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

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1 Abstract

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.

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

10 3. Our main results show that over past centuries sacred forests in Epirus underwent periods of varying tree

11 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 socioecological 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.

20

21 Keywords

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

24 1. Introduction

25 Ecological resilience is the capacity of an ecosystem to retain its structure and functionality after being 26 subjected to damage caused by disturbances, which alter one or more of its determining conditions 27 (Gunderson, 2000). This concept is particularly useful to understand how complex ecosystems react to 28 exogenous disturbances, such as climate change, other anthropogenic stresses, or natural disasters (Angeler 29 & Allen, 2016; Reyer et al., 2015; Seidl et al., 2016). Over recent decades numerous studies have assessed 30 spatial and temporal patterns of the ecological resilience of forest ecosystems worldwide, sometimes linked 31 to advocacy for greater efforts to tackle climate change and human disturbances to ecosystems (Muñoz et 32 al., 2021; Ratajczak et al., 2018; Seidl et al., 2016; Sterk et al., 2017; Willis et al., 2018). While human activities 33 are often the cause of system perturbation, they can also play an important role as a component of the 34 system (the so-called socio-ecological system, SES) and in its recovery (Berkes & Folke, 1998). This perspective 35 is becoming more prominent in resilience studies and acknowledges the fact that systems with both 36 ecological and social features need to be assessed and managed in an integrated and holistic way (Sterk et 37 al., 2017). Socio-ecological resilience has been assessed in many recent studies (e.g., Kelly et al., 2015; 38 Mngumi, 2021; Nikinmaa et al., 2023; Ruiz-Ballesteros, 2011), yet quantitative evidence on how the social 39 component influences the temporal and spatial dimensions of ecological recovery in forest SES is still lacking.

40 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 41 42 lakes, forests, caves, and islands and they range in scale from single trees, ponds or rocks, to wooded groves 43 or forests up to entire mountain ranges. They represent places of worship and memory and are not restricted 44 to any given region or culture (Bhagwat & Rutte, 2006). SNS are an exemplar of systems with a strong, 45 culturally-based social component that would be expected to have a major impact on their resilience. 46 Assessing socio-ecological resilience in SNS is extremely relevant to shed light on the social processes that 47 influence ecosystem recovery or degradation (e.g., traditional religious taboos; Marini Govigli et al., 2021), 48 with implications for forest management and nature conservation.

49 Sacred forests and groves are SNS that have been recognized as providers of important benefits related to 50 human-nature relationships (Wild & McLeod, 2008). These contributions to people's quality of life are even 51 more important in a context where urban populations are reviving forest-based spiritual practices (Roux et 52 al., 2022). Sacred forests in Europe and the Mediterranean region have been subject to a complex history of 53 successive cycles of decline associated with socio-economic instability and the undermining of existing 54 cultural values, followed by periods of recovery (Roux et al., 2022). While the role of sacred forests in 55 preserving traditional knowledge and management practices (cultural contributions) and environmental 56 resources (ecological contributions) have both been widely explored (e.g., Avtzis et al., 2018; Dudley et al., 57 2012; Sahle et al., 2021), there is little empirical evidence on the linkage between the two (e.g. Plieninger et 58 al., 2022; Stara, 2022; Alivizatou, 2021), and specifically of the impact of cultural praxes and processes (e.g., 59 traditional management, taboos and informal norms of forest conservation and management) on the socio-60 ecological resilience of sacred forests. This knowledge is crucial to predict how sacred forests will develop in 61 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 62 63 18th centuries. Assessing resilience in such a study setting is particularly novel because it provides us with the 64 opportunity to examine the system's resilience from its inception (i.e. the inception of sanctity), a dimension 65 that is often lost over time in most studies assessing the resilience of long-term spiritual SES. Our question 66 is: can we identify which cultural and social elements characterize sacred forest resilience in space and time? 67 Based on previous research conducted in Epirus, which reported the existence of strong cultural processes 68 that persisted through time and their influence on the floristic composition and structure of local sacred 69 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)

75 To test our first hypothesis, we used tree ages determined through dendrochronology and current tree 76 population size-class distributions as indicators of forest dynamics, and its legacy in the current structure of 77 the forests. To test the second hypothesis, we assessed the spatial relationship between a series of forest 78 structure indicators and the locus of cultural practices. The presence of a few spaced, old trees located near 79 a church (or icon stand or other religious structure) is typically identified as marking the cultural centre of 80 the site itself (Aerts et al., 2016; Lagopoulos, 2002). We hypothesised a decline in tree stature and density 81 with distance from the church, which may represent a dynamic equilibrium between the diminution of the 82 strength of cultural taboos on tree cutting and livestock grazing, and a process of more recent forest 83 expansion through natural colonization from the nucleus of protected forest adjacent to the church. Based 84 on these insights, we explore patterns of temporal and spatial resilience across the studied sacred forests. 85 Our results are valuable for forest conservation managers as they offer insights into the spatio-temporal 86 responsiveness of spiritual SES to significant external societal changes.

