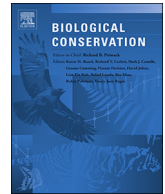




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## Quantifying the conservation value of Sacred Natural Sites

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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 amongst sacred groves than amongst 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.

## 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

Abbreviations: Sacred Natural Sites, SNS; Species Abundance Relationships, SAR

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

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

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

conservation objectives (Bhagwat and Rutte, 2006; Soury et al., 2007; Corrigan and Hay-Edie, 2013; Ormsby, 2013).

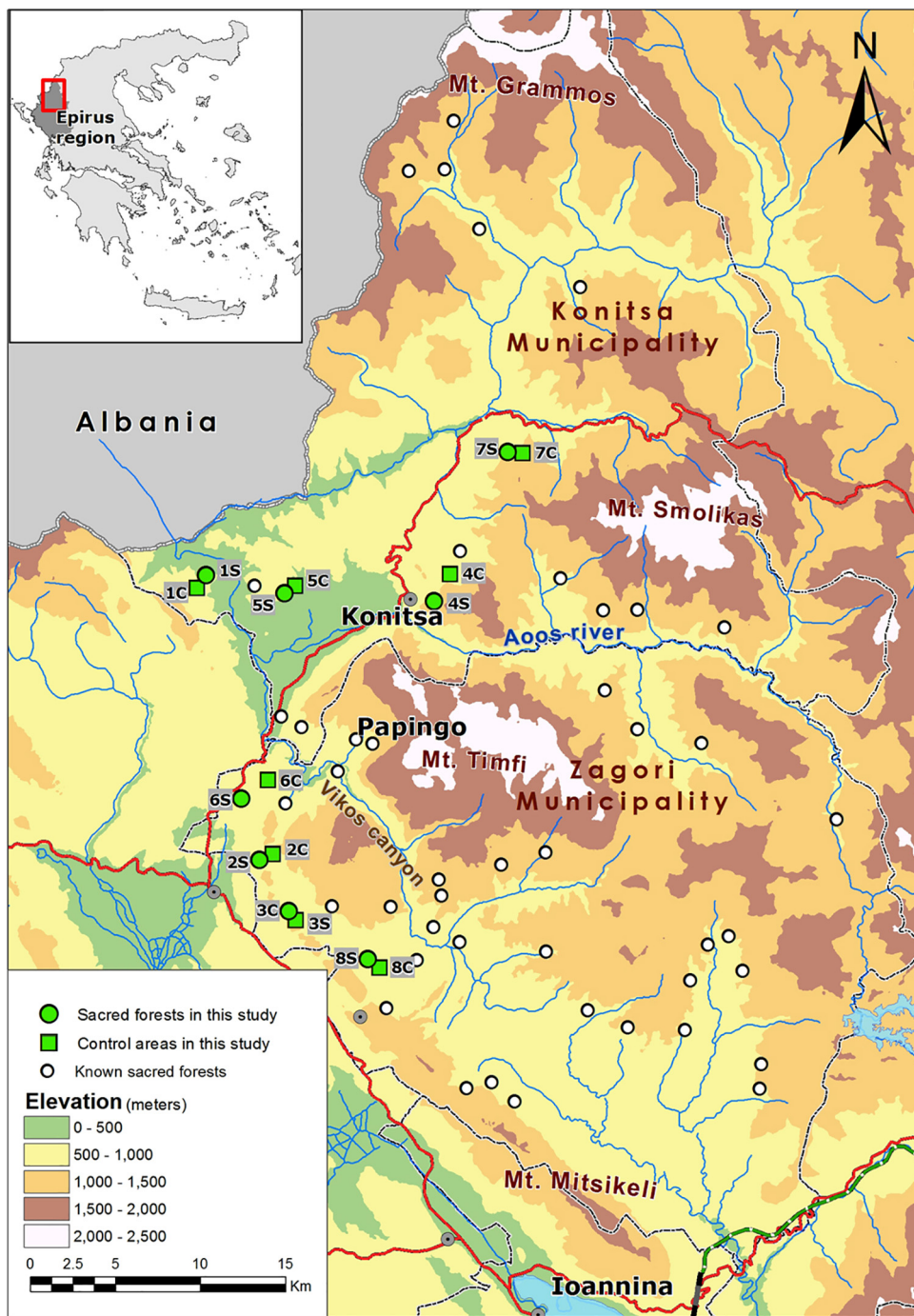
Despite the increasing interest in SNS as biodiversity refugia (Dudley et al., 2009), few studies have assessed their effectiveness across taxa, while most have focused on specific groups of organisms, such as plants (Boraiah et al., 2003; Khumbongmayum et al., 2006; Frascaroli et al., 2016), small mammals (Decher, 1997; Reed and Carol, 2004) or butterflies (Nganso et al., 2012). Most of these studies have been carried out in Asia, particularly India and China (Nganso et al., 2012; Gao et al., 2013; Karthikeyan and Dhamotharan, 2015), or Africa (Daye and Healey, 2015), with very little work in Europe (e.g. Frascaroli et al., 2016). 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



