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Healing Animals, Feeding Souls: Ethnobotanical Values at Sacred Sites in Central Italy[1]

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Healing Animals, Feeding Souls: Ethnobotanical Values at Sacred Sites in Central Italy. Ethnobotanical knowledge is a fundamental repository of the values and applications of different plants. This knowledge is often related to spiritual beliefs and religious sites, where plants have been nurtured and conserved for their use in rituals and traditional practices. While this link is well known for different areas of the global south, it has hardly been investigated in relatively more secular and modernized Western contexts. Here, we use first–hand vegetation surveys and published records to examine the occurrence of ethnobotanical values at 30 Catholic shrines in Central Italy, and compare them with an equal number of non–sacred control sites. We ask this: to what extent is there an association of useful plants with sacred places in Italy, as found in other cultural contexts? We show that a greater number of useful plants are found at sacred sites. While this is mainly a consequence of the higher species richness of sacred sites, an association with plants used in animal husbandry is particularly evident, and likely related to the deep historical connection between sacred places and pastoralist traditions in Central Italy. Also, we show that there are significant variations in the distribution of old trees; the largest specimens are found at the center of sacred sites, while tree size visibly decreases away from the shrines. This indicates also that individual trees have been actively managed and conserved at sacred sites, probably driven by the symbolic values that old trees frequently embody.

Guarire gli Animali, Nutrire le Anime: Risorse Etnobotaniche nei Luoghi Sacri Naturali del Centro Italia. Il sapere etnobotanico è un fondamentale archivio degli usi e delle applicazioni delle diverse piante. Questo sapere è spesso collegato a credenze soprannaturali e a luoghi di culto, in cui queste piante sono conservate o coltivate per essere usate in rituali e altre pratiche tradizionali. Mentre un tale legame è ben noto per diverse aree del Sud del globo, esso è stato a mala pena investigato nei contesti più moderni e secolarizzati del mondo occidentale. In questo contributo, utilizziamo appositi rilevamenti floristici per esaminare la presenza di risorse etnobotaniche in trenta eremi e santuari dell'Italia Centrale, e istituire un paragone con altrettanti siti di controllo. Ci chiediamo: c'è un legame tra luoghi sacri e piante utili in Italia simile a quello

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rinvenuto in altri contesti geografici e culturali? Dimostriamo che il numero di piante utili è in effetti maggiore nei siti sacri che nei siti di controllo. Mentre questo è in larga misura una conseguenza della più elevata ricchezza di specie presente nei luoghi sacri, un'associazione con piante usate per pratiche veterinarie è particolarmente evidente, e verosimilmente legata al profondo legame storico tra luoghi sacri e pastorizia nell'Italia Centrale. Dimostriamo inoltre che ci sono variazioni significative nella distribuzione degli alberi vetusti: gli esemplari più antichi si trovano generalmente verso il centro dei santuari, mentre il diametro degli alberi diminuisce progressivamente allontanandosi dai luoghi sacri. Questo suggerisce che anche singoli esemplari sono stati oggetto di particolare cura e conservazione, probabilmente in virtù del valore simbolico che gli alberi vetusti spesso incarnano.

Key Words: Sacred natural sites, ethnobotany, traditional ecological knowledge (TEK), old–growth forest, transhumance, Central Italy.

Introduction

Over the last five years, a growing number of contributions have emphasized the crucial role of sacred natural sites (henceforth, SNS) for the conservation of biocultural diversity and local livelihoods (Pungetti et al. 2012; Verschuuren et al. 2010; Wild and McLeod 2008). Here, SNS are defined as "areas of land or water having special spiritual significance to peoples and communities" (Wild and McLeod 2008). Both important ecological traits and traditional customs are often preserved at these revered places (Chouin 2002; Dudley et al. 2010; Fomin 2008; Ormsby and Bhagwat 2010). Furthermore, SNS are strictly related to traditional ecological knowledge (TEK) and indigenous ethnobiology (Berkes et al. 2000; Gadgil et al. 1993). SNS frequently provide local communities with fundamental "ecosystem services" (Dudley et al. 2010) or host high densities of medicinal plants (Anderson et al. 2005; Khumbongmayum et al. 2005), indicating that they might have been nurtured as repositories of knowledge and plant resources (Boraiah et al. 2003). The relation between SNS and TEK has been demonstrated in the "global south," especially in East Asia and Africa (Dudley et al. 2010), but remains relatively underexplored in Western non–traditional contexts, where modernization and secularization have been underway longer (Mallarach and Papayannis 2010). Exploring that relationship in other regions could help to conserve ethnobotanical knowledge in the face of accruing societal changes. In this study, we aim to address that gap by investigating the occurrence of useful plants (that is, plants with known ethnobotanical values) at SNS in Central Italy.