2. Material and methods

88 2.1 Study area

89 The study area is in the north of the Epirus region (northwestern Greece), within the local administrative 90 units of Zagori and Konitsa (Figure 1). In this area, recent studies have unveiled a large network of sacred 91 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 92 93 different forms of governance from strict religious regimes to community agreements resulting in 94 overlapping and varied restrictions ranging from controlled use to strict prohibition of trespassing (Stara et 95 al., 2016). Historical evidence indicates that the development of the sacred forests generally occurs 96 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).

114 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 119 the site's cardinal directions. Within each plot, all trees with a diameter at breast height (i.e. at 1.3 m, dbh) \geq 120 5 cm were identified and the dbh measured. A detailed description of the inventory procedures and variables 121 is provided by Marini Govigli et al. (2020). The inventory recorded 135 plots in total across the five study 122 sites. Size class distributions were obtained for the dominant tree taxon in each forest and an aggregation of 123 the remaining taxa, using 5 cm dbh classes. The distributions were calculated based on numbers of individual 124 stems, due to the presence of many multi-stemmed trees. The dominant tree taxa in each forest were 125 identified in Marini Govigli et al. (2020): deciduous Quercus spp. in Vitsa and Mazi (Quercus cerris, Quercus 126 frainetto, Quercus pubescens, and additionally Quercus trojana in Mazi), Pinus nigra in Vovoussa and 127 Palioseli, and Fagus sylvatica in Greveniti.

128 2.3 Estimation of tree ages from cores

129 To investigate the temporal relationship between forest structure and changing cultural practices (temporal 130 socio-ecological resilience), we used a combination of tree aging through dendrochronology and assessment 131 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 132 133 cored in year 2015), the tree with the largest diameter in each plot was selected for coring, whereas in the 134 oak- and beech-dominated forests (Vitsa, Mazi; year 2014 and Greveniti; year 2015) the second largest 135 individual in each plot was selected, as a high proportion of the largest trees were found to have cavities in 136 their centre. In such sites a second stage of sampling in 2015 added cores from an additional 86 individuals 137 to fill in gaps in the diameter size range of cored trees (with dbh \geq 5 cm). Only single-stemmed trees were 138 selected for coring with one core taken per tree, to respect the sensitivity of the local communities to 139 activities that may damage the trees in their sacred forests. This resulted in a total of 221 individual cores for 140 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 145 cores backwards from the first ring behind the bark to the pith. In this process, 16 cores were rejected, as 146 rotten, damaged, or with rings that could not be distinguished. This reduced the available dataset to 205 147 cores (Supporting Information- S2). As the oldest deciduous oaks were often rotten in the middle and the 148 angle of the core often did not intersect the oldest rings in the tree, not all the cores included the 149 chronological centre of the tree (i.e., the pith). To avoid repeat coring of trees in such culturally sensitive 150 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., 151 152 1987). In this study, we followed the method of Rozas (2003) to estimate partial (visible arch of the inner 153 rings) and incomplete (missing the inner arch and the pith) cores, which involved testing eight different 154 methodologies to estimate missing rings. The estimation methods and their results are provided in the 155 Supporting Information S3. Using the method which produced the smallest error, the ages of 89 partial and 156 54 incomplete cores were quantified (Supporting Information S4). Both linear and non-linear regression 157 models were used to establish the relationship between tree age and dbh of the dominant taxon at each site. 158 Model assumptions were tested and influential points showing a Cook's distance larger than 0.5 were 159 carefully investigated. If such outliers corresponded to incomplete cores, then they were interpreted as error 160 in the age estimation process and removed. Three error estimations of this kind were removed from the 161 sample. The power law regression was selected for the estimation process as it maximized the average model fit (R²) across the five sites. 162

163 Ages of all trees with stems \geq 5 cm dbh of the dominant taxon at each site were predicted from the site-164 specific power law age-diameter regressions. This was used to transpose the size class distributions of the 165 dominant taxon in each site to estimated age. These distributions were smoothed using non-parametric 166 kernel density estimations (KDE). KDE is a non-parametric estimation that enables the fitting of a smooth 167 curve (kernel density) to a set of observations, in this case the number of stems, allowing for the assessment 168 of emerging patterns across tree class distributions. By placing the age-frequency KDE curves against 169 historical village population data, we were able to assess whether drastic socio-economic changes in the 170 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 1868-2011¹.

