1.3 m) power law regressions for dominant trees from which wood cores were sampled in the five study sites. The 95% confidence intervals around each regression line are shown by the grey shading. The cores that were complete or for which ages were estimated from incomplete or partial cores are shown by different symbols.

The relationship between age and diameter presented in Figure 3 was used to generate kernel densities of estimated ages of all trees measured for dbh in each of the five sites (Figure 4). The results show comparable timing of tree establishment events across sites. Mazi and Vitsa (both oak-dominated) are characterized by two density peaks of tree ages: one of trees established in the middle of the 20th century (between 1975 and 1985 in Mazi, and 1940-1955 in Vitsa), and an earlier one occurring during the 19th century (between 1850 and 1900 in Mazi, and 1765-1845 in Vitsa), which is more clearly visible in Mazi. Vouvousa and Palioseli (both pine-dominated) are characterized by three density peaks: one of trees established around 1950-1960, another during 1890-1915, and the first between 1825 and 1850. The beech dominated site (Greveniti) is characterized by a single peak of trees established around 1950-1960 with peaks of lower intensity dating back to 1865 and 1880 respectively.

By comparing trends in tree age density with human population at the village level (Figure 4, secondary y-axis), a correlation between periods of tree establishment and drops in human population level is apparent in four out of the five sites. The 1940-1955 peak in Vitsa during and immediately following World War II was preceded by a population drop of 43.1% some 30 years earlier (between 1902 and 1913); the 1815-1850 peak in Vovoussa was preceded by a population drop of 72% some 10 years earlier (between 1812 and 1856); the 1940-1960 and 1890-1915 density peaks in Palioseli are associated with a population drop of 60.4% (between 1895 and 1928) and 38.9% (between 1940 and 1951) respectively. The increase in tree recruitment in Greveniti follows a drop in population of 43% between 1913 and 1920 and reaches its peak during 1950-1960 following a drop in population of 45% between 1940 and 1951.

