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Soil seed bank responses to coppice management in a Mediterranean oak forest

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ABSTRACT

The soil seed bank is a key component for forest dynamic processes, but the impact of management in Mediterranean woodlands is still poorly known. We investigated the effects of coppicing in a thermophilous oak forest in Italy. Seed germination from soil cores collected in young coppice (CWS) and long abandoned (UF) stands was monitored for eight months to determine seed density, species diversity, composition and ecological characteristics (i.e. life-forms, forest guilds and Ellenberg indicator values) of the soil seed bank community. Overall, a higher number of seedlings emerged from the CWS soil, and seed density was positively affected by light. Species richness increased with soil pH, higher in CWS. Species composition significantly diverged between the two stand types. In CWS, annual generalists of open habitats and non-native invasive weeds were dominant over forest specialist species. Contrastingly, these were more represented in UF, though light-demanding and early-successional species persisted in the soil as a legacy of former disturbances. Soil seed bank communities in CWS were more similar to extant understorey vegetation than in UF (Bay-Curtis similarity 0.078, 0.017 respectively), where abandonment led to stronger floristic divergence due to habitat filtering. Coppicing increased richness and heterogeneity of the soil seed bank, providing a pathway for colonization by ruderal species and invasive weeds. Management measures that limit the input of ruderal and invasive species, maintain higher canopy cover, and reduce post-harvest soil disturbance, will help preserve the native diversity and functional integrity of the soil seed bank in Mediterranean oak forests.

1. Introduction

The soil seed bank (SSB) consists of a reservoir of viable seeds stored in the soil until environmental conditions become favourable for germination or until the propagules lose their vitality (Simpson et al., 1989). SSBs represent a key functional component of many ecosystems, influencing vegetation dynamics (Anju et al., 2022; Gurnell et al., 2006) and contributing to the maintenance and regeneration of plant communities after disturbance (Grubb and Hopkins, 1986; Parker et al., 1989; Royo and Ristau, 2013; Saatkamp et al., 2014) through storage and rescue effects (Chesson, 2000). By maintaining viable propagules over time, they allow species to persist during unfavourable conditions and re-establish when suitable conditions return, potentially preserving species that have declined or disappeared from the aboveground vegetation (Bossuyt and Honnay, 2008; Plue et al., 2010; Royo and Ristau, 2013). By storing viable propagules over time, SSBs can enhance plant community richness and facilitate the temporal coexistence of species with different ecological requirements (Chesson, 2000; Plue et al., 2012).

SSB assemblages vary along environmental and temporal gradients (Gasperini et al., 2021; Royo and Ristau, 2013; Small and McCarthy, 2010), depending on the characteristics of local aboveground communities and habitats (Bossuyt and Honnay, 2008; Larson and Suding, 2022; Leckie et al., 2000; Thompson and Grime, 1979), and the site disturbance history (Bossuyt and Hermy, 2001; Heydari et al., 2013; Plue et al., 2010). Deterministic drivers such as soil properties and light availability, together with disturbance regimes, and stochastic processes such as burial depth, regulate seed survival, germination and recruitment, and ultimately shape species-specific trait assemblages; e.g. dormancy and persistence (Bekker et al., 2003; Bossuyt and Honnay, 2008; Gasperini et al., 2021; Larson and Suding, 2022; Mašková and Poschlod, 2022; Saska et al., 2020; Small and McCarthy, 2010; Thompson et al., 1993). Analysing the functional and ecological aspects of the SSB can help to link species and strategies to environmental filters and disturbance (Larson and Suding, 2022), providing insights into their role in community dynamics under changing conditions.

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In Mediterranean forests, disturbances include natural events such as fires (Pausas et al., 2008), windstorms and drought (Lloret et al., 2009), as well as forms of forest management that strongly impacts on the structure of the stands, like coppicing (Santi et al., 2024, 2025). The latter is a traditional silvicultural practice mainly aimed at firewood production and is still extensively applied in broadleaf forests of several areas, especially in Southern Europe (Zlatanov and Lexer, 2009; Nicolescu et al., 2018). Coppicing reduces the density and cover of the forest with temporal cycles of c. 15–20 years, recurrently creating favorable microhabitats for the germination of seeds of light-demanding and disturbance-adapted plants (Duncker et al., 2012; Blandino et al., 2022, Santi et al., 2024). Light availability is a key driver of seed germination and seedling establishment of generalist species, while the denser canopy of mature forests acts as a filter reducing the proportions of these species and promoting more shade-tolerant forest specialists (Gasperini et al., 2021, 2022).

Among soil properties, soil pH and organic matter content can influence the survival of buried seeds and the recruitment of seedlings (Kůrová, 2016; Yang et al., 2021; Pakeman et al., 2012; Plue et al., 2010). Soil pH and organic matter content are in turn potentially influenced by forest management, which modifies litter inputs and decomposition processes associated with changes in canopy structure and understory vegetation (Lucas-Borja et al., 2016; Santi et al., 2024). Previous studies have shown that coppice stands tend to have higher soil pH than mature forests, likely due to the regular removal of biomass, faster decomposition and mineralization under increased light and temperature, and reduced accumulation of acidifying litter (Hölscher et al., 2001; Baeten et al., 2009). In turn, higher soil pH has been reported to promote species richness in the soil seed bank of broadleaf forests in western Europe (Brown and Oosterhuis, 1981; Staaf et al., 1987).

Disturbance can have long-lasting effects on SSBs, as changes in species composition may persist in the soil long after aboveground vegetation has shifted. Species differ markedly in their ability to persist in the soil, from short periods to decades (Roberts, 1987; Bakker et al., 1996). Following widespread abandonment from the second half of the nineteenth century onwards (Buckley., 2020, Müllerová et al., 2014; Kamp, 2022), coppicing is returning in several southern European countries for socio-economic reasons (Buckley., 2020), pointing to the need for a better understanding of its impact on several components of the soil-vegetation system. Recent studies in coppice oak forests have reported warmer and more heterogeneous microclimatic conditions, increased light availability and significant shifts in leaf traits of understorey species, compared with high forest (Santi et al., 2024, 2025). However, the effects on SSBs have been rarely considered, particularly in thermophilous deciduous forests of the Mediterranean region. Accordingly, we compared the main SSBs characteristics of productive coppice stands and abandoned stands unmanaged for decades in a *Quercus cerris* forest of central Italy. Aim of this study was to address three main research questions:

Rq1: How does forest management (active coppicing vs long-term abandonment) affect SSB density, species diversity, composition, and their functional and ecological attributes? Rq2: How do environmental variables (light availability, soil pH, and total organic matter) influence SSB density and diversity?