173 2.4 Tree structural indicators

174 To investigate the spatial relationship between forest structure and the locus of cultural practices (spatial 175 socio-ecological resilience), we ran a series of linear Pearson correlation tests between four structural 176 indicators measured at the plot level and the plot's distance from the church building (for the three sacred 177 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 178 179 identifies the church as the spiritual focal point around which the sacred forest develops. In folk religion, the 180 church is personified as an epiphany (manifestation) of the deity (Stara et al., 2015), and villagers tend to be 181 reluctant to interfere with the forest in its visual proximity. For instance, as expressed in an interview (Stara, 182 2012, page 61): "[Husband]: Our field was downhill, close to the river but in view of the monastery, which 183 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, 184 but because of the view, I had the feeling that Virgin Mary was observing me. I cannot cut trees there' " 185 (Interview: 15/9/2006, Village Agios Minas). Furthermore, the largest trees in each sacred forest tend to be 186 187 those situated closer to the church, frequently positioned next to the altar (typically in the eastern part of 188 the building for Orthodox Christian churches).

189 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).

205 3. Results

206 3.1 Tree size-class distributions

207 In all five sites the stem size class distributions of all species showed an overall steep, approximately 208 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 210 distribution with a second peak in numbers in the 30-45 cm dbh range. When the distributions are restricted 211 to the dominant taxon in each forest, clear evidence of a second peak, in medium size ranges (varying from 212 213 20 70 dbh site), all five ca. to cm per is shown in sites (



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





218 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.

221 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 (R²) all above 0.5 (Figure 3).



231

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.

236 The relationship between age and diameter presented in Figure 3 was used to generate kernel densities of 237 estimated ages of all trees measured for dbh in each of the five sites (Figure 4). The results show comparable 238 timing of tree establishment events across sites. Mazi and Vitsa (both oak-dominated) are characterized by 239 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 240 241 and 1900 in Mazi, and 1765-1845 in Vitsa), which is more clearly visible in Mazi. Vouvousa and Palioseli (both 242 pine-dominated) are characterized by three density peaks: one of trees established around 1950-1960, 243 another during 1890-1915, and the first between 1825 and 1850. The beech dominated site (Greveniti) is 244 characterized by a single peak of trees established around 1950-1960 with peaks of lower intensity dating 245 back to 1865 and 1880 respectively.

246 By comparing trends in tree age density with human population at the village level (Figure 4, secondary y-247 axis), a correlation between periods of tree establishment and drops in human population level is apparent 248 in four out of the five sites. The 1940-1955 peak in Vitsa during and immediately following World War II was 249 preceded by a population drop of 43.1% some 30 years earlier (between 1902 and 1913); the 1815-1850 250 peak in Vovoussa was preceded by a population drop of 72% some 10 years earlier (between 1812 and 1856); 251 the 1940-1960 and 1890-1915 density peaks in Palioseli are associated with a population drop of 60.4% 252 (between 1895 and 1928) and 38.9% (between 1940 and 1951) respectively. The increase in tree recruitment 253 in Greveniti follows a drop in population of 43% between 1913 and 1920 and reaches its peak during 1950-254 1960 following a drop in population of 45% between 1940 and 1951.



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).

262 3.3 Forest structural indicators and church proximity

263 Significant associations between at least one of the four forest structural indices and distance from the 264 church were found in the three tested sites (Supporting information – S8). There is a significant negative 265 association between QMD and the distance of a plot from the central church in all three sites (trees get 266 smaller away from the church): Mazi (all species: Pearson's correlation coefficient -0.43, p = 0.021; Quercus 267 spp.: -0.35, p = 0.093), Vitsa (all species: -0.51, p = 0.008), and Vovoussa (*P. nigra*: -0.50, p = 0.018). There 268 was also evidence of a negative association between stem density (N) and plot distance (trees are less dense 269 further from the church) in Vovoussa (all species: -0.31, p = 0.099), and a positive association between BALM 270 and distance (higher proportion of larger trees closer to church) in Vitsa (Quercus spp.: -0.40, p = 0.05). 271 Significant results for GC (showing greater tree size inequality) are opposite in Mazi (positive correlation: 272 0.43, p = 0.04) and Vitsa (negative correlation: -0.56, p = 0.004) when calculated for the dominant Quercus 273 spp. taxon.

