

Conservation zones increase habitat heterogeneity of certified Mediterranean oak woodlands

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ABSTRACT

Forest certification is a conservation tool, which aims to promote the sustainable management and conservation of forest ecosystems. Establishing set-aside or lower intervention conservation zones to promote biodiversity conservation is a requisite of forest certification. We tested the effects of conservation zones on the tree biometrics and regeneration, as well as on the taxonomic, functional, and structural diversity of the shrub and herb understorey, in Mediterranean oak woodlands. We also assessed how oak biometrics, regeneration and understorey diversity varied among conservation zones established 10, 14, and 20 years before our sampling dates. Oak regeneration tended to be higher in conservation zones than in controls, but results varied with the age of conservation zones. For example, the abundance of oak seedlings and saplings was higher in 10-year-old conservation zones than in those established 20 years ago. Abundance of young oak trees was higher in 14-year-old conservation zones than in 10- and 20-year-old conservation zones. The understorey vertical diversity was significantly higher in 14- and 20-year-old conservation zones than in controls. Functional diversity differed significantly between conservation zones and controls, with a higher abundance of late-successional shrubs, namely fleshy-fruited species in 20-year-old conservation zones. The plant species composition of the shrub and the herb understorey was most dissimilar between older conservation zones and controls. Additionally, the cover and diversity of the understorey herb species decreased with the age of conservation zones. Conservation zones implemented under forest certification increase habitat structural complexity of oak woodlands, which may benefit wildlife species, but there will be trade-offs with the cover and diversity of the herb understorey. Forest managers must evaluate such trade-offs when establishing conservation zones in cork oak woodlands under forest certification schemes.

1. Introduction

Forests cover 30.8% of the world surface, harbour approximately 80% of the terrestrial biodiversity, and generate ecosystem services and functions on which all humankind depends (FAO and UNEP, 2020). Forest certification is a voluntary scheme aiming to promote sustainable forest management and forest conservation. Forest management under certification must comply with third-party audited environmental and socio-economic standards (Auld et al., 2008; Pollastrini et al., 2018). Forest products originated from certified forests have added market value, which is an incentive to certification (Auld et al., 2008). The Forest Stewardship Council (FSC) and the Programme for Endorsement

of Forest Certification (PEFC) are the main certification mechanisms in the world, covering approximately 222 million hectares (19%) and 331 million hectares (29%) of the productive forests in the world, respectively (FSC, 2020; PEFC, 2020). Forest certification usually requires forest managers to establish set-aside or lower intervention zones for biodiversity conservation (i.e., conservation zones) that generally comprise no less than 10% of the forest management unit area (Auld et al., 2008; FSC, 2015). Despite a continuous expansion of forest certification areas worldwide, there is still a lack of data on the effects of certification and conservation zones on biodiversity (di Girolami and Arts, 2018; van der Ven and Cashore, 2018), namely in Mediterranean forests and woodlands (but see Dias et al., 2015, 2016; Pollastrini et al.,

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2018; Sánchez-Almendro et al., 2018).

Cork oak (*Quercus suber* L.) is a tree species endemic to the western Mediterranean Basin that covers approximately 1.5 million hectares in Europe and 1 million hectares in North Africa. The largest cork oak cover occurs in Portugal (719 900 ha or 22% of the total forest cover of the country) from which approximately 100,000 ha are presently FSC-certified (APCOR, 2018; ICNF, 2019). Cork oak woodlands were first certified in Portugal 10 years before the present study (FSC, 2021).

Cork oak formations range from closed forests to open woodlands (Pasalodos-Tato et al., 2018). Cork oak open woodlands are silvopastoral systems, with tree densities varying between 20 and 80 trees per hectare, in which cork oak occasionally mixes with other tree species such as holm oak (*Quercus rotundifolia* Lam), umbrella (*Pinus pinea* L.) or maritime pine (*Pinus pinaster* Aiton) (Pinto-Correia and Mascarenhas, 1999; Bugalho et al., 2011a). The understory is a matrix of shrublands and herb species, sometimes mixed with crops (Pinto-Correia and Mascarenhas, 1999; Bugalho et al., 2009). Because of different and intermixed land uses, cork oak open woodlands form a heterogeneous habitat supporting high biodiversity, including endemic and threatened vertebrate species, and a diverse understory of shrub and herb species (Plieninger et al., 2010; Bugalho et al., 2011a; Dias et al., 2013; Leal et al., 2016). Cork (the outer tree bark) harvesting, used for wine bottle stoppers production, together with other uses such as livestock grazing, are the main production activities in cork oak woodlands. In the last decades, the sowing of permanent pastures in the understory of cork oak woodlands increased, sometimes by replacing natural grassland species, to support livestock production (Hernández-Esteban et al., 2019). Such pastures, rich in mixtures of legume species, usually require higher management intervention, namely through shrub clearing, fertilization, and grazing management. Despite being ecosystems of high socio-economic and biodiversity conservation value (Bugalho et al., 2011a), cork oak woodlands face both over-use and land-abandonment threats. While over-use, such as overgrazing or intensive shrub clearing for

pasture establishment, limits oak regeneration, land abandonment, and consequent shrub encroachment, increases the risk of severe wildfires and the probability of oak mortality (Bugalho et al., 2011a). Promoting the sustainable management of cork oak woodlands is fundamental for assuring their conservation, and forest certification may play a key role in achieving such aims (Leal et al., 2019).

Previous studies showed that conservation zones increase the abundance of oak seedlings and the shrub understory diversity in certified cork oak woodlands (Dias et al., 2016). In conservation zones, lower intensity management includes practices such as reduction or exclusion of grazing, or decreased shrub clearing, which may promote the diversity of the shrub understory (Santana et al., 2011; Moreno et al., 2016; Oksuz et al., 2020). However, it can also reduce the diversity of herbs of the understory (e.g., Ramírez and Díaz, 2008; Bugalho et al., 2011a,b). The few studies addressing how conservation zones in certified cork oak woodlands affect plant diversity focused on shrub taxonomic diversity and cover (e.g., Dias et al., 2016), not testing for the effects on the structural and functional diversity of the shrub or the herbage understory. Moreover, the effects of conservation zones on oak regeneration may depend on several other factors (Dias et al., 2016; Lecomte et al., 2022). For example, different shrub species may facilitate or inhibit oak regeneration (Rivest et al., 2011; Perea et al., 2016; Lecomte et al., 2022). Shrubs can facilitate oak regeneration by protecting acorns and seedlings from the predation of large herbivores, or by ameliorating micro-site conditions for seedling growth and survival (Gómez-Aparicio et al., 2004; Ramírez and Díaz, 2008; Smit et al., 2008; Plieninger et al., 2010). Conversely, shrubs can also decrease oak regeneration through increased competition or allelopathic interactions with oak seedlings (e.g., Gómez-Aparicio et al., 2004; Acácio et al., 2007, 2009). Therefore, shrub species composition and cover in conservation zones may have contrasting effects on oak regeneration success.