Rq3: How are SSB and understorey vegetation (UV) related in terms of species composition and functional characteristics under different management regimes? We hypothesized that H1 (Rq1): Active coppicing enhances SSB density and species diversity via effects on light availability, soil pH and organic matter content; H2 (Rq2): SSB species composition differ between management types, with recently coppiced stands hosting a more heterogeneous floristic pool with distinct functional and ecological characteristics; and, H3 (Rq3): Management is associated with differences in the SSB-UV relationships in terms of species composition and functional characteristics. The similarity between SSB and UV is expected to be stronger in active coppice stands due to recurrent disturbance maintaining a greater proportion of light-demanding generalist species, whereas unmanaged stands show greater divergence due to a stronger habitat filtering causing the UV to include more shade-tolerant specialists.

2. Materials and methods

2.1. Study site

This investigation was conducted in the forest of Berignone-Tatti in Tuscany, central Italy (43.347°N, 10.972°E)(Fig. 1). The area is characterised by a sub-Mediterranean bioclimate, with a mean annual temperature of 15.4 °C and mean annual precipitation of 846 mm. The forest extends over a hill system (415–534 m a.s.l.) formed by early Tortonian lacustrine deposits, mainly consisting of conglomerates and sandstones (Carmignani et al., 2004); soils deriving from this formation belong to the broad category of Cambisols. The examined stands belong to the European Environmental Agency category of "thermophilous deciduous forests" (Barbati et al., 2006) and represent different dynamic stages of the *Erico arboreae - Quercetum cerridis* association (Blasi, 2010). *Quercus cerris* (Turkey oak) is the dominant tree species, mixed with *Q. ilex, Fraxinus ornus* and other associated tree species in the subdominant layer. The shrub and herb layers are also well represented, including various woody and herbaceous species with different degrees of affinity for forest habitats. From the late Middle Ages until the second half of the 19th century, the entire forest was intensively exploited, especially for charcoal production and agro-silvopastoral activities, which often led to local degradation (Carrari et al., 2017). Based on information from the local forest administration, the area has not been affected by fire during the last 125 years (Bettini, *pers. comm.*).

Currently, part of the forest consists of privately owned stands that are still managed as coppice-with-standards. Here, the last cutting dates back to the winter 2016–2017. A large part of the forest is public, partly included in a Natura2000 site (IT5170006) and unmanaged for over 60 years for conservation purposes. Thanks to natural dynamic processes, these stands are close to the maturity stage, characterised by higher overstorey cover, density and multilayered vertical structure (Table 1). Hence, the forest consists of two management sectors (study sites) within the same continuous forest area that share similar environmental conditions and historical use, while markedly differing today in their structure due to the contrasting management types applied over the past 60 years.

2.2. Sampling design, soil collection and vegetation survey

Three plots (circular sampling areas of 10 m diameter) were randomly selected within each of the two sites under different management: the active coppice-with-standards (CWS) and the unmanaged forest close to the maturity stage (UF, Fig. 1). The six plots were at a distance of at least 100 m from a forest edge to exclude edge effects, and were separated from each other by at least 50 m to ensure spatial independence. Site conditions across the plots in terms of altitude, climate and major geomorphological features of the terrain were largely homogeneous (Table 1).

In each plot, we established four 5×5 m quadrats (25 m^2) to perform soil sampling and understorey vegetation surveys (24 quadrats in total). Soil samples were randomly collected between January and February 2024 in each quadrat. After removal of the litter layer (O horizon), 24 soil cores (4 cm diameter x 5 cm deep) per quadrat were gathered from mostly the A horizon, to obtain a total soil volume of 1.5 dm^3 per quadrat (18 dm^3 per management type) which corresponded to a total sampled surface of 0.03 m^2 per quadrat. Two additional cores (ca. 10 g) per quadrat were collected for the soil analyses. The 24 cores from each quadrat were then mixed and pooled in a single sample, resulting in a total of 13 pooled samples per management type (12 for the germination experiment and 1 for soil analyses). Once dried,

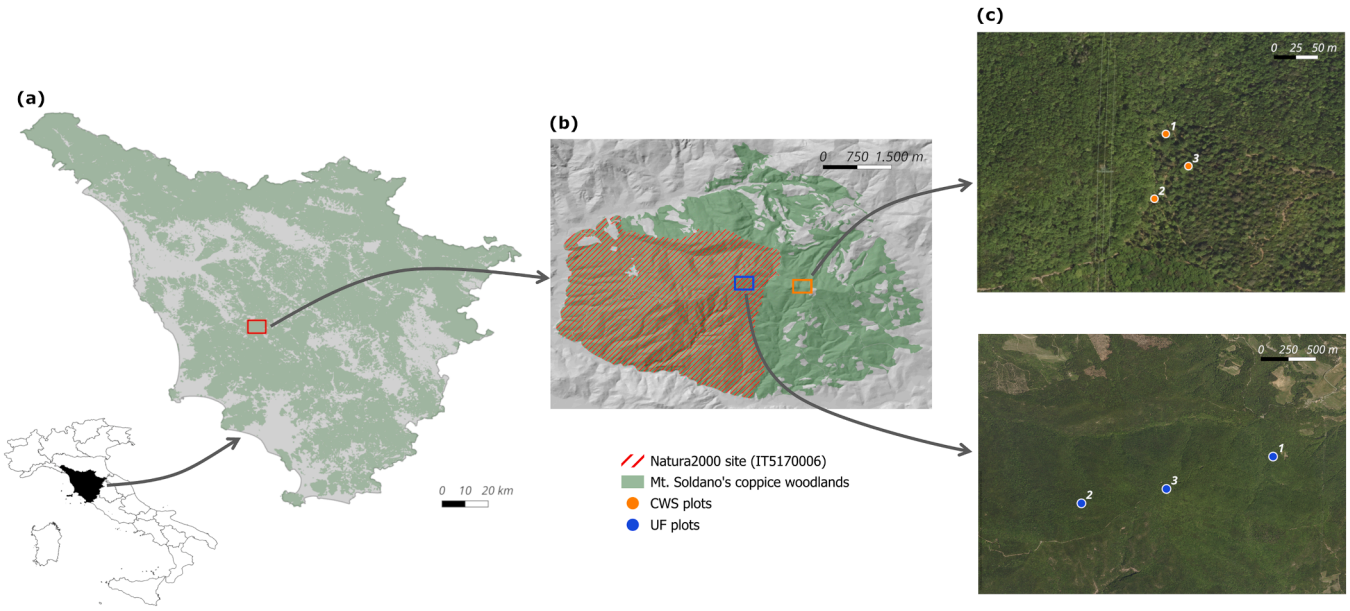

Fig. 1. Map of the two study sites located in the Tuscany region (a), representing different forest management types: coppice-with-standards (CWS; light green) and unmanaged forest (UF; red-striped) (b). The six sampling plots are also shown (three per management type), with CWS plots in orange and UF plots in blue (c).