4. Discussion

275 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

296 In Section 4.1, we reported a temporary reduction (about 50-100 years ago) in canopy tree recruitment with 297 decrease in grazing in the sampled sacred forests. Yet, when looking over the longest timescale (Figure 4), 298 we identify the opposite trend: strong vegetation recovery in all five sacred forests associated with two 299 historical periods of drastic reduction in human population pressure. The first is between 1850 and 1915. 300 This period coincides with an era of human population decline mainly driven by the combination of two 301 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, 302 303 2009) – during or soon after this period there is a marked increase in the rate of tree establishment at 304 Vovoussa, Palioseli, and to a lesser extent at Mazi, (Figure 4) and (ii) the turbulence, insecurity and economic 305 decline during the later years of the Ottoman occupation, up to 1913 in Epirus, after which there was a 306 marked increase in the rate of tree establishment in Vitsa and Greveniti (Figure 4). Both phenomena 307 contributed to regional population decline as people moved to Athens but also emigration to the USA and 308 Africa, reducing the population in the area by 30% from 1873 to 1902 (Supporting Information – S9) 309 (Damianakos et al., 1997; Papageorgiou, 1995).

During the mid-20th century there was another period of high tree establishment shared across the sites, 310 311 peaking between 1940-1960 for Vitsa, Palioseli, Vovoussa, and Greveniti and 1980 for Mazi (Figure 4). This 312 period includes two major historical events in the region: the Second World War (1940-1945), and the 313 subsequent Greek Civil War (1946-1949). During 1943-1945 many villages in the area were destroyed by the 314 German Nazis, while during the Civil War (1946-1949) all villages in the Zagori area were compulsorily 315 evacuated for political reasons (Stara, 2020). This period of intense social disruption was expressed in the 316 landscape as a period of ecological recovery of the sacred forest systems. Indeed, our study area is an 317 exemplar of the gradual but progressive increase in forest cover arising from the abandonment of rural areas, 318 due to wars and the subsequent rural exodus that characterized the whole rural economy of Greece 319 (Damianakos et al., 1997). The collapse of local economies also had a strong impact on the wood pasture

320 sacred forests (Vitsa and Mazi) which released the pressure of previous grazing practices (Papanastasis,321 2007).

322 The difference between the opposite trends in tree establishment observed over differing timescales might 323 be due to the intensity of human impacts. Historical events (wars and epidemics) caused a rapid and 324 extensive population decline in all the study areas. Major reduction in the intensity of human impacts 325 resulted in periods of strong ecological recovery in the sacred forests. In contrast, the rural depopulation of 326 Greece (and the wider Mediterranean region; Quintas-Soriano et al., 2022) over the last 100 years has been 327 a gradual yet continuous process characterised in particular by declining grazing pressure. The restriction on 328 the establishment rate of canopy tree species in sacred forests, resulting from decreased grazing pressure 329 and the consequent rise in competition from understorey shrubs, is likely a temporary phenomenon. Similar 330 processes in the past have been manifested as a delay in the recruitment response of canopy tree species. 331 This highlights the importance of the intensity and timescale of human disturbance on the ecological 332 dynamics of sacred forests, which is significant for their conservation management.

333 4.3 Spatial variation in forest structure

334 The ecological recovery of the sacred forest systems enabled by reduction in previous pressures, a result of 335 decline in local human populations, is expected to be marked by changes in spatial extent and structure 336 (Tsiakiris et al., in press). Assessing sacred forests as SES, our focus is on the spatial effect of the specific locus 337 of cultural practices marked by the church building in providing a culturally-defined ecological core to the 338 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 339 340 simultaneously the cultural and ecological nucleus of the forest – it is instructive to examine this further. The 341 sacred forests of Vitsa, Mazi and Vovoussa are each dedicated to the saints of their founding and now 342 centrally-located church, and are still used for annual religious celebrations (Stara, 2022; Stara, 2023). In this 343 sense the church building represents the cultural nucleus of each sacred forest, with local communities 344 treating the environment surrounding the church differently, as it symbolizes the area over which the 345 influence of the divine is strongest (Stara, 2012). As explained in Section 2.4, there are strong grounds for

346 considering the church to be the primary social component influencing people's behaviour in sacred forests, 347 particularly during their foundation when religion played a significant role in villagers' lives. Nowadays, other 348 infrastructure may have an influence, such as roads and paths potentially making the sacred forests more 349 susceptible to trespassers. However, due to the considerable depopulation of the study sites, these effects 350 are less important.