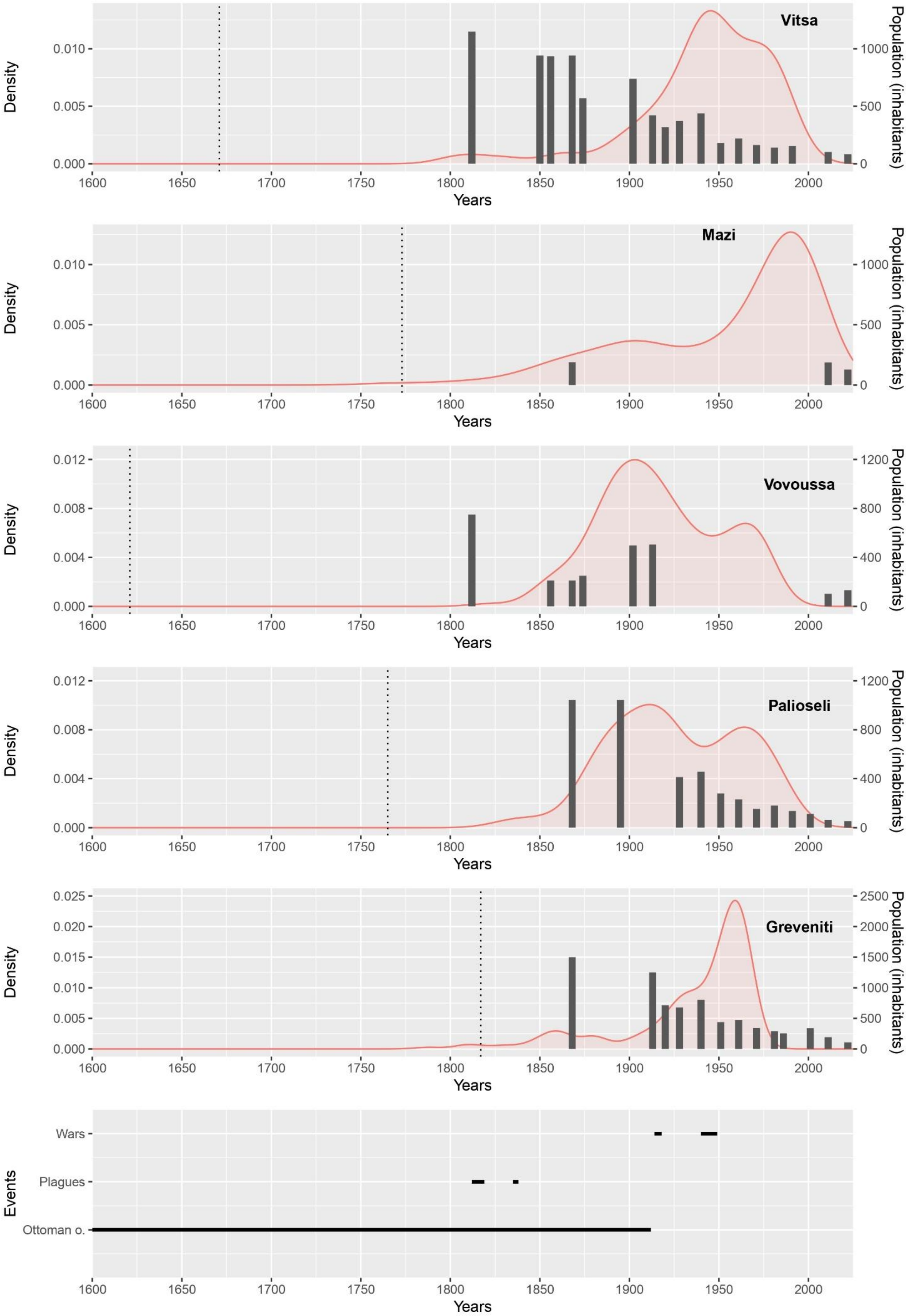

Vitsa
Mazi
Vovoussa
Palioseli
Greveniti
Density
Population (inhabitants)
Years
Events
Wars
Plagues
Ottoman o.

Figure 4. Kernel densities (red curves, left-hand y-axis) of the estimated dates of estabilishment of extant stems in each of the five study sites. Also shown are the human population numbers at village level (years 1812-2021; black bars, right-hand y-axis). The x-axis indicates year of tree establishment and human population census. Vertical dotted lines indicate the year of estabilishemnt of the oldest cored canopy tree for each site. The last panel shows the occurrence of major regional/national socio-economic events (Ottoman o = Ottoman occupation).

3.3 Forest structural indicators and church proximity

Significant associations between at least one of the four forest structural indices and distance from the church were found in the three tested sites (Supporting information – S8). There is a significant negative association between QMD and the distance of a plot from the central church in all three sites (trees get smaller away from the church): Mazi (all species: Pearson's correlation coefficient -0.43, p = 0.021; *Quercus* spp.: -0.35, p = 0.093), Vitsa (all species: -0.51, p = 0.008), and Vovoussa (*P. nigra*: -0.50, p = 0.018). There was also evidence of a negative association between stem density (N) and plot distance (trees are less dense further from the church) in Vovoussa (all species: -0.31, p = 0.099), and a positive association between BALM and distance (higher proportion of larger trees closer to church) in Vitsa (*Quercus* spp.: -0.40, p = 0.05). Significant results for GC (showing greater tree size inequality) are opposite in Mazi (positive correlation: 0.43, p = 0.04) and Vitsa (negative correlation: -0.56, p = 0.004) when calculated for the dominant *Quercus* spp. taxon.

4. Discussion

4.1 Determinants of change in tree population structures

All five study sites show a steep decline in all-species stem numbers with increasing diameter, as is typical for moderately undisturbed forests (Condit et al., 1998; Pulido & Díaz, 2005) where natural regeneration is continuous. However, this shape of size-class distribution is not apparent when considering only the individual dominant tree taxon per site (Supporting Information- S6) for which, as shown in Figure 4, regeneration is episodic rather than continuous. There is evidence in Figure 4 that the main dominant species in four of the five sites might have experienced an historical reduction in their rate of establishment associated with decreased human population occurring about 50 to 100 years prior to the sampling date (i.e. from 1915-1965). This appears counterintuitive but may be explained by the reduction in grazing pressure that accompanies human population decline leading to an increase in recruitment of shrubby and understorey species (e.g., *Quercus coccifera, Juniperus oxycedrus, Carpinus orientalis, Phillyrea latifolia*), which remain confined to the smallest diameter classes, as seen most clearly for Vitsa and Mazi in