Table 1
Location [latitude (Lat), longitude (Long), elevation (Elev)], stand [(Age, Basal area, total canopy cover (Cover), Photosynthetic Active Radiation (fPAR)] and soil [(pH; Total Organic Matter (TOM)] variables of the six study plots in the young coppice stands (CWS) and the unmanaged stands (UF). For fPAR and soil characteristics, values represent mean ± SD of 4 replicates per site.

Plot	Site location			Stand characteristics				Soil characteristics	
	Lat (°N)	Long (°E)	Elev (m a.s.l.)	Age (yrs)	Basal area (m^2 ha^{-1})	Cover (%)	fPAR (µm mol^{-2})	pH	TOM (%)
CWS1	43.3456	10.9826	482	8–10	19.8	30	0.43 ± 0.54	6.28 ± 0.29	17.5 ± 4.12
CWS2	43.3447	10.9823	470	8–10	32.7	25	0.25 ± 0.11	6.47 ± 0.57	15.5 ± 2.64
CWS3	43.3451	10.9828	480	8–10	35.3	35	0.23 ± 0.18	6.29 ± 0.14	16.2 ± 6.55
UF1	43.3516	10.9782	415	> 70	15.4	80	0.02 ± 0.01	5.96 ± 0.76	18.0 ± 8.52
UF2	43.3461	10.9545	505	> 70	8.5	90	0.02 ± 0.02	6.05 ± 0.21	17.7 ± 3.40
UF3	43.3477	10.9641	534	> 70	16.7	85	0.08 ± 0.13	6.16 ± 0.28	18.0 ± 3.74

soil samples were analysed for pH and Total Organic Matter (TOM). The soil was sieved through a 2 mm wire mesh and agitated in 25 ml of deionized water overnight using an orbital shaker. After the suspension settled, pH was measured using a benchtop pH meter (Buck et al., 2002). TOM was calculated as the weight difference of each air-dried soil sample, before and after calcination in a muffle furnace at 480 °C for 4 h, relative to the weight of the air-dried sample and expressed as a percentage.

Stand structural analyses were carried out in each plot in May 2024. The diameter at breast height (DBH) was measured for all trees > 3 cm, total vegetation cover was visually estimated to the nearest %. Light availability close to the forest floor was recorded between 12 a.m. and 14 p.m. under stable weather conditions. Photosynthetic Active Radiation (PAR, µmol m^{-2}) was measured with a FieldScout sensor (Spectrum Technologies, Aurora, IL, USA) and given as fraction of PAR (fPAR; Mõttus et al., 2013); the mean of three repeated 1-minute measurements taken at different locations inside the forest for each plot, relative to PAR measured in an open area, was used as a proxy for light conditions (following a protocol similar to Santi et al., 2025). Vegetation surveys were conducted in each quadrat of the six plots, identifying all vascular plant species and estimating their percentage of ground cover for the understorey vegetation (UV; < 1.3 m high).

2.3. Germination experiment

In February 2024, each pooled soil sample was sieved through a 5 mm wire mesh and divided into two subsamples of the same volume (a and b). Each subsample was spread as a 1 cm-thick layer in a plastic box (31 length× 24 width× 18 height cm), previously filled with approximately 11 dm^3 of sterilised potting soil. The bottom of each box was provided with holes and a thin layer of expanded clay to favour water drainage. To prevent seed contamination from external sources, the boxes were placed in a cold glasshouse in Florence (Italy). Four additional boxes with sterilised potting soil were randomly placed for contaminant species control (no contamination occurred). Daily irrigation was applied through an automated sprinkler system. Seed germination was monitored weekly for eight months (February to September 2024). At each monitoring point, we counted the seedlings that emerged from the soil and identified the species as soon as this was feasible. All seedlings were removed from the boxes after identification to reduce competition and maintain suitable conditions for germination and emergence of other seedlings in the soil. Seedlings that could not be quickly identified were transferred and grown in separate pots to allow their subsequent identification. The seedlings that died soon after emergence from the soil were included in the counts but usually not identified.

2.4. Data analysis

The number of seedlings emerging from each box (number of seedlings/0.015 m^2 of sampled surface) was used to estimate the seed density per unit area (number of seedlings/m^2) of the CWS and UF. The total number of species recorded in each quadrat was used to calculate the species density (number of species/0.03 m^2) of the CWS and UF. Because the total number of seedlings differed greatly between CWS and UF plots, we performed an individual-based rarefaction analysis to verify whether the observed richness differences were influenced by seedling abundance. This approach accounts for the large difference in total germinated seedlings between CWS and UF plots, allowing for a standardised comparison of species richness at the same number of individuals. In the understorey vegetation, species abundance in each quadrat was assessed using the Braun–Blanquet cover-abundance scale and subsequently converted to percentage for analyses. Taxonomic diversity was calculated by means of the Shannon index, using the number of seedlings as a measure of the species relative abundance for the SSB and the total plant cover for the understorey vegetation.

Linear mixed-effects models (LMMs) were then used to explore the relationship between forest management and fPAR, soil pH and total organic matter (TOM):

(1) Variable ~ Management + (1 | Plot)

Plot was included as a random effect to account for the nested sampling design and the consequent non-independence of observations within plots (four measurements per plot- one per quadrat). Results pointed to a significant positive effect of management on fPAR and soil pH, which were both higher in CWS plots (Table S1). Accordingly, linear mixed-effects models (GLMMs, LMMs) were applied to test the effect of these variables on SSB density (N_seedlings_SSB), species richness (SR_SSB), Shannon diversity (Shannon_SSB), as well as understorey vegetation ground cover (Ground cover_UV), species richness (SR_UV), and Shannon diversity (Shannon_UV) (Tables S2–S3). In addition, we tested the relationship between the two components using the ratio between the species richness in the SSB and in the understorey vegetation (SR_SSB/ UV) (Table S2). We used the R packages 'lme4' (Bates et al., 2015), 'MuMln' (Bartoń, 2025) and 'GlmmTMB' (Brooks et al., 2017). Continuous variables were scaled to allow comparison of effect sizes and to facilitate model fitting. The count data used to assess SSB density were overdispersed, hence GLMMs with a negative binomial distribution were fitted using Template Model Builder (*glmmTMB*). A Poisson distribution was used for species richness (SR) while a Gaussian distribution was applied for the other response variables:

(2) Variable ~ Management + pH + fPAR + (1 | Plot)

Plots and nested quadrats were included as random effects to account for the hierarchical design and the non-independence of observations.

