



Effect of bark harvest intensity on the formation of cavities and other microhabitats in cork oaks (*Quercus suber*)

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Abstract

Tree microhabitats associated with decay are rare in forests managed for timber because trees are often felled before reaching the age at which they naturally develop. Non-lethal tree management, such as harvesting non-timber forest products (NTFPs), can accelerate microhabitat formation in young trees. Cork bark is an important NTFP in Iberia that is harvested from cork oak trees (*Quercus suber*) every 9–14 years. Here we investigate the effect of bark harvesting coefficient (HC, harvest height/stem circumference) on the formation of cavities and other microhabitats in cork oaks in Los Alcornocales Natural Park, Spain. We surveyed 301 cork oaks and detected 1033 microhabitats (3.4 per tree), including 46 cavities. The number of unique microhabitats per tree significantly increased from 2.5 (± 0.25) at low intensity ($0 < HC \leq 1$) to 3.7 (± 0.15) at moderate intensity ($1 < HC \leq 2$, $p = 0.003$), but further increase to high intensity ($2 < HC \leq 3$), yielded no additional microhabitats. The probability of a tree having cavities exhibited a significant non-linear increase with harvest intensity. Cavities were low (< 5 m) and large (median entrance area 267 cm^2) and probably originated from wounds sustained during cork harvesting. A total of 57 cavities were identified in the study area, including an additional 3 in dead or unharvested cork oak and 8 in co-occurring gall oaks (*Q. faginea*). 11% ($n = 6$, $0.18 \text{ cavities ha}^{-1}$) had a suitable volume and entrance size for honey bee (*Apis mellifera*) colonies and other cavity-nesters with similar requirements. Our results indicate that bark harvesting, at moderate intensity, can be beneficial to wildlife in cork oak woodlands by increasing the supply of cavities and other microhabitats. However, even at moderate intensity, temporary benefits to wildlife might be offset by reduction in tree vigour and increased mortality.

Keywords Mediterranean oak forests · Tree microhabitats · Cork harvest · Non-timber forest products · Hollow-dependent fauna

Introduction

Non-excavated tree cavities originating from decay are ecologically important microhabitats that naturally develop over decades. Those usable by large vertebrates rarely occur in trees under 100 years old (Körkjas et al. 2021) and most pedunculate oak (*Quercus robur*) trees only start to develop cavities at 200–300 years old (Ranius et al. 2009). Cavities often occur at low densities in forests managed for

timber because trees are felled before reaching the age or size at which they naturally develop (Remm and Lõhmus 2011; Andersson et al. 2018). In contrast, other types of tree management such as pollarding, in which upper branches are repeatedly pruned to produce firewood (traditional) or for public safety (modern), can accelerate rot hole formation in young trees (Grüebler et al. 2013; Sebek et al. 2013; Avilés 2019; Großmann et al., 2020). Large pruning wounds (> 15 cm diameter) can develop into cavities suitable for cavity-nesting birds (Grüebler et al. 2013; Avilés 2019) and those containing wood mould are important for saproxylic invertebrates (Sebek et al. 2013; Della Rocca et al. 2023). Similarly, old trees that have been coppiced (repeatedly pruned at ground level) often develop basal cavities containing pools of rainwater (Maděra et al. 2017), which host the aquatic larvae of specialist flies and beetles (Schmidl et al. 2008).

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Non-timber forest products (NTFPs), including fruit, nuts, leaves, bark, resins and honey, are important for trade and subsistence in rural communities, especially in developing countries (Shackleton & Shackleton 2004). NTFP commercialisation can encourage forest conservation by providing an economically viable alternative to timber production or forest conversion (Peters et al. 1989). The effects of NTFP harvest on tree survival, growth rates and reproduction are well-studied (reviewed by Ticktin 2004). NTFP harvest can also be an important source of decay-related microhabitats in young trees. In southern Africa, where the bark of many tree species is harvested for medicinal uses (Grace et al. 2002), debarking wounds are frequently colonised by saproxylic fungi and invertebrates (Roux et al. 2005). Debarking does not usually increase tree mortality, unless it is done during the dry season or when trees are too young (Gaoue et al. 2013; Ngubeni 2015). In northern Europe, debarking has been used to increase the conservation value of oak trees by deliberately inducing decay and associated microhabitats in young trees without killing them (Bengtsson et al. 2012; Bengtsson and Wheeler 2021). Bengtsson et al. (2012) debarked over 100 oak trees in Sweden and England, most of which (98.4%) were still alive 8 years later and showing early signs of decay (Bengtsson and Wheeler 2021).

Cork oak (*Q. suber*) trees are evergreen trees native to southern Europe and northern Africa (Pausas et al. 2009). Cork oaks have a thick and spongy outer bark which has been harvested commercially since the mid-1800s to make wine bottle stoppers and building materials (Mendes and Graça 2009). Given its ability to regenerate, cork bark can be sustainably harvested at intervals of 9–14 years once a tree reaches 18–25 years old or a diameter at breast height (DBH) of c. 20 cm (Oliveira and Costa 2012). Cork oaks typically grow in forests and diverse savanna-type ecosystems called *montado* in Portugal, *dehesa* in Spain and *azaghar* in Morocco (Bugalho et al. 2009). However, due to increased drought and wildfires, and land abandonment following global cork devaluation in the late 2000s, many of these habitats have been replaced by persistent shrubland (Acácio et al., 2009; Bugalho et al. 2011). Therefore, shrub clearing and grazing are required to maintain habitat heterogeneity in cork oak ecosystems (Bugalho et al. 2011). Bark harvesting might also be important for maintaining biodiversity at the tree-level, by accelerating the formation of cavities and other important microhabitats for wildlife. Cavities in cork oaks are used by several mammals (Carvalho et al. 2014), birds (Segura 2017) and insects (Della Rocca et al. 2023), including threatened species such as the Iberian lynx (*Lynx pardinus*, Fernández and Palomares 2000) and hermit beetle (*Osmoderma eremita*, Chiari et al. 2012).