Central Italy has been indicated as a location in the Western world where a connection between ecological values and spiritual heritage remains especially evident (Frascaroli 2013). Rich ethnobotanical knowledge is also well rooted in the area, and locally correlated with its high floristic diversity (Idolo et al. 2010). Catholic shrines and monasteries in Central Italy are frequently associated with natural landscapes and features, such as forests, water springs, and high places; natural elements are objects of veneration at numerous sacred sites in this area (Frascaroli 2013; Nolan and Nolan 1989). The occurrence of rock, water, and plants in rituals and traditional healing is fairly common, and the world of nature and the rhythms of agricultural life feature prominently in popular rituals and devotions (De Waal 2012; Micati 2007). A connection of this kind is particularly evident between religious heritage and animal husbandry. Transhumance (that is, the seasonal migration of herds and people) has been practiced in the Mediterranean for 3,000years (Blondel et al. 2010), and a number of shrines and hermitages are thought to have risen along the ancient routes of transhumant herders (De Waal 2012). The cult of St. Michael the Archangel, one of the most rooted devotions in Italy, is also linked to traditional animal herding. For example, the Archangel is patron saint of shepherds and celebrated on May 8 and September 29, coinciding respectively with the movement of the herds to the mountain pastures and back to the plains (Marucci 2003). Although this mix of Catholicism, peasant culture, and folk beliefs has been waning following the massive social changes and rural abandonment of the last decades (Blondel et al. 2010), it remains vigorous in many parts of Central Italy (De Waal 2012).

In another study, we used floristic surveys to assess plant and habitat diversity at 30 SNS in

Central Italy and compare them with an equal number of similar non–sacred sites. We found that SNS differ from the control sites with regards to forest structure, habitat composition, and species richness, hosting a significantly greater number of giant trees, biotopes, and plant species (Frascaroli et al., forthcoming). This suggests that SNS in Central Italy have benefited from habitat–level management and conservation, and proves that SNS can have noticeable ecological importance also in modernized Western contexts. Here, we take a similar approach and rely on the available literature, to compare the occurrence of ethnobotanical values at the same 30 pairs of sacred and control sites. Our hypothesis, in line with the findings from other cultural contexts, is that there is a strong link between SNS and useful plants, as a consequence of selective management of ethnobotanical resources at SNS. Alongside species, we also consider tree sizes as an integral part of our analyses, as ancient trees are often charged with important symbolic values in spiritual traditions worldwide (Anderson 2004; Dudley et al. 2009; Nolan and Nolan 1989; Ramanujam and Cyril 2003; Salick et al. 2007; Schama 1995; Turner et al. 2009). We ask the following questions. (1) What species are most commonly associated with ethnobotanical uses across the study sites? What are their most frequent use values? (2) How do sacred and non–sacred control sites differ with regards to useful plant diversity and composition? (3) To what extent is the number of useful plant species directly related to total species richness or affected by other factors? (4) Are there additional micro distribution patterns, indicating that SNS might have been nurtured as repositories of ethnobotanical resources?

Methods

Study Area

Central Italy consists of five administrative regions: Tuscany, Marche, Umbria, Lazio, and Abruzzi. The surface area, which exceeds 70,000km^2, is dominated by hills (62.4 %) and mountains (34.2 %), whereas plains are limited to the coastline and valley–bottoms (3.3 %). Despite the considerable anthropogenic impacts that have affected the lowland areas, floristic diversity remains high overall, with more than 3,000 taxa of vascular plants being reported for each of Abruzzi, Lazio, and Tuscany, and more than 2,300 for each of the other regions (Conti et al. 2007). Typical biomes include: Mediterranean scrub along the coasts; Italian sclerophyllous and semi–deciduous forest (Olson and Dinerstein 2002) with *Quercus* spp., *Ostrya carpinifolia* Scop., and *Fraxinus ornus* L. in sub–mountainous areas; and Apennine montane forest above 1,000 MASL, with *Fagus sylvatica* L., *Acer opalus* Mill., and occasional relict stands of *Abies alba* Mill. This floristic wealth is mirrored by a high number of known ethnobotanical uses (Guarrera 2006), and a large proportion of protected land: nearly one–quarter of the total land surface is formally part of some protected area (PA).

Data Collection

Fieldwork was conducted in 2011–2012 at a sample of 30 shrines located in natural settings. Shrines are sacred sites that have become foci of veneration and destinations of pilgrimages for the presence of a relic or holy object (often a natural feature). Shrines in Central Italy can be as small as a cave or simple chapel but, unlike other sacred sites such as monasteries, do not necessarily host a community of monks or nuns. Rather, they tend to be directly linked to neighboring villages, and managed by lay associations of local people (Frascaroli 2013). We focused on shrines, as they resemble more closely the models of community–based resource management and folk spiritualities that characterize SNS in other parts of the world (Bhagwat and Rutte 2006; Ormsby 2011; Rutte 2011).

Sample shrines were selected so as to be evenly distributed across the region, located as equally as possible within and outside official PAs, representative of different habitat types, and characterized by different levels of religious importance (Frascaroli et al., forthcoming). Successively, each shrine was paired with a non–sacred control site nearby (≈1 km), having analogous elevation (mean ± SE of altitudinal difference: 54.7 ± 8.3 m), aspect, and habitat. Given the difficulty to clearly identify the borders of SNS in the region (Frascaroli 2013), we assumed a 25–m buffer around the perimeter of each shrine as its area of influence, leading to relevant surfaces varying between ca. 0.2 and 0.8 ha, depending on the size of the shrines themselves.

