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Quantifying the conservation value of Sacred Natural Sites

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Abstract

Many have asserted that Sacred Natural Sites (SNS) play an important role in nature protection but few have assessed their conservation effectiveness for different taxa. We studied sacred groves in Epirus, NW Greece, where a large number of such SNS have been identified. Based on historical, ethnographic and ecological criteria, we selected eight of these groves and matching control sites and in them we studied fungi, lichens, herbaceous plants, woody plants, nematodes, insects, bats and passerine birds. Our results reveal that the contribution of SNS to species conservation is nuanced by taxon, vegetation type and management history. We found that the sacred groves have a small conservation advantage over the corresponding control sites. More specifically, there are more distinct sets of organisms among sacred groves than among control sites, and overall biodiversity, diversity per taxonomic group, and numbers of species from the European SCI list (Species of Community Interest) are all marginally higher in them. Conservationists regard the often small size of SNS as a factor limiting their conservation value. The sizes of SNS around the globe vary greatly, from a few square meters to millions of hectares. Given that those surveyed by us (ranging from 5 to 116 ha) are at the lower end of this spectrum, the small conservation advantage that we testified becomes important. Our results provide clear evidence that even small-size SNS have considerable conservation relevance; they would contribute most to species conservation if incorporated in networks.

Keywords

Sacred Natural Sites; Conservation value; Biodiversity; Extinction Debt; Beta diversity

Research highlights

- Sacred Natural Sites (SNS) are thought to play an important role in conservation but quantitative analyses are rare.
- We studied the conservation capacity of SNS at multiple sites for multiple taxonomic groups.
- The SNS studied deliver a small but important conservation benefit compared with corresponding control areas.
- The contribution of SNS to species conservation is nuanced by taxon, vegetation type and management history.
- The best conservation strategy for small SNS is to join them as parts of networks within conventional conservation schemes.

Abbreviations

Sacred Natural Sites: SNS

Species Abundance Relationships: SAR

1. Introduction

Conservation is closely aligned with modern ecological thinking and over the last two centuries has become a major factor in policy decisions (Klein et al., 2009; Keppel et al., 2015). Before the arrival of the modern ecology-motivated concept, conservation has been practiced for many centuries in a variety of more traditional, community-based forms (Malhotra et al., 2007). One such form was through social taboos and religious beliefs that prescribed management regimes in sacred areas, often imposing limitations on certain activities, so as to secure important resources and services for the whole community (Berkes et al., 2000; Colding et al., 2001, Klepeis et al. 2016). These are the so-called sacred natural sites (SNS) that not only reflect the religious and social needs of the community but at the same time contribute important ecosystem services, from inspiration to air regulation, water and micro-climate quality, or conservation of biological diversity (Jim, 2003; Soury et al., 2007; Yuan and Liu, 2009; Wassie et al., 2010).

Sacred natural sites have been found in all inhabited continents (Hughes and Chandran, 1998) and woodland sacred groves can be traced back to the time when human society was still in a pre-agricultural state (Gadgil and Vartak, 1976). They have been associated with a wide range of faiths and beliefs, socio-cultural systems, institutions and ritual practices, and may be subject to changing conditions (Verschuuren et al., 2010). Around the Mediterranean basin, forests have long been recognized as a resource with a multifunctional role that needs particular care and protection. Groves or specific tree species, related mainly to sacrifice and burial, were considered as sacred and thus gained a special protection status (Blondel and Aronson, 1999). This was normally achieved through restrictions imposed by a local authority, usually a religious authority, threatening transgressors with supernatural consequences (Byers et al., 2001; Virtanen, 2002). At the same time, extended sacred forests served as a protective levee for the local community against natural disasters, such as landslides and floods (Stara et al., 2016). Sacred groves had flourished in Greece, since the Ottoman period, mainly in the mountainous regions, where the above-mentioned natural threats to local communities were much more severe and where historical circumstances allowed the involvement of the Church in their management.

Epirus is a mountainous region in northwestern Greece, in which sacred groves are a prominent component of the landscape; they form habitats dominated by mature trees that are unique within the historically intensively used landscapes (Stara et al., 2015; Stara et al.,

106 2016). These groves were established through a range of ritual praxes. Some were dedicated
107 to specific saints, some were little more than community agreements, while others were
108 protected by the threat of excommunication. Different management regimes prevailed
109 through time with some groves being strictly protected, some subjected to controlled
110 management, whereas for others only the protection of mature trees is reported. The groves
111 appear either in the form of protective forests above or close to villages or as groups of
112 veteran trees that accompany outlying churches or icon stands (Stewart, 1993; Nixon, 2006;
113 See also Appendix G). Nonetheless, they served in many cases as multifunctional forests for
114 local communities providing among others shaded grazing areas for livestock. Especially in
115 deciduous sacred forests, grazing could be intensive (Papanastasis et al., 2008).

116 Different cultural groups coexisted in Epirus contributing to the variability of the landscape,
117 but they were all associated with sacred groves. Long-term ethnographic research has
118 revealed that of the 80 villages in the mountainous municipalities of Zagori and Konitsa
119 almost all had at least one sacred grove; these groves mostly lie within a narrow range of
120 elevation, typically from 800 to 1200 m (Stara et al., 2016). This is also the zone where most
121 mountain settlements, characterized by a mixed system of agriculture-animal husbandry, have
122 developed historically (Nitsiakos, 2016).

123 Even though the role of SNS in the conservation of biodiversity has long been recognized
124 (Kosambi, 1962; Gadgil and Vartak, 1976; Haridasan and Rao, 1985), they have recently
125 gained more attention amongst conservation biologists because of the many threats to
126 biodiversity due to anthropogenic activities (Pimm et al., 1995; Gao et al., 2013). It has been
127 suggested that incorporating these SNS into existing protected area networks might increase
128 their effectiveness in achieving conservation objectives (Bhagwat and Rutte, 2006; Soury et
129 al., 2007; Corrigan et al., 2013; Ormsby, 2013).

130 Despite the increasing interest in SNS as biodiversity refugia (Dudley et al., 2009), few
131 studies have assessed their effectiveness across taxa, whilst most have focused on specific
132 groups of organisms, such as plants (Boraiah et al., 2003; Khumbongmayum et al., 2006;
133 Frascaroli et al., 2016), small mammals (Decher, 1997; Reed and Carol, 2004) or butterflies
134 (Nganso et al., 2012). Most of these studies have been carried out in Asia, particularly India
135 and China (Nganso et al., 2012; Gao et al., 2013; Karthikeyan and Dhamatharan, 2015), or
136 Africa (Daye and Healey, 2015), with very little work in Europe (e.g. Frascaroli et al., 2016).
137 It could be argued that, as most SNS tend to be small, their relevance to conservation, though

tangible, is limited compared to large reserves (Bossart et al 2006, Aerts et al 2006). Area is expected to affect the conservation effectiveness of SNS in several important ways. Firstly, the species-area relationship indicates that smaller areas cannot support as many species as larger ones. If a habitat shrinks, the level of biodiversity that it can sustain in the long term also shrinks, but, in the short term, the habitat retains more species than it can support. This surplus is called "extinction debt" (Diamond, 1972) and it must eventually be paid. The process takes time, with the magnitude of the delay being greater in larger fragments (Halley et al., 2016). Both the extinction debt and the time to the new equilibrium are also affected by the degree of isolation and the habitability of the "matrix" (i.e. the area between fragments; Koh and Ghazoul, 2010).

Focusing on a group of sacred groves in Epirus, the goal of this study is to investigate the conservation effectiveness of SNS. We do this by assessing their biodiversity and comparing them with matched control sites. For each sacred grove, a nearby woodland area without any sacred status but with similar characteristics was chosen to serve as a control site. To achieve a substantial breadth of studied organisms, eight different taxonomic groups were investigated simultaneously. Estimates of diversity were assessed per taxonomic group and per site. The importance of the size of the groves was also explicitly considered. In addition, extensive ethnographic research highlighted the impact of different management practices on the conservation status of these groves. The specific hypotheses that we are testing are as follows: (I) sacred groves have a higher alpha-diversity than their control sites because they enjoyed greater protection; (II) alpha-diversity differences will be accentuated for taxa, such as fungi or lichens, that benefit from the presence of trees of great age; and (III) sacred groves have higher beta-diversity than their control sites, since each sacred grove is expected to have its own distinctive land-use history (and therefore forest structure).

2. Materials and Methods

2.1. Study Areas and Sampling

Numerous sacred groves have been identified in a wide area of north-western Greece (Fig. 1), of which 22 were mapped. Of these, eight (1S-8S) were selected for the current study, based on an integrated set of historical, ethnographic, management and ecological criteria (Appendices A and G). Each of the selected sacred groves is situated in the mountainous region of Zagori and Konitsa (Fig. 1). Since our main hypotheses are that sacred-grove status involves higher biodiversity, for each grove we chose a single non-sacred site attempting an

assessment of biodiversity differences as practiced in other similar studies (Wortley et al. 2013, Derhé et al. 2016). We selected control sites (1C-8C) in close proximity; these matched each sacred grove in terms of substrate, topographic position and type of vegetation. In this study, we identified three types of groves in terms of vegetation: those dominated by (i) coniferous, (ii) evergreen broadleaved or (iii) deciduous broadleaved trees. We sampled in these eight pairs of sites over two consecutive years (2013 and 2014) following a sampling protocol that was adapted to the unique characteristics of each taxonomic group (Appendix B). The sampling effort was the same across all sites for any given taxonomic group, so that estimates of biodiversity are comparable.

2.2. Dataset

In total, eight taxonomic groups (fungi, lichens, herbaceous plants, woody plants, nematodes, insects, bats and passerine birds) were sampled in each sacred grove and the corresponding control site. All observed organisms of these groups were identified to species level, except for nematodes, which were identified to genus level. The data consist of abundance records per species, except for lichens, herbaceous plants (including ferns) and woody plants, for which only species presence was recorded.

2.3. Biodiversity analysis

The biodiversity we assess here is the total number of species recorded in each site, which we call the *species richness* of the site.

2.3.1. Ordination

To visualize the difference in composition between sites, multidimensional scaling analysis based on Bray-Curtis dissimilarity was conducted for each taxon, separately, and for all taxa combined. This index is widely used as a measure of multidimensional "distance" between samples for abundance data (e.g. Clarke et al., 2007; Birtel et al., 2015; Nicol et al., 2017); it has the advantage, over some other ordination techniques, that differences in abundance are scaled proportionally . The analysis was implemented in R 3.2.3 (R Core Team, 2015) using function *isoMDS* of the MASS package (Venables and Ripley, 2002) and function *vegdist* of the VEGAN package (Oksanen et al., 2016).

2.3.2. Species richness

Sacred groves and control sites were compared in terms of their species richness per site (across all taxa), total species richness per taxon (across all sacred and all control sites) and species richness per site per taxon.

Apart from their *type* (sacred or control), sites are characterized by their *location* within the region of Epirus (Fig. 1), their *vegetation* (three forest types) and the *area* of the site (being the area of the convex hull containing the sample plots within each site) (Table 1).

To investigate the effect of the different site characteristics on species richness, a generalized linear regression model $S \sim area + type + vegetation\ type + area{:}type$ with Poisson response and a logarithmic link function was used. The model is applied to the total species richness per site and to the species richness of each taxonomic group per site. In addition, we carried out a number of tests (regression and paired *t*-test) comparing species richness in sacred sites and control areas with and without conifer groves.

We also recorded the numbers of European SCI, Species of Community Interest (Official Journal of the European Union, 2009; Council Directive, 1992), for all sacred groves and corresponding control sites (Table E.1). We assessed the significance of the differences between them using a paired Students *t*-test.

2.3.3. Beta diversity

Apart from the species richness per site (alpha diversity) and the species richness across sites (gamma diversity), the sacred and control site communities were compared in terms of their beta diversity or species turnover (Magurran, 2004). Beta diversity between the local scale (sites) and the global scale (union of sites) was measured using Whittaker index and N^* index (Lazarina et al., 2013). Both indices give a measure of species turnover in space, which in this case measures the difference in species composition between the local scale (site) and global scale (the union of all sacred or all control sites). N^* is roughly defined as the sampling effort (number of samples) above which the samples accumulated will mostly contain species that have already been found. The advantage of the N^* index, as opposed to other indices, is that it is independent of the sampling effort, provided that there are enough samples for the index to be calculated (Lazarina et al 2013). The N^* index was computed using the R function provided by Lazarina et al (2013). We tested the significance of differences between sacred groves and control sites at the 5% level.

All statistical tests and analyses were performed in R 3.2.3 (R Core Team, 2015).