Andalusia is the southernmost region of Spain and the country's largest producer of cork (Sierra-Pérez et al. 2015). This region is also famous for its honey production and has a high density of managed honey bee (*Apis mellifera*) colonies, at over 0.06 colonies ha⁻¹ on average (Kukielka et al. 2008). Honey bees are traditionally managed alongside cork production and kept in cylindrical hives made of cork bark, although modern moveable-frame hives are now more common (Crane 1999). Wild colonies also occur in Spain, but at much lower densities than those of managed colonies (<0.01 colonies ha⁻¹, Rutschmann et al. 2022). Honey bee colonies require large cavities (> 15 L) with small entrances (< 10 cm diameter). In rural Spain, suitable nest sites can be found in man-made structures such as concrete power poles (Rutschmann et al. 2022), but no studies have investigated the availability of natural honey bee nest sites in trees or the processes that lead to their formation.

The aims of this study are to (i) assess the diversity of cavities and other microhabitats provided by cork oaks in Los Alcornocales Natural Park, Andalusia, Spain (ii) quantify the density of cavities, in both cork oaks and co-occurring gall oaks (*Q. faginea*), that are suitable for wild honey bee colonies and other cavity-nesters with similar requirements and (iii) analyse the effect of bark harvest intensity on microhabitat diversity, the probability of occurrence of different microhabitat groups and the height and size of cavities in harvested cork oaks. We predict that cork oaks subjected to higher harvest intensity will have more microhabitats, particularly those associated with debarking wounds such as bark structures and cavities. By extension, cork oak woodlands that are actively managed for cork production should have high conservation value for hollow-dependent fauna.

Methods

Study sites

Fieldwork was conducted in two cork oak woodlands of 14.8 ha (A) and 18.1 ha (B) in Los Alcornocales Natural Park, the largest protected cork oak habitat in the world at approximately 174,000 ha. Study sites were located approximately 250 m apart on the western (36.4327 N, 5.4640 W) and eastern (36.4303 N, 5.4576 W) side of the Hozgarganta river (Fig. 1). Study sites were chosen based on accessibility via public footpaths, lack of steep gradients and proximity to the town of Jimena de la Frontera where the authors were staying. We refer to sites as “woodland” because tree cover was between 40 and 45% at both sites and interspersed with shrubs, mainly rockrose (*Cistus* spp.) and heather (*Calluna* spp.). Cork oaks were the most common tree at both sites. Other tree species including semi-deciduous gall oaks, olive

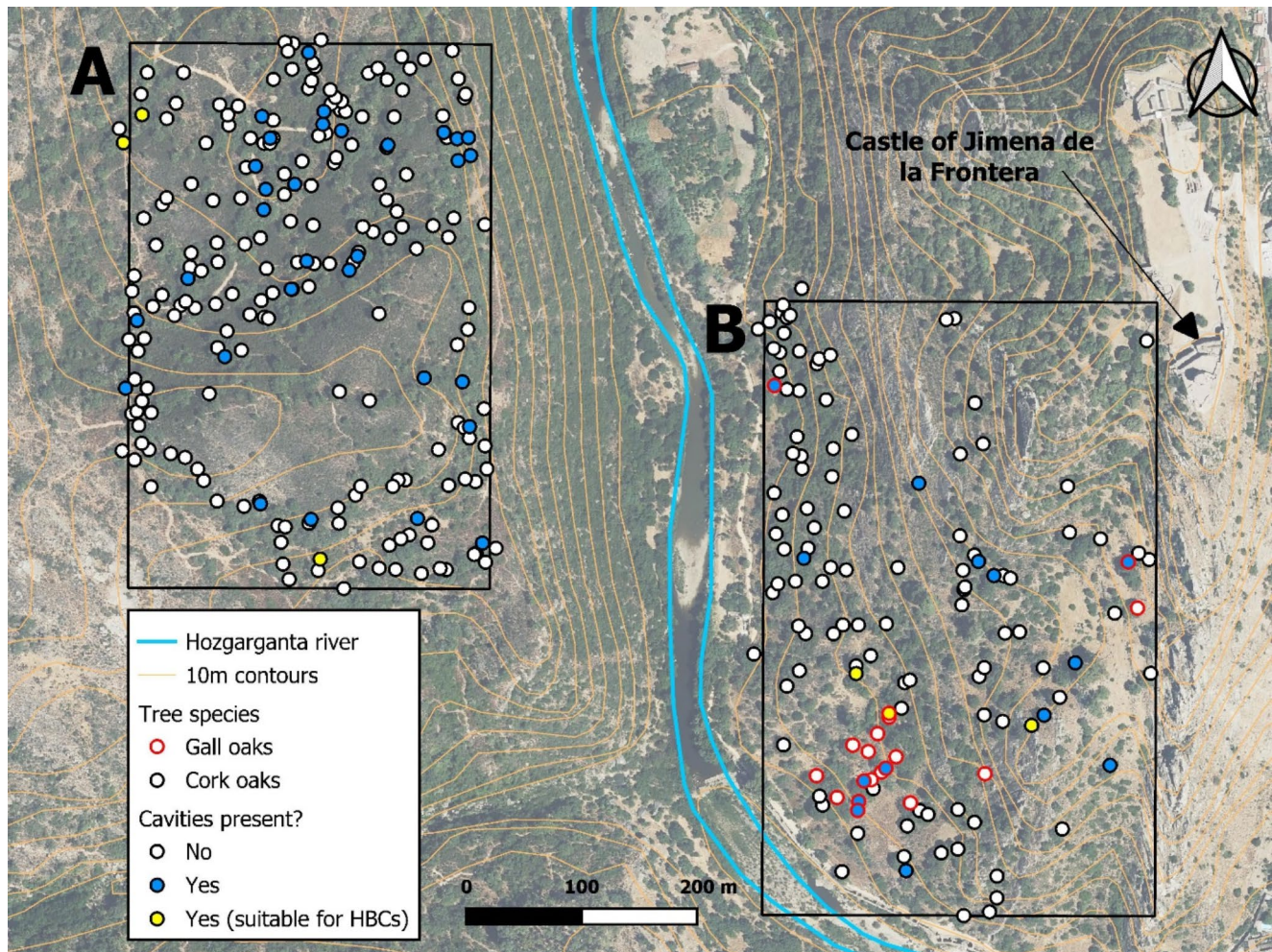


Fig. 1 Study sites near Jimena de la Frontera in Los Alcornocales Natural Park, Andalusia, Spain. Points show all oak trees with circumferences at breast height greater or equal to 1.57 m that were initially assessed, including gall oaks and dead or unharvested cork oaks. Blue points are trees with cavities and yellow points are trees with cavities

(*Olea europaea*) and *Eucalyptus* spp. were present in site B, which was part of the Chinchilla Nature Reserve. Gall oaks were included in the study because they were the only other tree species large enough to contain cavities in the study area and needed to be accounted for to accurately quantify cavity density.