In the present study, our main goal was to investigate the effects of

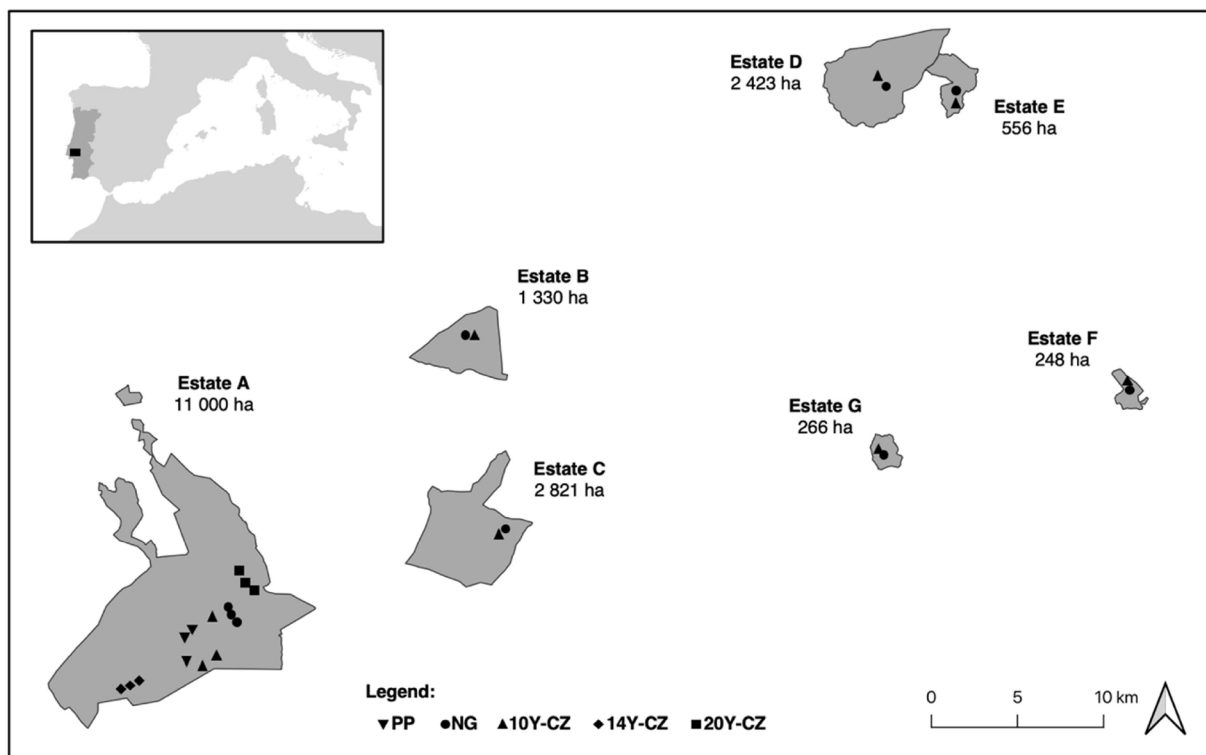


Fig. 1. Location of the study area (top left), of sampled estates (estates A to G), and estate area sizes. 10Y-CZ, 14Y-CZ, and 20Y-CZ are conservation zones established 10, 14 and 20 years before the study sampling date. 10Y-CZ occurred in all estates but 14Y-CZ and 20Y-CZ occurred only in Estate A. PP and NG are controls established in permanent pastures and natural grassland patches, respectively. Natural grassland patches occurred in all estates but permanent pastures only occurred in Estate A.

conservation zones, established under forest certification 10 years ago, on 1) oak regeneration and stand biometrics and 2) the taxonomic, functional, and structural diversity of the oak woodland shrub and herb understory. Additionally, we aim to know how 3) oak woodland regeneration and diversity responded to the increasing age of conservation zone (10, 14, and 20 years).

We expect higher oak regeneration, higher juvenile tree abundance, and an uneven oak age structure in conservation zones. We also hypothesize that shrub taxonomic, functional and structural diversity is higher in conservation zones than in control areas, with such differences increasing with the age of the conservation zones. Finally, we expect lower diversity and biomass of the herb understory in conservation zones, because of higher shrub cover in these zones.

2. Material and methods

2.1. Study sites

The study area comprised seven estates, with area sizes varying between 248 ha and 11,000 ha, located in the region of Coruche, Portugal (coordinates location: 38° 47' N; 8° 52' W to 39° 08' N; 8° 10' W). Soil and climatic conditions can display ecological gradients affecting cork oak stand dynamics (Matías et al., 2019; Moreno-Fernández et al., 2019). Therefore, we chose the study sites as homogeneous as possible by accounting for climate and soil type variation and the following factors: cork oak age and density, the density of other tree species, distance from trails or fire breaks, and slope based on data from aerial photography and field surveys. The climate in the region is the sub-humid Mediterranean, with a mean annual temperature of 16.0 °C and mean annual precipitation of 696.5 mm (1971–2000; IPMA, 2020). Soils in the region are dominantly haplic podzols (Panagos et al., 2011).