2.3.4. Conservation capacity of SNS

By the term "conservation capacity" we refer to the ability of a protected area to conserve biodiversity, assuming that management measures to protect the site are implemented. Conservation capacity involves two components: the number of species that an area of a given size can support at equilibrium, based on the species-area relationship (SAR, see for example Halley et al., 2013), and the duration for which the area can retain species (if fully protected). This is based on an estimation of the species relaxation curve for extinction debt (Halley et al., 2016), a prominent factor in extinction ecology and conservation (Newmark et al., 2017). Extinction debt becomes important when a fragment of habitat within a larger habitat network connected by dispersal gets isolated, with no further dispersal possible. Thereafter, the viability of each species is dependent on its population size within the fragment so that current species richness may be a relic of earlier biodiversity levels rather than true conservation capacity. The conservation capacity of the sacred groves was estimated for each taxonomic group, separately, using the Arrhenius SAR:

$$S = cA^z \quad \text{...(1)}$$

The constant z is typically between 0.2 and 0.3 for islands, while for continental areas it falls within the range of 0.1 to 0.15 (Halley et al., 2013). Calibration of the SAR was achieved by assuming a continental area with exponent 0.15; then c was determined by using the number of species found in the control sites through the formula $c = S/A^z$.

The first time-constant of relaxation is the expected time for half the extinction debt to be paid off, which actually is the half-life of extinction debt in a habitat remnant. In the absence of speciation and colonization, the half-life of extinction debt is equal to the time for species richness to fall to half its original value. Based on the models developed in Halley et al. (2016), this is approximately (in years):

$$t_{50} \approx 2.77\left(\frac{\rho A}{S_0}\right)^{\alpha} \tau \quad \text{...(2)}$$

Here, A is the area of the remnant forest, ρ is the typical total density of individuals of the relevant taxonomic group, τ is the average generation time and S_0 is the initial number of species in the area A at the time of area reduction or isolation. The factor $\rho A/S_0$ is important, being the number of individuals per species. If the initial number of species, S_0, is not known, the alternative is to use the SAR and substitute Eq. (1) for species number:

$$t_{50} = 2.77\left(\frac{\rho A^{1-z}}{c}\right)^{\alpha}\tau \quad \text{... (3)}$$

In order to get ρ and τ, we assume a single average for each taxonomic group (Halley et al., 2016). For passerine birds, herbaceous and woody plants, ρ and τ values are as in Halley et al. (2016). For nematodes, our measurements indicated typical densities of 7.5×10^9 individuals per ha and we used a generation time of 19 days (Lee, 2002), while for bats we used ρ=0.105 individuals per ha and for the generation time we used τ=8 years, which is half the average longevity (Austad and Fischer, 1991). For insects, the value of τ=1 year was typical of the species in our study, while $\rho=7.83\times10^4$ individuals per ha that we used is clearly a conservative number as it refers to ground-dwelling beetles (Didham et al., 1998). We did not compute curves for lichens or fungi owing to known complications of defining individuals and generation times for these groups.

2.3.5. SNS and National Parks (NP) size worldwide

To see how the size of the sacred groves that we studied fits into the global picture, using a literature search, we assembled a database of SNS from various countries, for which we could find the area (Table F.1) as well of National Parks in three countries: Greece, the United Kingdom and the United States (Table F.2).

3. Results

In total, across all taxonomic groups studied, 816 species were observed and identified within the eight pairs of sacred groves and control sites (Table C.1). There was great variability in the species richness of the sacred sites relative to their respective control sites for different taxonomic groups: in five of them, the total number of species observed was higher in the sacred groves, and in three groups, it was higher in the control sites (Fig. 2a), but these differences were not statistically significant except for fungi (p=0.001, see Table C.2), for which richness was higher in sacred groves. Combining species across the taxonomic groups, all except two localities had higher species richness in the sacred grove than the corresponding control site (Fig. 2b). The two exceptions are localities 4 and 7 (Fig. 1) that are associated with steeper slopes and are dominated by conifers. The other six pairs are associated with the lowland or southern-aspect slopes and are dominated by broadleaved trees. There is a strong correlation (Fig. 2b) between the species richness of the sacred groves (x) and control sites (y) in each locality for the six pairs dominated by broadleaved trees,

290 reflecting the success of their matching in the sample design (y=0.727x+30.56, R^2=0.912,
291 p=0.003). For these localities, there is also a significant difference between overall species
292 richness in the sacred groves and control sites (t-test, p=0.0085). These tests show a
293 consistent trend for greater overall species richness in the sacred groves than the control sites.

294 Ordination shows that the patterns of species composition amongst the three vegetation types
295 (Fig. D.1) varied by taxonomic group. However, with species of all groups combined, there
296 was a clear distinction between the vegetation types. Regarding the site type, there were no
297 consistent differences in composition between sacred groves and control sites for the
298 individual groups of species or for all species combined (Figs D.1 and D.2). The generalized
299 linear regression analysis shows (Table C.2) that the site area and type do not affect
300 significantly the total species richness per site (at a 5% significance level). However, their
301 interaction is significant meaning that the relationship between species richness and area
302 differs depending on the type of the site (sacred or control). As sacred sites are mostly
303 smaller in area than control sites (Table 1). The total species richness is also significantly
304 affected by vegetation type. On a taxonomic group level, the locality is not significant for any
305 group. The type of the site (sacred or control) is significant only for fungi, whereas vegetation
306 type is significant for lichens, herbaceous plants, and woody plants; none of these predictors
307 is significant for nematodes, insects, passerine birds or bats. The interaction between site
308 locality and type is also significant for herbaceous plants and lichens, as was also the case for
309 total species richness.

310 Of the 13 European SCI species that were encountered in the study area, more were found in
311 the sacred groves (eleven) than in their control sites (nine) especially for passerine birds (8
312 versus 4). However, overall the difference was not significant (paired t-test; p=0.30).

313 The Whittaker and N* indices of species turnover reveal significantly greater beta diversity
314 amongst the sacred groves than amongst the control sites (at the 5% level for both indices)
315 (Fig. 3). More specifically, beta diversity is greater in the sacred groves for five taxonomic
316 groups (lichens, herbaceous plants, woody plants, passerine birds and bats); it is slightly less
317 for insects, and very similar between the two site types for nematodes and fungi. Notably,
318 beta diversity is much lower for the nematodes than for all the other taxonomic groups of
319 species, presumably because nematodes were identified only to genus level and, hence, the
320 majority of nematode genera are found in all samples.

The area of the sacred groves was small, ranging from 4.9 ha to 115.7 ha with a median size of 18.4 ha. Both the area and the taxonomic group are expected to affect the half-life of species loss following habitat isolation (Fig. 4a) and, hence, their conservation capacity. The predicted half-life varied greatly amongst taxonomic groups being low for bats and passerine birds, under 100 years for most of the sacred groves, but very high, above 1000 years, for nematodes and herbaceous plants (because of their large populations) and for woody plants (because of large generation times)). However, the general linear modelling analysis did not find a significant relationship between area and species richness.

In our literature search, we found 104 SNS for which the area was recorded or could easily be inferred; these occur in all inhabited continents. To these we added the 22 sacred groves in Epirus that we mapped, including the 8 whose biodiversity we studied in detail. The histogram for this ensemble (Fig 4a) shows that the size of SNS varies greatly, ranging from a few square metres to over 100,000 km^2, with the groves that we studied falling in the smaller part of the range. By contrast, National Parks are always at least 10 km^2 (Fig. 4b).

4. Discussion

Globally, this is the first study to evaluate the conservation capacity of SNS by use of a large and taxonomically broad set of species. Regarding Hypothesis (I), our study shows that while sacred groves contained more species overall, the difference between them and control sites was not statistically significant unless the north-facing conifer sites were omitted from the analysis. Similar statistical issues have arisen in a previous study comparing protected and unprotected areas for several taxonomic groups (Gray et al., 2016), despite the expected differences between such areas. These results suggest that the advantage of protected over unprotected areas becomes blurred when more than one taxonomic group is examined (Khumbongmayum et al., 2005; Gao et al., 2013). To avoid the bias of masking differences when pooling together data from different taxonomic groups, in the present study, biodiversity was assessed for each group separately. While species richness was higher for most groups in sacred groves, only for fungi was this difference significant. This lends support to Hypothesis (II), except that for lichens, the other taxon that should benefit from the presence of older trees, the differences were not significant. For plants, this lack of strong distinction contrasts with an earlier study (Frascaroli et al., 2016) reporting significantly more species in sacred groves than in reference sites. In contrast to the nuanced difference in

353 species richness between sacred groves and control sites, there was a clear biodiversity
354 benefit when beta diversity was considered (Hypothesis III). Its higher value for sacred
355 groves suggests that there is a greater distinction (in the sets of species) between sacred
356 groves than between control sites. This might be explained by the groves different histories of
357 usage, which have a significant effect on sacred grove's vegetation structure and therefore on
358 the ecological community structure, thus increasing the dissimilarities between groves.
359 Different patterns of land abandonment could also play a role. By contrast, the ~~non-sacred~~
360 control areas arose largely through natural regeneration in the last 100 years and thus have a
361 more uniform structure.

362 Given the lack of evidence of a strong difference in species richness or composition between
363 sacred groves and control sites, other factors were explored to explain the results found. The
364 most obvious candidate was vegetation type, as the eight pairs of sites were stratified between
365 topographic locations, with three different vegetation types being distinguished, dominated
366 by coniferous, evergreen broadleaved or deciduous broadleaved trees. In all of the analyses,
367 and for many of the species groups examined separately, a clear distinction was found in
368 species richness and composition between the six site pairs dominated by broadleaved trees
369 (with either similar overall richness between the site types or higher richness in the sacred
370 groves) in contrast to the two site pairs with conifer-dominated vegetation (where control
371 sites had higher richness). Other than the nature of coniferous forests *per se*, a number of
372 features might also contribute to the distinct biodiversity pattern in these two site pairs.
373 Firstly, these two groves and their control sites are in closer proximity to the nearest village
374 than is the case for the other sites. This could have led to more intense anthropogenic
375 influence or, alternatively, it might have increased the effectiveness of the protection
376 associated with religious prohibitions (Frosch et al., 2016). Secondly, they are located on
377 very steep slopes, so these groves would require strict protection to fulfil the role of erosion
378 or landslide control. Looking closely at each sacred grove, it becomes apparent that its current
379 status has been individually shaped by its history. For example, despite a long history of
380 protection, one of the conifer groves is the forest of Konitsa (4S) was heavily logged for
381 timber and fuel wood in the 1940s, during the Second World War and the following Greek
382 Civil War. Subsequently, in 1953, the municipality decided to manage the forest by removing
383 mature trees in an effort to raise funds for enforcing its protection, particularly of its most
384 degraded parts. Our review of the management history of the eight sacred groves also reveals
385 site-specific variation in the enforcement of restrictions on tree cutting or livestock grazing,

386 which are likely to have influenced considerably the habitat properties and, hence,
387 conservation capacity.

388 Land abandonment is another driving force in the evolution of the landscapes of this area. In
389 the postwar period, as agriculture in Western Europe entered a productivity-orientated phase,
390 agricultural change in the study area coincided with decline of agricultural activity or simply
391 of its abandonment. Crop fields disappeared and grasslands gradually developed into
392 shrublands and forests due to a decrease in animal grazing and subsequent natural succession.
393 An exception to that is Konitsa, where the surrounding fertile lowlands remain agricultural to
394 this day (Zomeni et al., 2008). This homogenization of the landscape may explain the
395 differences between sacred and control sites being only marginal. Photos from 1945 and 2007
396 (Fig. H.1) reveal a changing forest landscape with the forest areas around the groves most
397 often expanding. Thus, a possible hypothesis is that the sacred groves acted as nuclei of
398 expansion and dispersal of biodiversity into newly regenerated forest areas.

399 Because sacred groves along the mountainsides of Epirus were established for their benefits
400 in terms of cultural and religious beliefs, hill-slope protection, recreation or even scenery
401 (visual amenity), rather than for biodiversity conservation *per se*, they can be described as
402 suffering from a kind of "rocks and ice syndrome" (Terborgh, 1999). Biodiversity
403 conservation was not the priority in delimiting these areas; this has emerged as a secondary
404 benefit. For that reason, the sites chosen for sacred status were not selected according to
405 conservation criteria. This is especially the case with respect to their size. Size is a major
406 factor limiting conservation capacity (Halpern, 2003; Ramesh et al., 2016), both with respect
407 to the number of species that can be supported in the long-term and in the length of time an
408 extinction debt can be sustained following isolation (Fig. 4). However, people establishing
409 sacred groves might settle for much smaller areas than are necessary in conservation terms, as
410 can be seen at a global scale in Fig 4.