Tree survey

We initially assessed all oak trees in the study area with circumferences at breast height (CBH) ≥ 1.57 m, 95% of which were cork oaks and 5% were gall oaks. The whole sample is used for descriptions of cavities and calculations of cavity density. We then narrowed down the sample by excluding gall oaks and dead or unharvested cork oaks for descriptions of other microhabitats and analyses of bark harvesting coefficient (HC). Crown height and maximum

that have a suitable volume and entrance size for honey bee colonies (HBCs). Map was created using QGIS (v3.32.1) with topography data and satellite imagery downloaded from the Spanish National Centre for Geographic Information (CNIG, 2024)

debarking heights above 2 m were measured using a clinometer. HC was calculated by dividing maximum harvest height by CBH, which is typically measured over cork bark prior to harvesting (Oliveira and Costa 2012). However, this was not possible in our study, so HC was overestimated slightly. The CBH of multi-stem trees was estimated from crown height using the slope and intercept produced by a linear regression analysis of CBH and crown height in single-stem trees. CBH was converted to diameter at breast height (DBH) by dividing it by π . Trees with diameters of $0.5 \text{ m} \leq \text{DBH} < 0.6 \text{ m}$ were classed as “medium” and trees with diameters of $0.6 \text{ m} \leq \text{DBH} < 1.0 \text{ m}$ were classed as “large”. The health of living trees was assessed on a scale of 1 to 4 following Oleksa et al. 2013. Health scores (HS) of 1 were assigned to trees with no cavities, deadwood or other signs of decay. Health scores from 2 to 4 were based on the amount of deadwood in the crown (HS=2: 25%, HS=3:

50%, HS=4: 75%). Raw health scores are included in statistical models, whereas a binary variable (HS=1: “healthy” or HS>1: “unhealthy”) is used for figures and descriptive statistics.

The whole tree was assessed for potential microhabitats, although upper branches may have been under represented due to their greater distance from observers (see discussion). Microhabitats were recorded by a single pair of observers using a field guide by Kraus et al. (2016) containing 64 microhabitats which we grouped into 16 categories (Table 1) following Larrieu et al. (2018). Bark-related microhabitats, including bark loss (IN11-14), bark shelters (BA11), bark pockets (BA12) and coarse bark (BA21), were only recorded for the inner layer of bark (not the outer cork bark). An additional microhabitat category was created for pennywort epiphytes (*Umbilicus* spp.). Descriptions of all microhabitat groups are included in Table 1 and photos of common microhabitats in bark-harvested cork oaks are shown in Fig. 2.

Cavity survey

We defined cavities as dry holes with internal dimensions that greatly exceeded the entrance. This excludes woodpecker (Picidae) feeding holes (CV14), insect exit holes (CV5) and water-filled holes (CV4). The height and orientation of the cavity entrance were measured using a tape measure and compass, respectively. Cavity entrance area (cm²) was approximated from vertical (VD_e) and

horizontal (HD_e) diameters using the equation for an ellipse ($area = 1/4 \cdot \pi \cdot VD_e \cdot HD_e$). Cavity volume (litres) was approximated from internal height (H_i) width (W_i) and depth (D_i) using the equation for an ellipsoid ($volume = 1/6 \cdot \pi \cdot H_i \cdot W_i \cdot D_i$). Internal dimensions were measured by inserting wire into the cavity in different directions. A cavity was considered suitable for a honey bee colony if the volume was 15–80 L (Seeley and Morse 1976; McNally and Schneider 1996; Ratnieks et al. 1991) and the entrance 10–60 cm² (Seeley and Morse 1976; Gambino et al. 1990; Ratnieks et al. 1991; Baum et al. 2005).

Statistical analysis

All statistical analyses were done in R (v4.3.1, R core team 2023) and plots were made using *ggplot2* (Wickham 2016). Generalised linear models (GLMs) were used to analyse the linear, non-linear and categorical effects of HC on three response variables with different error distributions: (i) the number of unique microhabitats per tree (microhabitat diversity, Poisson), (ii) the probability of occurrence of different microhabitat groups (binomial) and (iii) the height, entrance area and volume of cavities (gamma). For brevity, we only report the results of binomial models for microhabitat groups that were significantly affected by HC. Variables included in global models were health score (ordinal), DBH (linear), HC (linear) and HC² (quadratic). Variance inflation factors (VIF) were calculated for each variable in the global model to test for multicollinearity. HC (linear) was centred

Table 1 Microhabitats recorded in two cork oak woodlands in Los Alcornocales Natural Park, Andalusia, Spain. Microhabitats were recorded on living bark-harvested cork oaks (*Quercus suber*) using a field guide by Kraus et al. (2016). Cavities include woodpecker breeding holes (CV1, *excluding CV14), trunk and mould cavities (CV2) and branch holes (CV3). Injuries and wounds include trunk and crown breakage (IN2) and cracks and scars (IN3). “Other” microhabitats recorded include bird nests (NE1), water-filled holes (CV4) and Ivy (EP33)

Microhabitat	Description	Code	Site A	Site B	Total
Bark loss	Loss of inner bark exposing area of sapwood > 25 cm ²	IN1	139	53	192
Bark pockets	Inner bark (> 100 cm ²) detached from sapwood by > 1 cm (top open)	BA12	137	54	191
Bark shelters	Inner bark (> 100 cm ²) detached from sapwood by > 1 cm (bottom open)	BA11	130	41	171
Coarse bark	Fissures of > 2 cm in the bark surface	BA21	83	23	106
Moss	Non-vascular epiphytes (> 10% coverage)	EP31	79	14	93
Insect holes	Small (ϕ < 2 cm) tubular entrance or exit holes created by xylophagous insects	CV5	52	28	80
Cavities	Large (ϕ > 2 cm) dry holes with an interior larger than the entrance hole	CV1-3*	37	9	46
Sap flow	Sap flowing from inner bark (> 10 cm length)	OT1	20	18	38
Breakages and scars	Broken stem/branches (ϕ > 20 cm). Scars on the stem > 30 cm long, > 10 cm deep, > 1 cm wide	IN2-3	13	8	21
Woodpecker feeding holes	Conical excavation in deadwood with entrance ϕ > 10 cm	CV14	16	2	18
Pennyworts	Flowering epiphyte in genus <i>Umbilicus</i>	EP36	9	9	18
Deadwood	Dead branches (ϕ > 10 cm) usually in shaded parts of the crown	DE1	14	2	16
Ferns	Vascular non-flowering epiphyte (> 5 fronds)	EP34	17	0	17
Cankers	Cancerous growth (ϕ > 20 cm) with rough surface	GR3	13	0	13
Fungi	Fruiting bodies of both annual and perennial fungi (ϕ > 5 cm)	EP1	5	1	6
Other	-	-	4	3	7
Total			768	265	1033