In all models (1, 2), assumptions were checked by visual inspection of residuals. The lowest Akaike information criterion (AIC) and Bayesian information criterion (BIC) were used to select the best-fitting model by displaying a selection (delta AIC > 2) with the dredge function of the R package MuMin (Bartoń, 2025; Fieberg and Johnson, 2015). For each model, marginal (R^2m) and conditional (R^2c) coefficients were calculated to quantify the variance explained by fixed effects alone and by both fixed and random effects combined (Nakagawa and Schielzeth, 2013).

Next, functional and ecological characterisation of the SSB communities was based on Raunkiær life-forms (according to Pignatti, 2017), Ellenberg indicator values for light, temperature, moisture, continentality, soil reaction and nutrient content (after Pignatti et al., 2005), and the forest guilds according to Heinken et al. (2022) for the central European flora. The Raunkiær life-forms classification system groups plants based on the position of their perennating buds during the unfavorable season (phanerophyte = buds above ground; chamaephyte = buds close to the ground; hemicryptophyte = buds at soil surface; geophyte = buds below ground; therophytes = annuals).

Heinken et al. (2022) is based on 5 categories reflecting the degree of affinity to forest habitats. Categories '1.1′ and '1.2′ include specialists growing exclusively in forest interiors and species of forest edges and openings, respectively. Generalist species are included in guilds '2.1′ and '2.2′, while species of open habitats are classified as 'O'. Missing species were evaluated based on information in *Flora d'Italia* (Pignatti, 2017), our previous research (Gasperini et al., 2023; Santi et al., 2024) and personal unpublished data. For each quadrat, the relative abundance of each life-form and forest guild was calculated as the percentage of individuals belonging to that category relative to the total number of seedlings. The weighted mean Ellenberg indicator values per quadrat, based on the number of seedlings, was also calculated. Raunkiaer life-forms, forest guilds and Ellenberg indicator values were compared between CWS and UF using either *t*-tests or Mann–Whitney U tests, depending on data normality (assessed with the Shapiro–Wilk test) and homogeneity of variances (assessed with Levene's test).

Finally, species composition of the SSB and the established understorey communities in each quadrat was compared to assess the level of floristic divergence and the main associated variations in functional and ecological characteristics. The stronger the convergence, the higher the number of species whose seeds can germinate under the current forest conditions and develop into seedlings that enter the realised understorey vegetation (UV) (Hopfensperger, 2007). Analyses were based on standardized species abundances to account for the different abundance metrics used for the two layers (e.g., seedling counts for soil seed bank [SSB] and percent cover for the understorey vegetation [UV]). Differences in species composition between CWS and UF SSBs and understoreys were analysed using Non-metric Multidimensional Scaling (NMDS) based on Bray-Curtis dissimilarities among quadrats. To test the significance of overall compositional differences and among the pairwise combinations of the four groups (CWS SSB, UF SSB, CWS UV, and UF UV), PERMANOVA was applied with 9999 permutations. A betadisper test (vegan R package) was used to confirm that results were not driven by differences in data dispersion in the multivariate space (Legendre and Gallagher, 2001). Pairwise comparisons between groups were corrected for multiple testing using the Benjamini-Hochberg (FDR) procedure. Species contributing most to compositional differences were identified using *simper* function in *vegan* package (Legendre and Gallagher, 2001). All analyses were performed in R 4.4.2 (R Core Team 2023).

3. Results

3.1. Soil seed bank density and species diversity

The total number of seedlings that emerged from the soil at the end of the experiment was 2.8 times higher in CWS than in UF stands (1272 vs. 453 seedlings in total, on average 4034 ± 3839 seedlings/m^2 in the CWS and 1588 ± 1159 seedlings /m^2 in the UF). The cumulative seedling emergence graph (Fig. 2) shows that differences in seed density were maintained for the entire duration of the experiment. Based on model results, density at the quadrat level was negatively affected by UF management, though marginally ($p < 0.10$, Fig. 3a, Table S2). Density was instead positively affected by fPAR ($p < 0.05$, Fig. 2b, Table S2).

The size of the species pool in CWS was larger than in UF (60 vs. 39 species, respectively). However, rarefaction curves indicated that this apparent difference in species richness between treatments could be largely explained by differences in SSB density (Fig. S1). The UF stands showed a slightly stronger increase in species richness in the central portion of the curve. At the quadrat level, however, the difference in mean species richness (19 ± 10 vs. 12 ± 3, mean ± SD in CWS and UF, respectively) was not supported by model results, showing that neither richness nor Shannon diversity was affected by forest management

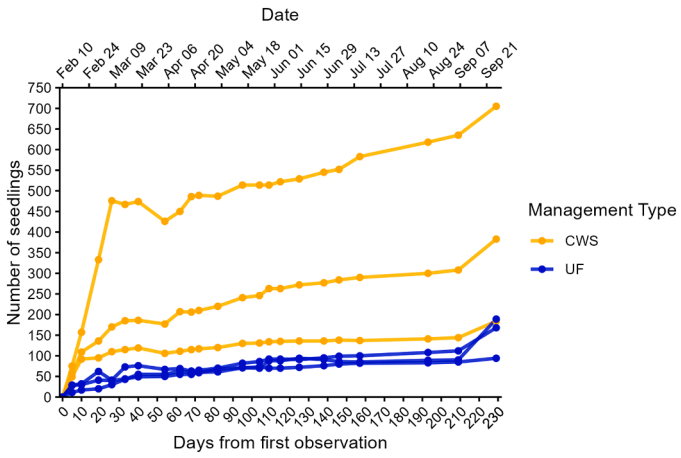

Fig. 2. Cumulative seedling emergence over time from the SSB of young coppice-with-standards (CWS, orange line) and unmanaged stands (UF, blue line) showing the average number of seedlings emerged over time across the plots. Concave sections occur when seedling mortality exceeds seedling emergence.

(Table S2). Both latter variables were instead positively affected by soil pH, with higher values in less acidic soils (Fig. 3c,e, Table S2). No effects of TOM on density and species diversity were detected (Table S2).

