



Impact of coppicing on microclimate and understorey vegetation diversity in an ancient Mediterranean oak forest

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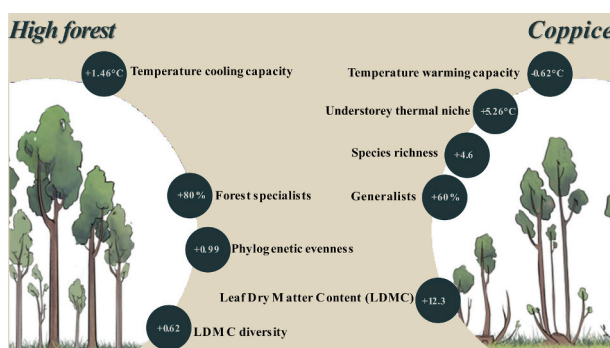
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HIGHLIGHTS

- Impact of coppicing on oak forest microclimate and understorey was analyzed.
- Temperature buffering capacity was reduced, compared to high forest.
- Understorey species richness was increased, but many forest specialists were lost.
- Phylogenetic evenness was reduced by habitat filtering processes.
- Leaf Dry Matter Content was enhanced.

GRAPHICAL ABSTRACT



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ABSTRACT

Coppicing is one of the oldest silvicultural practices and is still widely applied to produce renewable energy from broadleaf forests. However, the consequences on microclimate and understorey vegetation are still poorly understood, especially in Mediterranean oak forests. With the ongoing changes in the climate system and global biodiversity loss, a better understanding of how the forest temperature buffering capacity and below-canopy plant community are impacted by coppicing is crucial. Here we quantify microclimate and understorey vegetation changes in adjacent ancient coppice-with-standards and high forest stands dominated by oaks in Italy, where these systems have been applied for a long time. Air and soil temperatures were recorded for 2.5 years, and nested vegetation plots were used to analyse coppicing effects on species composition, taxonomic, phylogenetic, and functional diversity. Coppicing significantly reduced the forest temperature buffering capacity. The mean of the daily maximum temperatures over the entire period was 1.45 °C higher in the coppiced sites, whereas the mean of the daily minimum temperatures was 0.62 °C lower than in the high forest. Coppicing increased understorey species richness by favouring generalist taxa, but significantly decreased the proportion of forest specialists. The understorey community in coppiced forests consisted of more warm-adapted species. Moreover, coppicing also led to a loss of phylogenetic evenness and to shifts in diversity and community weighted mean Leaf Dry Matter content, pointing to habitat filtering and acclimation processes. In sum, we show

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that coppicing affects microclimate and understory vegetation in a direction that can exacerbate the effects of climate change, negatively affecting the oak forest specialist flora and its phylogenetic evenness.

1. Introduction

Forest coppicing is one of the oldest forms of land use, adopted since at least the early Middle Age, to obtain regular supplies of firewood and charcoal as a source of energy, material for building, fencing, tan-bark, turnery and crafts (Hamer, 1995). In many regions, coppicing is applied as part of traditional agro-silvo-pastoral systems and contributes to create “cultural forest landscapes” (Muys et al., 2022). Coppicing was abandoned approximately after World War 2 in most northern and central European countries but is still widely applied in Mediterranean and South-Eastern Europe (Zlatanov and Lexer, 2009; Nicolescu et al., 2018; Strimbu and Nicolescu, 2023). In Italy, 42.3 % of the total forest surface is managed as coppice-with-standards (Gasperini et al., 2022; Chelli et al., 2023). Mainly due to the energy-related problems caused by the current socio-economic circumstances, coppice management is today widely returning as a sustainable way to produce renewable energy and biomass from woodlands (Slach et al., 2021). Together with other sustainable energy sources such as wind, solar or hydro power, biomasses are considered essential to substitute climate-impacting fossil fuels (Amjith and Bavanish, 2022).

Coppice forests are formed by various species of broadleaved trees that are cut at regular time intervals (usually every 10 to 30 years), leading to cycles of vegetative regeneration by means of sprouting or suckering from the tree stumps. This practice creates an artificial disturbance regime of medium to high intensity (Duncker et al., 2012), with similarities to canopy gap formation by natural events (e.g. wind damage), but with higher frequency and on shorter time scales (Joys et al., 2004). Despite its broad use, the short and long-term consequences of this disturbance regime on ecosystem functioning and biodiversity of oak-dominated forests of the Mediterranean region are still not well understood.