Fig. 2 Common microhabitats recorded on bark-harvested cork oaks (*Quercus suber*). (A) Loss of inner bark exposing large area (>600cm²) of sapwood (IN12) at the base of a tree. (B) Breeding hole excavated by a woodpecker (CV13). (C) Pennywort (*Umbilicus* spp.) epiphytes (EP36) growing on virgin (unharvested) cork bark. (D) Wound wood

around an injury causing inner bark to lift and starting to create bark pockets (BA12). (E) Dead tree with several woodpecker feeding holes (CV14). (F) Large trunk cavity (CV24). (G) Fire bugs (*Pyrrhocoris apterus*) sheltering in a deep fissure in bark (BA21)

around zero to reduce collinearity with HC² (quadratic) to within an acceptable range of 1 to 5. Likelihood ratio tests were used to determine whether the removal of a variable resulted in a significant change in the model's ability to

explain variation in the response (model quality). Summaries for each GLM, including model coefficients, statistical significance and VIF, are shown in the supplementary material (Table S1). GLMs were run again with HC included as a

categorical variable with 3 levels: low ($0 < HC \leq 1$), moderate ($1 < HC \leq 2$) and high ($2 < HC \leq 3$). HC categories were chosen based on the limits in different countries, which are $HC \leq 2$ in Portugal, Spain and Italy, and $HC \leq 3$ in France, Morocco, Tunisia (Oliveira and Costa 2012). Tukey tests were used to test for significant differences in the mean ($\pm$ SE) of each response variable between HC categories. *P* values are adjusted for multiple comparisons using the Bonferroni method.

Results

Microhabitat diversity

Of the total 349 oak trees assessed, 301 were living cork oaks with evidence of bark harvesting (211 in site A, 90 in site B). A total of 1033 microhabitats (3.4 per tree) were recorded on living bark-harvested cork oaks (768 in site A, 265 in site B). Most (73%) tree microhabitats catalogued by Kraus et al. (2016) were identified in our study area. Absences include root buttress cavities (GR1), witches' brooms (GR2) and microsoil (OT2). Most microhabitats occurred on harvested parts of the tree. However, non-fungal epiphytes, deadwood and breakages almost exclusively occurred on virgin cork (never harvested).

A total 57 cavities were found in the study area, including an additional 8 in gall oaks and 3 in dead or unharvested cork oaks. Seven cavities (12%) were located at the base of the tree with ground contact (CV21–22), 5 (9%) were cavities excavated by woodpeckers (CV1), 11 (19%) were open cavities with large entrances that did not prevent rain from reaching the interior (CV25–26) and 34 (60%) were decay cavities or branch holes in the trunk or major branches (CV23–24, CV31–32). Cavity entrances were not orientated at random ($R=0.3$, $p=0.023$) and had a mean bearing of 32 degrees (northeast; Fig. S1, supplementary material). Entrance heights ranged from 0 to 4.8 m (median 0.9 m, Fig. 3). Entrance area varied greatly from 4.7 to 2350 cm² (median 267 cm²) with 27% suitable for honey bee colonies (Fig. 3). Volume was less variable, 7 to 673 L (median 66 L, 41% suitable, Fig. 3). Overall, 11% of cavities (0.18 cavities ha⁻¹) met the nesting requirements of honey bee colonies, although none were occupied.

Effect of HC

A total of 172 bark-harvested cork oaks were classed as healthy ($HS=1$) and 129 were classed as unhealthy ($HS>1$). Crown height ranged from 4.7 to 26.5 m (mean 12.1) and was highly correlated with CBH in single-stem cork oaks ($F=13.2$, $p<0.001$). DBH, including estimated values for

multi-stem cork oaks ($n=62$), ranged from 0.50 to 0.99 m (mean 0.61 m) with 178 trees being classed as medium and 123 large. HC ranged from 0.44 to 3.02 (mean 1.6), excluding two outliers at 3.99 and 4.80, with 52 trees harvested at low intensity, 162 moderate and 87 high. There was no significant collinearity between health score, DBH, HC and study site in any of the global models ($VIF<2$, Table S1, supplementary material).

Increased HC corresponded with a non-linear increase in the number of unique microhabitat groups per tree (microhabitat diversity, Fig. 4). Poisson GLMs (Table S1, Model 1) were significantly worse at explaining variation in microhabitat diversity after removing the quadratic component of HC (Model 1b, $\chi^2=12.7$, $p<0.001$) but not after removing the linear component (Model 1c, $\chi^2=0.5$, $p=0.491$). When considering HC categories, microhabitat diversity significantly increased from low (2.5 ± 0.25) to moderate intensity (3.8 ± 0.15 , $p=0.003$) but not from moderate to high (3.4 ± 0.19 , $p=0.746$).

Of the 16 microhabitat groups recorded, 6 were significantly affected by HC. Increased HC corresponded with a linear increase in the occurrence of bark pockets, a non-linear increase in the occurrence of bark shelters and cavities, a non-linear decrease in the occurrence of coarse bark and insect holes, and a linear decrease in the occurrence of pennyworts (Fig. 5). Binomial GLMs (Table S1, Model 2–7) were significantly worse at explaining variation in the occurrence of bark shelters (Model 3b, $\chi^2=23.4$, $p<0.001$), cavities (Model 4b, $\chi^2=10.1$, $p=0.002$), coarse bark (Model 5b, $\chi^2=7.6$, $p=0.006$) and insect holes (Model 6b, $\chi^2=8.2$, $p=0.004$) after removing the quadratic component of HC, and bark pockets (Model 2d, $\chi^2=9.1$, $p=0.003$), bark shelters (Model 3d, $\chi^2=5.0$, $p=0.025$) and pennyworts (Model 7d, $\chi^2=5.7$, $p=0.016$) after removing the linear component. Differences in microhabitat probability between HC categories were only significant for bark pockets and bark shelters, both of which significantly increased from low (shelters: 0.27 ± 0.06 , pockets: 0.44 ± 0.07) to moderate intensity (shelters: 0.66 ± 0.04 , $p<0.001$; pockets: 0.65 ± 0.04 , $p=0.030$) but not from moderate to high (shelters: 0.57 ± 0.05 , $p=0.651$; pockets: 0.71 ± 0.05 , $p=0.777$).