To sample those areas, we laid out one to three 100–m^2 (25 m x 4 m) rectangular plots at each site, starting at the border of the shrine and stretching 25 m away from it. When feasible, the orientation of the first plot was randomly determined, and the following ones positioned so as to evenly cover the remaining space. Although we always aimed to maximize sampling intensity, the number of plots was often limited by topography (e.g., where a SNS was located along a cliff, it was possible to lay plots only on a limited area of the site). The same sampling scheme used at each SNS, including extent of the sampled area and number and location of the plots used, was replicated at the matching control site. The species, the diameter at breast height (DBH), and the distance from shrine border were recorded for all mature tree specimens (i.e., ≥10 cm DBH) rooted within the rectangular plots. Additionally, three 1–m^2 quadrats were nested within each rectangular plot to sample understory vegetation. The quadrats were located so there was one at each end of the rectangular plots as well as one in the middle so as to obtain systematic vegetation samples at different distances from the shrines (0.5, 12.5, and 24.5m). We collected specimen vouchers of vascular plants inside the quadrats, including herb and shrub layers as well as canopy projections, and estimated their percentage cover. The collected samples were dried for later identification, and deposited at the Herbarium of the Botanical Garden of the University of Zurich.

As our study questions and design hinged on the pairwise comparison of matching SNS and control sites, we accepted varying sample sizes across different pairs, as long as the same number and collocation of plots were used at each pair. While this pragmatic approach might have led to underrepresenting species composition at some of the sites, it enabled us to systematically contrast SNS with similar non–sacred patches across a wide area and range of habitats, while at the same time maximizing the size of the sample for the entire region. Similarly, the 25–m buffer on which we focused around each shrine was probably an underestimation of the real extent of most SNS, but provided a safe conservative standard for delimiting relevant areas of investigation across all the study system.

Data Analysis

Possible ethnobotanical uses were determined for each identified taxon at each site, based on the exhaustive synthesis of the available literature presented by Guarrera (2006). This work is a collation of published accounts of known ethnobotanical uses, subdivided by regional relevance. For each taxon, therefore, we recorded only the uses relevant to the specific regional context where the specimen had been collected. The uses inventoried were divided in five use categories: (1) "animal–related," including all plants used either as animal fodder or for veterinary purposes; (2) "domestic," including resources used for arts, crafts, and construction; (3) "human food," including all plants used in human alimentation; (4) "human medicine," including plants with medicinal, toxicological, and anti–parasitical applications; and (5) "information," including plants used for playing, featuring in mottos or beliefs, or employed in religious and ritual activities, and coinciding with the definitions of "information services" (de Groot et al. 2002) or "cultural services" (MEA 2005).

To assess how frequently the species inventoried are associated with ethnobotanical uses, we calculated a "use frequency" summary, loosely mirroring the metrics of "cultural value of ethnospecies" elaborated by Reyes–García et al. (2006), and "use value" proposed by Byg and Balslev (2001) and Araujo and Lopes (2012). We defined one use record as the association of one species with one use category at one study site. Associations of one species with more use categories at the same site were also counted, so that each species could have a maximum total of five use records at each site. The use frequency for each species was obtained by adding up the number of use records encountered across all of the study sites. We preferred considering as distinct records only the general use categories, rather than the single uses reported for each plant, to avoid the generalization of specifically local uses, which could have resulted in overestimation of use records for certain plant species.

To analyze the ethnobotanical difference between SNS and control sites, and test the hypothesis that useful plants are more common at SNS, we established paired comparisons between matching sites. We used paired t–tests for normally distributed and equal variance data, and Wilcoxon sign–rank tests for two related samples if the data had non–parametric distributions. To account for the influence of total species richness on useful plants diversity, we divided the number of useful species in each use category by the number of all species at each site, and based an additional comparison on those figures.

To assess the strength of the relationship between species richness and useful plants diversity, and test what other geographical variables (altitude, habitat type, region), anthropogenic variables (site religious importance, presence of PA), and external factors (sampling location) affect the latter, we fitted a linear model, having confirmed the assumptions of normality and equal variance of the data.

Finally, to further test the hypothesis that specific plant taxa and individual specimens have been selectively managed at SNS, we analyzed the occurrence of useful plants and tree sizes at different distances from each shrine. We used Kruskal–Wallis analysis of variance (ANOVA) by ranks for testing the former, and a simple linear regression for the latter.

Since multiple tests were executed on the same sample data, we applied Holm correction for multiple comparisons (Holm 1979) to the resulting p–values. This is a modified Bonferroni procedure that grants slightly higher statistical power, while maintaining effective control on the overall Type I error rate (Olejnik et al. 1997).

All statistical analyses were performed with the software R version 2.15.2 (R Core Team 2012).

Results

Ethnobotanical Species and Use Values

Out of an available pool of 352 species previously sampled in the study area, we compiled an inventory of 118 plant taxa that were associated with some use value, based on the published sources collated by Guarrera (2006). Also see the Appendix ("Electronic Supplementary Material", ESM). Human medicine uses were relevant for 100 of the species in question, human food for 46 species, crafts and domestic uses for 45 species, animal veterinary and feeding purposes for 44 species, while information values could be related to only 36 species (Appendix ESM). Human medicine also had the highest use frequency across the study sites (423), followed by craft and domestic uses (197), animal veterinary and feeding purposes (182), human food (157), and information values (100) (Appendix ESM).