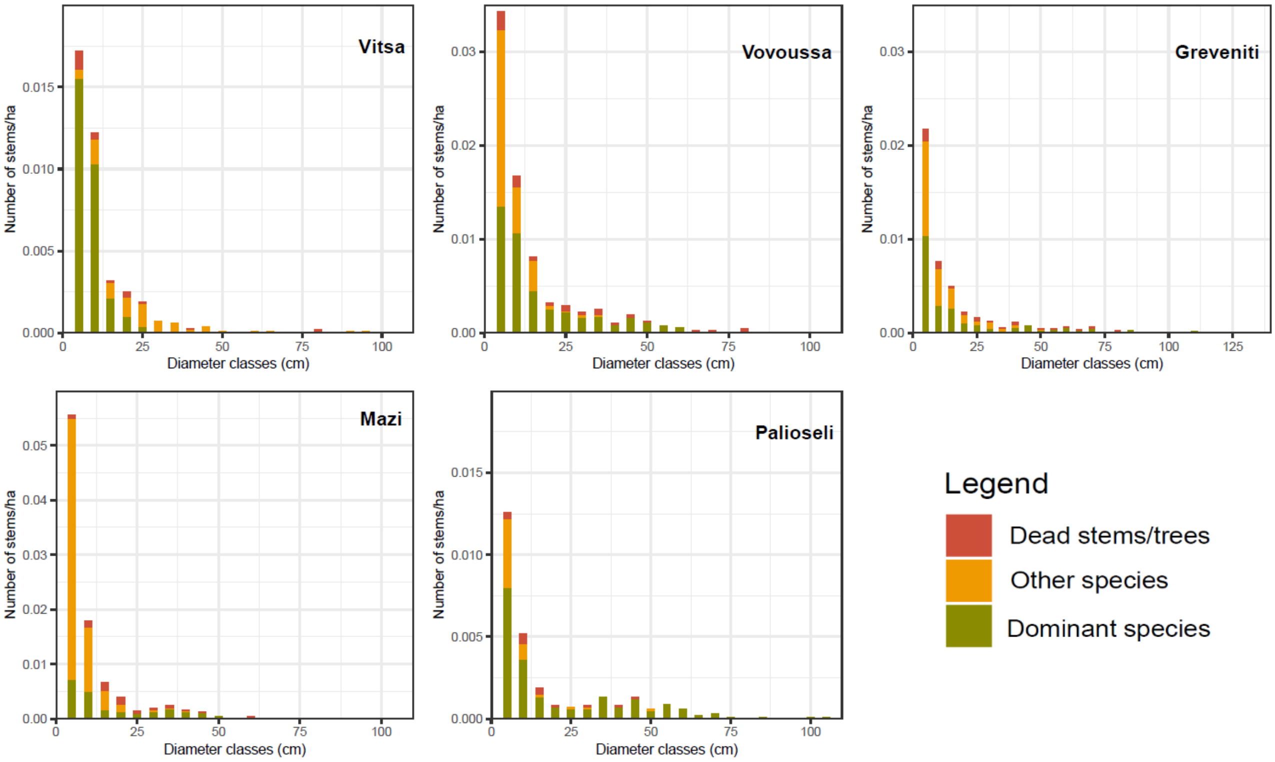


Figure **2**. Historical evidence shows that the understorey species were formerly kept at a low abundance by local management practices, such as active grazing and trampling in Vitsa and Mazi (Pion, 2014). With the progressive reduction in human activities in the area and change in management practices, these shrubs would have increase in density and size thereby increasing competition with saplings of the main canopy tree species reducing their rate of tree recruitment. A similar process has been observed elsewhere in the Mediterranean (e.g., Dehesa wood pastures in Spain; Pulido & Díaz, 2005). This finding suggests that simplistic interpretations of tree size-class distributions may obscure more complex stand histories.