Increased HC corresponded with a linear increase in cavity entrance height (Fig. 3) and a linear decrease in cavity entrance area but had no effect on cavity volume. Gamma GLMs (Table S1, Model 8–10) were significantly worse at explaining variation in cavity entrance height (Model 8c, $\chi^2=4.8$, $p=0.003$) and cavity entrance area (Model 9c, $\chi^2=4.4$, $p=0.043$) after removing the linear component of HC, but not after removing the quadratic component (cavity entrance height: Model 8b, $\chi^2<0.1$, $p=0.943$; cavity entrance area: Model 9b, $\chi^2=0.4$, $p=0.540$). HC had no effect on cavity volume (linear: Model 10c, $\chi^2=0.4$,

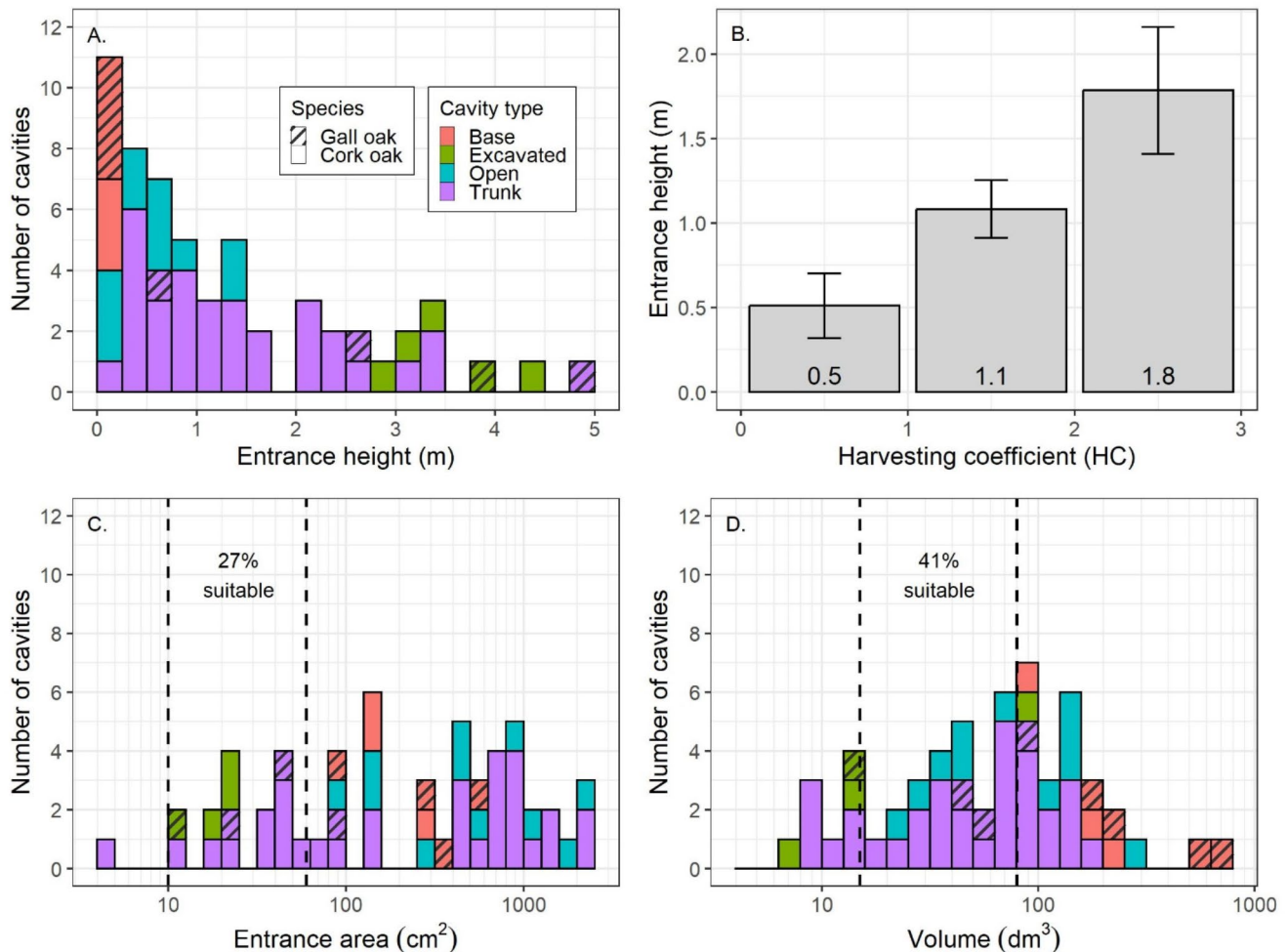


Fig. 3 Entrance height (A), entrance area (C) and volume (D) of 57 cavities in oak trees (*Quercus* spp.) surveyed in two cork oak woodlands in Los Alcornocales Natural Park, Andalusia, Spain. Solid bars show cavities in cork oaks (*Q. suber*, $n=49$), and dashed bars show cavities in gall oaks (*Q. faginea*, $n=8$). Seven (12%) were basal cavities with ground contact (CV21-22), 5 (9%) were cavities excavated by woodpeckers (CV1), 11 (19%) were open cavities with large entrances (CV25-26) and 34 (60%) were decay cavities or branch holes in the trunk or co-dominant stems (CV23-24, CV31-32). Entrance height was recorded for all cavities, ranging from 0 to 4.8 m (median 0.9 m),

and had a significant positive correlation with harvest intensity in living bark-harvested cork oaks (B). Entrance area and volume were recorded for 56 cavities and are shown on a log scale with minor increments of 1, 10 and 100. Dashed lines show honey bee colony nesting requirements (entrance area: 10–60 cm², volume: 15–80 L). Entrance area ranged from 4.7 to 2350 cm² (median 267 cm², 27% suitable). Volume ranged from 7 to 673 L (median 66 L, 41% suitable). Overall, 6 cavities (10%, 0.18 cavities ha⁻¹) met honey bee colony nesting requirements, although none were occupied

$p=0.475$, quadratic: Model 10b, $\chi^2=0.1$, $p=0.763$) and there was no significant difference in any cavity dimensions between HC categories ($p>0.05$).