**Fig. 1.** Identified sacred groves (circles) in the broad area of Zagori and Konitsa. For the current study, biodiversity was measured in eight of these sacred groves (green circles) and in eight corresponding control sites (squares). Shown in the inset is the location of the Epirus study area in Greece. Red lines denote major roads. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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, multi-dimensional 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., 2006; 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  $S \sim \text{area} + \text{type} + \text{vegetation type} + \text{area}:\text{type}$  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 Student's *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

**Table 1**

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

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

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:

$$S = cA^z \quad (1)$$

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  $c = S/A^z$ .

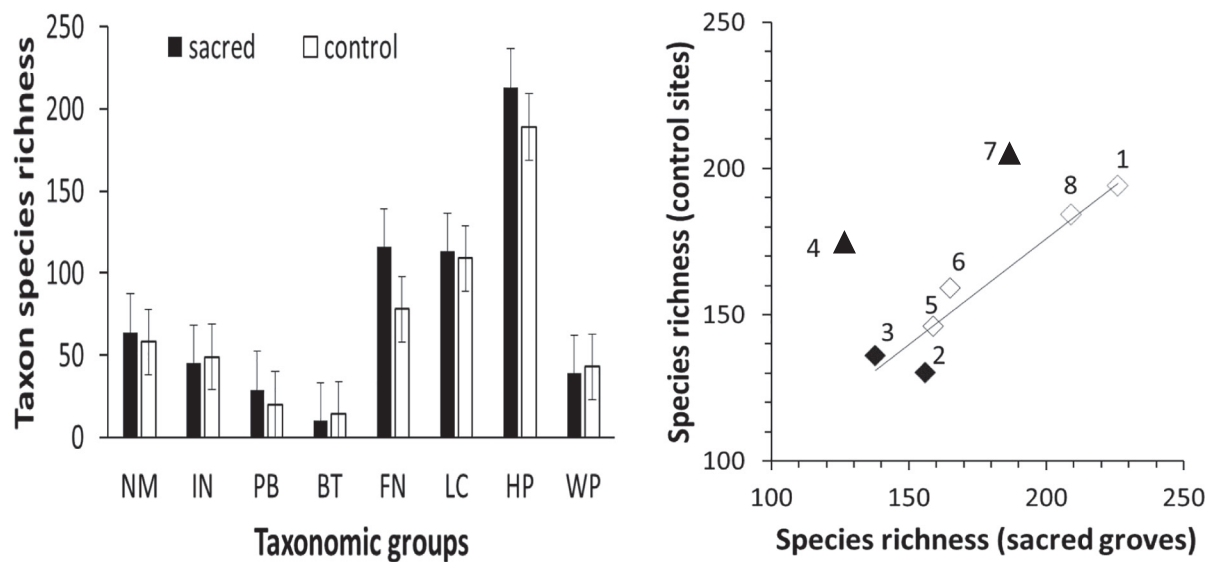
The first time-constant of relaxation is the expected time for half the extinction debt to be paid off, which actually is the half-life of extinction debt in a habitat remnant. In the absence of speciation and colonization, the half-life of extinction debt is equal to the time for species richness to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

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

Here,  $A$  is the area of the remnant forest,  $\rho$  is the typical total density of individuals of the relevant taxonomic group,  $\tau$  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:

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

In order to get  $\rho$  and  $\tau$ , we assume a single average for each taxonomic group (Halley et al., 2016). For passerine birds, herbaceous and woody plants,  $\rho$  and  $\tau$  values are as in Halley et al. (2016). For nematodes, our measurements indicated typical densities of  $7.5 \times 10^9$  individuals per ha and we used a generation time of 19 days (Lee, 2002), while for bats we used  $\rho = 0.105$  individuals per ha and for the generation time we used  $\tau = 8$  years, which is half the average longevity (Austad and Fischer, 1991). For insects, the value of  $\tau = 1$  year was typical of the species in our study, while  $\rho = 7.83 \times 10^4$  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.



**Fig. 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.

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

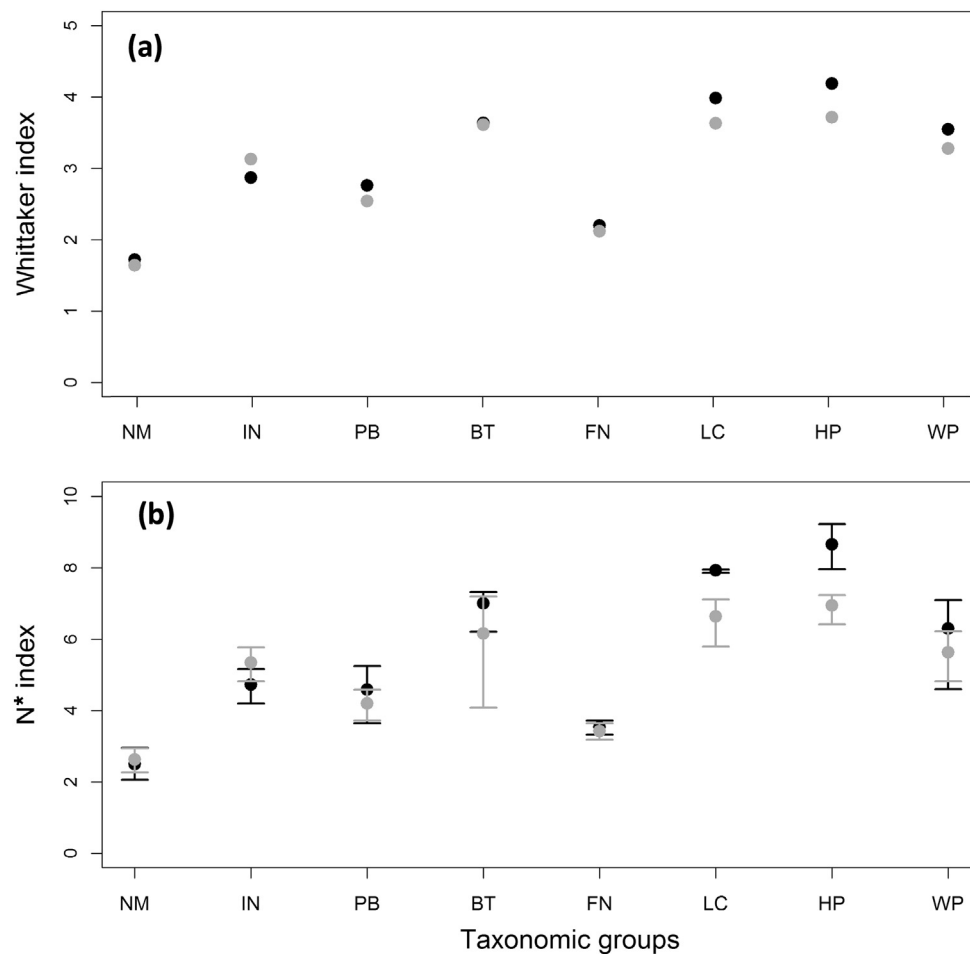
Ordination shows that the patterns of species composition amongst the three vegetation types (Fig. D.1) varied by taxonomic group. However, with species of all groups combined, there was a clear distinction between the vegetation types. Regarding the site type, there were no consistent differences in composition between sacred groves and control sites for the individual groups of species or for all species combined (Figs D.1 and D.2). The generalized linear regression analysis

shows (Table C.2) that the site area and type do not affect significantly the total species richness per site (at a 5% significance level). However, their interaction is significant meaning that the relationship between species richness and area differs depending on the type of the site (sacred or control). As sacred sites are mostly smaller in area than control sites (Table 1). The total species richness is also significantly affected by vegetation type. On a taxonomic group level, the locality is not significant for any group. The type of the site (sacred or control) is significant only for fungi, whereas vegetation type is significant for lichens, herbaceous plants, and woody plants; none of these predictors is significant for nematodes, insects, passerine birds or bats. The interaction between site locality and type is also significant for herbaceous plants and lichens, as was also the case for total species richness.