4.2 Recurring recovery periods of accelerated tree establishment in the forests

In Section 4.1, we reported a temporary reduction (about 50-100 years ago) in canopy tree recruitment with decrease in grazing in the sampled sacred forests. Yet, when looking over the longest timescale (Figure 4), we identify the opposite trend: strong vegetation recovery in all five sacred forests associated with two historical periods of drastic reduction in human population pressure. The first is between 1850 and 1915. This period coincides with an era of human population decline mainly driven by the combination of two historical events: (i) the effect of plague epidemics during the Ottoman occupation (1812-1819 and 1835-1838, the last strands of the Black Death pandemic that hit Europe from the 14th century; Ágoston & Masters, 2009) – during or soon after this period there is a marked increase in the rate of tree establishment at Vovoussa, Palioseli, and to a lesser extent at Mazi, (Figure 4) and (ii) the turbulence, insecurity and economic decline during the later years of the Ottoman occupation, up to 1913 in Epirus, after which there was a marked increase in the rate of tree establishment in Vitsa and Greveniti (Figure 4). Both phenomena contributed to regional population decline as people moved to Athens but also emigration to the USA and Africa, reducing the population in the area by 30% from 1873 to 1902 (Supporting Information – S9) (Damianakos et al., 1997; Papageorgiou, 1995).

During the mid-20th century there was another period of high tree establishment shared across the sites, peaking between 1940-1960 for Vitsa, Palioseli, Vovoussa, and Greveniti and 1980 for Mazi (Figure 4). This period includes two major historical events in the region: the Second World War (1940-1945), and the subsequent Greek Civil War (1946-1949). During 1943-1945 many villages in the area were destroyed by the German Nazis, while during the Civil War (1946-1949) all villages in the Zagori area were compulsorily evacuated for political reasons (Stara, 2020). This period of intense social disruption was expressed in the landscape as a period of ecological recovery of the sacred forest systems. Indeed, our study area is an exemplar of the gradual but progressive increase in forest cover arising from the abandonment of rural areas, due to wars and the subsequent rural exodus that characterized the whole rural economy of Greece (Damianakos et al., 1997). The collapse of local economies also had a strong impact on the wood pasture sacred forests (Vitsa and Mazi) which released the pressure of previous grazing practices (Papanastasis, 2007).

The difference between the opposite trends in tree establishment observed over differing timescales might be due to the intensity of human impacts. Historical events (wars and epidemics) caused a rapid and extensive population decline in all the study areas. Major reduction in the intensity of human impacts resulted in periods of strong ecological recovery in the sacred forests. In contrast, the rural depopulation of Greece (and the wider Mediterranean region; Quintas-Soriano et al., 2022) over the last 100 years has been a gradual yet continuous process characterised in particular by declining grazing pressure. The restriction on the establishment rate of canopy tree species in sacred forests, resulting from decreased grazing pressure and the consequent rise in competition from understorey shrubs, is likely a temporary phenomenon. Similar processes in the past have been manifested as a delay in the recruitment response of canopy tree species. This highlights the importance of the intensity and timescale of human disturbance on the ecological dynamics of sacred forests, which is significant for their conservation management.

4.3 Spatial variation in forest structure

The ecological recovery of the sacred forest systems enabled by reduction in previous pressures, a result of decline in local human populations, is expected to be marked by changes in spatial extent and structure (Tsiakiris et al., in press). Assessing sacred forests as SES, our focus is on the spatial effect of the specific locus of cultural practices marked by the church building in providing a culturally-defined ecological core to the system and whether this acts as a nucleus from which spatial expansion of the system occurs during periods when ecological recovery is released. This presents a paradox as the most intensely used area is simultaneously the cultural and ecological nucleus of the forest – it is instructive to examine this further. The sacred forests of Vitsa, Mazi and Vovoussa are each dedicated to the saints of their founding and now centrally-located church, and are still used for annual religious celebrations (Stara, 2022; Stara, 2023). In this sense the church building represents the cultural nucleus of each sacred forest, with local communities treating the environment surrounding the church differently, as it symbolizes the area over which the influence of the divine is strongest (Stara, 2012). As explained in Section 2.4, there are strong grounds for considering the church to be the primary social component influencing people's behaviour in sacred forests, particularly during their foundation when religion played a significant role in villagers' lives. Nowadays, other infrastructure may have an influence, such as roads and paths potentially making the sacred forests more susceptible to trespassers. However, due to the considerable depopulation of the study sites, these effects are less important.