One major effect of coppicing is expected on microclimate buffering, since this is significantly affected by the forest structure, density and canopy cover of the stands, via modifications of albedo, evapotranspiration, air turbulence and radiation absorption (Ehbrecht et al., 2017; Greiser et al., 2018; Davis et al., 2019). Alteration of stand structure due to management can influence various aspects of the below-canopy microclimate, with cascading effects on associated biodiversity and ecosystem processes (Davis et al., 2019; Christiansen et al., 2022; Sanczuk et al., 2023). This is a major issue in the present era of climate warming (Kempainen et al., 2023). According to Senf and Seidl (2020), natural and anthropogenic disturbances causing widespread canopy opening will accelerate and amplify the effects of climate change on forest biodiversity through their impact on microclimates. Because of this, Selva et al. (2020) argued that forest management policies should aim at reducing the rate of forest degradation by tree harvesting, and support biomass-rich forests with closed canopies. Based on current knowledge, when canopy cover drops below c. 75 % the degree to which forest microclimates and biodiversity will be buffered from climatic extremes is in fact severely reduced (Zellweger et al., 2019; De Frenne et al., 2021). This becomes crucial in the Mediterranean countries, where it is expected that temperatures will warm by 0.9–5.6 °C, compared with the last decades of the 20th century, by the end of 2100, and there will be an increasing frequency and intensity of heatwaves and drought spells (Ali et al., 2022).

To mitigate the impact of these events on woodlands (see Pollastrini et al., 2019; Iacopetti et al., 2021; Peñuelas and Sardans, 2021; Bussotti et al., 2023), policymakers and forest administrators in the Mediterranean countries should be informed about the consequences of silvicultural practices that cause a drastic and repeated reduction of canopy cover, tree stock and structural complexity of the stands, such as

coppicing.

Coppicing also suddenly alters the sunlight regime at the forest floor, which is the other key factor determining rapid effects on the herb layer (Gilliam, 2007; De Frenne et al., 2015; Valladares et al., 2016; Landuyt et al., 2019; De Pauw et al., 2021). Changes in resource availability usually activate dynamic processes and interspecific competition in the understory community, resulting in directional shifts in its diversity, composition, and functional profile (Barbier et al., 2008). In temperate forests, the understory layer is a key reservoir of the forest plant diversity, harbouring on average 80 % of the total plant species richness (Gilliam, 2007; Landuyt et al., 2019). Understanding and predicting the responses of this layer to disturbances is thus crucial to adapt management and support the conservation of forest diversity. In Europe, however, the effects of coppicing on understory vegetation at different timescales are still unclear and based on studies in mesophilous oak forests of Central Europe (Decocq et al., 2004; Baeten et al., 2009), or in mountain beech forests of the Apennines (Bartha, 2008; Campetella et al., 2016; Cervellini et al., 2017; Bricca et al., 2020; Chelli et al., 2023). On the other hand, investigations in thermophilous oak forests of the Mediterranean region focused on the interaction between coppicing and grazing (Debussche et al., 2001; Ainalis et al., 2010). Moreover, most of the studies above focused on single aspects of diversity, while multifaceted approaches are still scarcely implemented in forest ecosystems (Ottaviani et al., 2019). Taxonomic diversity, often measured as species richness, is the most studied side of diversity, although it ignores community evolutionary history and ecosystem functioning, namely phylogenetic and functional diversity (Jarzyna and Jetz, 2016). The former is considered as a “deep” component of diversity that can affect ecosystem processes (Srivastava et al., 2012), services (Faith et al., 2010) and stability (Cadotte et al., 2012). Preserving and maximising phylogenetic diversity of communities is a major goal in conservation biology, since this may enhance stability under changing habitat conditions across evolutionary time scales (Rodrigues and Gaston, 2002; Coppi et al., 2019). Functional diversity is a fundamental determinant of ecological processes, influencing ecosystem dynamics, stability, productivity, nutrient balance and other processes (Tilman, 2001). Examining ecosystem responses to habitat changes and disturbances should always consider the multifaceted nature of biodiversity because facets can be affected in different ways (De Pauw et al., 2021). In temperate forests, for example, understory species richness is usually positively affected by light availability at the forest floor (Suding, 2001; Hamřík et al., 2023), while harsher environmental conditions may lead to a reduction of phylogenetic and functional diversity (Ottaviani et al., 2019; Lanta et al., 2023). Overall, we know little on how coppicing in thermophilous deciduous forests impacts on these understory diversity facets, despite the extent of this forest type in Europe (40 % of the ICP Forests Level I plots in Italy; International Cooperative Programme on Assessment and Monitoring of Air Pollution Effects on Forests; Barbati et al., 2007), its rich flora and vulnerability to increasing heat and drought (Pollastrini et al., 2019; Iacopetti et al., 2021). This hampers the adoption of strategies and policies for the conservation of their biodiversity and functional integrity in the face of climate change.