Discussion

Our results show that cork oak woodlands provide many microhabitats for wildlife with an average of 3.4 unique microhabitat groups per tree. Microhabitat diversity significantly increased from low to moderate bark harvest intensity, as did the occurrence of microhabitats associated with debarking wounds such as bark structures and cavities.

However, microhabitat diversity did not increase from moderate to high intensity and some microhabitat groups, such as epiphytes that only grow on virgin cork, decreased in occurrence at high intensity. Therefore, whilst bark harvesting at moderate intensity can be beneficial to biodiversity in cork oak woodlands, high intensity harvests (HC > 2) should be avoided as they potentially jeopardize tree health without providing additional habitats for wildlife.

Despite active management being beneficial for wildlife in cork oak woodlands, over-exploitation can be detrimental (Bugalho et al. 2009). At the ecosystem-scale, excessive grazing and acorn collecting (for both human and animal consumption) can decrease natural regeneration (Bugalho

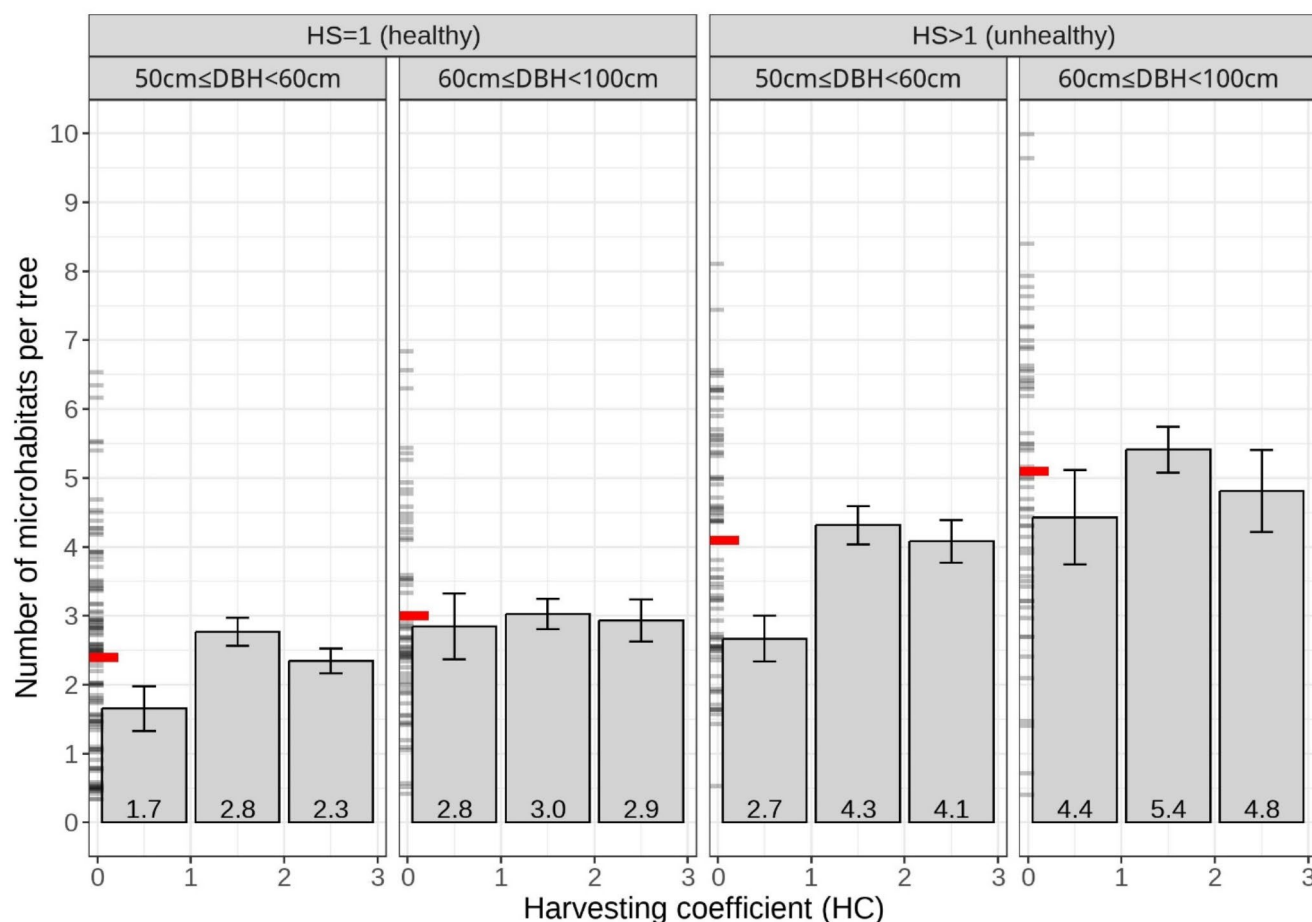


Fig. 4 Effect of bark harvest coefficient (HC, harvest height/stem circumference) on the number of unique microhabitats per tree (microhabitat diversity) in living bark-harvested cork oaks (*Quercus suber*). Trees are categorised based on health score (HS), which ranged from 1 (healthy trunk and crown) to 4 (75% crown deadwood), and stem diameter at breast height (DBH). Microhabitat diversity is shown as horizontal lines on the y axes (random noise included for visualisation)

tion), with the mean for each tree category in red. Mean microhabitat diversity (vertical bars, $\pm$ SE) significantly increased from 2.5 (± 0.25) per tree at low harvest intensity ($0 < HC \leq 1$) to 3.7 (± 0.15) per tree at moderate harvest intensity ($1 < HC \leq 2$, $p=0.003$), but further increase to high intensity ($2 < HC \leq 3$) yielded no additional microhabitats ($p=0.746$)

et al. 2011). At the tree-level, canopy pruning can decrease the abundance of foliage-gleaning birds (Leal et al. 2013) and trees that have been recently debarked are less likely to recover after a wildfire (Barberis et al. 2003; Moreira et al. 2007; Catry et al. 2012). Los Alcornocales Natural Park has a fire return interval of 15–25 years (Marañón 2009) and cork oaks are harvested every 9–14 years in Spain (Oliveira and Costa 2012). Given the frequency of the two events, they are likely to coincide within typical cork oak rotation periods of 150–200 years (Pereira & Tome, 2004). Harvest intensity might also be an important factor determining post fire survival and resilience to drought, given that it correlates with increased water loss (Oliveira 1995) and decreased bark thickness (Pizzurro et al. 2010) in cork oaks. However, no studies have investigated the effect of harvest intensity (as opposed to harvest vs. no harvest) on cork oak mortality and there are currently no legal limits regarding

HC in Spain, unlike other cork producing countries such as Portugal and Italy, where HC must not exceed 3 (Oliveira and Costa 2012).