The results of the spatial resilience analysis provide strong evidence of the role of the traditional social component (i.e., the cultural praxis associated with the church) in determining the spatial extent of the forests' current recovery phase, and thus the overall resilience of the system. Thus, the presence of the church and associated rites protects a physical core of larger, older trees that provides the ecological nucleus of forest structural recovery and spatial expansion. The marked and highly significant decline in quadratic mean diameter of tree stems with distance from the church in all three tested sites was supported by observations made during the fieldwork that the largest (and oldest; 17^{th}-18^{th} century) trees were located close to the central church in Vitsa, Mazi, and Vovoussa. This generally fits with available historical reconstructions. Sacred forests are believed to have been established during the Ottoman occupation (1430-1913), being related to settlements in certain cases now ruined or coagulated into the location of present villages during the 16^{th} and 17^{th} centuries (Lambridis, 1870). Therefore, the largest extant trees could be part of the first generation of trees constituting the sacred forests.

This ecological – socially generated and preserved – forest nucleus will have driven ecological recovery and expansion by ecological processes such as dispersal of seeds from mature mother trees with high fecundity or moderation of physical environmental constraints (such as high insolation and low moisture) that limit rates of tree seedling establishment (Corbin & Holl, 2012). There was some evidence of the effect of these processes amongst the sites, with a general tendency for increased relative abundance of smaller trees with distance from the church, however reduced tree stem density with distance from the church was only found for one of the three sites (Vovoussa). The importance of site- or species-specific factors in mediating such mechanisms was evidenced by the opposite significant trends in the Gini coefficient for the dominant taxon with distance from the church found between two of the sites.

4.4 Linking spatial to temporal dynamics: towards a socio-ecological resilience assessment of sacred forests

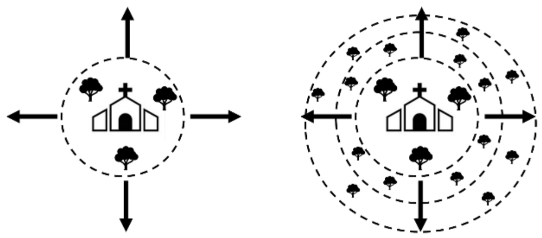
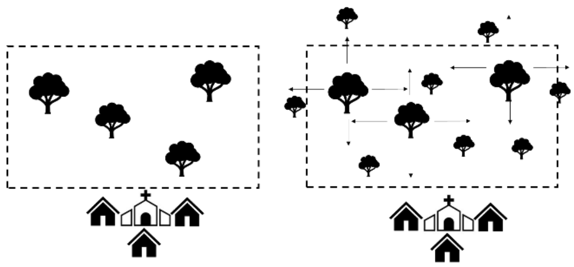
By considering both temporal and spatial dynamics of the studied sacred forests we can assess how social processes are linked to their resilience and structural development during the recovery phase (Table 1).

- Sacred forests with central churches (Vitsa, Mazi, Vovoussa) expand following a **concentric** model, with the oldest trees located in proximity to the central church (cultural core of the forest) with expansion occurring through younger generations of trees (established during the second half of the 19th century, and then during the second half of the 20th century) predominantly in the area immediately outside the core, as a response to the space available due to sudden societal changes (rural depopulation after pandemics and/or wars).
- The two sacred forests without a central church were belts of wooded land located above the village, ostensibly to protect downslope settlements from landslides and rockfalls. The forests of Palioseli and Greveniti were established and sustained through an excommunication ritual, that is remembered in the collective memory of their rural communities (Marini Govigli et al., 2021; Stara et al., 2016). These forests are characterised by a **diffuse** model of infilling of open areas from dispersed mature trees within the forest boundary that originated in the pre-existing wood pasture. Thus, recovery occurring in response to social changes is most obvious within the forest boundaries or spilling over into adjacent abandoned pastureland (Marini Govigli et al., 2021).

While the process of forest expansion (ecological recovery) through both models is enabled by regional socioeconomic changes - first and foremost population decline - the spatial pattern of recovery in the landscape depends on the type of ritual protection and the original configuration of the forests. This indicates the importance of the role of social processes when assessing forest socio-ecological resilience.

Table 1. Sacred forests' spatiotemporal dynamics and suggested models for forest recovery and expansion.