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

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



**Fig. 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.

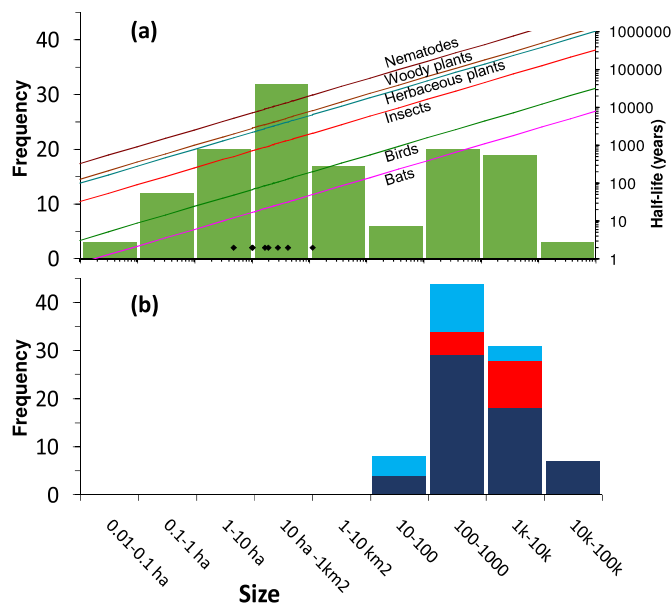
In our literature search, we found 104 SNS for which the area was recorded or could easily be inferred; these occur in all inhabited continents. To these we added the 22 sacred groves in Epirus that we mapped, including the 8 whose biodiversity we studied in detail. The histogram for this ensemble (Fig. 4a) shows that the size of SNS varies greatly, ranging from a few square meters to over 100,000 km<sup>2</sup>, with the groves that we studied falling in the smaller part of the range. By contrast, National Parks are always at least 10 km<sup>2</sup> (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 species richness between sacred groves and control sites, there was a clear biodiversity benefit when beta diversity was considered (Hypothesis III). Its higher value for sacred groves suggests that there is a greater distinction (in the sets of species) between sacred groves than between control sites. This might be explained by the groves different histories of usage, which have a significant effect on sacred grove's vegetation structure and therefore on the ecological community structure, thus increasing the dissimilarities between groves. Different patterns of land abandonment could also play a role. By contrast, the non-sacred control areas arose largely through natural regeneration in the last 100 years and thus have a more uniform structure.

Given the lack of evidence of a strong difference in species richness or composition between sacred groves and control sites, other factors were explored to explain the results found. The most obvious candidate was vegetation type, as the eight pairs of sites were stratified between topographic locations, with three different vegetation types being distinguished, dominated by coniferous, evergreen broadleaved or deciduous broadleaved trees. In all of the analyses, and for many of the species groups examined separately, a clear distinction was found in species richness and composition between the six site pairs dominated



**Fig. 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 ha to 100,000 km<sup>2</sup>. 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. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

by broadleaved trees (with either similar overall richness between the site types or higher richness in the sacred groves) in contrast to the two site pairs with conifer-dominated vegetation (where control sites had higher richness). Other than the nature of coniferous forests per se, a number of features might also contribute to the distinct biodiversity pattern in these two site pairs. Firstly, these two groves and their control sites are in closer proximity to the nearest village than is the case for the other sites. This could have led to more intense anthropogenic influence or, alternatively, it might have increased the effectiveness of the protection associated with religious prohibitions (Frosch et al., 2016). Secondly, they are located on very steep slopes, so these groves would require strict protection to fulfil the role of erosion or landslide control. Looking closely at each sacred grove, it becomes apparent that its current status has been individually shaped by its history. For example, despite a long history of protection, one of the conifer groves is the forest of Konitsa (4S) was heavily logged for timber and fuel wood in the 1940s, during the Second World War and the following Greek Civil War. Subsequently, in 1953, the municipality decided to manage the forest by removing mature trees in an effort to raise funds for enforcing its protection, particularly of its most degraded parts. Our review of the management history of the eight sacred groves also reveals site-specific variation in the enforcement of restrictions on tree cutting or livestock grazing, which are likely to have influenced considerably the habitat properties and, hence, conservation capacity.