As predicted, cork oaks subjected to higher harvest intensity were more likely to have microhabitats associated with debarking wounds (bark structures and cavities). Intense bark harvesting is more likely to produce wounds, especially when done by inexperienced workers (Oliveira and Costa 2012). Debarking wounds of 40 cm in diameter may take 20 years to heal (Natividade 1938), during which the tree is vulnerable to attack by insects and fungi (Sousa and Debouzie 1999; Martin et al. 2005). Therefore, high intensity harvests might be more likely to increase tree mortality through wounding than physiological effects like water loss. In addition, debarking wounds can decrease cork production and make cork planks more difficult to remove (Costa et al. 2004). Cork bark is traditionally harvested by skilled

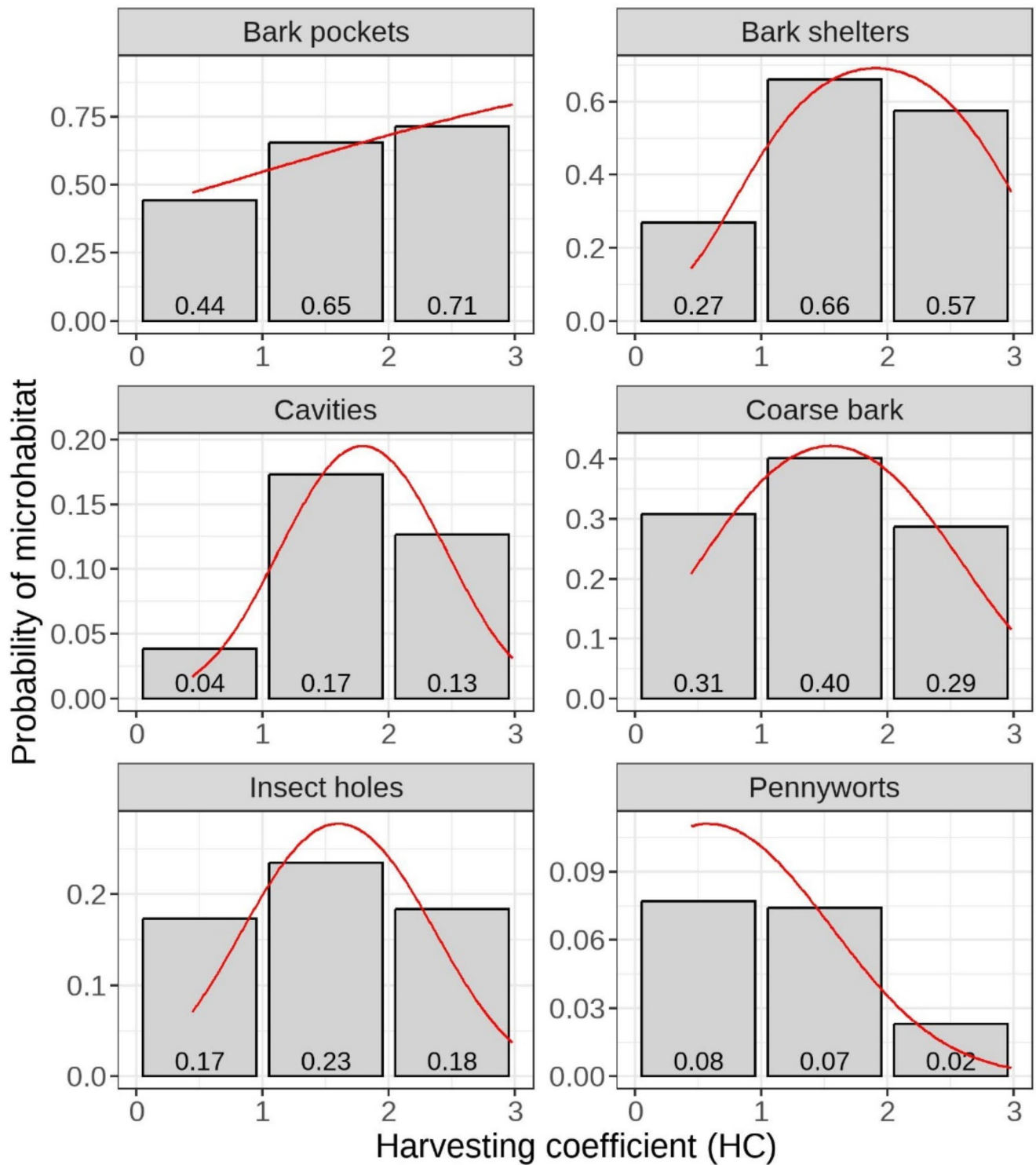


Fig. 5 Effect of bark harvest coefficient (HC, harvest height/stem circumference) on the probability of occurrence of 6 microhabitat groups in living bark-harvested cork oaks (*Quercus suber*). Grey bars show observed probabilities at low ($0 < HC \leq 1$), moderate ($1 < HC \leq 2$) and high ($2 < HC \leq 3$) harvest intensity. Red lines show predicted probabilities produced by binomial generalised linear models across the range

of observed HCs. Increased HC corresponded with a linear increase in the occurrence of bark pockets, a non-linear increase in the occurrence of bark shelters and cavities, a non-linear decrease in the occurrence of coarse bark and insect holes, and a linear decrease in the occurrence of pennyworts

workers using a hand axe, but the process can be mechanised using a modified chainsaw which reduces the risk of wounding the tree (Beira et al. 2014).