411 No size dependence was observed for the diversity of sacred groves. This was initially
412 surprising, given the expected dependence of species richness and relaxation time on area.
413 However, as the actual sampling area (given any taxonomic group) is the same in each site
414 we expect this to increase only weakly with site area (Phillips et al., 2017). Furthermore, we
415 should not think of these groves as islands of forest in a landscape of cultivation. The groves
416 have always existed in a matrix of habitable or partially-habitable landscape, so for this
417 reason also, it is not so surprising that measurements of diversity fail to show the limiting

418 effect of size expected from Eq. 1. Finally, consistent with historical and photographic
419 evidence, the area of groves is not constant. Most have expanded since 1945 while some were
420 not isolated even in 1945. Also, the variability of areas is not so great (Fig 4a), so that area
421 dependence is not easily detectable if statistical power is low. Thus, while Eqs (1-3), based on
422 isolated fixed-area island models, can illuminate our understanding of conservation capacity
423 and relaxation time, they must be used in conjunction with historical and landscape
424 information when their basic assumptions are not met.

425 These results show a conservation benefit of SNS, which is variable amongst taxa and is
426 affected by the type of grove and by management history. Other SNS in Epirus or elsewhere
427 are likely to behave similarly, particularly if they are of similar size. Thus, in the wider
428 context, if SNS are to play a role in modern conservation, these factors must be carefully
429 assessed. Extension of the analyses reported here should prioritize a landscape-scale
430 assessment of the relative fragmentation of the different sacred groves and control sites, and
431 the extent to which this explains the variation in their species composition and diversity
432 (Echeverría et al., 2007; Daye and Healey, 2015). A fuller knowledge of the historical context
433 can help in this, especially regarding changes in management regime. The issue of vegetation
434 type should be also addressed so as to clarify if it really plays an important role in
435 conservation efficiency.

436 The sacred groves studied here are small in size and have been affected by changing degrees
437 of protection and management throughout their history. Many of them could not function as a
438 reserves or conservation areas by themselves. However, following another modern paradigm,
439 that of the European Natura 2000 system (Official Journal of the European Union, 2011), a
440 network of protected areas existing in an agricultural matrix (following the “countryside
441 SAR” principle) (Pereira et al., 2014) offers an alternative approach. If SNS were
442 incorporated into wider parks or networks, the small conservation advantage that we
443 observed here could become more important. Moreover, a conservation network based
444 around such areas might gain local recognition more readily than a park or network
445 developed on a purely scientific basis. As a large proportion of SNS are small, this approach
446 is likely to be important globally.

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448

449

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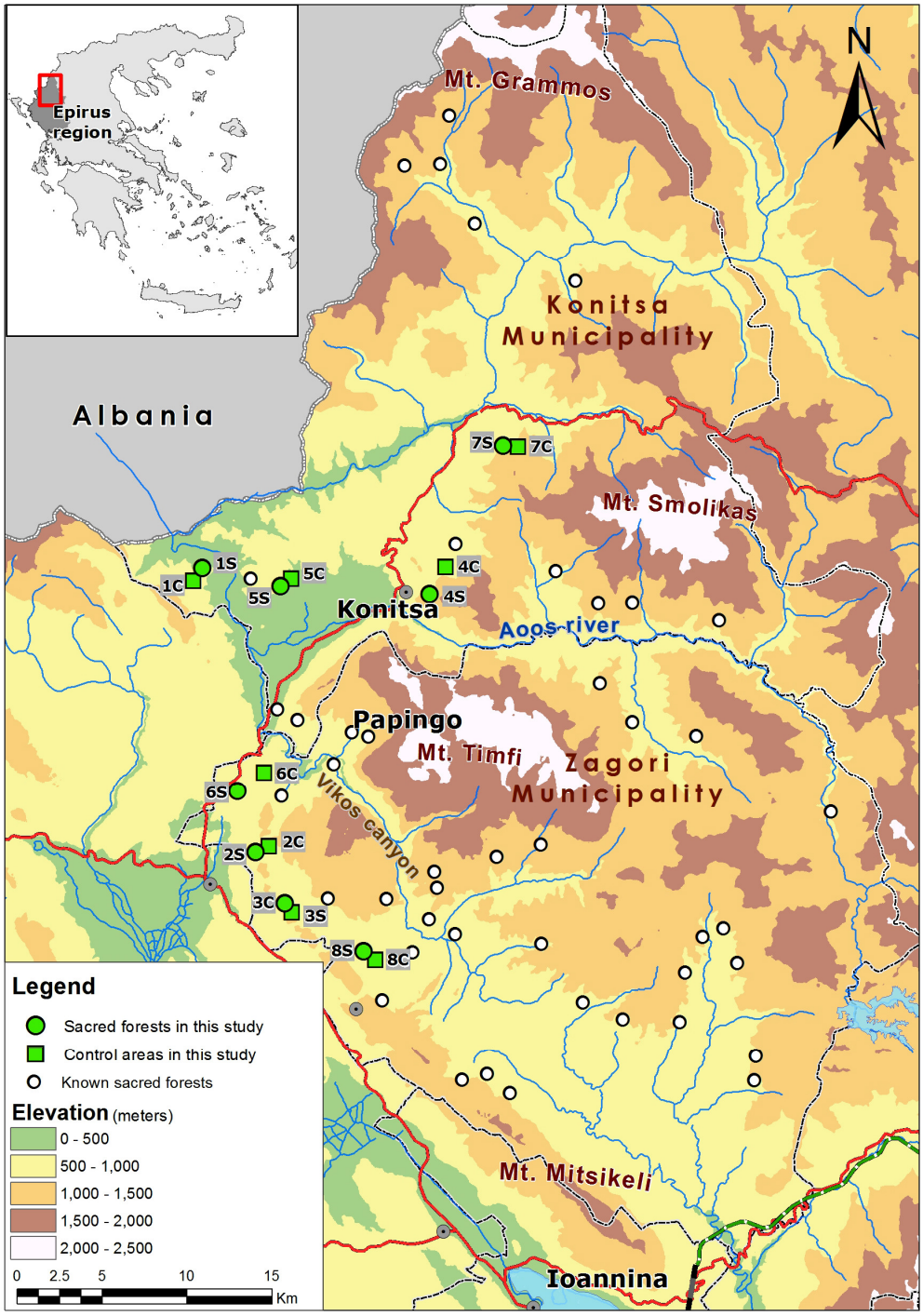

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691 **Figure 1** Identified sacred groves (circles) in the broad area of Zagori and Konitsa. For the
692 current study, biodiversity was measured in eight of these sacred groves (green circles) and in
693 eight corresponding control sites (squares). Shown in the inset is the location of the Epirus
694 study area in Greece. Red lines denote major roads.

695

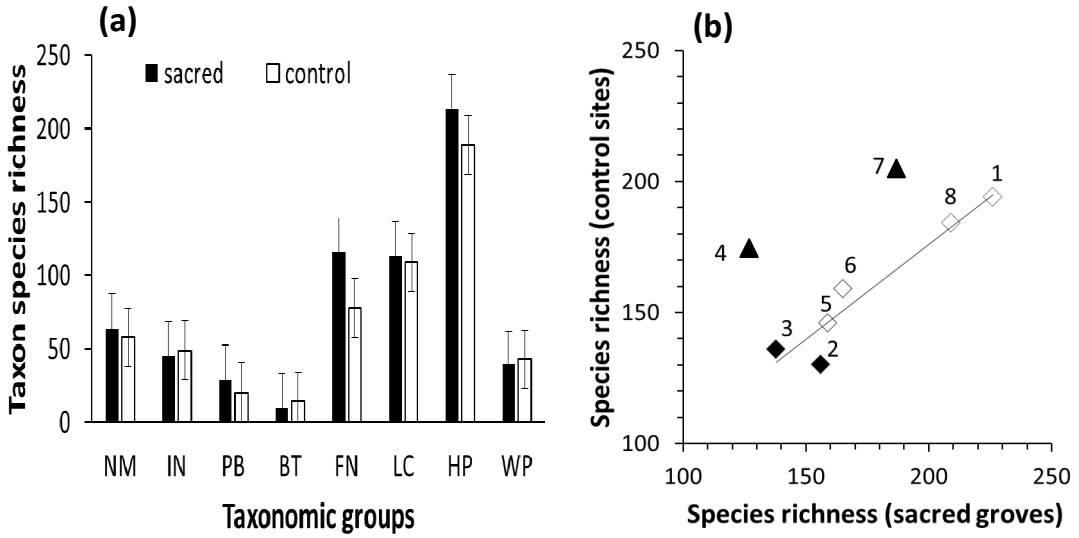


Figure 2 Representations of biodiversity in the sacred and control sites for various taxonomic groups: **(a)** Total species richness (genus richness for nematodes) in each group of species across all eight sacred groves and their respective control sites (with mean and standard error bars). Taxonomic groups are: NM, nematodes; IN, insects; PB, passerine birds; BT, bats; FN, fungi; LC, lichens; HP, herbaceous plants; WP, woody plants. (**b**) Scatterplot of species richness recorded in sacred groves and their respective control sites. The fitted line (y=0.727x+30.56, R^2 = 0.912) was calculated after the two pairs of sites dominated by conifers (4 and 7) were excluded. Open diamonds are deciduous broadleaved sites, closed diamonds evergreen broadleaved sites and closed triangles coniferous sites.

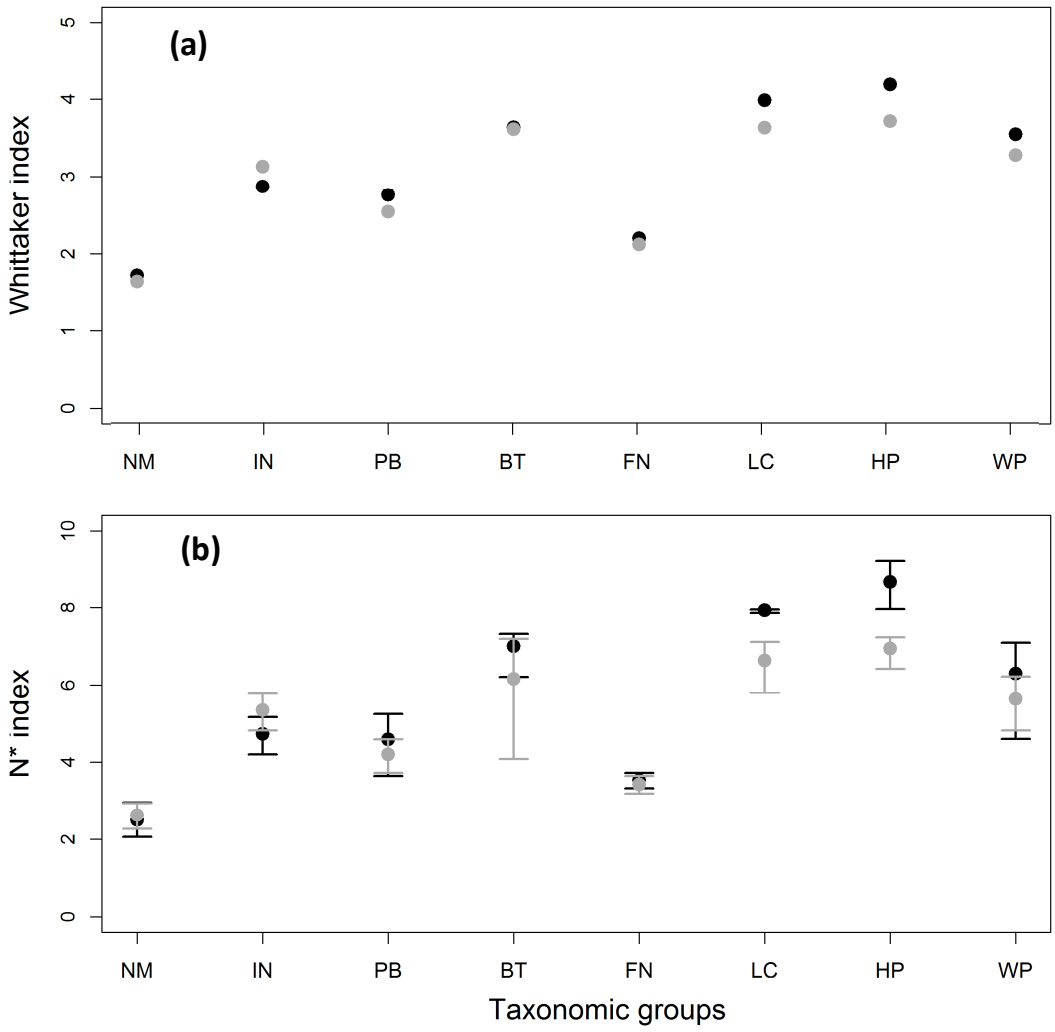


Figure 3 Species turnover measured as the beta diversity between the local scale (sites) and global scale (union of sites): (**a**) Whittaker index and (**b**) *N** index for the sets of eight sacred groves (black) and respective control sites (gray), by taxonomic group (NM, nematodes; IN, insects; PB, passerine birds; BT, bats; FN, fungi; LC, lichens; HP, herbaceous plants; WP, woody plants) with error bars corresponding to the standard deviation of the species accumulation curve used to estimate the *N** index. In the case of nematodes, genus turnover is shown.