3.2. Soil seed bank species composition

We found significant compositional differences between management types (Table S4B) with no significant differences in multivariate dispersion (Table S4B). Most seedlings in the SSB of both stand types belonged to a few species, resulting in an uneven distribution of abundances (Fig. 4). These dominant taxa accounted for most of the compositional differences between CWS and UF (Fig. S3). In CWS, *Erigeron canadensis, Juncus bufonius* and *Erica arborea* accounted for ~61% of the total number of seedlings (Fig. 4a). These three species contributed most to the compositional dissimilarity from UF, together accounting for more than 40% of the cumulative dissimilarity (Table S5). In contrast, UF soil seed banks were more strongly associated with shade-tolerant species, including *Cardamine hirsuta*, *Moehringia pentandra* and *Luzula forsteri* (Table S5). Despite the high abundance of *Erica arborea* also in the UF stands, the SSB of UF was less strongly dominated by a few taxa, requiring ten additional species to reach 70% of cumulative abundance (Fig. 4b).

3.3. Functional and ecological characteristics of the soil seed bank

In terms of life-forms and functional groups, the SSB of the CWS stands was mainly characterised by significantly higher abundance of perennials (phanerophyt es) and short-lived winter annuals (therophytes), while the proportion in the other forms was similar (Table 2). Concerning ecological groups, forest specialists of edges and clearings (category 1.2) were more represented in the UF stands, while species of mainly open vegetation (2.2) showed a higher proportion in the CWS stands (Table 2). Moreover, Ellenberg indicator values showed that the UF stands included more shade-adapted and thermophilous species (Table 2).

3.4. Relationships between the soil seed bank and the understorey vegetation

Based on model results, all understorey vegetation variables were significantly affected by forest management. Compared with CWS, ground cover, species richness and Shannon diversity all decreased in the UF stands (Table S3). Species richness was positively related to fPAR (Table S3).

The NMDS ordination showed a clear separation among the four analysed groups, CWS-SSB, UF-SSB, CWS-UV, and UF-UV (Fig. 5). Besides forest management effect, two-way factorial PERMANOVA indicated significant differences between species pools (SSB vs UV), and

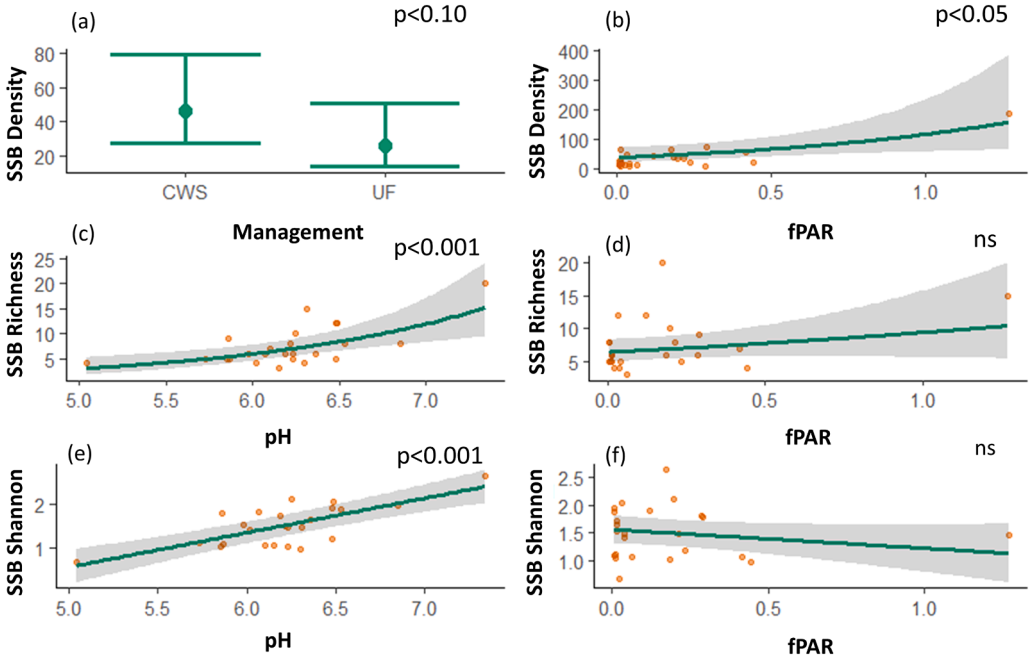

Fig. 3. Soil seed bank density (a–b), species richness (c–d), and Shannon diversity (e–f) in relation to forest management, soil pH, and light availability (fPAR). Bars and lines show model predictions for categorical (management) and continuous (pH, fPAR) predictors, respectively. Points represent observed values. The mean values of pH and fPAR (in μmol m^{-2}) were scaled for the analysis and back-transformed into the original scale for data visualisation. Shaded areas and error bars indicate 95% confidence intervals. Only predictors included in the mixed-effects models (Table S2) are shown: management and fPAR for seedling density (a, b); pH and fPAR for species richness and Shannon diversity (c, d, e, f).

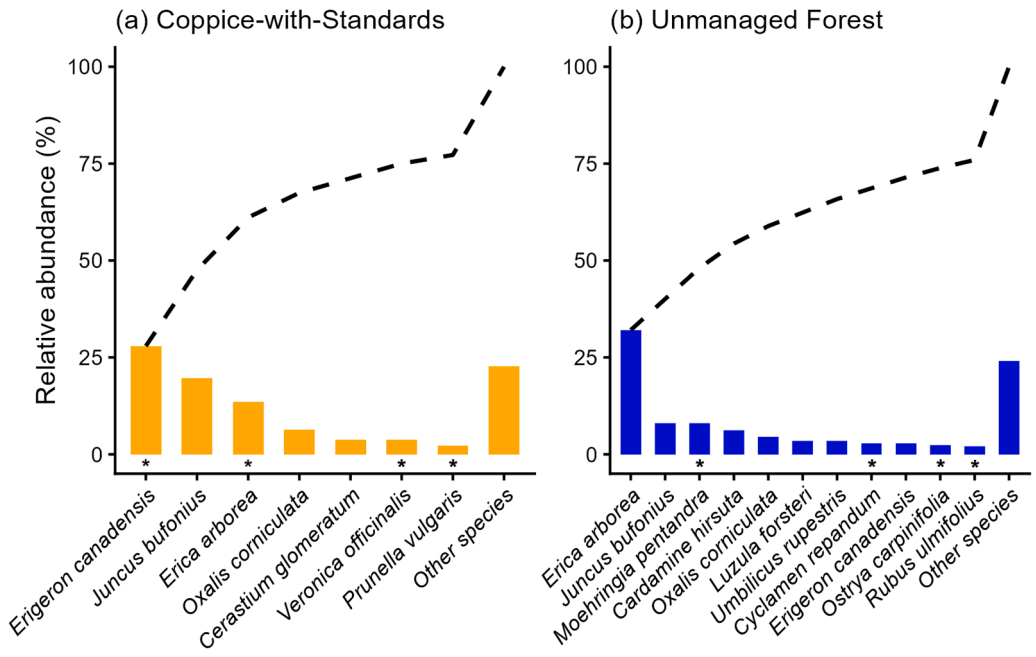

Fig. 4. Most frequent species found in the SSB of (a) the coppice-with-standards and (b) the unmanaged forest stands, expressed as percentage of the total number of seedlings identified in each stand type. The top species were selected to reach approximately 70% of total abundance. Species below a 2% abundance threshold are grouped as "Other species". The dashed line indicates the cumulative percentage, i.e. the progressive sum of each species contribution to the overall seedling abundance. Asterisks (*) indicate species present in both the soil seed bank and aboveground vegetation.