2.2. Sampling design

To investigate the effects of conservation zones, established under forest certification, on oak regeneration stand biometrics and diversity of the understory, we compared conservation zones (hereafter CZ) with control areas in each of the seven study estates. To control for the initial conditions of the study sites we collected all the information available from the estate owners and forest producers association on the management history of each estate. In six of these estates, we sampled one CZ implemented 10 years before our sampling dates (hereafter 10Y-CZ), and in the largest estate we sampled three 10Y-CZ. In this estate, the forest manager had already established conservation zones 14 and 20 years before our sampling dates (hereafter, 14Y-CZ, 20Y-CZ, respectively). These conservation zones were established before the implementation of the FSC in Portugal but followed the same forest management practices (e.g., grazing exclusion, low shrub clearing) as the FSC conservation zones. Although there is no grazing, cork harvesting and low shrub clearing (for fire prevention) may occur in conservation zones. Control plots were located the nearest as possible to each of the conservation zones. The herb understory was of two types: natural grassland species (NG) and permanent pastures (PP). While natural grassland species occurred in all estates, permanent pastures only occurred in estate A. Permanent pastures are mixtures of mainly legume nitrogen-fixing species (e.g., *Trifolium* spp, *Ornithopus* spp) sown in the understory of oak woodlands to increase plant productivity and the potential for livestock grazing of cork oak woodlands. These permanent pastures require higher management intervention (e.g., fertilization, high cattle grazing) than natural grassland species of the understory (Hernández-Esteban et al., 2019). We sampled the 10-, 14- and 20-year conservation zones (10Y-CZ, 14Y-CZ, and 20Y-CZ, respectively) established in the estate A to assess how the stand biometrics, oak regeneration, shrub and herb understory diversity varied with time since implementation of conservation zones (Fig. 1).

2.3. Field sampling

We located one circular 2500 m² plot (28.2 m radius) in the centroid of each conservation zone and controls in each estate. Six 20 m transects, 10 m apart from each other, were located in each of these circular plots.

For estimating oak tree stand biometrics, we measured the diameter at breast height (DBH) of all adult oak trees (DBH ≥ 7.5 cm) found in the 2500 m² circular plots, both in conservation zones and control areas. We used tree basal area as a proxy for tree cover.

To estimate cork oak regeneration, we counted all cork oak seedlings (height < 10 cm) and saplings (10 ≤ height < 50 cm) found in ten 1 m² square plots, established at 1 m intervals along each of the 20 m length transects (overall, sixty 1 m² plots in each CZ and paired controls). We also counted all young oak trees (DBH < 7.5 cm and height ≥ 50 cm) within the 2500 m² circular plots and classified these oak trees into two height classes: 50–150 cm and taller than 150 cm.

We estimated shrub cover and diversity with the line-intercept method (Canfield, 1941), by measuring the canopy projection of each shrub species along each line transect, also recording shrub species height.

As shrub fruits are a valuable source of food for wildlife (e.g., Herrera, 1984, 1989; Pereira et al., 2014), we classified shrub species into four functional groups according to fruit type: acorn (e.g., *Quercus cocifera* L., *Quercus lusitanica* Lam.), fleshy (e.g., *Arbutus unedo* L., *Myrtus communis* L.), legume (e.g., *Ulex australis* (Planch.) Esp.Santo, Cubas, Louã, C.Pardo & J.C.C, *Genista triacanthos* Brot.), and “other fruit” shrubs (e.g., capsules or small dry fruits; e.g., *Cistus salvifolius* L., *Lavandula stoechas* L.; Castroviejo, 2012).

All these measurements were conducted in 2018.

Additionally, in estate A, we recorded the herb species occurring in the understory of CZs and controls. For this purpose, we used the point-intercept method (Goodall, 1953), by placing a rod every 50 cm along each of the 20 m transects used in the shrub monitoring (see above) and by recording the frequency of touches of the rod in each herb species, which we grouped into grasses, legumes and forbs.

We measured the species composition and cover of the herb understory in the Spring of 2018 and 2019.

2.4. Tree size, plant species and habitat structural diversity

To estimate adult tree stand heterogeneity, as well as shrub vertical and horizontal diversity, we used an adaptation of the diversity Shannon-Wiener index (Magurran, 2013) as follows. To estimate adult tree size heterogeneity, we replaced tree species abundance in the Shannon-Weaver diversity index by DBH class (Plieninger et al., 2010) and classified trees according to the following DBH classes: 7.5–15 cm, 15.1–22.5 cm, 22.6–30 cm, 30.1–37.5 cm, 37.6–45 cm, larger than 45 cm. For estimating shrub vertical diversity, we replaced species abundances in the Shannon-Weaver diversity index by cover per height class. We divided shrub height classes as: less than 50 cm, 51–100 cm, 101–150 cm, 151–200 cm, 201–400 cm, and above 400 cm. In the case of shrub horizontal diversity, we replaced species abundance in the index by the number of shrub patches per length size class. We considered as a shrub patch, the length of the shrub canopy projection measured uninterrupted along each of the 20 m transects, regardless of shrub species. Patches of shrubs were classified according to their length into the following length classes: 1–20 cm, 21–50 cm, 51–100 cm, 101–200 cm, 201–400 cm, and larger than 400 cm.

We estimated understory taxonomic diversity using the Simpson's diversity index (Magurran, 2013). For assessing the dissimilarity of plant communities between CZ and control areas, we used the Bray-Curtis distance index (Magurran, 2013).

2.5. Statistical analysis

The study area, where the seven estates are located, has no evident

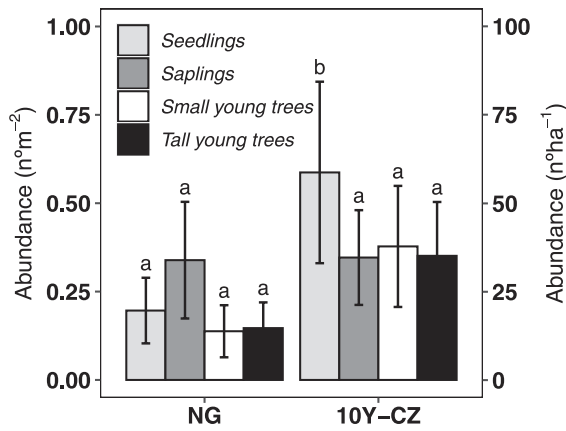


Fig. 2. Oak regeneration in 10-year-old conservation zones (10Y-CZ) and natural grassland (NG) controls (mean ± SEM). Number of oak seedlings (height < 10 cm) and saplings (10 ≤ height < 50 cm) per m² (left y-axis; n = 108); abundance of young trees (DBH < 7.5 cm; number of individuals per ha (right y-axis; n = 18) by height classes (50 ≤ height < 130 cm – small young trees, height ≥ 130 cm – tall young trees). Different letters represent significant differences between sites (Table A.1).

climatic or edaphic gradients. Moreover, we tested the effect of treatments (CZs and controls) using linear mixed models, including the estate as a random factor (Jiang, 2007). For the tested variables, the estate effect as a random factor was not significant, so we chose to keep the most parsimonious models without the estate as a random factor.