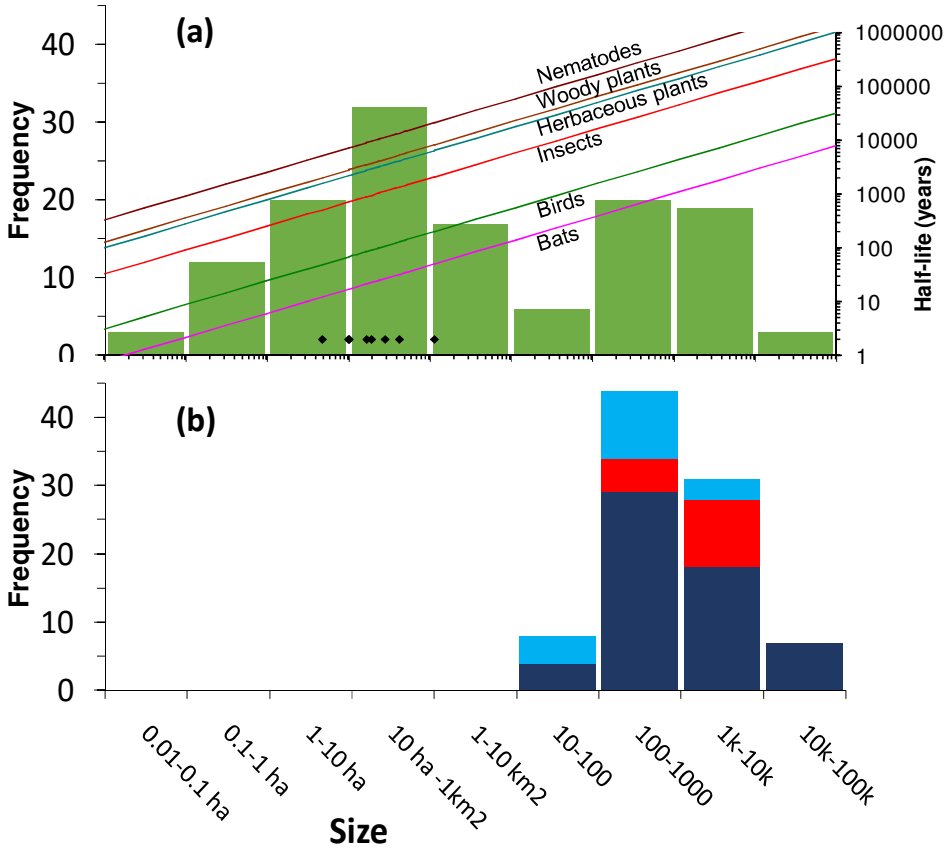


Figure 4 (a) Histogram of area for 126 SNS: 22 mapped in Epirus and 104 found in our literature search. Superimposed on this is the expected half-life of species loss following habitat isolation using Eq. 3 for all taxonomic groups except fungi and lichens for areas ranging from 0.01 hectare to 100,000 km^2. The taxonomic group name appears below the line except for nematodes and woody plants for which it is above the line. The sizes of the eight sacred groves of Epirus in this study are shown as black dots just above the horizontal axis. **(b)** Histogram of area for the national parks in Greece (light blue), Great Britain (red) and the USA (dark blue). The main divisions (powers of 10) in the horizontal axis are the same for both panels.

738 **Table 1.** Location, area and vegetation type of the eight sacred groves (S) and their respective
739 control sites (C). For vegetation type, D = deciduous broadleaf, E = evergreen broadleaf, C =
740 coniferous forests.

741

Associated village	Vegetation type	Sacred groves		Control sites	
		Code	Area (ha)	Code	Area (ha)
Aidonohori	D	1S	19.8	1C	16.24
Elafotopos	E	2S	29.11	2C	69.09
Kato Pedina	E	3S	10.33	3C	55.23
Konitsa	C	4S	115.7	4C	538.9
Mazi	D	5S	10.37	5C	54.24
Mesovouni	D	6S	17.02	6C	22.01
Molista	C	7S	43.29	7C	41.29
Vitsa	D	8S	4.87	8C	41.38

742

Appendix A – Selection of sacred groves, control sites and sampling points

Sacred sites

We identified sacred grove sites across the landscape based on archival and ethnographic fieldwork. We further identified and mapped the borderline of these groves using ortho-rectified aerial photographs from the year 1945, which is the oldest complete set of aerial photographs of the area. From these identified sacred groves, eight were selected on the basis of a number of criteria. Firstly, we excluded those less than 3.5 hectares in size, as estimated for 1945, so as to secure at least one permanent bird observation point of 100 m radius (see Appendix B) in each grove. Secondly, we excluded all sites for which there was evidence of substantive felling of trees during the last 60 years, according to the Forestry Department management plans and records or earlier ethnographic or field research. To the remaining sites, we applied the criteria of a minimum threshold of 70% current tree cover and lack of degradation, based on recent ethnographic and field data. From the initial shortlist of sites, a stratified set of sacred groves was selected so as to cover a range of cultural diversity (cultural units, ritual praxes and management regimes) according to ethnographic data (See Appendix E). Where possible (all criteria being satisfied), groves closer to roads were chosen so as to reduce field work and allow more time for sampling. The final set of sacred groves that were selected was limited to eight because of time constraints.

Fig A1. View from inside three sacred groves of different types: (left) Elafotopos, a broadleaved evergreen forest (2S), (middle) Molista, a coniferous forest (7S), and (right) Aidonochori, a deciduous forest (1S). (Photos K. Stara 2015)

Control sites

Since our main hypotheses concern biodiversity, we define a control site for each sacred grove so as to assess the biodiversity difference relative to a non-sacred, reference forest. This approach has been used widely in similar studies of biodiversity comparisons (Wortley et al. 2013, Derhé et al. 2016). Here, the selection priority is to find a non-sacred forest for which the environmental factors are as close as possible to the sacred grove. Thus, for each of the eight sacred groves, we identified the best matched control site (without sacred status but with similar site environment and vegetation characteristics) according to a series of criteria: (a) the site had to be close to the respective sacred site (less than 4 km), (b) its area should be

as large or larger than the respective sacred site, (c) tree cover in it should be no less than 70%, (d) it should be of the same vegetation type (dominated by coniferous, evergreen broadleaved or deciduous broadleaved trees) as the sacred grove, (e) it should have the same geological bedrock, and also (f) similar slope and aspect. Selection was based on the analysis of ortho-rectified aerial photos from 2007, existing forest vegetation maps, digitized geological maps of 1:5000 scale, and the Google Earth digital elevation model, supplemented by observations during field visits. Their boundaries were defined using all of the above criteria. Control sites were usually part of larger contiguous woodland areas and except for one, they were larger in area than the sacred sites.

Fig A2. View from the outside of two sacred groves of different types: (left) Molista, a coniferous forest (7S) lies behind slope above village, and (right) the evergreen broadleaved grove of Kato Pedina (3S) rises upwards to the right along the slope above the village. See also Appendix H. (Photos K. Stara 2015)

Sampling points

Inside each sacred site and in each corresponding control site, a set of points was chosen by random placement. These points were subject to the additional constraints that they should be located at least 100 m from the woodland edge and separated from any other by at least 300 m. These criteria define a maximum number of independent sample plots that can fit in each site. A heuristic algorithm [Generate Random Points, provided by the online software 'Geospatial Modelling Environment' (www.spatialecology.com)] was employed to provide the sequence of potential sampling points for each taxon. A common sequence of random points was generated for each site and provided to all the teams working on different taxonomic groups. However, the teams were not constrained to use the same points. For each taxonomic group, the same sampling effort was used in all sites and the total number of species that were found in the site was recorded.

Appendix B – Sampling protocols

Nematodes

Four sampling points were chosen at each site (sacred and control) and at each a plot of 100 m^2 was established. In each plot, a composite soil sample of five soil cores, 3 cm in diameter

and 12 cm in depth, was collected, so that four composite samples were taken from each site. In all cases, the litter layer was removed before sampling. Nematodes were extracted from 200 cm^3 of each composite soil sample. For extraction, the modified Cobb's sieving and decanting method (S'Jacob and van Bezooijen, 1984) was employed. After counting total abundance of nematodes, samples were fixed with 4% formaldehyde solution. From each sample, 150 nematodes were selected and identified to the genus level using an identification key (Bongers, 1994). In cases where the number of specimens of a sample was less than 150, we identified them all.

Insects

One sampling point was chosen at each site. Insect sampling was conducted using a modified Pollard sampling scheme (Caldasa and Robbins, 2003), following transects in four directions (N, S, E, W) of 200 m, with a width of 10 m on each side of the center line, lasting exactly 45 minutes. Sites were visited twice (early summer 2013 and late summer 2014) for five days each time, in order to include species that appear in different periods during the year, while the order at which sites were sampled differed each time, so as to avoid a bias induced by the specific time of the day. Flying adult insects were collected in nets, whereas soil dwelling and wood-boring adult insects were retrieved with the help of a knife and a tweezer. Specimens were then put into plastic bags and were given a label that described the site, the time and the number of individuals observed for each species. Identification was conducted at the Laboratory of Forest Entomology (Forest Research Institute - HAO Demeter, Greece) using the appropriate morphological keys for each insect order.

Passerine birds

One sampling point was chosen at each site. Point counts of a fixed radius of 100 m were carried out, recording all bird species observed or identified from their calls and breeding songs for a fixed time period of 10 minutes. One point-count was conducted per site, at the same fixed point, in early morning (from 30 min before dawn and for a duration of 3 h) on two dates, in early and late spring (with the interval between replicates being less than 30 days). Breeding songs were considered to indicate a pair of birds, whereas all other observations indicated one individual. The sum of individuals that were recorded on the two sampling dates, in each site, were taken as the measure of abundance in the analysis.

Bats

One sampling point was chosen at each site. Starting from there, another four sampling points were selected on a line with an approximate distance of 100 m between them. Echolocation calls of bats were recorded at each point for 15 minutes as well as between points (while walking from one point to the next), using the ultrasound receiver Batcorder (ecoObs). Recordings started half an hour after sunset and lasted approximately one and a half hours in each site. Sampling was conducted from mid to late summer and was repeated twice in each site, in 2013 and 2014. Calls were analyzed and species were identified by use of the ultrasound analysis software bcAnalyze v.2 (ecoObs).

Fungi

Sampling was conducted at eight sampling points within each sacred and control site. At each point, a plot of 200 m² was clearly marked along its edges and carefully examined for fungal carpophores. The area was visited twice during the year: in autumn, when most Basidiomycetes fruit, and again in spring in order to observe the fruiting Ascomycetes. Sampling was thus carried out four times in each of the 16 sites: autumn 2013, spring and autumn 2014 and autumn 2015. The exact timing of the visits relied on the information given by local collaborators about the occurrence of fruiting. Carpophores on all substrates (soil, leaf litter, dead wood) were sampled. Their identification was based on their macroscopic features in the field. Specimens of each species were counted and recorded. Specimens whose identification was in doubt were kept in portable coolers and taken to the Laboratory of Forest Pathology & Mycology (Forest Research Institute - HAO Demeter, Greece) for further laboratory examination and verification.

Lichens

In each site, one sampling point was chosen as the centroid of a 250 m^2 sample plot. Lichen sampling was carried out on tree trunks up to 2 m above ground, on five individuals of each tree species present in the plot. The sampling followed a random time- and species recovery-constrained strategy: on the set of sampled trees, all crustose, foliose or fruticose species observed were collected until no additional species could be detected. All collecting sites were visited once. The identification of the lichen material was carried out using stereo- (Zeiss Stemi) and light-microscopes (Zeiss Axioscope). Standard chemical spot tests, based on potassium hydroxide, bleach, iodine and para-phenylenediamine, and thin layer chromatography (Orange et al., 2001) were applied, and results were compared with those from literature (Clauzade and Roux, 1985; Nimis, 1987; Purvis et al., 1992; Wirth, 1995). Specimens are stored at the GZU Herbarium of the Institute of Plant Science, Karl-Franzens University of Graz (Austria).