Here we analyse shifts in temperature buffering capacity and understory diversity in an ancient oak forest of central Italy. This represented an optimal model system because stands with coppice-with-standards and high forest are next to each other and applied for a long time and in homogeneous site conditions. For a deeper understanding of the effects of coppicing we focused on all the three major dimensions of diversity, taxonomic, phylogenetic and functional, as these often respond differently to environmental changes and ecological factors (De Pauw et al., 2021). Accounting for stand structure, light and soil

conditions, we could therefore test the following hypotheses: i) air and soil temperature buffering is lower in coppice stands because of lower canopy density; ii) coppicing positively affects understorey taxonomic diversity by increasing species richness (SR) due to a greater proportion of generalist and thermophilous plants; iii) understorey phylogenetic and functional diversity are lower in coppice stands, since more phylogenetically and functionally diverse communities commonly develop in more favourable conditions (Lanta et al., 2023).

2. Materials and methods

2.1. Study site and forest characteristics

The “Bosco ai Frati” forest is located in a plain area of central Italy (43.98 N, 11.30E, altitude 250–270 m a.s.l.), close to the city of Florence, and is included in the “Tuscan Basin” biogeographical section of the Temperate Division, according to the Italian Ecoregional classification (Blasi et al., 2014). The climate of the area is sub-mediterranean, with a mean annual temperature of 12.4 °C and 870 mm of precipitation. The geological substrate is formed by sandy-clayey alluvial deposits and lignite, from which a leached and more or less acid brown soil develops under forest cover (Cambisol). The forest is included in the EU site network of Natura2000 (ZPS, IT5140006) for its historical, cultural, and naturalistic value. It represents a characteristic example of the habitat “thermophilous deciduous forest” (type 8.2: “Turkey oak, Hungarian oak and Sessile oak forest”) according to EEA (2006), of the habitat “Northern Italian *Quercus cerris* forests” (code T1941) in the EUNIS habitat classification (EEA, 2021), and of habitat 91 M0 (“Pannonian-Balkan Turkey oak-sessile oak forests”) of the Natura 2000 system. On syntaxonomical grounds, it is representative of the association *Hieracio racemosi-Quercetum petraeae* Pedrotti et al. (order *Quercetalia pubescenti-petraeae* Klika), an acidophilous forest community typically found on fluvio-lacustrine deposits of continental valleys in central Italy (Pignatti, 1998; Blasi et al., 2010). The locally dominant and most frequent tree species are *Quercus cerris* and *Q. petraea*, usually associated with non-dominant trees as *Fraxinus ornus*, *Sorbus torminalis*, *S. domestica*, *Carpinus betulus*, *Acer campestre*, *Malus sylvestris* and others, as typical for this forest type (Carrari et al., 2016). The shrub layer is also well developed and species-rich, including *Crataegus laevigata*, *C. monogyna*, *Cornus mas*, *Euonymus europaeus*, *Pyracantha coccinea*, *Ligustrum vulgare*, *Lonicera caprifolium*, and others.