We compared oak stand biometrics (basal area and DBH diversity) and shrub species richness between CZ and control areas with the Welch’s *t*-test (Ruxton, 2006). When data did not meet assumptions of normal distributions, even after transformation, we used non-parametric tests.

For comparing effects of CZ age on oak stand biometrics (basal area, DBH diversity), regeneration (small tree abundance), understory diversity (shrub and herb Simpson’s diversity index and species richness) and structure (shrub vertical diversity, cover of herb species), we used one-way ANOVA, followed by Tukey’s test post-hoc for testing for individual differences between ages of CZ (Zar, 2010). To compare oak regeneration (abundance of oak seedlings and saplings), shrub richness, shrub structure (horizontal diversity, cover of functional groups) and herb cover among CZ ages, we used the Kruskal-Wallis test, followed by Dunn’s test for multiple post-hoc comparisons (Zar, 2010).

We used linear regression analysis to investigate the relationship between age of CZ with the diversity and cover of the shrub and herb understory.

Finally, to assess which shrubs species were positively or negatively associated with the abundance of oak seedlings, we related oak regeneration with the cover of shrub species by using the Spearman’s Rank correlation, for shrub species present in at least 80% of the plots. A positive or negative association between shrub cover and abundance of oak seedlings may indicate potential facilitation or competition, respectively, of shrubs with oak seedlings (e.g., Gómez-Aparicio et al., 2004; Acácio et al., 2007).

All statistical analyses were performed in R version 4.1.0 (R Core Team, 2021), using the Vegan package (Oksanen et al., 2018) to estimate the Simpson’s, Shannon-Wiener, and Bray-Curtis indexes.

3. Results

3.1. Effects of 10-year-old conservation zones

3.1.1. Oak regeneration and stand biometrics

We did not find significant differences between 10Y-CZ and NG controls in adult oak basal area (10Y-CZ = 11.8 ± 1.2 m² ha⁻¹ vs NG

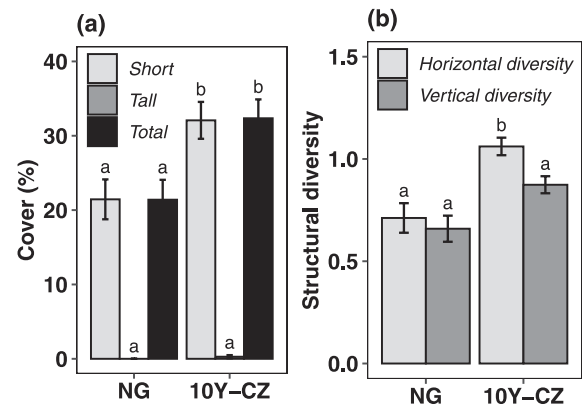


Fig. 3. Cover of short (height ≤ 200 cm) and tall (height > 200 cm) shrubs and shrub structural diversity in 10-year-old conservation zones (10Y-CZ) and natural grassland (NG) controls: a) total shrub cover (%) and cover by height; b) shrub horizontal and vertical diversity. Different letters represent significant differences between 10Y-CZ and NG controls (Table A.1).

controls = 12.8 ± 0.7 m² ha⁻¹; *t* (12.997) = - 0.672, *p* = 0.514) nor in DBH diversity (10Y-CZ = 1.6 ± 0.1 vs NG controls = 1.4 ± 0.1, *t* (14.384) = 1.480, *p* = 0.160).

The abundance of oak seedlings was significantly higher in 10Y-CZ than in NG controls (*W* = 1782.5, *p* = 0.034) (Fig. 2). Although the abundances of younger oak trees (saplings, small and tall young trees) tended to be higher in 10Y-CZ than in NG controls, such differences were not significant (Fig. 2).

3.1.2. Shrub understory

We identified 35 shrub species in total, of which 33 species in 10Y-CZ and 22 species in NG control areas (Supporting Information Table A.2). Shrub species richness and Simpson’s diversity index did not differ significantly between 10Y-CZ and NG controls (*t* (15.018) = 1.457, *p* = 0.166 and *W* = 41, *p* = 0.965 for species richness and Simpson’s diversity index, respectively; Table A.3). There was 61% dissimilarity in shrub species composition between 10Y-CZ and NG controls (Table A.4), and total shrub cover was significantly higher in 10Y-CZ than in NG control plots (*W* = 1956.5, *p* = 0.002; Fig. 3-a). Tall shrubs (taller than 200 cm) were almost absent from the 10Y-CZ and NG controls, and the cover of short shrubs (shorter than 200 cm) was significantly higher in 10Y-CZ (*W* = 1961.5, *p* = 0.002; Fig. 3-a).

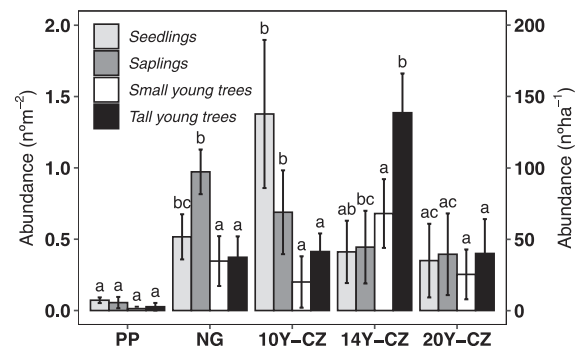


Fig. 4. Oak regeneration in conservation zones (CZ) of different ages, permanent pastures (PP) controls and natural grasslands species (NG) controls (mean SEM). Oak regeneration is shown as abundance (number of individuals m⁻²; left y-axis; n = 108) of seedlings (height < 10 cm) and saplings (10 cm ≤ height < 50 cm); abundance of young trees (DBH < 7.5 cm; number of individuals ha⁻¹; right y-axis; n = 18) by height classes (50 ≤ height < 130 cm – small young trees, height ≥ 130 cm – tall young trees). 10Y, 14Y and 20Y are 10-, 14- and 20-year-old CZ, respectively. Different letters represent significant differences between sites (Table A.1).