Herbaceous and Woody Plants

In each site, two sampling points were selected. At each, a plot of 250 m^2 was set up. Within these plots, every vascular plant, whether a seed plant (Spermatophyta) or a fern (Pteridophyta), was identified to species level and recorded. Species were further divided into herbaceous and woody plants.

Appendix C - Species richness and its analysis

The location of the eight selected sacred groves of Konitsa and Zagori, in Epirus, northwestern Greece, and of their matching control sites are presented in Table C.1. Given are for each site (sacred grove or control) the number of species that were recorded for each of the eight taxonomic groups examined per site and overall.

887 A generalized linear regression model was built to test the effect of site area (area containing
888 the sampling locations within each site), site type (sacred or control) and vegetation type
889 (dominated by coniferous, evergreen broadleaved or deciduous broadleaved trees) on the total
890 species richness (*S*) and on the species richness within each taxonomic group (for nematodes
891 this was genus richness). The model used is $S \sim area + type + vegetation\ type + area{:}type$,
892 with a Poisson response and a logarithmic link function. The results are summarized in Table
893 C.2. The significance of each predictor variable is judged on a 5% significance level.

Table C.1. Number of species* recorded in the eight sacred groves (S) and their respective control sites (C) by taxonomic group. Total corresponds to the total species richness across all sites of each type for each taxonomic group (columns), and across all species groups for each site (rows). The grand total is the number of species in each group found across all 16 sites. For vegetation type, D = deciduous broadleaf, E = evergreen broadleaf, C = coniferous forests.

Type	Site	Number of species								
		Nematodes*	**Insects**	**Passerine birds**	**Bats**	**Fungi**	**Lichens**	**Herbaceous plants**	**Woody plants**	**Total**
sacred groves	Aidonohori (1S)	39	9	14	2	33	48	70	11	**226**
	Elafotopos (2S)	48	10	7	3	14	19	46	9	**156**
	Kato Pedina (3S)	32	11	6	2	21	12	47	7	**138**
	Konitsa (4S)	35	7	9	4	13	20	30	8	**126**
	Mazi (5S)	37	9	10	5	8	33	46	11	**159**
	Mesovouni (6S)	39	11	9	1	20	21	49	15	**165**
	Molista (7S)	37	11	14	2	22	24	58	16	**184**
	Vitsa (8S)	35	7	15	3	27	50	61	11	**209**
	Total	**64**	**45**	**29**	**10**	**116**	**113**	**213**	**39**	**629**
control sites	Aidonohori (1C)	31	8	9	2	11	42	74	17	**194**
	Elafotopos (2C)	46	10	6	5	12	15	28	8	**130**
	Kato Pedina (3C)	42	9	7	6	12	23	28	9	**136**
	Konitsa (4C)	36	11	8	4	17	29	48	10	**163**
	Mazi (5C)	25	5	9	6	10	23	57	11	**146**
	Mesovouni (6C)	31	8	5	2	20	27	50	16	**159**
	Molista (7C)	38	11	9	2	12	42	63	19	**196**
	Vitsa (8C)	34	11	10	4	12	39	59	15	**184**
	Total	**58**	**49**	**20**	**14**	**78**	**109**	**189**	**43**	**560**
	Grand total	**72**	**69**	**29**	**14**	**159**	**152**	**270**	**51**	**816**

*Number of genera for nematodes.

Table C.2. Summary statistics and ANOVA results of the generalized linear regression model predicting species richness (total and per taxonomic group) from the site area (extent of sampling area), the site type (S for sacred; control is baseline) and the vegetation type (E, evergreen broadleaved forest; D, deciduous broadleaved forest; coniferous forest is baseline). The model coefficient estimates (Estimate), standard error of the estimate (Std. error), associated *p*-value (Pr(>|z|)) and ANOVA *p*-values (Pr(>Chi)) are given.

Taxonomic group	Summary statistics				ANOVA	
		Estimate	Std. Error	Pr(>|z|)		Pr(>Chi)
All species	(Intercept)	2.358	0.444	1.09E-07		
	Area	-0.042	0.037	0.252	Area	0.582
	type S	-0.843	0.475	0.076	Type	0.788
	vegetation D	0.262	0.230	0.253	vegetation	**0.001**
	vegetation E	-0.500	0.331	0.131	area:type	**0.018**
	area:type S	0.123	0.052	0.017		
Nematodes	(Intercept)	3.571	0.150	0		
	Area	0.00004	0.0004	0.931	Area	0.994
	type S	0.088	0.108	0.418	Type	0.412
	vegetation D	-0.090	0.150	0.549	vegetation	0.097
	vegetation E	0.126	0.150	0.399	area:type	0.771
	area:type S	-0.001	0.002	0.772		
Insects	(Intercept)	2.398	0.276	0		
	Area	-1.17E-05	0.001	0.988	Area	0.644
	type S	0.186	0.218	0.393	Type	0.751
	vegetation D	-0.319	0.281	0.256	vegetation	0.694
	vegetation E	-0.140	0.285	0.623	area:type	0.255
	area:type S	-0.005	0.005	0.269		
Passerine birds	(Intercept)	2.398	0.276	0		
	Area	-1.17E-05	0.001	0.988	Area	0.644
	type S	0.186	0.218	0.393	Type	0.751
	vegetation D	-0.319	0.281	0.256	vegetation	0.694
	vegetation E	-0.140	0.285	0.623	area:type	0.255
	area:type S	-0.005	0.005	0.269		
Bats	(Intercept)	2.398	0.276	0		
	Area	-1.17E-05	0.001	0.988	Area	0.492
	type S	0.186	0.218	0.393	Type	0.277
	vegetation D	-0.319	0.281	0.256	vegetation	0.584
	vegetation E	-0.140	0.285	0.623	area:type	0.278
	area:type S	-0.005	0.005	0.269		
Fungi	(Intercept)	2.589	0.232	0		
	Area	0.0004	0.001	0.506	Area	0.671
	type S	0.585	0.163	0.0003	Type	**0.001**
	vegetation D	-0.021	0.227	0.927	vegetation	0.357

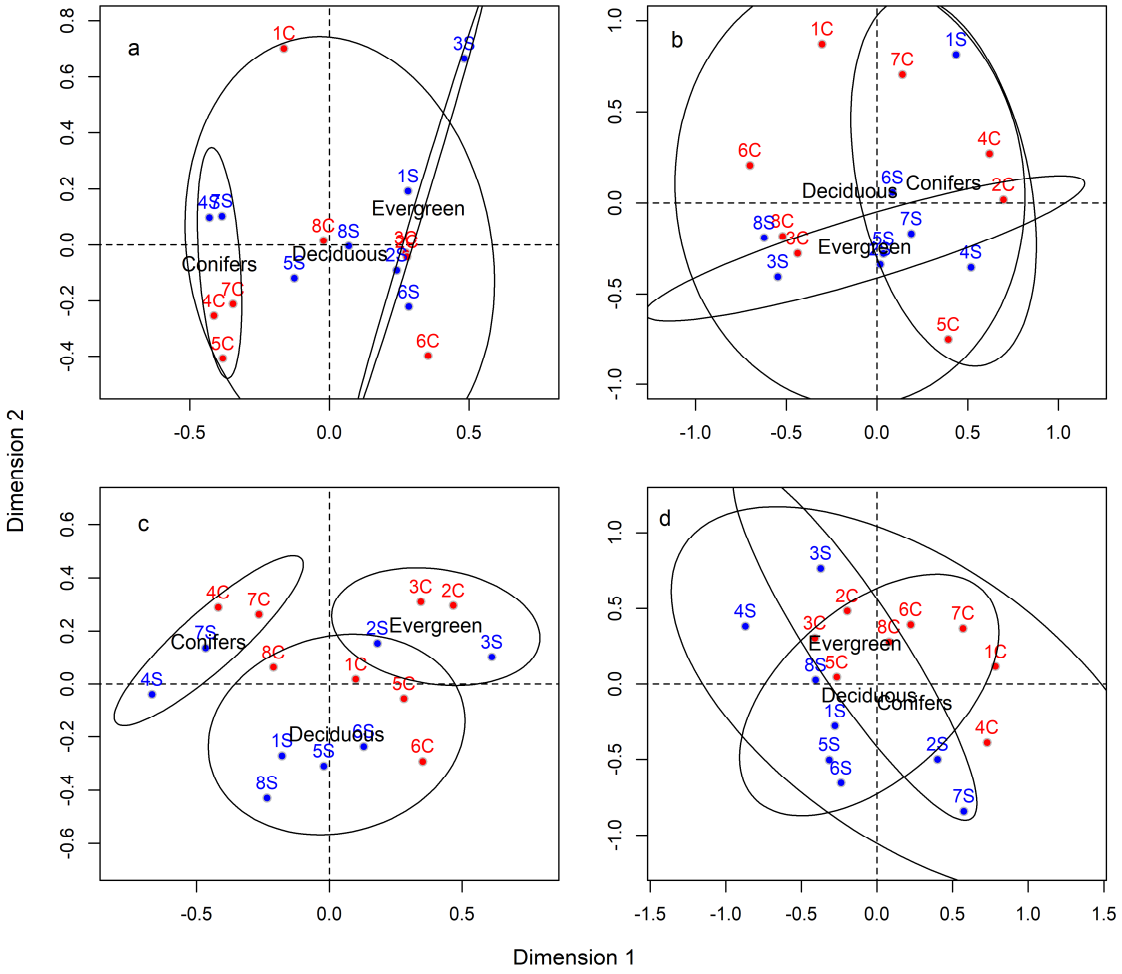
	vegetation E	-0.186	0.236	0.431	area:type	0.130
	area:type S	-0.005	0.003	0.139		
Lichens	(Intercept)	3.635	0.153	0		
	Area	-0.001	0.0004	0.270	Area	0.443
	type S	0.104	0.121	0.389	Type	0.390
	Vegetation D	-0.065	0.154	0.672	vegetation	**1.01E-07**
	Vegetation E	-0.754	0.179	2.61E-05		
	area:typeS	-0.007	0.003	0.015	area:type	**0.0113**
Herbaceous plants	(Intercept)	4.173	0.117	0		
	Area	-0.001	0.0005	0.093	Area	0.166
	type S	0.147	0.092	0.109	Type	0.676
	vegetation D	-0.126	0.117	0.285	vegetation	**7.6E-06**
	vegetation E	-0.542	0.130	3.03E-05	area:type	**0.001**
	area:type S	-0.006	0.002	0.002		
Woody plants	(Intercept)	3.051	0.215	0		
	Area	-0.001	0.001	0.055	Area	0.377
	type S	-0.119	0.190	0.531	Type	0.125
	vegetation D	-0.336	0.221	0.129	Vegetation	**0.012**
	vegetation E	-0.778	0.255	0.002	area:type	0.211
	area:type S	-0.005	0.004	0.225		