Woody plants appeared prominently as useful taxa. *Fraxinus ornus* was the species with the highest use frequency across all sites, and alone accounted for over 9 % of all use records in the inventory (Fig. 1). Twelve more species totaled over 2 % of all use records each, including other four deciduous trees (*Quercus pubescens* Willd., *Cornus mas* L., *Ostrya carpinifolia*, and *Quercus ilex* L.), and one shrub species (*Juniperus communis* L.).

According to published ethnobotanical records, *F. ornus* is or used to be associated in all the study regions both to medicinal applications (for its diuretic properties) and animal veterinary purposes (either as a laxative or to treat particular disturbances in hens). In addition, uses of *F. ornus* locally included other medicinal applications (e.g., treatment of arthritis, rheumatisms, cough, fever, hemorrhage, and wounds), as well as domestic crafts (e.g., weaving of baskets, carving of shepherd staffs, and green dyeing). The treatment of human pathologies was often indicated in the sources in relation to *Q. pubescens* also. These medical uses were diverse, including applications for sore throat, respiratory disorders, contusions, and skin and gums infections. *Q. pubescens* was extensively mentioned in the sources also for having been employed for crafts and domestic uses; feeding to pork, sheep, and rabbits; and ritual protection against witches and evil eye. According to the available accounts, finally, *O. carpinifolia* and *Q. ilex* have been used in the study area mainly for domestic purposes, such as crafting of ploughs and handles for different tools, and the feeding of animals in the case of the acorns of *Q. ilex*.

Comparison of Sacred and Control Sites

Overall, plant richness accumulated faster at SNS (Fig. 2), and species richness was higher in the plots at SNS (mean ± SD: 273 ± 8.9) than at control sites (224 ± 7.8). A greater number of useful taxa were also recorded at SNS (mean ± SE: 9.1 ± 0.7 versus 8 ± 0.6; t =–2.2205, df =29, p =.172). In particular, SNS hosted more plants used for animal veterinary and feeding (mean ± SE: 3.4 ± 0.4 versus 2.6 ± 0.3; t =–2.6582, df =29, p < .10), whereas the mean differences for other use categories were not significant (Fig. 3a). Control sites, in contrast, had a higher concentration of useful taxa calculated as the number of useful species divided by the total species richness at each site, both in overall (mean ± SE: 0.56 ± 0.03 versus 0.5 ± 0.3; t =1.5553, df =29, p =.654) and for each use category except for animal veterinary and feeding uses (Fig. 3b), although none of these differences were significant. These results are based on the α values adjusted by Holm correction.

Influence of Plant Diversity and Other Factors on Useful Taxa

There was an evident correlation between species richness and the number of useful taxa recorded at each site. This relation alone accounted for nearly 65 % of the total variability in the number of useful plants (F=153.402, df=1, p<.001, Table 1). There was also a negative relation between the occurrence of useful taxa and increasing altitude (F=15.36, df=1, p<.001), whereas the influence of elevation on total species richness had an opposite sign.tgroup

Further, useful plant diversity varied significantly in relation to habitat type (F=3.777, df=6, p<.01). After standardizing by species richness, deciduous forest assemblages showed the highest concentrations of useful taxa (mean ± SE: from 0.625 ± .03 for *Q. ilex*-dominated forests to 0.475 ± 0.02 for mixed deciduous forests; Fig. 4), while the ratio between useful taxa and species richness was generally lower for grassland habitats. Finally, there were significant differences across study regions (F=3.178, df=4, p<.05), while other anthropogenic factors (including official protection and religious importance of the site) did not significantly affect the number of useful taxa.

Modeling the number of use records instead of useful species at each site yielded similar results. Only the correlation with total species richness, despite remaining significant, explained less of the variability (R^2=0.21, N=60, p<.001).

Micro–Spatial Patterns in the Distribution of Useful Plants and Tree Sizes

There were no significant differences in the number of plant species sampled at different distances from shrines (Kruskal–Wallis ANOVA by ranks: χ^2=1.539, df=2, p=.463), and very similar numbers of useful plants in each use category were also found at different sampling distances (χ^2=1.5018, df=2, p=.472).

Tree size, in contrast, was significantly correlated with distance from shrines (R^2=0.106, N=501, p<.0001; Fig. 5). On average, tree diameter was larger at SNS than at control sites, and the largest specimens were located visibly closer to the shrines (Fig. 5).