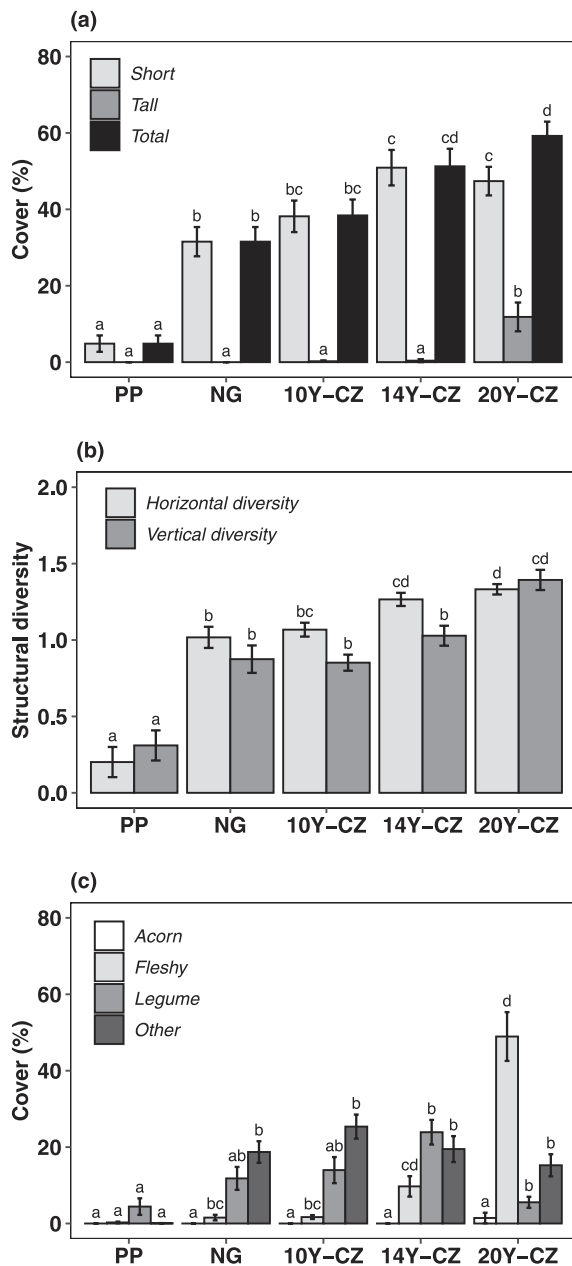


Fig. 5. Structural and functional diversity of the shrub understory in conservation zones (CZ) of different ages, permanent pastures (PP) controls and natural grasslands species (NG) controls: a) total shrub cover (%) and cover by height classes (short shrubs: $h \leq 200$ cm, tall shrubs: $h > 200$ cm); b) shrub horizontal and vertical diversity; c) shrub functional diversity (shrub cover %) by type of fruit: acorn, fleshy, legume, other fruits (mean \pm SEM; $n = 90$). 10Y, 14Y and 20Y are 10-, 14- and 20-year-old CZ, respectively. Different letters represent significant differences between sites (Table A.1).

Shrub horizontal diversity was significantly higher ($W = 1990$, $p = 0.001$), and shrub vertical diversity tended to be higher ($W = 1758$, $p = 0.065$), in 10Y-CZ than in NG controls (Fig. 3-b). There were no differences in shrub functional groups between 10Y-CZ and NG controls.

3.2. Effects of age of conservation zones

3.2.1. Oak regeneration and stand biometrics

The effect of age of conservation zones (10Y-, 14Y-, 20Y-CZ) was only assessed in estate A (see methods). Oak basal area did not vary between sites ($F_{(4, 10)} = 1.309$, $p = 0.331$), ranging from 10.4 ± 0.2 m².

ha⁻¹ in 20Y-CZ and 13.9 ± 0.6 m².ha⁻¹ in 14Y-CZ (Tables A.1 and A.5). DBH diversity was significantly lower in PP controls than in NG controls or CZ ($p < 0.01$).

There was not a consistent pattern in the variation of oak regeneration among the age of CZ. Oak seedlings and saplings abundance was highest in 10Y-CZ (significantly different from 20Y-CZ, $p < 0.05$), and tall young oaks abundance was highest in 14Y-CZ (significantly different from all other CZ ages, $p < 0.05$; Fig. 4). CZ age did not affect the abundance of small young oaks. The abundance of oak seedlings and saplings (but not of young oak trees) was significantly higher in NG controls than in PP controls ($p < 0.05$).

The abundance of all classes of oak regeneration was positively related to total shrub cover ($p < 0.05$) and cover of some individual shrub species (Table A.6). For example, there was a strong positive correlation between the abundance of all regeneration classes and the cover of *Cistus crispus* L. ($p < 0.01$), and of the abundance of oak seedlings and saplings with the cover of *C. salvifolius* ($p < 0.001$) and of *Ulex australis* ($p < 0.001$). There was also a positive association between the abundance of oak saplings and tall young oaks and the cover of *Daphne gnidium* L. ($p < 0.01$) (Table A.6).

3.2.2. Shrub understory

We found five shrub species in PP controls, 12 species in NG controls, and 14, 17, and 19 shrub species in 10Y-CZ, 14Y-CZ, and 20Y-CZ, respectively. Overall, we found a total of 26 shrub species in all sites (Supplementary Information Table A.2).

The richness of shrub species was significantly higher in 14Y-CZ than in PP controls ($p < 0.05$), but there were no significant differences between other CZ (10Y, 20Y) and NG or PP controls. Additionally, shrub Simpson's diversity index was significantly lower ($p < 0.01$) in PP controls than in NG controls and as compared to all CZ ages. Shrub species richness and Simpson's diversity index were not significantly different between CZ of different ages ($p > 0.05$; Table A.3).

The dissimilarity of shrub communities increased with age of CZ. This dissimilarity was highest at 20Y-CZ either as compared with PP controls (91 % dissimilarity) or NG controls (71 % dissimilarity) (Table A.4).