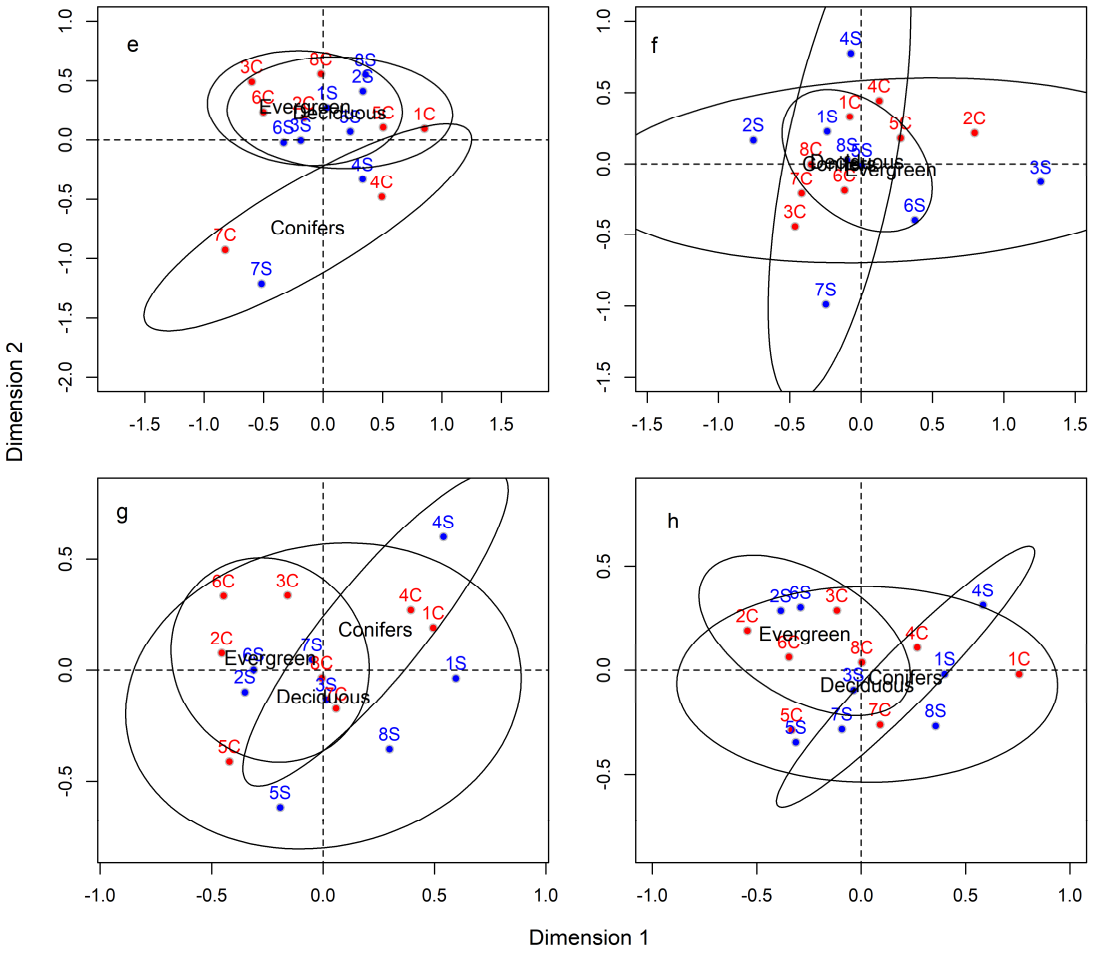
Appendix D - Ordination analysis

To visualize the difference in composition between sites, multidimensional scaling analysis based on Bray-Curtis dissimilarity was conducted for each taxon, separately, and for all taxa combined. The analysis was implemented in R 3.2.3 (R Core Team, 2015) using function *isoMDS* of the MASS package (Venables and Ripley, 2002) and function *vegdist* of the VEGAN package (Oksanen et al., 2016).

For herbaceous and woody plant species, ordination showed a surprising lack of differentiation in floristic composition between the three vegetation types corresponding to different topographic positions (Fig. D.1). This is possibly due to the fact that we have only presence counts for these taxonomic groups. For the other species, patterns of species composition amongst sites varied notably by taxonomic group. For lichens, insects and bats, there was no clear pattern, with much overlap amongst the pairs and the vegetation types. For passerine birds, there was a clear distinction amongst the three vegetation types, but the two sites within each pair were not closely clustered. Notably, for passerine birds there is a separation between sacred groves and control sites. For the remaining two taxonomic groups, the conifer-dominated sites were distinct from the broadleaf tree-dominated ones, but whereas for the fungi the two sites within each pair were quite well clustered, for the nematodes they tended to be split. For all species combined, there is a clear distinction in the species composition of the three vegetation types and for the majority of the eight pairs (Fig. D.2). However, the ordination analyses did not reveal any consistent differences in

composition between the two types of sites (sacred groves and control) for the individual groups of species or for all species combined.

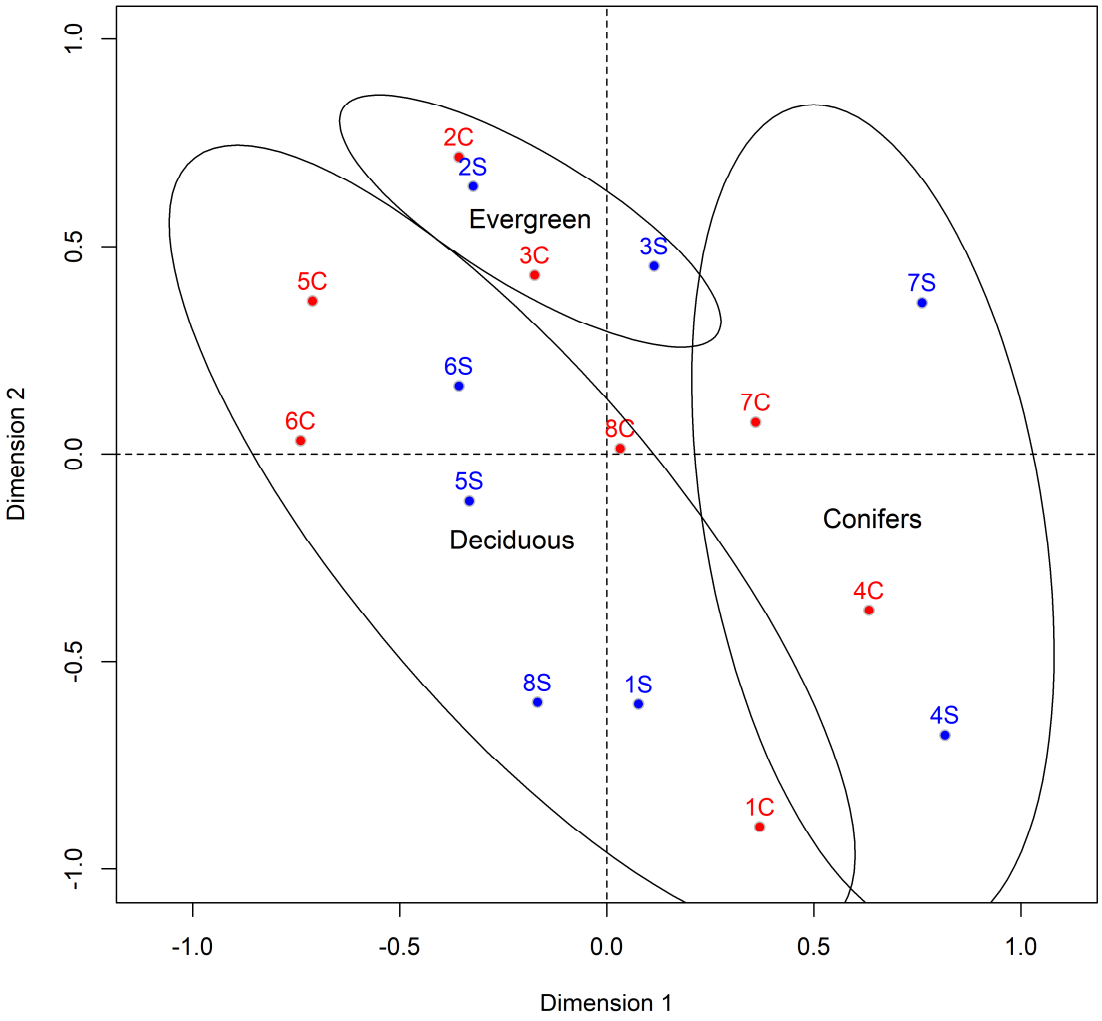




931

932 **Figure D.1.** Ordination of sacred groves (S) and respective control sites (C) using
933 multidimensional scaling with the Bray-Curtis dissimilarity index as a measure of the
934 distance between sites for (**a**) nematodes, (**b**) insects, (**c**) passerine birds, (**d**) bats, (**e**) fungi,
935 (**f**) lichens, (**g**) herbaceous plants, (**h**) woody plants. Ellipses define 90% intervals of the
936 distribution of scores within the three vegetation types dominated by different tree types (C,
937 coniferous; E, evergreen broadleaved; D, deciduous broadleaved). The analysis was
938 implemented in R using function *isoMDS* in the MASS package.

939



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941

942 **Figure D.2.** Ordination of sacred groves (S) and respective control sites (C) using
943 multidimensional scaling with the Bray-Curtis dissimilarity index as a measure of the
944 distance between sites. Data from all taxa were reduced to presence-only before carrying out
945 the analysis. Ellipses define 90% intervals of the distribution of scores within the three
946 vegetation types dominated by different tree types (coniferous, evergreen broadleaved and
947 deciduous broadleaved). The analysis was implemented in R using function *isoMDS* in the
948 MASS package.

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950

Appendix E – SCI species

Table E.1. Species of Community Interest (SCI) identified in each sacred grove and respective control site of this study. Of the 8 taxa investigated, SCI species were identified only for bats, insects, passerine birds (Passer.), herbaceous plants (P-herb) and woody plants (P-Wood), as nematodes were identified at the genus level and in some cases also lichens and fungi.

Type	Location	Code	Number of SCI					
			Bats	Insects	Passerine birds	Herbaceous plants	Woody plants	Total
sacred groves	Aidonohori	1S	0	0	1	0	0	1
	Elafotopos	2S	1	0	0	0	1	2
	Kato Pedina	3S	1	0	1	0	1	3
	Konitsa	4S	0	0	1	0	1	2
	Mazi	5S	0	0	3	0	1	4
	Mesovouni	6S	0	0	2	0	1	3
	Molista	7S	0	0	3	0	0	3
	Vitsa	8S	0	1	1	0	1	3
	Total		**1**	**1**	**8**	**0**	**1**	**11**
control sites	Aidonohori	1C	0	0	1	0	1	2
	Elafotopos	2C	1	0	0	0	1	2
	Kato Pedina	3C	1	0	1	0	1	3
	Konitsa	4C	0	0	1	0	0	1
	Mazi	5C	0	0	0	0	1	1
	Mesovouni	6C	0	0	1	0	1	2
	Molista	7C	0	0	2	0	0	2
	Vitsa	8C	0	2	1	0	1	4
	Total		**2**	**2**	**4**	**0**	**1**	**9**
	Grand Total		**2**	**2**	**8**	**0**	**1**	**13**

Appendix F – Size of sacred natural sites and national parks size worldwide

Table F.1. Sacred natural sites (SNS) included in the comparative analysis. SNS mapped by us in the study area are in italics (for these, the names are in two parts: [village name]-[sacred forest name]). Those whose biodiversity we surveyed also are in bold.

Name	Area (ha)	Country	Continent	Reference
Tsodilo Hills	9,000.0	Botswana	Africa	WWF 2005
Zaïpobly	12.3	Côte d'Ivoire	Africa	WWF 2005
Gufae	33.5	Ethiopia	Africa	Daye & Healey 2015
Tele	12.6	Ethiopia	Africa	Daye & Healey 2015
Osha-Ocha	5.3	Ethiopia	Africa	Daye & Healey 2015
Akasie	4.9	Ethiopia	Africa	Daye & Healey 2015
Ula	1.8	Ethiopia	Africa	Daye & Healey 2015

Qimme	0.7	Ethiopia	Africa	Daye & Healey 2015
Bortianor	164,892.0	Ghana	Africa	O'Neal Campbell 2005
Oshiye	772.0	Ghana	Africa	O'Neal Campbell 2005
Asantemanso Sacred grove	295.0	Ghana	Africa	Bossart et al. 2006
Boabeng-Fiema	190.0	Ghana	Africa	Larsen et al. 2009
Gyakye Sacred grove	11.5	Ghana	Africa	Bossart et al. 2006
Bonwire Sacred grove	8.0	Ghana	Africa	Bossart et al. 2006
Kajease forest	6.0	Ghana	Africa	Bossart et al. 2006
Kokrobite	0.1	Ghana	Africa	O'Neill Campbell 2005
Abiriw	0.04	Ghana	Africa	Nganso et al. 2012
Odumante	0.03	Ghana	Africa	Nganso et al. 2012
Mount Kenya	142,020.0	Kenya	Africa	Dudley et al. 2009
Mijikenda Kaya forests	6,000.0	Kenya	Africa	Githitho 2003
Nyika National Park	313,400.0	Malawi	Africa	Dudley et al. 2009
Sacred groves of Oshogbo	55.0	Nigeria	Africa	Dudley et al. 2009; WWF 2005
Limpopo's Modjadji Reserve	439.0	South Africa	Africa	Dudley et al. 2009; WWF 2005
Misali Island marine conservation area	2,158.0	Tanzania	Africa	Dudley et al. 2009
Mude Lhong	330.0	Thailand	Asia	Junsongduang et al. 2013
Jigme Dorji Wildlife Sanctuary	790,495.0	Bhutan	Asia	Dudley et al. 2009
Angkor	40,000.0	Cambodia	Asia	WWF 2005
Xishuangbanna	247,439.0	China	Asia	Dudley et al 2009; WWF 2005
Meghalaya	100,000.0	India	Asia	Mishra et al. 2004
Periyar Tiger reserve	77,700.0	India	Asia	Dudley et al. 2009
Mawsmai Syiem	122.0	India	Asia	Ormsby 2013
Law Lyngdoh	77.0	India	Asia	Ormsby 2013
Ayappa	41.7	India	Asia	Ormsby 2013
Ayyapa devarakadu	16.6	India	Asia	Ormsby 2013
Betekurubara devarakadu	15.9	India	Asia	Ormsby 2013
Khloo Langdoh	15.7	India	Asia	Ormsby 2013
Khloo Blai Phlong	10.0	India	Asia	Ormsby 2013
Ayyapa Kadanoor	10.0	India	Asia	Ormsby 2013
Poonya Bhagavathi	7.0	India	Asia	Ormsby 2013
Law Lyngdoh	4.4	India	Asia	Ormsby 2013
Battemaki	3.6	India	Asia	Ormsby 2013
Periya Mudaliar	3.2	India	Asia	Ramanujan et al. 2003
Karekud	3.0	India	Asia	Ormsby 2013
Koorvale	3.0	India	Asia	Ormsby 2013
Bhagavathi temple	2.0	India	Asia	Ormsby 2013
Kadenkad	1.6	India	Asia	Ormsby 2013
Kundachappa	1.4	India	Asia	Ormsby 2013
Kilialamman	1.0	India	Asia	Ramanujan et al. 2003
Keezhbuvanagiri	1.0	India	Asia	Ramanujan et al. 2003
Mahadevara	1.0	India	Asia	Ormsby 2013
Kikut Aiyappa	1.0	India	Asia	Ormsby 2013
Pammangalathamme	0.8	India	Asia	Ormsby 2013