Table 2
Relative abundance of seedlings per quadrat (mean ± sd) for each life-form and forest guild; Ellenberg indicator values per quadrat (mean ± sd), weighted on seedling number. Significance of the differences between coppice (CWS) and unmanaged (UF) stands was determined using either *t*-tests (t) or Mann–Whitney U tests (U), depending on data normality (assessed with the Shapiro–Wilk test) and homogeneity of variances (assessed with Levene's test). Significance level: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Each management type is represented by 12 quadrats. Forest guilds are 1.1: forest specialists of forest interiors;1.2: species of forest edges and openings; 2.1: generalist species mainly occurring in forests but not restricted to them; 2.2: generalist species typical of open habitats but also occurring in forests; O: species of open habitat.

	CWS	UF	Sign level	Test type
Life-form				
Phanerophyte	21.3 ± 12.9	40.2 ± 23.9	*	t = 2.33
Chamaephyte	10 ± 13.3	5.4 ± 7.5	n.s.	U= 55
Hemicryptophyte	13.2 ± 10.1	12.5 ± 10.4	n.s.	t = 0.23
Geophyte	1.2 ± 2.2	7.5 ± 8.2	n.s.	U= 44.5
Therophyte	54.4 ± 17.9	34.5 ± 24.2	*	U= 34.5
Forest guild				
1.1	3.1 ± 3.1	10.4 ± 12.5	n.s.	U= 55
1.2	0.2 ± 0.4	8.7 ± 19.8	*	U= 68
2.1	23.6 ± 11.6	36 ± 23.9	n.s.	U= 55.5
2.2	50.5 ± 16.3	24.6 ± 14	***	t = 3.97
O	27.7 ± 18	20.3 ± 17.6	n.s.	U= 67
Ellenberg indicator values				
Light	6.9 ± 0.6	5.8 ± 0.6	***	U= 10,0
Temperature	6.7 ± 0.3	7.3 ± 0.3	***	t = 5.1
Continentality	4.4 ± 0.4	4.3 ± 0.5	n.s.	U= 59.5
Soil moisture	4.4 ± 0.5	4.1 ± 0.6	n.s.	t = 1.5
Soil pH	4 ± 0.6	3.4 ± 0.8	n.s.	t = 1.4
Soil nutrient content	4.6 ± 1.1	3.6 ± 1.2	n.s.	t = 1.9

significant interaction between the latter and forest management ($p < 0.001$ for all terms). *Erigeron canadensis*, *Erica arborea, Fraxinus ornus* and *Quercus ilex* accounted for 35% of dissimilarity between the SSB and the UV (Table S6). The two latter tree species contributed significantly to compositional differences between management types (Table S7). Pairwise comparisons showed that all group combinations differed significantly ($p < 0.001$, FDR-corrected, Table S4) with no significant differences in within-group variability (Table S4B). Compositional similarity between the SSB and the UV was low in both stand types, especially in the UF stands (Bray–Curtis similarity = 0.017 vs. 0.078 in the CWS stands).

In CWS stands, the floristic pool in the UV was larger than in the SSB (SSB:UV species richness ratio=0.7), whereas in the UF stands it was smaller than in the SSB (ratio = 1.3). At the quadrat level, the mean SSB: UV species richness ratio was < 1 in both stand types, but significantly lower in CWS (Table S2, Figure S2).

Annual species (therophytes) were significantly more represented in the SSB than in the established UV, in both stand types (Table 3). Hemicryptophytes showed a similar trend, though the difference was significant only for the UF stands. Phanerophytes were instead more abundant in the UV than in the SSB of both stand types. Trends in forest guild proportions were consistent in the two stand types (Table 3). In both stand types, SSBs contained significantly more taxa of open habitats (guilds O and 2.2)(Table 3). In contrast, UVs were dominated by more shade-tolerant species of forest interiors (1.1), along with taxa mostly indifferent to light conditions (2.1) or typical of forest edges and openings (1.2; Table 3).

Finally, the comparison of community-averaged Ellenberg indicator values showed that species of the SSB are more preferential of acid soils, light demanding, and with lower temperature requirements than those of the UV (Table 3).

4. Discussion

A first main finding of this study was that SSB density was positively associated with light availability (fPAR), while forest management weakly influenced this variable with lower values in UF stands

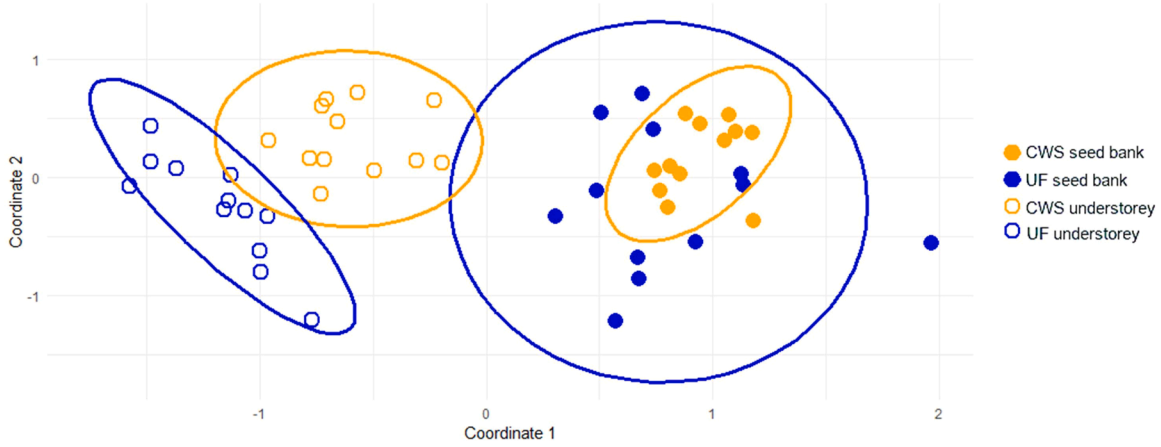

Fig. 5. Non-metric Multidimensional Scaling (NMDS) ordination based on Bray-Curtis dissimilarities among quadrats. Quadrats are grouped into: CWS soil seed bank, UF soil seed bank, CWS understorey vegetation, UF understorey vegetation. Pairwise PERMANOVA comparisons of community composition among the soil seed bank and understorey vegetation groups across forest management types (CWS and UF) and the relative homogeneity of group dispersions are shown in Table S4.