90% of bark-harvested cork oaks had at least one microhabitat associated with debarking wounds, with bark structures being the most benign as the inner bark is still relatively intact. It is important to distinguish between bark pockets (top open) and shelters (bottom open) because wood mould can accumulate in the former (Kraus et al. 2016). Bark shelters are used for roosting by forest-dwelling bats (Dietz et al. 2018), whereas bark pockets with mould are important larval sites for saproxylic beetles (Winter and Möller 2008). Both microhabitats are probably formed via the same processes and over relatively short time periods. Bark structures may form immediately after a tree is wounded (Körkjäs et al. 2021) or once the wound has started to heal and surrounding bark begins to lift (Bengtsson and Wheeler 2021). The formation of bark structures does not necessarily depend on tree age as they occur in small trees (DBH < 20 cm; Michel and Winter 2009; Michel et al. 2011). Bark structures probably do not remain on a tree for very long (< 1 year) before falling off and our results suggest that intensive management might accelerate this process. Unfortunately, no studies have investigated the long-term persistence of bark structures (Körkjäs et al. 2021).

Cavities were less common, occurring in 13% of bark-harvested cork oaks, and represent more advanced debarking wounds where decay has progressed to the heartwood. Körkjäs et al. (2021) reviewed cavity formation rates and found that medium (5 cm entrance diameter) and large (10 cm) cavities naturally develop at approximately 90 and 170 years of age, respectively, in species with available data (mainly rosids). Zheng et al. 2016 estimated that tree cavities originating from wounds in Fagaceae require a minimum of 56 years to develop a volume of 6 L. Given that the first bark harvest in cork oaks occurs at 18–25 years, one can expect to see relatively large cavities in trees as young as 75 years. Once a cavity has developed, it will typically be usable for 10 to 20 years until it is destroyed, for example by stem breakage, or degraded by excavators, advanced decay, or hole occlusion (Wesołowski 2012).

A limitation of our study, which applies to most ground-based microhabitat surveys, is that microhabitats groups occurring higher in the canopy are less likely to be detected. This is particularly true for cork oaks as bark is only removed from lower parts of the tree, leaving a bare region where microhabitats are more obvious. This region is larger at higher harvest intensities so microhabitats might be more likely to be noticed, which could be partly responsible for the significant increase in microhabitat diversity from low to moderate intensity. Most of the microhabitats we detected were associated with debarking wounds, so it

is not surprising that they increased with harvest intensity. We found that the occurrence of pennyworts, which only grow on virgin cork, significantly decreased at higher intensity and it is possible that less conspicuous microhabitats exhibited a similar trend but were undetected. Whilst a few trees had crown heights of over 25 m, the vast majority (85%) were less than 15 m and their canopies could be adequately assessed from the ground with binoculars, so we don't expect this bias to have a large effect on our results. In addition, microhabitats were recorded by a pair of observers, following recommendations by Paillet et al. (2014), to minimise detection errors.

We found 57 cavities in our 33 ha study area, which results in a density of 1.7 cavities ha⁻¹. This density is comparable to those recorded in European forests (median 5.6 cavities ha⁻¹, Remm and Lõhmus 2011) and within the range of cavity densities (1.1 to 3.9 cavities ha⁻¹) reported in Iberian holm oak (*Quercus rotundifolia*) *dehesa* by Avilés (2019). Six (11%) cavities were determined to be suitable for honey bee colonies and other cavity-nesters with similar requirements (small entrance, large volume). This results in a honey bee nest site density of 0.18 nest sites ha⁻¹. Honey bee nest site densities reported in the literature range from 0.014 to 0.1 nest sites ha⁻¹ in European forests (Requier et al. 2020; Kohl et al. 2022; Suppl.) and 0.17 to 0.23 nest sites ha⁻¹ in open oak woodland in southern United States (Baum et al. 2005; Rangel et al. 2016; Dickey et al. 2023). In addition to a high density of suitable nest sites, Iberian cork oak woodlands support a range of understory formations (pasture, shrubland, cropland etc.) and high floral diversity, making them ideal for pollinators.

Our results indicate that the main process driving cavity formation in cork oak woodlands is decay, presumably originating from wounds sustained during bark harvesting. All cavities were below 5 m, which corresponds with maximum cork harvest heights observed in the study area (< 6 m in 98% of trees). Indeed, cavity entrance height had a significant positive correlation with harvest intensity. Although cavities in *Q. faginea* were also below 5 m, even though bark from this species is not harvested. Cavities had a median height of just 0.9 m and were orientated towards the northeast, away from prevailing south westerly winds. This suggests that some cavities originated from fire scars, which typically form at the base of the tree on the leeward side where turbulent hot air accumulates (Gutsell and Johnson 1996). We did not see any other evidence of fire damage, but this may have been removed in previous bark harvests. The significant bias towards northeast could also be explained by decreased sun exposure and increased humidity, both of which favour decay in living trees (Zheng et al. 2016).

Many cavities had large entrances of up to 2,500 cm² and 19% were not completely buffered from external

environmental conditions. Axe wounds sustained during cork harvesting are typically larger (15–40 cm long) (Costa et al. 2004; Natividade 1938) than those originating from pruning cuts (Grüebler et al. 2013; Avilés 2019) and can take decades to heal completely (Natividade 1938). Indeed, most cavities were too large (both volume and entrance size) and low for honey bee colonies and other species that are susceptible to predation and require a stable microclimate (e.g., passerines), but probably usable as den sites by large mammals like the common genet (Carvalho et al. 2014) and the Eurasian lynx (Fernández and Palomares 2000). Cavity-users might temporarily avoid nest sites in cork oaks during cork removal due to increased disturbance (Godinho and Rabaça 2011; Carvalho et al. 2014) but usually only for a single breeding season (Godinho and Rabaça 2011).

Conclusion

Cork oak woodlands are important agroforestry systems throughout the Mediterranean Basin that support rural livelihoods through commercial cork production. Active land management, such as grazing and shrub clearing, has been shown to be crucial in sustaining the high levels of biodiversity associated with cork oak habitats. Our results suggest that moderate levels of bark harvesting can also benefit wildlife, particularly cavity-nesting species and those depending on dead and decaying wood habitats. In some cases, these habitats might be in oversupply, as shown by the many cavities suitable for wild honey bee colonies, none of which were occupied. If possible, high-intensity bark harvests ($HC > 2$) should be avoided as this can compromise tree vitality without producing many additional habitats for wildlife. Even at moderate intensity, temporary benefits to wildlife in cork oak woodlands might be offset by long-term reduction in tree vigour and increased mortality.

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Data availability The data that supports the findings will be uploaded to a repository upon acceptance.

Declarations

Competing interests The authors declare no competing interests.

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