The forest has a very long temporal continuity, existing since at least the early Middle-Age thanks to the cares by the local monks and Franciscans friars: it thus represents a typical ancient forest sensu Peterken (1974), Hermy et al. (1999) and Wulf (2003). For a long time, two contrasting management approaches have been adopted, one oriented to the production of firewood and one oriented to the conservation of a more natural structure, biotic components and functional processes of the forest. The former is applied in the privately owned part, as traditional coppice-with-standards. The forest is therefore composed of sprouters of approximately the same age and standard trees, either originated from seed or tree stumps released from the previous utilizations, to support the regeneration of the forest. When the sprouters are felled at intervals of ca. 18 years, the younger standards are retained for one or two more coppice rotations, whereas most of the older ones are harvested; the standards density does not exceed 60 trees per hectare. The other part of the forest is instead managed by the local public forest administration and has been left to its natural dynamics since 1985, when it was converted from coppice-with-standards to high forest through the selection of one sprouter per stump. From that time, only minor thinning interventions were applied to the subdominant tree and shrub layers, since the management is oriented to nature conservation rather than timber production.

2.2. Sampling design and data collection

A total of six main sampling sites were established in representative parts of the coppice forest (three sites), and the high forest (three sites; details in Fig. 1a and in Appendix A, Table A.1). The two groups of sites were in the forest core and in homogeneous site conditions in terms of other environmental factors including elevation, macroclimate, fine morphology of the terrain and soil type. This allowed us to exclude major ecological factors as confounding variables and to separate the effect of forest management on the examined response variables. The three coppice sites were representative of different temporal stages of the firewood production cycle, one being young (4 years since the last cut), one intermediate (8 years) and one old (12 years). We adopted a nested sampling design with two levels, to characterise: i) forest structure and microclimate, and ii) understorey diversity and composition (Fig. 1b). In each main site we established a circular macro-plot of 13 m radius (531 m²; Gasperini et al., 2022) in which all woody plants with a diameter > 3 cm diameter at breast height (DBH) were measured to determine stem density and basal area; ground cover was visually estimated as the percentage of space occupied by the canopy of all trees and shrubs >1.3 m high (values of basal area, stem density and ground cover per macroplot are available in Appendix A, Table A.1).

For microclimate, we followed the protocol of Meeussen et al. (2021). In May 2020, two temperature loggers (USB Lascar EasyLog EL-USB-1, with an accuracy of ±0.5 °C between −35 to +80 °C) were installed at the centre of each macro-plot to measure air and soil temperature. The air sensor was attached to the north side of a wooden pole at 1 m above the forest floor and protected by a plastic white shield to avoid direct solar radiation on the sensor. The soil sensor was placed in a protective, transparent plastic tube and horizontally buried at 5 cm depth in the soil, next to the pole; data (°C) were continuously recorded at hourly intervals, until October 1, 2023. In total, 12 temperature loggers were installed.

In May and June 2022, understorey vegetation surveys were conducted in four 5 × 5 m quadrats regularly placed within each of the six macroplots, resulting in a total of 24 quadrats, 12 in coppice and 12 in high forest. In each plot, all vascular plant species below 1.3 m were recorded and scored for percentage of ground cover (Ampoorter et al., 2016). Identification and nomenclature were based on Pignatti (2017–2019) and Euro+Med Plant Base (<https://euoplusmed.org/>). Next, two samples of bulk soil (100 g each) were randomly collected in each quadrat at 2–10 cm depth (after removing the litter layer), for determination of soil pH-H₂O. Soil was first dried and sieved with a 2 mm mesh sieve; pH was measured on 10 g samples of mixed soil in deionized water (25 ml) (values per quadrat are available in Appendix A, Table A.12).

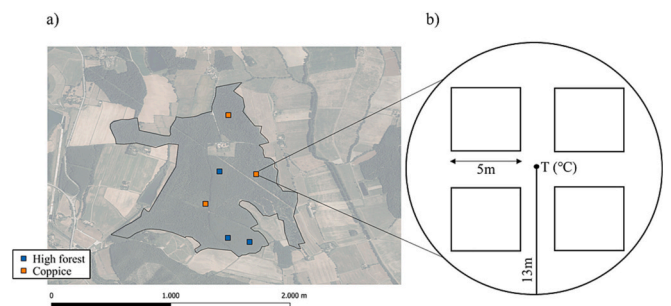


Fig. 1. a) Study area and location of the six plots in coppice and high forest; b) nested sampling design to analyse forest structure, air and soil temperature, understorey diversity and composition.