Table 3
Relative frequency of species classified into life-forms and forest guilds (average number of SSB species per quadrat ± sd vs. average number of UV species per quadrat ± sd) and Ellenberg indicator values per quadrat (mean ± sd, weighted on seedling number), calculated for the SSBs of CWS and UF. Differences between CWS and UF were tested using either *t*-tests (t) or Mann–Whitney U tests (U), depending on data normality (assessed with the Shapiro–Wilk test) and homogeneity of variances (assessed with Levene's test). Significance level: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s., non-significant. Each management type is represented by 12 quadrats. Forest guilds are 1.1: forest specialists of forest interiors;1.2: species of forest edges and openings; 2.1: generalist species mainly occurring in forests but not restricted to them; 2.2: generalist species typical of open habitats but also occurring in forests; O: species of open habitat.

	SSB CWS	UV CWS	Sign. level	Test type	SSB UF	UV UF	Sign. Level	Test type
Life-form								
Phanerophyte	16.5 ± 12.7	46.2 ± 12	***	U= 13.0	24.1 ± 14.7	84.9 ± 7.2	***	U= 0
Chamaephyte	10.1 ± 8	10.4 ± 4.8	n.s.	t = 0.1	7.6 ± 5.9	3.4 ± 5.1	n.s.	U= 41.5
Hemicryptophyte	31.7 ± 11.9	30.5 ± 9.9	n.s.	t = 0.6	19.7 ± 12.1	3.2 ± 4.7	***	U= 10.5
Geophyte	3.2 ± 4.6	9.1 ± 3.2	**	U= 21.0	9.9 ± 9.8	7 ± 4.4	n.s.	U= 62.5
Therophyte	38.5 ± 12.6	3.8 ± 4.7	***	U= 1.0	38.7 ± 17.6	1.6 ± 3.7	***	U= 2.0
Forest guild								
1.1	5.5 ± 4.6	15.8 ± 5	***	t = 5.3	10.8 ± 11.4	30.8 ± 11.2	***	t = 4.4
1.2	5.8 ± 7.9	14.1 ± 5.4	*	U= 27.5	4.8 ± 6.2	16.8 ± 7.5	**	U= 19.0
2.1	22.6 ± 13.4	42.9 ± 7.4	***	U= 14.0	22.4 ± 15.6	51.5 ± 9.1	***	t = 5.7
2.2	49.1 ± 18.2	25.6 ± 9.1	***	t = 4.1	45.2 ± 13.1	0.9 ± 3.2	***	U= 0
O	17.1 ± 8.4	1.6 ± 2.5	***	U= 8.0	16.8 ± 11.8	0 ± 0	***	U= 6.0
Ellenberg indicator values								
Light	6.5 ± 0.5	5.8 ± 0.5	***	t = 5.2	6.2 ± 0.6	4.9 ± 0.3	***	t = 7.1
Temperature	6.4 ± 0.4	7 ± 0.3	*	t = 2.7	7.1 ± 0.2	7.5 ± 0.3	***	U= 15.0
Continentality	4.3 ± 0.2	4.6 ± 0.1	n.s.	U= 58.5	4.4 ± 0.3	4.6 ± 0.2	n.s.	U= 54.5
Soil moisture	4.1 ± 0.5	4 ± 0.2	n.s.	t = 1.8	4.2 ± 0.2	3.9 ± 0.2	**	t = 3.1
Soil pH	4.6 ± 0.5	5.6 ± 0.2	***	t = 5.2	4.8 ± 0.5	5.7 ± 0.2	***	t = 5.7
Soil nutrient content	4.4 ± 0.6	4.4 ± 0.3	n.s.	t = 1.2	4.4 ± 0.5	4.3 ± 0.3	n.s.	U= 65.5

compared with coppice stands. Species diversity was instead under the stronger control of soil pH. A second key result was that SSB species composition was significantly different between the two stand types, with associated shifts in functional and ecological characteristics. Third, the compositional similarity between the SSB and the UV was low in both stand types but lower in the UF stands, due to stronger habitat filtering.

4.1. Effects of management, light and soil conditions on SSB density and species diversity

Consistent with our first hypothesis, SSB density in young coppice stands was greater than in unmanaged forest. However, the influence of management was secondary with respect to the direct effect of light in controlling the density of the SSB. Similar evidence was recently provided by Gasperini et al. (2022), who detected a weak effect of stand structure (density and canopy cover) on the overall density of the soil seed bank of European deciduous forests, with more pronounced differences emerging between the forest edge and interior, mediated by light and soil properties such as litter quality and C:N ratio.

Concerning species richness and diversity, we found no significant direct effects of management. Based on rarefaction curves, the larger floristic pool in the CWS was likely associated with higher variation in SSB density between quadrats, compared with the UF. Increased light availability and reduced soil acidity can also explain the more heterogeneous SSB floristic composition of the coppice forest, in line with our hypothesis. These results are in line with previous studies showing that coppicing maintains higher pH than mature forests (Hölscher et al., 2001; Baeten et al., 2009) and that reduced soil acidity may be a relevant driver of soil seed bank density and diversity (Brown and Oosterhuis, 1981; Staaf et al., 1987; Wang et al., 2024). Several studies have shown that species-rich soil seed banks are a common feature of open forests and, more in general, disturbed ecosystems (Bossuyt et al., 2002; Bossuyt and Honnay, 2008; Donelan and Thompson, 1980; Gasperini

et al., 2021; Royo and Ristau, 2013; Small and McCarthy, 2010). Instead, the impoverished floristic pool in the SSB of the unmanaged forest supports that significant losses of species can occur in oak coppice stands after several decades of abandonment (Brown and Warr, 1992).

4.2. Effects on species composition and ecological characteristics

As expected from our second hypothesis, species composition of the SSB was significantly divergent between the two stand types. Differences were likely the result of the cyclic reduction of tree density and canopy cover in the coppice stands, favouring the establishment of light and temperature demanding species. This supports that the relative abundance of generalist versus specialist species in SSB of temperate forests is a strongly management-dependent parameter (Leckie et al., 2000; Olano et al., 2002; Plue et al., 2010). Generalist proliferation often increases overall SSB species richness in stands subject to disturbance (Bossuyt and Honnay, 2008; Gasperini et al., 2021). By enhancing flowering, seed production, germination and seedling establishment, coppicing promotes their cyclic replenishment of the soil seed bank (Traba et al., 2004).