Type of ritual protection	Spatial dynamics	Temporal dynamics	Forest recovery and expansion model

Dedicated to Saints/Virgin (Vitsa, Mazi, Vovoussa)	Oldest/largest trees clustered around central church	Two main tree establishment periods: second half of the 19th century and second half of the 20th century.	CONCENTRIC 
Excommunication ritual (Palioseli, Greveniti)	No central church. Largest trees dispersed within the forest		DIFFUSE 

Sacred forests as SES are the combined outcome of both ecological and social processes, whose relationships are continuously evolving. Their resilience depends on the occurrence of positive feedbacks between social drivers and ecological variables (Nikinmaa et al., 2023; Sterk et al., 2017). Notable positive ecological-to-social feedbacks are the ecological recovery of the forests in periods of low demographic pressure and their expansion into formerly open areas. Positive social-to-ecological feedbacks include strong social memories of the sacred forest folklore and traditions, which are passed from generation to generation and serve to preserve the sites' heritage and their social purpose. Preserving the sacred forests' capacity to retain their *ecological structure* and *social functionality* after being subjected to damage caused by disturbances entails acknowledging that both aspects of resilience (social and ecological) should be assessed and managed. The concept of "applied nucleation" is well established in forest restoration ecology (e.g. Benayas et al. 2008; Corbin & Holl, 2012) but it tends to be considered in an entirely physical ecological sense. The implications of the present study are that greater attention should be paid to the role of the social component of SES in both providing a nucleus of established forest habitat and the conditions necessary for it to nucleate forest recovery and restoration.

5. Conclusions

The results of this study shed light on the temporal and spatial dimensions of socio-ecological resilience of sacred forests in northwestern Greece. The study presents evidence of distinct temporal waves of tree establishment over historical time linked to regional socio-economic changes. We also uncovered compelling evidence highlighting the role of the social component, particularly the presence of the church and its associated cultural practices, in determining the spatial extent of the current recovery phase of the forests.

The linkage of sacred forests' ecological resilience with changing socio-cultural practices over both temporal and spatial scales is crucial for guiding conservation and restoration strategies. In the case of the studied sacred forests, we found strong evidence of the transition from historical periods of overpopulation and landscape scarcity of forest resources, which imposed high anthropogenic pressure on sacred forest systems, to periods of severe regional depopulation and deruralization, during which sacred forests generally fade from people's memories as they blend into the surrounding landscape through spontaneous natural establishment of forests in formerly open areas. The varied spatial responsiveness of the forests to such drastic exogenous societal changes should inform communication and management actions aimed at preserving sacred forests and other SNS undergoing both cultural abandonment and ecological expansion. These actions should include public awareness campaigns to promote cultural resilience and active forest management measures, including at the landscape scale, to enhance ecological resilience. Such measures may include clearing flammable shrubs from border areas, suppressing the forest understory of competitive tree and shrub species through periodic light grazing to enable the establishment of canopy tree species, and methods such as tree species selection and boundary maintenance in order to maintain the socio-ecological identity of individual SNS within an increasingly tree-dominated matrix. The implementation of such restoration measures is especially important as the regulatory environment shifts towards the conservation of such sites[2], given that their intrinsic dynamism can challenge the simple concept of preservation as the basis for forest protection.

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[2] Since 2015 the sacred forests of Zagori and Konitsa have been included in the national index of Intangible Cultural Heritage (ICH, 2015), and in 2023 the Zagori Cultural Landscape was inscribed on the UNESCO World Heritage List (Bendermacher-Gerousi et al., 2022).

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8. Statement on inclusion

Our study brings together authors from a number of different countries, including scientists currently or formerly based in the country where the study was carried out (Greece and specifically the Epirus region). All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent was considered from the onset. Literature published by scientists from the region was cited including relevant work published in the local language.

9. Author contributions

Marini Govigli, V., Healey, J.R., Wong, J.L.G, and Stara, K. conceived the ideas and designed methodology; Marini Govigli, V. collected the data; Marini Govigli, V. analysed the data; Marini Govigli, V. and Healey, J.R.

led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

10. Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this article.

11. Data availability statement

The data associated with this manuscript are archived in Zenodo. Marini Govigli, V., Cullen, R., Healey, J. R., Kyparissis, A., Markos, N., Pion, N., Stagakis, S., Stara, K., Tsiakiris, R., Vanikioti, T., Wong, J. L. G., & Halley, J. M. (2024). Forest inventory and tree age datasets from selected Sacred Forests in NW Greece [Data set]. Zenodo. https://doi.org/10.5281/zenodo.10564919