Total shrub cover increased with the age of CZ ($38.41 \pm 4.17\%$ vs. $59.23 \pm 3.72\%$ in 10Y-CZ and 20Y-CZ, respectively; $p < 0.01$) being significantly higher in 14Y-CZ and 20Y-CZ than in NG controls ($p < 0.01$) (Fig. 5-a). PP controls had a significantly lower shrub cover than NG controls, and lower than CZ of all ages ($p < 0.001$; Fig. 5-a).

The differences in shrub cover were mainly due to the contribution of the short shrubs (<200 cm). However, the cover of tall shrubs (>200 cm) was significantly higher in 20Y-CZ than in other CZ ages or controls (PP and NG) ($p < 0.001$; Fig. 5-a).

Total shrub cover, horizontal and vertical diversity increased significantly with CZ age ($p < 0.001$; Fig. 5-b and A.1). Horizontal and vertical shrub diversity was lower in PP controls than in NG controls ($p < 0.05$).

The cover of shrubs that produce acorns was not significantly different between sites ($p > 0.05$; Fig. 5-c), but that of fleshy-fruited shrubs tended to increase with the age of CZ, being significantly higher in 20Y-CZ than in the other CZ ages or controls ($p < 0.05$). Legume shrub species' cover was significantly higher in 14Y-CZ and 20Y-CZ than in PP controls ($p < 0.05$). Shrubs that produce other types of fruits (e.g., capsules) had significantly lower cover in PP controls comparing to of the other sites ($p < 0.05$).

3.2.3. Herb understory

Monitoring of the species composition and cover of herb species was conducted only in estate A. Here, we recorded an overall of 148 herb species (135 species in 2018 and 64 species in 2019) (Table A.2). The highest number of species occurred in the PP controls, with 77 and 35 species found in 2018 and 2019, respectively. The lowest number of species occurred in 14Y-CZ, with 26 and 12 species recorded in 2018 and

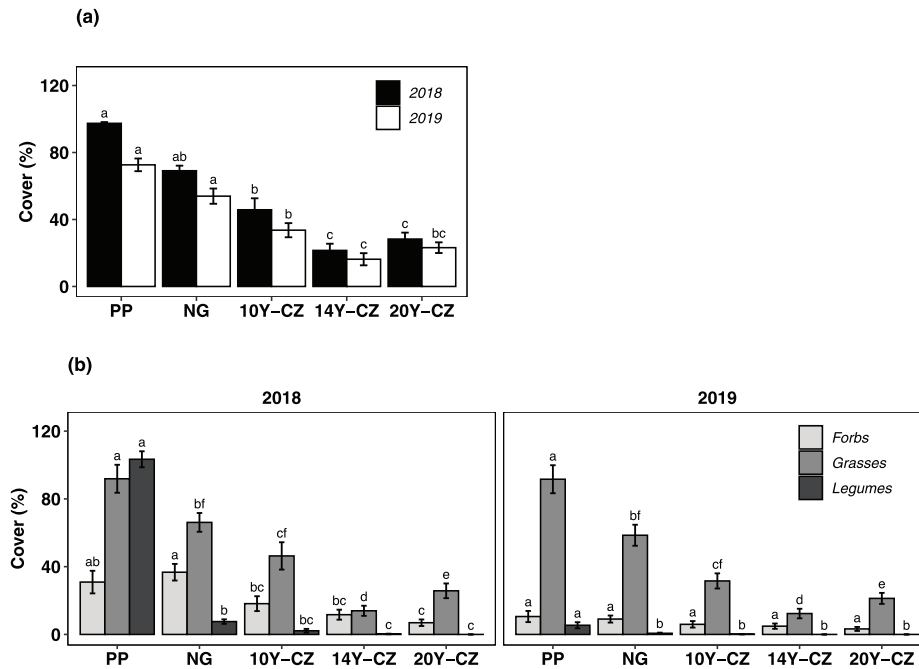


Fig. 6. Herb cover in conservation zones (CZ) of different ages (10Y, 14Y, 20Y), controls of permanent pastures species (PP) and controls of natural grasslands species (NG) in the years of 2018 and 2019: a) total herb cover, b) cover of forbs, grasses and legumes (%), mean \pm SEM, $n = 90$. Different letters represent significant differences between sites (Table A.1).

2019, respectively.

Neither species richness nor Simpson's diversity index differed between CZ and NG controls or among CZ ages in 2018 or 2019 ($p > 0.05$; Table A.1), but species richness of PP controls was significantly higher than that of 14Y-CZ in 2018 (40.0 ± 3.3 species vs. 13.0 ± 1.6 ; mean \pm SEM; $p < 0.05$).

The highest dissimilarity in herb species occurred between PP controls and 20Y-CZ in 2018 (93% dissimilarity). The dissimilarity of herb species increased with CZ age in both sampling years (Table A.4).

Cover of herb species was lower in 2019 than in 2018 and decreased with CZ age ($p < 0.001$; Fig. 6-a, and Figure A.2) but that of PP controls was significantly higher than in CZ, for all CZ ages ($p < 0.05$), both in 2018 and 2019. In NG controls, herb cover was significantly higher than that of CZ, for all CZ ages, in 2019 ($p < 0.05$) and significantly higher than 14Y-CZ and 20Y-CZ, in 2018 ($p < 0.05$).

Grasses dominated in most of CZ and controls (except for PP controls in 2018, when legumes were the dominant cover) (Fig. 6-b), but grass cover decreased significantly with the age of CZ in both years ($p < 0.05$). The age of CZ did not significantly affect the cover of forbs and legumes.

Cover of grasses, forbs, and legumes tended to be significantly higher in NG and PP controls than in CZ, with differences varying with age of conservation zone (Fig. 6-b). Additionally, the cover of grasses and legumes, but not of forbs, was significantly higher in PP controls than in NG controls ($p < 0.05$).