Our findings show that coppicing increases the abundance of annual generalists of open habitats (category 2.2), allowing their rapid reproduction and, for some species, the formation of persistent soil seed banks. In particular, the small seeds of species with high dispersal ability can be accumulated in the soil in large amounts, remaining viable until light availability and temperature fluctuations promote dormancy break and germination (Moro et al., 2024; Murdoch and Ellis, 2000). In the present study, the SSB was in fact dominated by a few, highly fecund species of open habitats, such as *J. bufonius, E. arborea*, *O. corniculata* and *E. canadensis*. Especially, the massive presence of the former species, a North American invasive weed (Regehr and Bazzaz, 1979), may have relevant ecological consequences once established in the coppice understorey vegetation. These include alterations in soil nutrient availability, shifts in soil microbial communities (Zhang et al., 2020; Liu et al., 2025), and allelopathic suppression of co-occurring plant species (Wang et al., 2017). Moreover, our findings showed that *E. canadensis* and the cosmopolitan invasive weed *O. corniculata* (Groom et al., 2019) are able to persist in the SSB of the unmanaged stands after decades of abandonment, though with reduced density. This presence is a legacy effect of former disturbances such as intense coppicing, charcoal production or grazing by cattle, pigs or other animals in the forest, that have prompted the establishment of these species into the native community. Similarly, the abundance of *E. arborea* and *J. bufonius* in the SSB of the unmanaged stands supports that the seeds of early-successional and light-demanding species can remain viable in the forest soil for decades, as previously reported (Grime, 2006; Baskin and Baskin, 2014). Large amounts of seeds of *J. effusus* and *J. bufonius* were found in the SSB of coppice oak forests in England (Brown and Warr, 1992), and both species were reported to form dense soil seed banks in European forests, with several thousand seeds per square meter (Bossuyt et al., 2002; Decocq et al., 2004; Gasperini et al., 2022).

Notably, however, the dominance of these generalist species in the SSB of the coppice stands did not lead to the exclusion of shade-tolerant species, as observed in similar Italian oak forests (Santi et al., 2024, 2025). The occurrence of *Luzula forsteri*, *Carex sylvatica*, *Brachypodium sylvaticum*, *Moehringia pentandra* and *Viola reichenbachiana* supports that the SSB may contribute to the re-establishment of forest-specialist communities with canopy closure during the coppice cycle. Our findings show that when this type of management is interrupted or abandoned, the SSB becomes gradually richer in forest specialists (Table 3), either hemicryptophytes (those mentioned above), or shade-tolerant geophytes such as *Cyclamen repandum*.

4.3. Relationships between soil seed bank and understorey vegetation

Based on our third hypothesis, management was associated with differences in the SSB-UV relationships in terms of species composition and functional characteristics. Altogether, our findings support that the compositional divergence between the SSB and the UV tends to increase with time of free forest dynamics. This is due to differences in seed persistence among species and the ecological filtering driven by light and soil conditions that limit seed germination in the unmanaged forest. Differences in SSB and UV composition were also found in previous studies of Brown and Warr (1992) and Plue et al. (2017). As expected, however, floristic dissimilarity was stronger in the unmanaged forest due to habitat filtering, while coppicing limited it thanks to a greater proportion of generalist species in the SSB. Differences in seed persistence among species may also explain the above result. Persistent seeds are often considered an adaptation of light-demanding species to situations in which sufficiently open conditions in a forest matrix are only intermittent, caused by occasional disturbances to the vegetation cover and/or the soil (Brown and Warr, 1992). Hence, species associated with more disturbed or open environments, like coppice forests, tend to form more persistent soil seed banks (Dölle and Schmidt, 2009; Murdoch and Ellis, 2000). In contrast, shade-tolerant forest species generally form transient soil seed banks and are therefore less likely to accumulate in the soil (Bossuyt and Hermy, 2001; Pickett and McDonnell, 1989). In our study, short seed persistence may explain the absence from the SSB of the UF stands of forest specialists like *Symphytum bulbosum*, *Ilex aquifolium*, *Sorbus torminalis* and *Carpinus betulus*, despite their frequent presence in the established vegetation (Table S8). On the contrary, a notable case of long seed persistence in the UF stands was that of *Erica arborea*, which was the most abundant species in the SSB despite its total absence in the realized forest community (Table S8). *E. arborea* is in fact a shade-intolerant shrub often forming a transient seed bank in Mediterranean maquis affected by fire (Moreno et al., 2023), but able to persist in the soil of shady evergreen forests for decades (Arévalo and Fernández-Palacios, 2000).

4.4. Implications for forest management

In terms of species diversity, coppicing increases the size of the floristic pool of the SSB by enhancing the presence of generalists, while allowing the persistence of at least some forest specialists. Abandonment leads instead to a general impoverishment due to progressively stronger filtering determining unsuitable conditions for seed persistence and germination of most species. However, whether increased competition by early-successional generalists over forest specialists can lead to their rarefaction or even exclusion from the SSB of coppice stands in the long term remains unknown. Moreover, coppicing prompts the dispersal and population growth of also non-native invasive weeds (Radtke et al., 2013, Vacchiano et al., 2016) that can disrupt the soil-vegetation system and remain in the forest soil for decades (Bakker et al., 1996). This process of invasion and ruderalization can seriously undermine the forest native biodiversity and its functioning (Radtke et al., 2013; Sitzia et al., 2016; Vacchiano et al., 2016).

Management in Mediterranean oak forests would therefore take advantage from the mitigation of these effects, by either restricting coppice management to small areas not in direct contact with urbanized or agricultural land and/or adopting specific measures during and after the utilisation. These may include the retention of un-harvested forest edges around the coppiced areas to physically intercept and slow down the "seed rain" of both generalist and invasive species, which are mostly wind-dispersed (Pyšek and Hulme., 2005). Besides, maintaining a higher canopy cover through the retention of standard trees in clusters rather than as isolated individuals, along with the adoption of longer utilization cycles, could support native forest specialists. Finally, reducing as much as possible the mechanical disturbance to soil after the utilisation would help to maintain suitable conditions for these species (Venanzi et al., 2020). Together, these measures may contrast the process of ruderalization of the SSB in coppice forests.

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CRediT authorship contribution statement

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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.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123912.

Data availability

Research Link Provided

Supporting data to the paper "Soil seed bank responses to coppice management in a Mediterranean oak forest" (Figshare)

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