Aiyappa (Mythadi)	0.8	India	Asia	Ormsby 2013
Ayappa Temple	0.6	India	Asia	Ormsby 2013
Chamundi	0.6	India	Asia	Ormsby 2013
Kalath Bhagavathi	0.5	India	Asia	Ormsby 2013
Periya Kattupalayam Chavadi	0.4	India	Asia	Ramanujan et al. 2003
Bhagavathi temple Kadanoor	1.0	India	Asia	Ormsby 2013
Alagar hills	4,500.0	India-Tamil Nadu	Asia	Swamy et al. 2003
Kandanur	33.0	India-Tamil Nadu	Asia	Swamy et al. 2003
Solai-Anadaver kovil	12.0	India-Tamil Nadu	Asia	Swamy et al. 2003
Ayaanar kovil	10.0	India-Tamil Nadu	Asia	Swamy et al. 2003
Danau Sentarum National Park	80,000.0	Indonesia	Asia	Wadley and Colfer 2004
Mount Hakusan	14,826.0	Japan	Asia	Dudley et al. 2009
The sacred forest of Kashima	1,500.0	Japan	Asia	WWF 2005
Kii Mountain range	265.0	Japan	Asia	Mallarach & Papayannis 2006
Kinabalu National Park	75,370.0	Malaysia	Asia	Dudley et al. 2009
Khovsgol Lake	838,070.0	Mongolia	Asia	WWF 2005
Sagarmatha National Park	114,800.0	Nepal	Asia	Dudley et al. 2009; WWF 2005
Peak wilderness park	22,380.0	Sri Lanka	Asia	Dudley et al. 2009
Mihintale	1,000.0	Sri Lanka	Asia	WWF 2005
Mae tae hai	325.0	Thailand	Asia	Junsongduang et al. 2013
Kata Tjuta National Park	132,566.0	Australia	Australasia	Dudley et al. 2009
Deen Maar	453.0	Australia	Australasia	WWF 2005
Tongarino National Park	76,504.0	New Zealand	Australasia	Dudley et al. 2009
Hunstein Range Wildlife Management Areas	220,000.0	Papua New Guinea	Australasia	WWF 2005
Čertova stěna	105.0	Czech republic	Europe	WWF 2005
Gammelstadsviken	435.0	Estonia	Europe	Mallarach et al. 2010
Hiiemägi	25.0	Estonia	Europe	Mallarach et al. 2010
Northern Karelia	350,000.0	Finland	Europe	Dudley et al. 2009
Pyätunturi National Park	4,340.0	Finland	Europe	WWF 2005
Mt Athos	33,563.0	Greece	Europe	WWF 2005
Meteora	375.0	Greece	Europe	WWF 2005
Greveniti – Eftapapado	117.2	Greece	Europe	Tsiakiris et al. 2013
Konitsa – Kouri (4S)	115.7	Greece	Europe	Tsiakiris et al. 2013
Manasi- Livadi	53.7	Greece	Europe	Tsiakiris et al. 2013
Kalouta – Livadi	51.7	Greece	Europe	Tsiakiris et al. 2013
Molista – Trafos (7S)	43.3	Greece	Europe	Tsiakiris et al. 2013
Tristeno – Livadi	39.1	Greece	Europe	Tsiakiris et al. 2013
Kalovrisi - Ag. Nikolaos	38.8	Greece	Europe	Tsiakiris et al. 2013
Elafotopos-Kri Panagias (2S)	29.1	Greece	Europe	Tsiakiris et al. 2013
Aristi – Pournaria	25.1	Greece	Europe	Tsiakiris et al. 2013
Palioseli - Mereáo	24.4	Greece	Europe	Tsiakiris et al. 2013
Kapesovo – Gradista	23.6	Greece	Europe	Tsiakiris et al. 2013
Leptokaria - Ekklisiastiko	23.3	Greece	Europe	Tsiakiris et al. 2013
Aidonochori-Aidonolalousa (1S)	19.8	Greece	Europe	Tsiakiris et al. 2013
Mesovouni-Ag Charálampos	17.0	Greece	Europe	Tsiakiris et al. 2013

(6S)				
Iliochori - Proph. Elias	16.6	Greece	Europe	Tsiakiris et al. 2013
Kavasila – Panagia	13.0	Greece	Europe	Tsiakiris et al. 2013
Vrysochori – Livadi	11.4	Greece	Europe	Tsiakiris et al. 2013
Mazi – Panagia (5S)	10.4	Greece	Europe	Tsiakiris et al. 2013
Kato Pedina – Anilia (3S)	10.3	Greece	Europe	Tsiakiris et al. 2013
Aetopetra - Ag. Paraskevi	8.6	Greece	Europe	Tsiakiris et al. 2013
Vovousa - Ag. Paraskevi	6.8	Greece	Europe	Tsiakiris et al. 2013
Vitsa – Livadakia (8S)	4.9	Greece	Europe	Tsiakiris et al. 2013
Mt Carmel	26,600.0	Israel	Europe	Dudley et al. 2009
Benedictine monastery Monte Oliveto Maggiore	500.0	Italy	Europe	Frascarolli 2013
Quercus ilex forest	100.0	Italy	Europe	Frascarolli 2013
Yuganskiy Kanthy	648,700.0	Russia	Europe	Dudley et al. 2009; WWF 2005
Laponian area	940,000.0	Sweden	Europe	Dudley et al. 2009
Coconino National Forest	747,061.0	USA	N. America	Dudley et al. 2009; WWF 2005
Wupatki National Monument	14,267.0	USA	N. America	Dudley et al. 2009; WWF 2005
Lanin National Park	379,000.0	Argentina	S. America	Dudley et al. 2009; WWF 2005
Kaa-lya del Gran Chaco	1,954,875.0	Bolivia	S. America	WWF 2005
Isiboro-sécure	1,200,000.0	Bolivia	S. America	WWF 2005
Sajama National Park	100,230.0	Bolivia	S. America	WWF 2005
Tumucumaque	2,700,000	Brasil	S. America	WWF 2005
Laguna De la cocha	39,000.0	Colombia	S. America	Dudley et al. 2009; WWF 2005
Arenal	12,010.0	Costa Rica	S. America	WWF 2005
Cayapas Mataje	51,300.0	Ecuador	S.America	WWF 2005
Tikal	55,005.0	Guatemala	S. America	WWF 2005
Lagunas de Montebello	60,022.0	Mexico	S. America	WWF 2005
Kuna Park	60,000.0	Panama	S. America	WWF 2005
Lake Titikaka	460,000.0	Peru	S. America	WWF 2005
Machu Pichu	32,592.0	Peru	S. America	Dudley et al. 2009

Table F.2. National Parks (NP) in Greece, UK and the USA used in the analysis and their size (in km^2).

Name	**km^2**	**Country**
Lakes Volvi & Koroneia	2,120	Greece
Northern Pindos National Park	1,970	Greece
Rodopi Mountain Range National Park	1,731	Greece
National Park of East Macedonia - Thrace	930	Greece
Lake Kerkini National Park	831	Greece
National Park of Tzoumerka, Peristeri and Arachthos Gorge	820	Greece
Chelmos-Vouraikos National Park	544	Greece
Dadia – Lefkimi – Soufli Forest National Park	428	Greece
Axios-Loudias-Aliakmon National Park	338	Greece

Prespa National Park	327	Greece
Olympus National Park	238	Greece
Evros Delta	200	Greece
Parnitha National Park	180	Greece
Mt Oiti National Park	70	Greece
Parnassos National Park	36	Greece
Ainos National Park	29	Greece
National Park of Schinias – Marathon	14	Greece
Cairngorms	4,528	UK
Lake District	2,362	UK
Yorkshire Dales	2,179	UK
Snowdonia	2,176	UK
Loch Lomond and the Trossachs	1,865	UK
South Downs	1,624	UK
Peak District	1,437	UK
North York Moors	1,434	UK
Brecon Beacons	1,344	UK
Northumberland	1,048	UK
Dartmoor	953	UK
Exmoor	694	UK
Pembrokeshire Coast	621	UK
New Forest	570	UK
Broads	303	UK
Wrangell - St. Elias	53,370	USA
Gates of the Arctic	34,398	USA
Denali	24,398	USA
Katmai	16,552	USA
Lake Clark	16,370	USA
Death Valley	13,759	USA
Glacier Bay	13,275	USA
Yellowstone	8,991	USA
Kobuk Valley	7,082	USA
Everglades	6,105	USA
Grand Canyon	4,927	USA
Glacier	4,102	USA
Olympic	3,731	USA
Sequoia & Kings Canyon	3,495	USA
Big Bend	3,242	USA
Joshua Tree	3,213	USA
Yosemite	3,027	USA
North Cascades	2,768	USA
Kenai Fjords	2,456	USA
Isle Royale	2,314	USA
Great Smoky Mountains	2,110	USA
Canyonlands	1,366	USA
Grand Teton	1,255	USA

Rocky Mountain	1,076	USA
Channel Islands	1,009	USA
Badlands	989	USA
Capitol Reef	979	USA
Mount Ranier	954	USA
Voyageurs	882	USA
Hawaii Volcanoes	880	USA
Shenandoah	794	USA
Crater Lake	741	USA
Biscayne	700	USA
Zion	593	USA
Redwood	439	USA
Great Sand Dunes	433	USA
Lassen Volcanic	430	USA
Petrified Forest	379	USA
Saguaro	370	USA
Guadalupe Mountains	350	USA
Great Basin	312	USA
Arches	309	USA
Theodore Roosevelt	285	USA
Dry Tortugas	262	USA
Mammoth Cave	214	USA
Mesa Verde	211	USA
Acadia	193	USA
Carlsbad Caverns	189	USA
Bryce Canyon	145	USA
Cuyahoga Valley	134	USA
Black Canyon of the Gunnison	123	USA
Haleakala	122	USA
Wind Cave	115	USA
Pinnacles	108	USA
Congaree	90	USA
Virgin Islands	52	USA
American Samoa	43	USA
Hot Springs	22	USA

Appendix G – Ethnographic Research

Methods

Ethnographic study of the sacred groves of Epirus aiming to describe people's valuation and perception of different tree species and to identify the sacred natural sites and their emblematic trees (Stara et al., 2015) started in 2005, involving initially 23 villages in Zagori. Work resumed in 2012 and covered the rest of Zagori and the adjacent area of Konitsa.

975 Research for this study of the archives of municipalities, the Forestry Service and the Church,
976 and of local libraries targeted at finding references to the sacred groves and their history, in
977 general, and of those selected for the study, in particular. Ethnographic research involved
978 interviews with local people. They were asked about their community's sacred groves, the
979 reasons for their maintenance, also about their history and the ritual activities, the
980 supernatural guardians, acceptable and non-acceptable uses, and stories or taboos about
981 trespassing in the groves (Stara et al., 2016).