351 The results of the spatial resilience analysis provide strong evidence of the role of the traditional social 352 component (i.e., the cultural praxis associated with the church) in determining the spatial extent of the 353 forests' current recovery phase, and thus the overall resilience of the system. Thus, the presence of the 354 church and associated rites protects a physical core of larger, older trees that provides the ecological nucleus 355 of forest structural recovery and spatial expansion. The marked and highly significant decline in quadratic 356 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; 17th-18th century) trees were located 357 358 close to the central church in Vitsa, Mazi, and Vovoussa. This generally fits with available historical 359 reconstructions. Sacred forests are believed to have been established during the Ottoman occupation (1430-360 1913), being related to settlements in certain cases now ruined or coagulated into the location of present villages during the 16th and 17th centuries (Lambridis, 1870). Therefore, the largest extant trees could be part 361 of the first generation of trees constituting the sacred forests. 362

363 This ecological – socially generated and preserved – forest nucleus will have driven ecological recovery and 364 expansion by ecological processes such as dispersal of seeds from mature mother trees with high fecundity 365 or moderation of physical environmental constraints (such as high insolation and low moisture) that limit 366 rates of tree seedling establishment (Corbin & Holl, 2012). There was some evidence of the effect of these 367 processes amongst the sites, with a general tendency for increased relative abundance of smaller trees with 368 distance from the church, however reduced tree stem density with distance from the church was only found 369 for one of the three sites (Vovoussa). The importance of site- or species-specific factors in mediating such 370 mechanisms was evidenced by the opposite significant trends in the Gini coefficient for the dominant taxon 371 with distance from the church found between two of the sites.

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

373 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, 382 383 ostensibly to protect downslope settlements from landslides and rockfalls. The forests of Palioseli 384 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 385 et al., 2016). These forests are characterised by a diffuse model of infilling of open areas from 386 387 dispersed mature trees within the forest boundary that originated in the pre-existing wood pasture. 388 Thus, recovery occurring in response to social changes is most obvious within the forest boundaries 389 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	Spatial		
protection	dynamics	Temporal dynamics	Forest recovery and expansion model



395

396 Sacred forests as SES are the combined outcome of both ecological and social processes, whose relationships 397 are continuously evolving. Their resilience depends on the occurrence of positive feedbacks between social 398 drivers and ecological variables (Nikinmaa et al., 2023; Sterk et al., 2017). Notable positive ecological-to-social 399 feedbacks are the ecological recovery of the forests in periods of low demographic pressure and their 400 expansion into formerly open areas. Positive social-to-ecological feedbacks include strong social memories of 401 the sacred forest folklore and traditions, which are passed from generation to generation and serve to 402 preserve the sites' heritage and their social purpose. Preserving the sacred forests' capacity to retain their 403 ecological structure and social functionality after being subjected to damage caused by disturbances entails 404 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; 405 406 Corbin & Holl, 2012) but it tends to be considered in an entirely physical ecological sense. The implications of 407 the present study are that greater attention should be paid to the role of the social component of SES in both 408 providing a nucleus of established forest habitat and the conditions necessary for it to nucleate forest recovery 409 and restoration.

410 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.

416 The linkage of sacred forests' ecological resilience with changing socio-cultural practices over both temporal 417 and spatial scales is crucial for guiding conservation and restoration strategies. In the case of the studied 418 sacred forests, we found strong evidence of the transition from historical periods of overpopulation and 419 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 420 421 from people's memories as they blend into the surrounding landscape through spontaneous natural 422 establishment of forests in formerly open areas. The varied spatial responsiveness of the forests to such 423 drastic exogenous societal changes should inform communication and management actions aimed at 424 preserving sacred forests and other SNS undergoing both cultural abandonment and ecological expansion. 425 These actions should include public awareness campaigns to promote cultural resilience and active forest 426 management measures, including at the landscape scale, to enhance ecological resilience. Such measures 427 may include clearing flammable shrubs from border areas, suppressing the forest understory of competitive 428 tree and shrub species through periodic light grazing to enable the establishment of canopy tree species, and 429 methods such as tree species selection and boundary maintenance in order to maintain the socio-ecological 430 identity of individual SNS within an increasingly tree-dominated matrix. The implementation of such 431 restoration measures is especially important as the regulatory environment shifts towards the conservation

of such sites², 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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620 7. Acknowledgements

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635 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.

641 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 forpublication.

646 10. Conflict of Interest

- 647 The authors declare that they have no known competing financial interests or personal relationships that
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649 11. Data availability statement

- The data associated with this manuscript are archived in Zenodo. Marini Govigli, V., Cullen, R., Healey, J. R.,
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