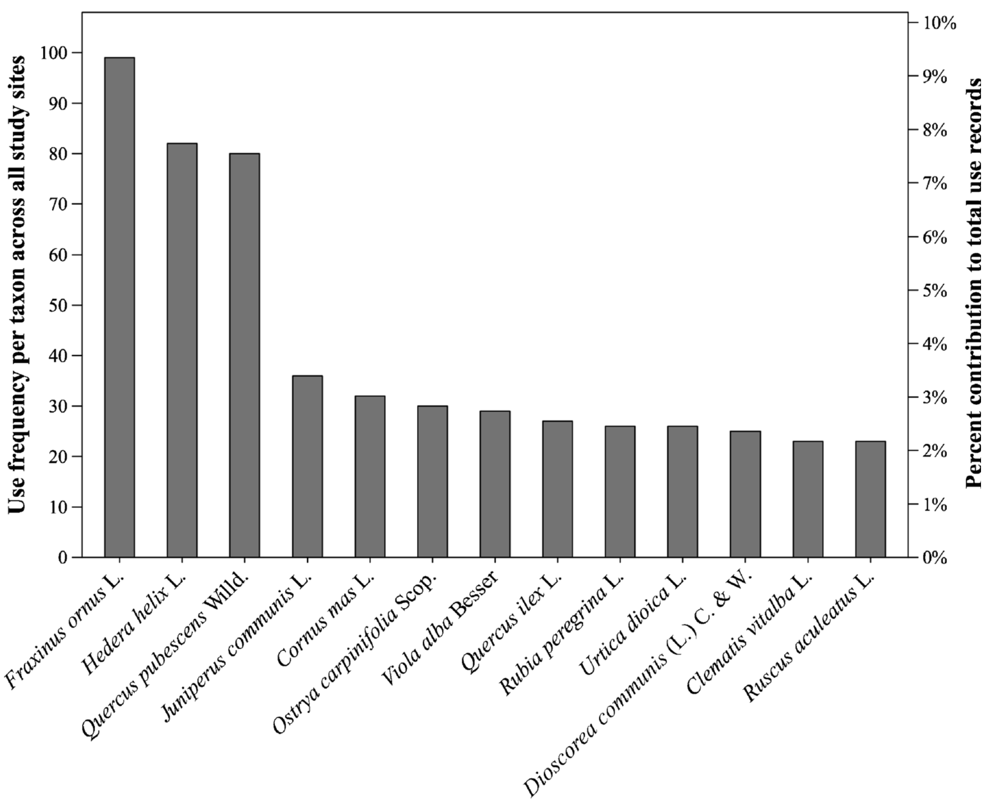

Fig. 1. Use frequency of different taxa across all study sites, and percent contribution of each taxon to all use records in the inventory. Only taxa accounting for more than 2 % of all use records are displayed.

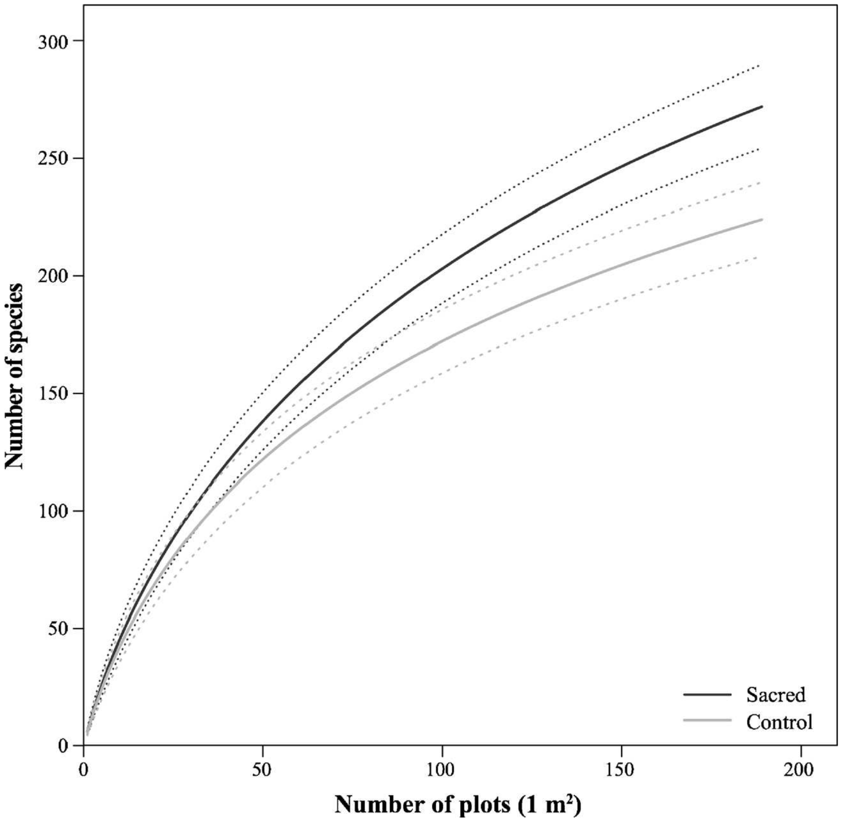

Fig. 2. Sample–based accumulation curves of total plant richness at sacred natural sites and control sites. Solid lines represent expected species richness; dashed lines represent 95 % confidence intervals.