Land abandonment is another driving force in the evolution of the landscapes of this area. In the postwar period, as agriculture in Western Europe entered a productivity-orientated phase, agricultural change in the study area coincided with decline of agricultural activity or simply of its abandonment. Crop fields disappeared and grasslands gradually developed into shrublands and forests due to a decrease in animal grazing and subsequent natural succession. An exception to that is

Konitsa, where the surrounding fertile lowlands remain agricultural to this day (Zomeni et al., 2008). This homogenization of the landscape may explain the differences between sacred and control sites being only marginal. Photos from 1945 and 2007 (Fig. H.1) reveal a changing forest landscape with the forest areas around the groves most often expanding. Thus, a possible hypothesis is that the sacred groves acted as nuclei of expansion and dispersal of biodiversity into newly regenerated forest areas.

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

No size dependence was observed for the diversity of sacred groves. This was initially surprising, given the expected dependence of species richness and relaxation time on area. However, as the actual sampling area (given any taxonomic group) is the same in each site we expect this to increase only weakly with site area (Phillips et al., 2017). Furthermore, we should not think of these groves as islands of forest in a landscape of cultivation. The groves have always existed in a matrix of habitable or partially-habitable landscape, so for this reason also, it is not so surprising that measurements of diversity fail to show the limiting effect of size expected from Eq. 1. Finally, consistent with historical and photographic evidence, the area of groves is not constant. Most have expanded since 1945 while some were not isolated even in 1945. Also, the variability of areas is not so great (Fig. 4a), so that area dependence is not easily detectable if statistical power is low. Thus, while Eqs. (1)–(3), based on isolated fixed-area island models, can illuminate our understanding of conservation capacity and relaxation time, they must be used in conjunction with historical and landscape information when their basic assumptions are not met.

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

The sacred groves studied here are small in size and have been affected by changing degrees of protection and management throughout their history. Many of them could not function as a reserves or conservation areas by themselves. However, following another modern paradigm, that of the European Natura 2000 system (Official Journal of the European Union, 2011), a network of protected areas existing in an agricultural matrix (following the “countryside SAR” principle) (Pereira et al., 2014) offers an alternative approach. If SNS were incorporated into wider parks or networks, the small conservation advantage that we observed here could become more important. Moreover, a conservation network based around such areas might gain local recognition more



readily than a park or network developed on a purely scientific basis. As a large proportion of SNS are small, this approach is likely to be important globally.

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## Appendix. Supplementary Information