4. Discussion

4.1. Oak regeneration and stand biometrics

Our work suggested higher oak regeneration in CZ such as found in other studies (e.g., Dias et al., 2016), but results were not consistent among regeneration classes nor ages of CZ. Such results do not only relate with shrub cover, *per se*, but most probably with shrubs species identity. We found a positive correlation between the abundance of regeneration with shrub total cover and specific shrub species (e.g., *Cistus crispus*, *C. salvifolius* and *Ulex australis*), which may suggest facilitation processes in such cases. Facilitative or "nurse shrubs" are

important for shade, ameliorating light, heat, and water stress conditions (Gómez-Aparicio et al., 2004; Acácio et al., 2007). The lower oak regeneration in PP controls may be due to a lower protective shrub cover in these areas and higher predation by livestock (Gómez-Aparicio et al., 2004; Smit et al., 2008; Bugalho et al., 2009; Arosa et al., 2015). Livestock presence also increases soil compaction, which might impede the establishment of oak seedlings (Pausas et al., 2009). Higher herb cover and biomass, particularly in PP controls, may also induce increased competition with oak seedlings, further inhibiting oak regeneration (Pulido et al., 2010; Caldeira et al., 2014). Additionally, DBH diversity and abundance of small adult oak trees (DBHs < 22.5 cm; Supporting Information Table A.5) in PP controls was significantly lower than in NG controls and CZ which confirm the decreased oak regeneration in the PP controls (Plieninger et al., 2010).

Shrub encroachment, however, may also prevent oak regeneration (e.g., Acácio et al., 2007, 2009) if shrub species compete with seedlings for resources such as light or water. Our results showed lower oak regeneration in 20Y-CZ, suggesting that the higher tall shrubs species abundance and denser shrub cover prevented oak regeneration in 20Y-CZ compared to the younger ages of CZ. We expected an increase in young tree abundance in older CZ, assuming that the time since the establishment of CZ would increase the successful transition from seedlings to young trees. However, except for the 14Y-CZ, the abundance of young trees was similar among conservation zones. These results suggest that intermediate ages of CZ may be more favorable to promote oak regeneration than older CZ. Assessing how shrub species may vary from facilitative to competitive with the age of CZ is therefore worth investigating in the future. Moreover, oak regeneration success depends on other biotic factors (e.g., seed production, seed dispersers availability) and abiotic conditions (e.g., climatic conditions, soil, slope) (e.g., Acácio et al., 2007; Caldeira et al., 2014; Arosa et al., 2015; Simões et al., 2016). Further studies are necessary to disentangle the effects of the age of CZ and the effects of site location.

4.2. Shrub understory

Shrub diversity did not differ, in general, between CZ and control

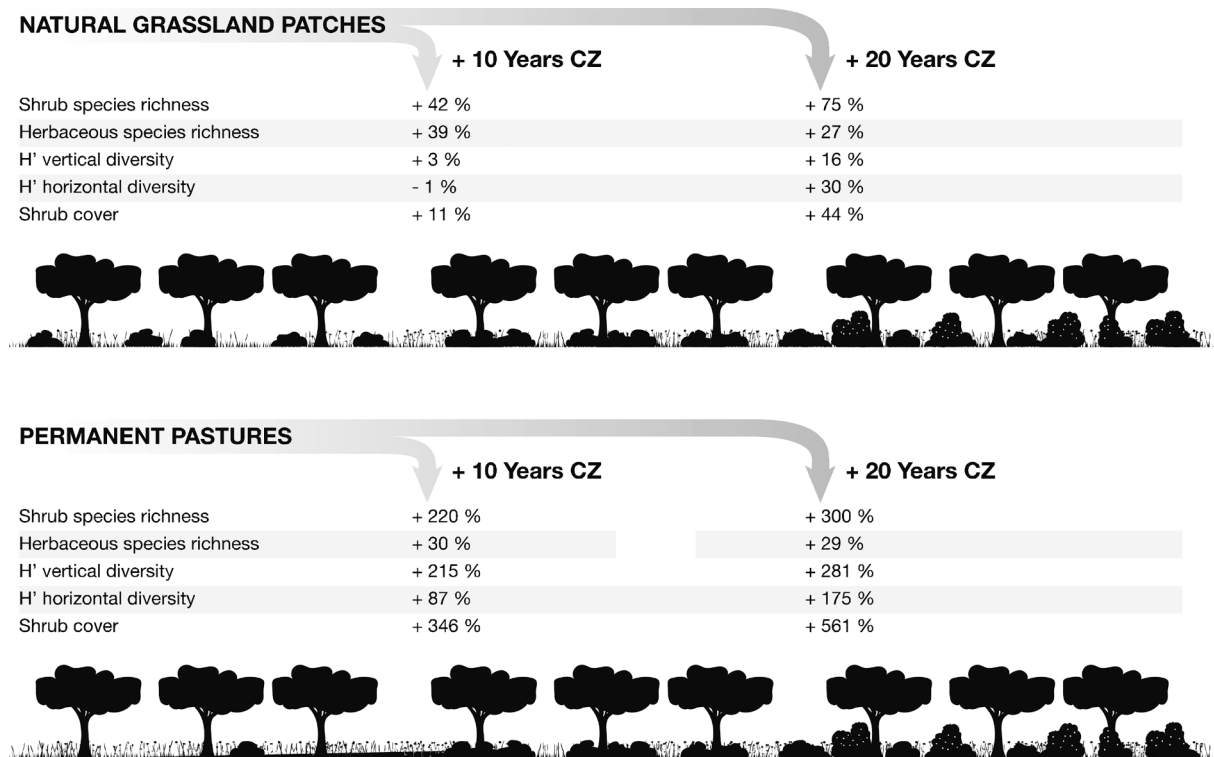


Fig. 7. Summary of the main effects of age of conservation zones (10 years CZ and 20 years CZ) on the shrub and herb species and structural diversity of the understory of cork oak woodlands. The baseline (controls) are the two most frequent understory herb management types: a) natural grasslands (NG) species or b) permanent pastures (PP). The structural diversity and cover of shrubs increased from areas dominated by natural grassland species or by permanent pastures to CZ. In PP, which have higher management intervention, responses to set aside are more obvious than in areas dominated by NG species. The positive effect of older ages of conservation zones is more evident on the richness of shrub species than on that of herb species.

areas, with a significantly higher number of shrub species recorded only in 14Y-CZ than in PP controls. Limited shrub control (i.e., regular periodicity, but locally restricted) in CZ may contribute to prevent shrub encroachment by dominant species and promote species co-existence (e.g., different light or shade-tolerant species) (Canteiro et al., 2011; Santana et al., 2011). This may result in a higher diversity of shrubs (e.g., Canteiro et al., 2011; Dias et al., 2016; Köbel et al., 2021) as observed in 14Y-CZ.