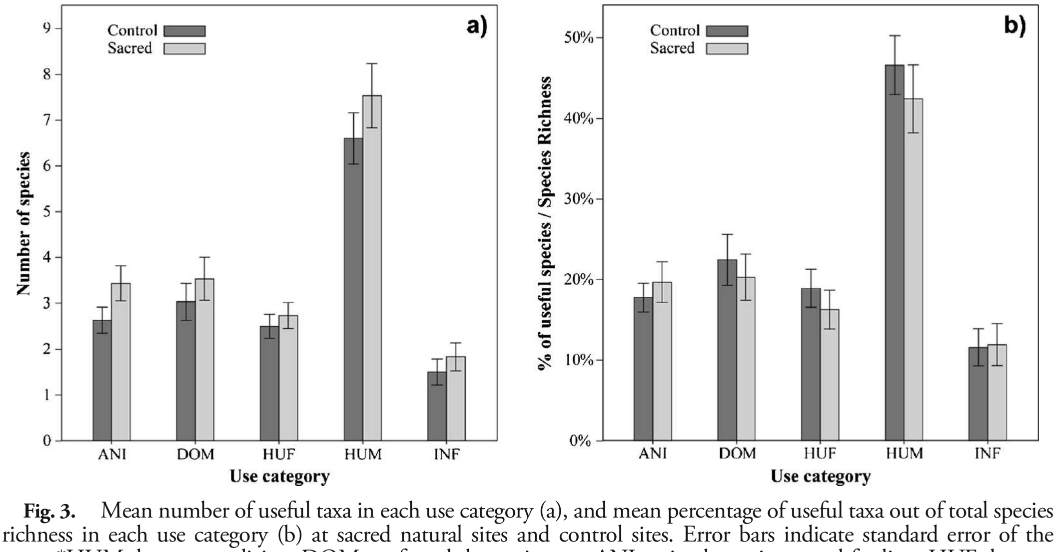

Fig. 3. Mean number of useful taxa in each use category (a), and mean percentage of useful taxa out of total species richness in each use category (b) at sacred natural sites and control sites. Error bars indicate standard error of the mean.*HUM: human medicine; DOM: craft and domestic uses; ANI: animal veterinary and feeding; HUF: human food; INF: information values.

Table 1. SEQUENTIAL SUM OF SQUARES ANOVA, TESTING THE INFLUENCE OF OVERALL SPECIES RICHNESS, ANTHROPOGENIC AND ENVIRONMENTAL VARIABLES, AND GEOGRAPHICAL LOCATION ON THE OCCURRENCE OF USEFUL PLANTS.

Explanatory Variable	*df*	*SS*	*F*	*p*
Species richness	1	429.89	153.402	<0.001*
Site type (sacred vs. control)	1	0.00	0.000	0.990
Religious importance	1	0.80	0.287	0.597
PA	1	1.27	0.454	0.507
Altitude	1	43.05	15.360	<0.001*
Habitat type	6	63.50	3.777	<0.01*
Region	4	35.62	3.178	<0.05*
Location	21	86.13	1.463	0.191
Site type : PA	1	4.93	1.758	0.198
Residuals	22	61.65		

*Significant variables; p ≤0.05.

Discussion

SNS are considered bastions of biocultural diversity (Pungetti et al. 2012; Verschuuren et al. 2010) and TEK. A growing body of research has shown how these places have been key in providing ethnobotanical resources and other ecological services to local populations in different parts of the global south (Dudley et al. 2010; Lebbie and Guries 1995; Ormsby and Bhagwat 2010). Our analyses suggest that a relation between SNS and ethnobotanical values is prominent also in a Western non–traditional context, although with significant differences and specificities.

Relation with Pastoralist Traditions

The first evident association between SNS and ethnobotanical resources in Central Italy is represented by plants with animal–related applications. Indeed, we found that these species are more numerous at SNS both as an absolute count and a proportion of all available species (Fig. 3a–b). Veterinary uses appear with particular frequency at SNS, and are associated with plants in the families of Lamiaceae (*Clinopodium nepeta* [L.] Kuntze, *Melissa officinalis* L., *Teucrium chamaedrys* L., *Thymus serpyllum* L.), Ranunculaceae (*Clematis vitalba* L., *Helleborus* spp.), Rosaceae (*Agrimonia eupatoria* L., *Rosa canina* L., *Sanguisorba minor* Scop.), and Urticaceae (*Parietaria officinalis* L., *Urtica dioica* L.), as well as *Quercus pubescens* and *Hedera helix* L.

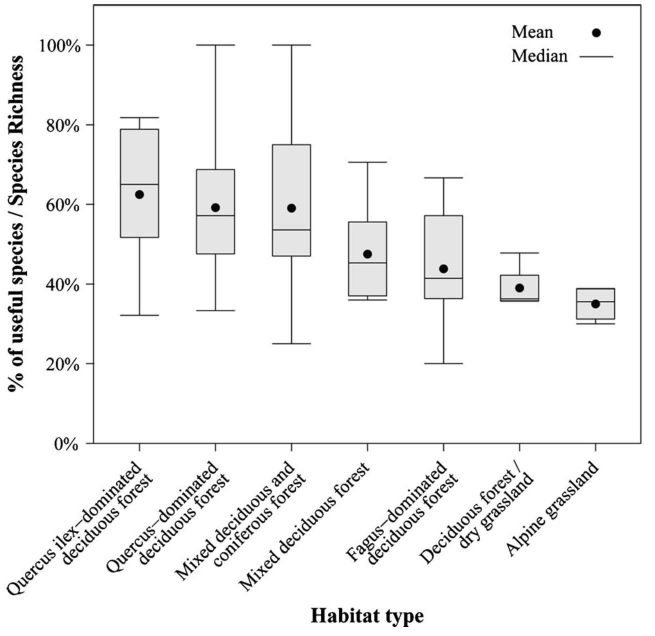

Fig. 4. Boxplots of useful plant diversity divided by total species richness for different habitat types, summarizing median, mean, upper and lower quartiles, and minimum and maximum data values.