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## References

- Aerts, R., Van Overtveld, K., Haile, M., Hermy, M., Deckers, J., Muys, B., 2006. Species composition and diversity of small Afromontane forest fragments in northern Ethiopia. *Plant Ecol.* 187, 127–142.
- Austad, S.N., Fischer, K.E., 1991. Mammalian aging, metabolism, and ecology: evidence from the bats and marsupials. *J. Gerontol.* 46, 47–53.
- Berkes, F., Colding, J., Folke, C., 2000. Rediscovery of traditional ecological knowledge as adaptive management. *Ecol. Appl.* 10, 1251–1262.
- Bhagwat, S.A., Rutte, C., 2006. Sacred groves: potential for biodiversity management. *Front. Ecol. Environ.* 4, 519–524.
- Birtel, J., Walsler, J.-C., Pichon, S., Bürgmann, H., Matthews, B., 2015. Estimating bacterial diversity for ecological studies: methods, metrics and assumptions. *PLoS One* 10 (4), e0125356. <http://dx.doi.org/10.1371/journal.pone.0125356>.
- Blondel, J., Aronson, J., 1999. *Biology and Wildlife of the Mediterranean Region*. Oxford University Press, Oxford, UK.
- Boraiah, K.T., Vasudeva, R., Bhagwat, S.A., Kushalappa, C.G., 2003. Do informally managed sacred groves have higher richness and regeneration of medicinal plants than state-managed reserve forests? *Curr. Sci.* 84, 804–808.
- Bossart, J., Opuni-Frimpong, E., Kuudaar, S., Nkrumah, E., 2006. Complementarity of fruitfeeding butterfly species in relic sacred forests and forest reserves of Ghana. *Biodivers. Conserv.* 15, 333–359.
- Byers, B.A., Cunliffe, R., Hudak, A.T., 2001. Linking the conservation of culture and nature: a case study of sacred forests in Zimbabwe. *J. Hum. Ecol.* 29, 187–218.
- Clarke, K.R., Somerfield, P.J., Chapman, M.G., 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *J. Exp. Mar. Biol. Ecol.* 330, 55–80.
- Colding, J., Folke, C., 2001. Sacred taboos: 'invisible' systems of local resource management and biological conservation. *Ecol. Appl.* 11, 584–600.
- Corrigan, C., Hay-Edie, T., 2013. A Toolkit to Support Conservation by Indigenous Peoples and Local Communities: Building Capacity and Sharing Knowledge for Indigenous Peoples' and Community Conserved Territories and Areas (ICCAS). UNEP-WCMC, Cambridge, UK.
- Council Directive, 1992. Council Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora (Available at): <http://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX:01992L0043-20070101>.
- Daye, D.D., Healey, J., 2015. Impacts of land-use change on sacred forests at the landscape scale. *Global Ecol. Conserv.* 3, 349–358.
- Decher, J., 1997. Conservation, small mammals, and the future of sacred groves in West Africa. *Biodivers. Conserv.* 6, 1007–1026.
- Derhé, M.A., Murphy, H., Monteith, G., Menéndez, R., 2016. Measuring the success of reforestation for restoring biodiversity and ecosystem functioning. *J. Appl. Ecol.* 53 (6), 1714–1724.
- Diamond, J.M., 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific islands. *PNAS* 69, 3199–3203.
- Didham, R.K., Hammond, P.M., Lawton, J.H., Eggleton, P., Stork, N.E., 1998. Beetle species responses to tropical forest fragmentation. *Ecol. Monogr.* 68, 295–323.
- Dudley, N., Higgins-Zogib, L., Mansourian, S., 2009. The links between protected areas, faiths, and sacred natural sites. *Conserv. Biol.* 23, 568–577.
- Echeverría, C., Newton, A.C., Lara, A., 2007. Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. *Glob. Ecol. Biogeogr.* 16, 426–439.
- Frascaroli, F., Bhagwat, S., Guarino, R., Chiarucci, A., Schmid, B., 2016. Shrines in Central Italy conserve plant diversity and large trees. *Ambio* 45, 468–479.
- Frosch, B., Holger, J., Mhamdi, A., Achhal El Kadmiri, A., Rudner, M., Deil, U., 2016. Sacred sites in north-western Morocco – naturalness of their vegetation and conservation value for vulnerable plant species. *Feddes. Repert.* 127, 83–103.
- Gadgil, M., Vartak, V.D., 1976. Sacred groves of Western Ghats of India. *Econ. Bot.* 30, 152–160.
- Gao, H., Quyang, Z., Chen, S., van Koppen, C.S.A., 2013. Role of culturally protected forests in biodiversity conservation in Southeast China. *Biodivers. Conserv.* 22, 531–544.
- Gray, C.L., Hill, S.L.L., Newbold, T., Hudson, L.N., Börger, L., Contu, S., Hoskins, A.J., Ferrier, S., Purvis, A., Schaler, J.P.W., 2016. Local biodiversity is higher inside than outside terrestrial protected areas. *Nat. Commun.* 7, 12306.
- Halley, J.M., Sgardeli, V., Monokrousos, N., 2013. Species-area relationships and extinction forecasts. *Ann. N. Y. Acad. Sci.* 1286, 50–61.
- Halley, J.M., Monokrousos, N., Mazaris, A.D., Newmark, W.D., Vokou, D., 2016. Dynamics of extinction debt across five taxonomic groups. *Nat. Commun.* 7, 12283.
- Halpern, B.S., 2003. The impact of marine reserves: do reserves work and does reserve size matter. *Ecol. Appl.* 13, 117–137.