Lack of significant differences among remaining ages of CZ may relate with differences in shrub species composition between sites, but not to its overall number of species, as shown by the high dissimilarity indexes found among CZ and control plots. Pioneer shrub species (e.g., Cistaceae and Fabaceae) dominated controls and younger CZ, while late successional species (e.g., *Pistacia lentiscus* L., *Myrtus communis* L., *Phyllirea angustifolia* L., and *Arbutus unedo* L.) only occurred in older CZ, following the ecological succession transitions observed in long-term set-aside studies (e.g., Santana et al., 2011). This suggests that having CZ of different ages increases habitat heterogeneity (Peco et al., 2006; Castro et al., 2010) in certified oak woodlands.

Shrub cover became significantly higher in CZ than in controls after 10 years of the implementation of CZ, with differences increasing with time (increases of 7 % and 28 %, after 14 and 20 years of CZ implementation, respectively). Previous work on the effects of certified CZ on the understory of cork oak woodlands showed no significant differences in shrub cover after six years of CZ implementation (Dias et al., 2016). In our work, shrub cover becomes significantly higher after 10 years of CZ implementation, as found in longer-term set-aside areas (e.g., Castro and Freitas, 2009; Köbel et al., 2021).

Shrub horizontal and vertical diversity were higher in older CZ. In these areas, shrub patchiness was more diverse, and shrubs taller than 200 cm were more abundant, confirming results found in similar ecosystems (Castro and Freitas, 2009; Lecomte et al., 2019). Higher shrub

horizontal and vertical heterogeneity, in turn, can generate more ecological niches and benefit different wildlife species (e.g., Beja et al., 2007), which is a plus for wildlife conservation. Moreover, tall shrubs in older CZ were mainly late-successional species, such as *P. lentiscus*, *P. angustifolia*, and *A. unedo*, which generate fleshy fruits used for food by wildlife, namely over-wintering and fall migrant birds and mammals (Herrera, 1984, 1989; Santana et al., 2012; Pereira et al., 2014).

4.3. Herb understory

Our results confirmed the typical high plant richness found in the herb understory of cork oak woodlands (Díaz-Villa et al., 2003; Ramírez and Díaz, 2008; Bugalho et al., 2011a; Peco et al., 2012). There was a higher cover and number of herb species in controls than in CZ, as in the latter the expansion of shrub cover can outcompete herb species (Díaz-Villa et al., 2003; Castro et al., 2010). Additionally, grazing in controls may increase the plant diversity by favoring particular functional groups (e.g., annuals, prostrated species) (Pykälä, 2005; Díaz et al., 2007; Tárrega et al., 2009; Bugalho et al., 2011b; Pérez-Camacho et al., 2012). Nevertheless, some authors found the same herb species richness before and after grazing abandonment (e.g., Peco et al., 2006). The richness of herb species was only significantly higher in PP controls than in 14Y-CZ in 2018. However, the species composition dissimilarity increased with the age of CZ (as compared to controls) with a transition from dominance of annual to perennial species as found in other studies (e.g., Canteiro et al., 2011).

As expected, while the cover of shrubs increased in CZ, the cover of herb species decreased (Castro and Freitas, 2009), with lowest values in 20Y-CZ. The cover of herb species was also lower in 2019 than in 2018, most probably due to different climatic conditions between years. While precipitation and temperature in 2018 were within the average values for 1971–2000, 2019 was a drier and warmer year (IPMA, 2019), which

may have inhibited herb germination and growth (Nogueira et al., 2018). The variability in herb cover between 2018 and 2019 was lowest in 20Y-CZ and highest in PP controls, which might be related to herb species composition. Annual herb species, which are very dependent on intra- and inter-annual climatic variations (e.g., frequency of high temperatures, dry years) (Peco et al., 2006; Nogueira et al., 2018), dominated PP controls, while perennial species dominated 20Y-CZ. Perennial herb species tend to be more resilient to environmental inter-annual variability than annual species (Canteiro et al., 2011), which can explain these results. Conversely, in PP controls, legume species dominated the herbaceous cover in 2018, decreasing abruptly in the dry year of 2019, following a pattern observed in other studies addressing the variability of herb layer composition in Mediterranean areas (e.g., Nogueira et al., 2018).

4.4. Management implications

Forest certification expanding in cork oak woodlands, associated with conservation zones of different ages, can promote variability in herb and shrub species composition and habitat structure complexity, therefore contributing to biodiversity conservation (Fig. 7).

Increasing shrub cover, however, may imply trade-offs with the cover and diversity of herb species. Shrub encroachment, more likely to occur in longer-term conservation zones, may outcompete herb species decreasing plant diversity, cover, and productivity (Peco et al., 2006; Bugalho et al., 2011a). A decrease in herb cover and reduced grassland patches within the oak woodland understory may, in turn, negatively affect grassland dependent wildlife species (e.g., Palma et al., 2006; Bugalho and Abreu, 2008). Such effects can be avoided by establishing conservation zones of different ages. Conservation zones interspersed with areas dominated by herb species, can contribute to maintain the typical shrubland-grassland matrix that characterizes the understory of the oak woodland ecosystem that benefits biodiversity conservation (Bugalho et al., 2011a). Biodiversity gains resulting from establishing conservation zones must also be assessed relative to other trade-offs such as wildfires. Indeed, the higher cover of tall shrubs in older conservation zones may lead to an increased probability of severe oak canopy fires (Agee and Skinner, 2005; Bugalho et al., 2011a; Lecomte et al., 2019).

Mediterranean oak woodlands are threatened by low regeneration, adult oak mortality, and loss of canopy cover (Caldeira et al., 2014; Moreno-Fernández et al., 2019; Acácio et al., 2021). Low management intervention and reduced grazing in conservation zones can benefit oak regeneration and survival of adult oak trees (e.g., Acácio et al., 2021), which is of critical importance for the conservation of these ecosystems.

CRedit authorship contribution statement

Teresa Mexia: Methodology, Investigation, Formal analysis, Writing – original draft. **Xavier Lecomte:** Supervision, Methodology, Investigation, Writing – review & editing. **Maria Conceição Caldeira:** Supervision, Conceptualization, Methodology, Writing – review & editing. **Miguel Nuno Bugalho:** Funding acquisition, Supervision, Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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