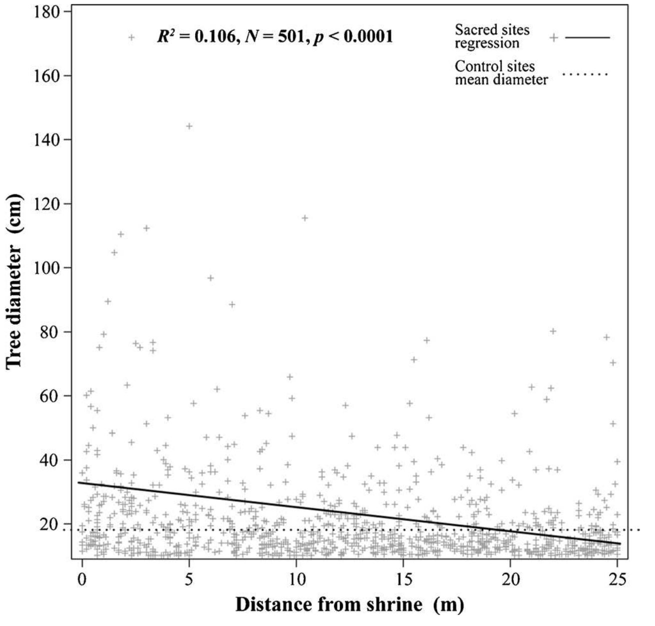

Fig. 5. Linear regression of tree size by distance from shrine for 30 sacred natural sites, and mean tree diameter at 30 non–sacred control sites.

While a relation between veterinary practice and SNS had not been hypothesized, it is not overly surprising and can be explained by the historical origins of many SNS in the area. A historical connection between transhumance and SNS is known in many parts of Central Italy, although written sources in this regard are scarce. Memory of that link remains especially vivid in oral and religious heritages, including the foundation stories of numerous sacred sites (which feature herders, herds, or individual animals as main subjects), and the rich pastoralist symbolism that characterizes the devotion to St. Michael the Archangel (De Waal 2012; Marucci 2003).

Also in our sample, at least 12 sites show evident traces of the cult of St. Michael and herding traditions, such as an explicit dedication to the Archangel, being located along transhumance routes, and the celebration of religious rituals that fall on the key dates of transhumance or entail cattle fairs and the blessing of animals. The influence of transhumance and animal husbandry on ethnobotanical patterns is not unusual and has been reported for other parts of the world (Fairhead and Leach 1996; Ladio and Lozada 2004a, 2004b). Consistently, we found that the proportion of plants with animal–related uses is noticeably higher at the 12 SNS with an ascertained connection to pastoralism, suggesting that this pattern might be directly related to those past activities of animal herding.

Symbolic Value of Giant Trees and Importance of Deciduous Forests

Another distinctive association between SNS and ethnobotanical values emerged with regards to ancient trees. Old–growth forests and monumental trees have often exercised a fascination that transcends cultural barriers (Schama 1995), and entails spiritual, symbolic, and aesthetic appreciations rather than utilitarian motives alone (Blicharska and Mikusiński 2013). In Central Italy, a reflection of this symbolic prominence is found in the fact that trees of different species (commonly *Fagus sylvatica* and *Quercus* spp.) figure as loci of a divine apparition in the foundation stories of numerous SNS (Salvatore 2002), including two in our sample.

Our analysis of tree sizes showed that SNS have been key in conserving patches of old–growth forest (Frascaroli et al., forthcoming), as well as preserving outstanding specimens. A total of 17 trees larger than 70 cm DBH were sampled at SNS (against only three at control sites), which rival in size others considered "patriarchal" or "monumental" trees in the respective regions (CFS 2013). A micro–scale spatial pattern is also evident in the distribution of these trees, as the majority are located in the immediate proximity of the shrines, and only five are at a distance greater than 5 m from shrine borders

(Fig. 5). This suggests that individual tree specimens have been selectively managed and conserved in the shrines' vicinity as carriers of symbolic values (Turner et al. 2009), or because the very act of conserving them untouched is an expression of the veneration for the sanctity of the place (Hughes and Chandran 1998). This further supports the hypothesis that specific ethnobotanical values have been nurtured at SNS in Central Italy. Some of the values in question, however, are intangible rather than utilitarian, and related to other attributes (size, age) than just species.

While the symbolic prominence of trees was especially evident at SNS, our results in general highlighted the crucial role played by *Quercus*–dominated woodlands and other deciduous forest assemblages for traditional livelihoods in the region. Indeed, despite being species–poorer habitats than open–range grasslands, we found that deciduous forests tend to harbor a significantly higher proportion of useful taxa (Table 1 and Fig. 4). The co–evolution of deciduous forests and human cultures in the Mediterranean is well documented (Blondel et al. 2010; Naveh 1987). While these forests are scarcely productive compared to central– and north–European forests for what concerns wood mass (Llédo et al. 1992), they stand out for the diverse range of non–timber products that they provide (Blondel et al. 2010). This is clearly reflected in the high proportion of useful species that we found in forest habitats, and in the many use values associated with deciduous trees, such as *Fraxinus ornus*, *Quercus pubescens*, *Quercus ilex*, and *Ostrya carpinifolia*, throughout all of the study area (Fig. 1).