- Haridasan, K., Rao, R.R., 1985. *Forest Flora of Meghalaya*. Vol. 1 Dehra Dun, Scientific Publishers, Bishen Singh and Mahendrapal Singh.
- Hughes, J.D., Chandran, M.D.S., 1998. Chapter 5: sacred groves around the earth: an overview. In: Ramakrishnan, P.S., Saxena, K.G., Chandrashekhara, U.M. (Eds.), *Conserving the Sacred for Biodiversity Management*. Oxford & IBH, New Delhi and UNESCO, Paris.
- Jim, C.Y., 2003. Conservation of soils in culturally protected woodlands in rural Hong Kong. *For. Ecol. Manag.* 175, 339–353.
- Karthikeyan, C., Dhamotharan, R., 2015. Density, species richness and diversity of Trees in a Sacred Grove-Tropical Dry Deciduous Forest, Dharmapuri District, Tamil Nadu, South India. *Scholars Acad. J. Biosci.* 3, 536–540.
- Keppel, G., Mokany, K., Wardell-Johnson, G.W., Phillips, B.L., Welbergen, J.A., Reside, A.E., 2015. The capacity of refugia for conservation planning under climate change. *Front. Ecol. Environ.* 13, 106–112.
- Khumbongmayum, A.D., Khan, M.L., Tripathi, R.S., 2005. Survival and growth of seedlings of a few tree species in the four sacred groves of Manipur, Northeast India. *Curr. Sci.* 88, 1781–1788.
- Khumbongmayum, A.D., Khan, M.L., Tripathi, R.S., 2006. Biodiversity conservation in sacred groves of Manipur, northeast India: population structure and regeneration status of woody species. *Biodivers. Conserv.* 15, 2439–2456.
- Klein, C.J., Wilson, K.A., Watts, M., Stein, J., Carwardine, J., Mackey, B., Possingham, H.P., 2009. Spatial conservation prioritization inclusive of wilderness quality: a case study of Australia's biodiversity. *Biol. Conserv.* 142, 1282–1290.
- Klepeis, P., Orłowska, I.A., Kent, E.F., Cardelús, C.L., Scull, P., Wassie Eshete, A., Woods, C., 2016. Ethiopian church forests: a hybrid model of protection. *Hum. Ecol.* 44, 715–730.
- Koh, L.P., Ghazoul, J., 2010. A matrix-calibrated species-area model for predicting biodiversity losses due to land-use change. *Conserv. Biol.* 24, 994–1001.
- Kosambi, D.D., 1962. *Myth and Reality*. Popular Press, Bombay, India.
- Lazarina, M., Sgardeli, V., Kallimanis, A.S., Sgardelis, S.P., 2013. An effort-based index of beta diversity. *Methods Ecol. Evol.* 4, 217–225.
- Lee, D.L., 2002. *The Biology of Nematodes*. CRC Press.
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwell, Oxford.
- Malhotra, K.C., Gokhale, Y., Chatterjee, S., Srivastava, S., 2007. *Sacred Groves in India*. Aryan Books International, New Delhi, India.
- Newmark, W.D., Jenkins, C.N., Pimm, S.L., McNeally, P.B., Halley, J.M., 2017. Targeted habitat restoration can reduce extinction rates in fragmented forests. *PNAS* 114, 9635–9640.
- Nganso, B.T., Kyerematen, R., Obeng-Ofori, D., 2012. Diversity and abundance of butterfly in the Abiriri and Odumant sacred groves in the Eastern Region of Ghana. *Res. Zool.* 2, 38–46.
- Nicol, E., Stevens, J.R., Jobling, S., 2017. Riverine fish diversity varies according to geographical isolation and land use modification. *Ecol. Evol.* 7, 7872–7883.
- Nitsiakos, V., 2016. *Peklari, Social Economy in a Greek Village*. Lit Verlag, Zurich.
- Nixon, L., 2006. *Making a Landscape Sacred. Outlying Churches and Icon Stands in Sphakia*. Oxbow Books, Oxford, Southwestern Crete.
- Official Journal of the European Union, 2009. Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the Conservation of Wild Birds (Available at): <http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:32009L0147>.
- Official Journal of the European Union, 2011. Commission Implementing Decision of 11 July 2011 Concerning a Site Information Format for Natura 2000 Sites (Available at): <http://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX%3A32011D0484>.
- Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Helene Wagner, H., 2016. *Vegan: Community Ecology Package*. R package version 2.3-3. <https://CRAN.R-project.org/package=vegan>.
- Ormsby, A., 2013. Analysis of local attitudes toward the sacred groves of Meghalaya and Karnataka, India. *Conserv. Soc.* 11, 187–197.
- Papanastasi, V.P., Yiakoulaki, M.D., Decandia, M., Dini-Papanastasi, O., 2008. Integrating woody species into livestock feeding in the Mediterranean areas of Europe. *Anim. Feed Sci. Technol.* 140, 1–17.
- Pereira, H.M., Ziv, G., Miranda, M., 2014. Countryside species-area relationship as a valid alternative to matrix-calibrated species-area model. *Conserv. Biol.* 28, 874–876.
- Phillips, H.R.P., Halley, J.M., Urbina-Cardona, N.J., Purvis, A., 2017. The effect of fragmentation area on site-level biodiversity. *Ecography*. <http://dx.doi.org/10.1111/ecog.02956>.
- Pimm, S.L., Russell, G.J., Gittleman, J.L., Brooks, T.M., 1995. The future of biodiversity. *Science* 269, 347–350.
- R Core Team, 2015. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Ramesh, T., Kalle, R., Downs, C.T., 2016. Predictors of mammal species richness in KwaZulu-Natal South Africa. *Ecol. Indic.* 60, 385–393.