982 *Management regimes in the sacred groves of Epirus*

983 The groves appear either in the form of protective forests above or close to villages or as
984 groups of veteran trees that accompany outlying churches ("xoklissia") or icon stands
985 ("eikonismata", shrines comprising boxes containing icons and an oil lamp that remains lit
986 most evenings; Stewart, 1993; Nixon, 2006) retaining a protection value through association
987 with various Orthodox saints (Politis, 1904; Kyriakidou-Nestoros, 1989). Management
988 regimes in the sacred groves of Epirus vary from strict protection to controlled management.
989 These regimes are site-dependent and related to the specific reasons for which these groves
990 were established and maintained, to the type of religious dedication, the perceived personality
991 of the protector saint or saints, historical circumstances and community needs. When a
992 church with a sacred grove was founded on the epiphany of the divine, then the protection
993 was strict. For example, for the grove in Vovoussa in East Zagori, dedicated to the saint Agia
994 Paraskevi, local people argue that Agia Paraskevi herself chose the exact point, where the
995 church should be built, through various manifestations, such as repeatedly moving her icon
996 there. The local cult remains very much alive today linked to that grove and all harvests (e.g.
997 from hunting, collecting honey from wild bee hives, plants, mushrooms, dead wood etc.) are
998 still strictly prohibited (Stara et al., 2016). Strict regimes also tended to prevail for protective
999 forests on very steep slopes (e.g. at Molista, site 7S; Table S1, Fig S3). In contrast, the regime
1000 in some groves is much more relaxed (e.g. at Mazi, 5S; Table S1, Fig. S3); for instance,
1001 grazing is allowed without restrictions during certain time periods. Harvesting of branches
1002 ("shredding") of evergreen tree species during harsh winters (for fuelwood or animal fodder)
1003 was allowed occasionally by church and community councils, whereas shredding of
1004 deciduous tree species during early spring was always considered a trespass. In extreme
1005 cases, controlled management might permit timber harvesting for necessary public works.
1006 Some tolerance of breaking these rules was extended to members of lower social strata.
1007 Finally, collective trespassing could be allowed in abnormal situations. For example, in times
1008 of war or during festivals that are characterized by the ceremonial reversal of social order, the
1009 collection of dead wood and flammable branches of shrubs for use might be allowed (e.g. at
1010 Christmas or for carnival bonfires). Several hamlets in the area were consolidated during the
1011 16th to 17th century forming the present villages. Where settlements are abandoned, their
1012 associated sacred groves are often gradually neglected and only mature trees in the vicinity of
1013 the church itself are protected (Stara et al., 2016).

1014

Excommunication

Excommunication is the exclusion of a person from the Church and the deprival of its mysteries. In the Orthodox Church, it is the heaviest punishment that can be imposed on a Christian. From the later Byzantine period, and particularly under the Ottoman rule, excommunication was commonly employed for offenses of economic or social character, as are cases of theft, rape, livestock stealing, defamation, trespassing etc. It was also used as a threat in order to protect trees and other natural resources from trespassing and interference (Mihailaris, 2004; Stara et al., 2012).

Appendix H – Aerial Photos of sacred groves in 1945 and 2007

The exact borders of the sacred groves studied were identified and mapped using ortho-rectified aerial photographs from the year 1945, the oldest complete set of aerial photographs of the area (source: Hellenic Military Geographical Service, digital aerial photo 1945 - orthorectified) and compared with the most recent set of 2007 (Hellenic Cartographic and Cadastral Organisation, digital orthorectified image 2007). The scale for all photographs is 1:7,500 except for the site 4S (Konitsa) for which it is 1:20,000.

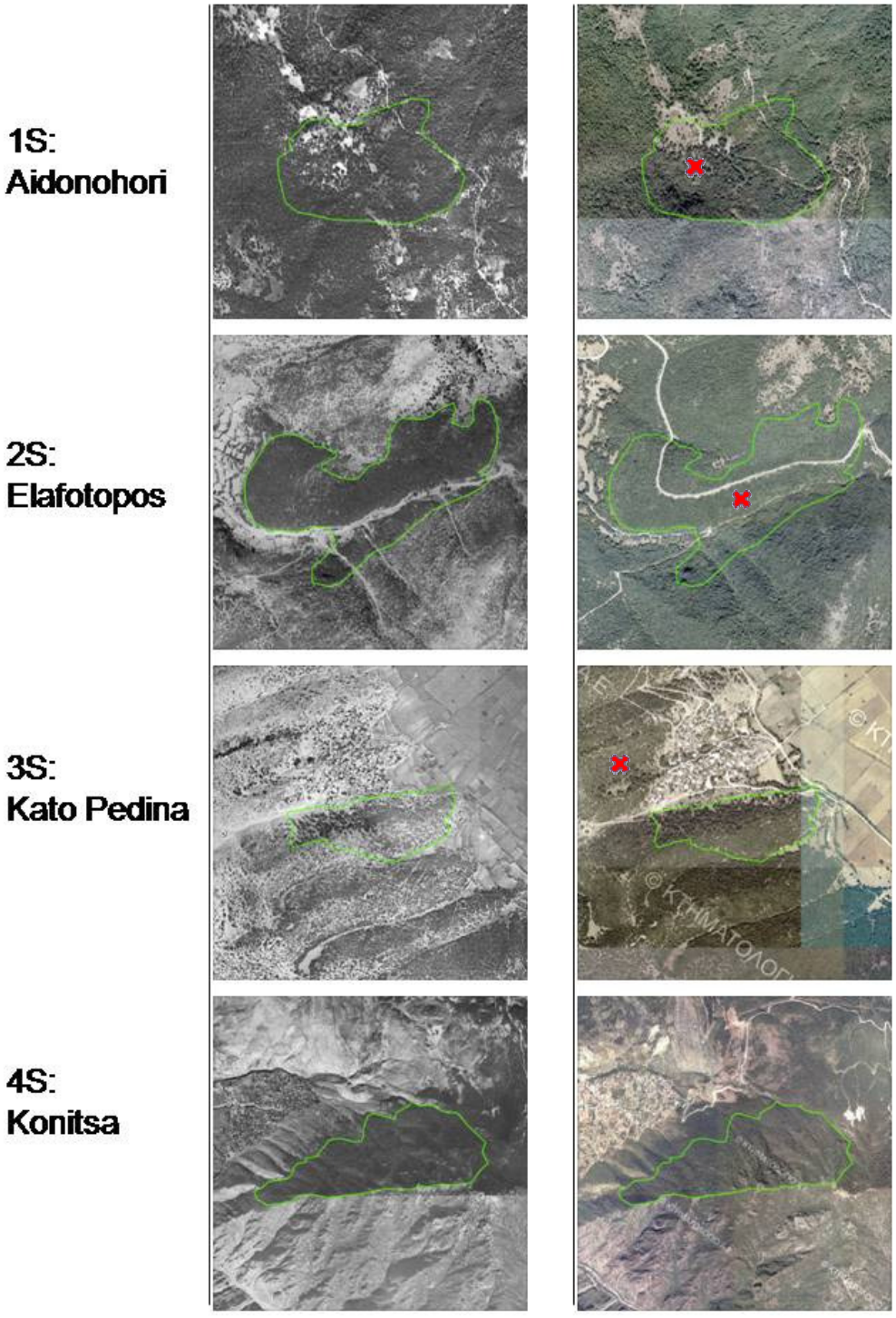
These photos reveal a changing forest landscape, with the forest areas around the groves often expanding. Sites 1S, 4S, 5S and 7S were not isolated from the surrounding forest areas even in 1945.

Sites 1S and 5S show little net change in cover but exhibit a pattern of patchy increase or decrease in tree cover within the sacred grove. The area surrounding site 5S changed in vegetation structure, from a dense scrubland to a young forest as grazing by goats decreased.

In sites 2S, 4S and 7S, forest cover remained high within the sacred grove but with substantial changes in the surrounding matrix. Whereas the sacred groves in 1945 were largely isolated (surrounded mainly by rangelands, scrublands or wood-pastures with minimum tree cover), by 2007, much of this surrounding matrix was covered by trees. This is predominantly because of the cessation of grazing that allowed the regrowth of forests. In the case of conifer forests (sites 4S, 7S), trees in the sacred groves could have been an important seed source, while for the other types, existing shrubs (e.g. around site 2S) can take tree form once grazing stops.

Sites 3S and 6S show a similar trend of a large increase in tree cover between the two dates, both inside the sacred grove and in the surrounding matrix.

Around site 8S, there is substantial increase in tree cover in the surrounding matrix, with just patchy changes in tree cover inside the sacred grove, as grazing (goats, sheep and cows) is still active forming an open extensive wood pasture characterized by scattered trees and scrubs.



1051

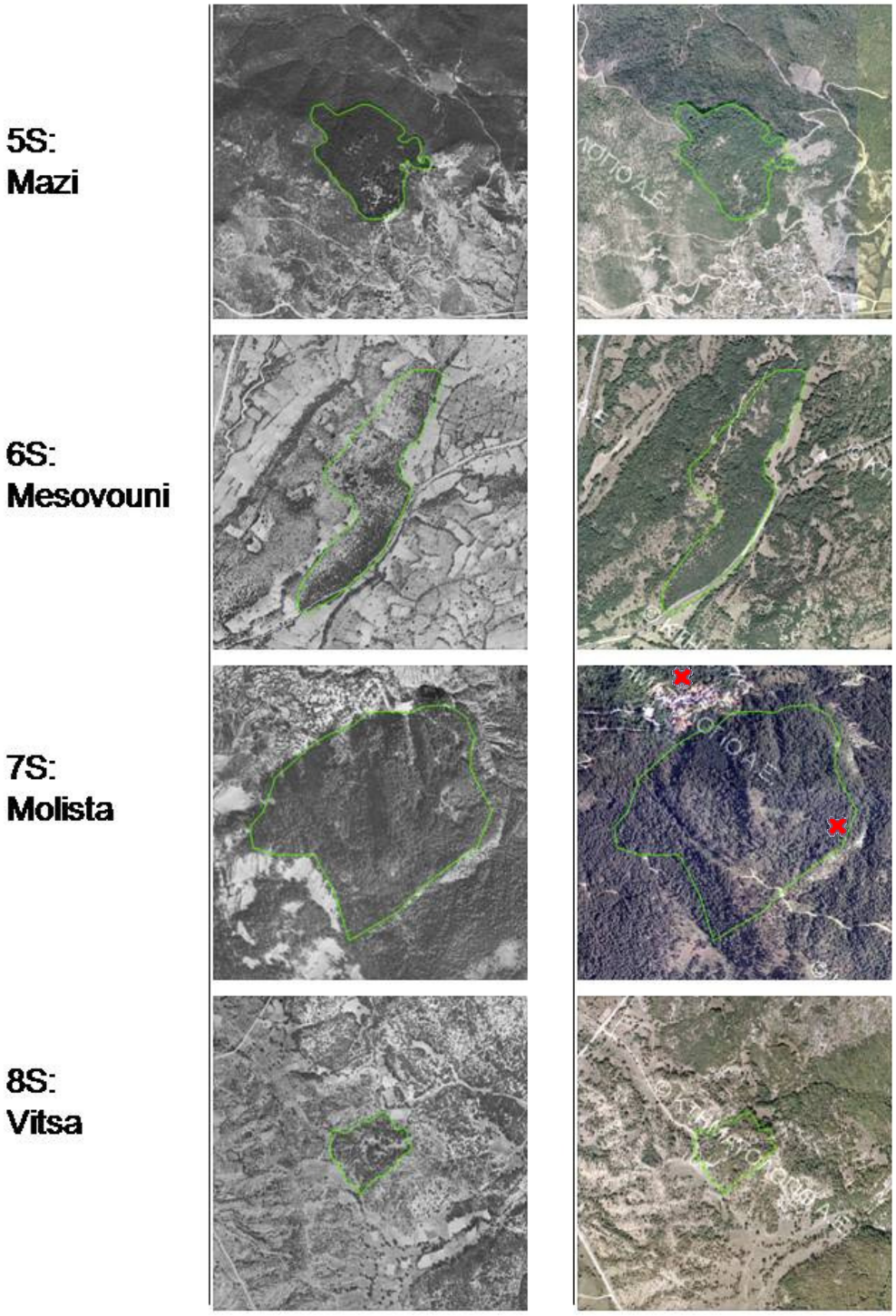


Figure H.1. Changes in and around sacred groves between 1945 (left panels) and 2007 (right panels). Sacred groves are marked by the green line. Lettering inside is from the official state agency that issued the 2007 maps. The X's in groves 1S, 2S, 3S and 7S correspond to the vantage points from which the photos in figures A1 and A2 were taken.

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