Occurrence of Other Ethnobotanical Values at SNS

Other ethnobotanical values were not specifically related to SNS. Although SNS had a greater number of useful taxa in each use category (Fig. 3a), this seems mostly a consequence of their higher species richness. Indeed, we had previously found that SNS tend to host a significantly higher number of plants (Fig. 2). In particular, the richness of herbaceous species is considerably greater at SNS, while shrub and tree diversities remain nearly constant between SNS and control sites (Frascaroli et al., forthcoming). Low–intensity anthropogenic pressures are a possible driver of these differences, as it is known that moderate rates of disturbance can positively influence the diversity of a system (Grime 1973; Naveh and Whittaker 1980). Although our control plots are also partially disturbed sites (for example, being located near walking tracks, or showing traces of light logging), human interventions such as weeding, selective thinning, and trampling (related to both individual visits and collective rituals) are far more evident at SNS, and likely to drive the patterns in question (Frascaroli et al., forthcoming).

Similarly to other studies (Begossi 1996; Sheil and Salim 2012), a strong relation between overall species richness and number of useful species at a site emerged also from our analyses (Table 1). Such a relation accounts for the greater diversity of useful plants recorded at SNS, and is consistent with the insight that disturbed anthropogenic sites often serve as repository areas where ethnobotanical resources thrive (Marshall and Hawthorne 2012; Olupot et al. 2009; Voeks 2004). Unexpectedly, however, we found that this greater diversity is not also accompanied by a higher proportion of useful species at SNS. Rather, the proportion of taxa with ethnobotanical applications was slightly higher at control sites, with the exception of animal–related uses (as discussed above; Fig. 3b). This contrasts, for example, with the findings of Boraiah et al. (2003) from the Western Ghats of India, where sacred groves had similar species richness to non–sacred patches, but significantly higher proportions of medicinal species.

The different floristic composition of SNS and control sites could offer a first explanation of this pattern. Indeed, whereas SNS have a considerably higher number of herbaceous species, usefulness is more frequently attributed to trees and ligneous species in the study area (as illustrated above), which are equally common at SNS and control sites. This would explain why the latter hosts fewer species overall, but exhibits a higher proportion of useful plants. A complementary interpretation could also be sought in the spatial patterns of SNS in the area. Remote settings are especially common for SNS in Central Italy (Nolan and Nolan 1989), due to their origin as hermitages of local saints or resting posts on the transhumance routes to mountain pastures (Frascaroli 2013). Consequently, most of the SNS investigated are visited by pilgrims only once or a few times per year, usually in occasion of annual festivities. As opposed to the sacred groves found at village borders in other cultural contexts, these specific characters would have made SNS in Central Italy less suitable as repositories of plants used for daily applications.

Comparable considerations can also explain the negative influence of altitude on useful plants diversity, in spite of the greater species richness recorded at higher elevations. While a negative relation of this kind does not necessarily occur in other contexts (Salick et al. 1999; Santos et al. 2008), some studies have highlighted a significant link between local availability and reported usefulness, and the relevance of proximity on the collection of ethnobotanical resources (De Lucena et al. 2007; Weckerle et al. 2006). The fact that plants located in more accessible habitats or closer to settlements are more likely to be recognized as useful could be a reason why useful taxa in our sample are more numerous at low or mid altitudes (i.e., <1,000 MASL), in spite of increasing floristic diversity at higher elevations.

Conclusions

SNS in Central Italy are important patches for the conservation of particular habitats and species–rich plant assemblages. Our present findings reveal that these sites also have a significant association with specific ethnobotanical values. Plants used for animal veterinary purposes are particularly frequent at SNS in Central Italy, probably due to an ancient connection between religious traditions and animal herding, and the fact that shrines were often established along transhumance routes. Similarly, we found evidence that ancient trees have been most actively preserved in the immediate vicinity of shrines, likely driven by the aesthetic and spiritual values that old trees carry (Moore 2007). These results indicate that a link between SNS, ecological knowledge, and ethnobotanical values has profound roots also in a Western and relatively modernized context. Also, they underline the prominence of intangible values of biodiversity in the management of the investigated SNS (Wild and McLeod 2008), and the importance of botanical traits beyond species alone. The cultural significance of extra–taxonomic traits should be an important avenue for future research in ethnobiology and the symbolic links between people and biodiversity (see also Ghirardini et al. 2007; Pieroni 2001; Reyes–García et al. 2006).

Broadening the scope, our study also emphasized the primary role played by Mediterranean deciduous forests as sources of both material livelihoods and symbolic or cultural "services." The remarkable body of traditional forest knowledge, beliefs, and practices, into which this has translated, represents a rich heritage threatened by the dramatic social changes of the last century (Parrotta and Agnoletti 2007). Preservation of this heritage should represent an ecological and cultural priority: the survival both of distinctive cultural landscapes, and of the habitat diversity that is associated with them, is known to depend on it (Otero et al. 2013; Schmitz et al. 2012).

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