- Reed, L.W., Carol, J.P.C., 2004. Sacred forest, hunting, and conservation in west Kalimantan, Indonesia. *Hum. Ecol.* 32, 313–338.
- Soury, A., van Koppen, K., Tchiboza, M.S., Cotonou, B., 2007. Sacred Forests: A Sustainable Conservation Strategy? The Case of Sacred Forests in the Quémé Valley, Benin. Wageningen University, Wageningen.
- Stara, K., Tsiakiris, R., Wong, J.L.G., 2015. The trees of the sacred natural sites of Zagori, NW Greece. *Landsc. Res.* 40, 884–904.
- Stara, K., Tsiakiris, R., Nitsiakos, V., Halley, J.M., 2016. Religion and the management of the commons - the sacred forests of Epirus. In: Agnoletti, M., Emanuelli, F. (Eds.), *Biocultural Diversity in Europe*. Springer International Publishing, Switzerland, pp. 283–302.
- Stewart, C., 1993. *Demons and the Devil. Moral Imagination in Modern Greek Culture*. Princeton University Press, Princeton, New Jersey.
- Terborgh, J., 1999. *Requiem for Nature*. Island Press, Washington DC.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S*, fourth ed. Springer, New York.
- Verschuuren, B., Wild, R., McNeely, J.A., Oviedo, G., 2010. *Sacred Natural Sites: Conserving Nature and Culture*. Earthscan, London.
- Virtanen, P., 2002. The role of customary institutions in the conservation of biodiversity: sacred forests in Mozambique. *Environ. Values* 11, 227–241.
- Wassie, A., Sterck, F.J., Bongers, F., 2010. Species and structural diversity of church forests in a fragmented Ethiopian Highland landscape. *J. Veg. Sci.* 21, 938–948.
- Wortley, L., Hero, J.-M., Howes, M., 2013. Evaluating ecological restoration success: a review of the literature. *Restor. Ecol.* 21 (5), 537–543.
- Yuan, J., Liu, J., 2009. Fengshui forest management by the Buyi ethnic minority in China. *For. Ecol. Manag.* 257, 2002–2009.
- Zomeni, M., Tzanopoulos, J., Pantis, J.D., 2008. Historical analysis of landscape change using remote sensing techniques: an explanatory tool for agricultural transformation in Greek rural areas. *Landsc. Urban Plan.* 86, 38–46.