2.3. Data analysis

2.3.1. Microclimate

Time series of temperature data from the 12 loggers were first visually checked using the EasyLogUSB software. As in Meeussen et al. (2022), biased measurements showing deviating trends or clear outliers (due to the uprooting of the sensors from the soil by animals) were removed from the dataset. Daily minima (Tmin), maxima (Tmax) and mean temperatures (Tmean) were determined to calculate the monthly averages (spring: March, April and May; summer: June, July and August; autumn: September, October and November; winter: December, January and February); the air and soil temperature dataset were available for 97.92 % and 90.93 % of the days, respectively. After that, the relationship between temperature means (Tmax, Tmean, Tmin) of each season and structural variables (BA/ha and Number of plants/ha) was tested using a linear model (temperature ~ structural variable). Analyses were performed with R software (R Core Team, 2021).

2.3.2. Site variables and understorey diversity

All analyses were performed with R version 4.2.2 software (R Core Team, 2021).

Stand structural variables (ground cover of woody layers >1.3 m, stem density, BA), soil pH were compared both by plot and type of management, using Anova test or Kruskal Wallis, and t-test or Wilcoxon, when data were normally distributed (Shapiro-Wilk test) or not, respectively (results regarding the differences between coppice and high forest of structural variables and pH are presented in Appendix A, Table A.13).

Understorey taxonomic diversity and composition were examined using the data collected in the 5 × 5 m quadrats. Gamma (γ)-diversity of the coppice and high forest understorey was determined as overall species richness (SR) of the groups of plots, followed by calculation of plot-level α -diversity as SR, Shannon index (H') and Evenness (J). Variations in species composition were analyzed at the quadrat level using the Lennon distance as beta-diversity measure based on species presence/absence (Lennon et al., 2001). This metric quantifies true compositional turnover and is not influenced by richness differences among quadrats that create nestedness patterns (Ampoorter et al., 2016). Results were then visualised with non-metric multidimensional scaling using the *metaMDS* function in the Vegan R package (Oksanen et al., 2019). Differences in the position of plots of the two types (coppice and high forest) in the multivariate space were tested using a permutational analysis of variance (PERMANOVA) with 999 permutations (*Adonis* function in *Vegan*), followed by a multivariate dispersion homogeneity test using *betadisper* (Warton et al., 2012). Ellipses were drawn on the non-metric multidimensional scaling graph using the function *ordiellipse*, depending on their standard deviation. The indicator species analysis (Dufrene and Legendre, 1997) was performed (function *multipatt* in *Indicspecies* package; Cáceres and Legendre, 2009) to identify the species significantly associated with coppice and high forest in terms of frequency and cover. Ellenberg indicator values for all species in the plots (modified after Pignatti et al., 2005; light, L; temperature, T; soil humidity, H; soil reaction, R; nutrients, N) were used to infer the main ecological differences between the two groups of plots. For a more detailed analysis of the thermal shifts of the understorey community induced by coppicing, the ClimPlant database (Vangansbeke et al., 2021) was used to calculate the mean of the temperature preferences of each understorey species (retrieved from https://figshare.com/articles/dataset/ClimPlant_realized_climatic_niches_of_vascular_plants_in_European_forest_understoreys/12199628?file=38936309); thermal niche data were available for 87.34 % of the species in our dataset (10 out of 79 species were missing). Community weighted mean of annual mean and maximum temperatures were obtained using species abundance (cover percentage) in the coppice and high forest. Next, two density curves were generated to display the distribution of the average values of Tmean, Tmax and Tmin in the high

forest and in coppice quadrats. In addition, all species were assigned to the guilds of European forest plants (following Heinken et al., 2022), to detect shifts of the understorey ecological composition associated with management, focusing on forest specialists (guilds 1.1 and 1.2) vs. generalists (2.1 and 2.2 species according to Heinken et al., 2022). The relative frequency and abundance of each guild was calculated for each plot and compared in coppice vs. high forest using a Wilcoxon/t-test. A few Mediterranean species not included in the list by Heinken et al. (2022) were classified based on Pignatti et al. (2017-2019) and our expert evaluation (guilds attributed to each species are present in Appendix A, Table A.14). Next, phylogenetic diversity metrics were calculated to assess the forest management influence on the amount of evolutionary distance and phylogenetic structure of the understorey. To this purpose a phylogenetic tree (Appendix B, Fig. B.1) of all species in the pool of plots was built based on the megaphylogeny of vascular plants (PhytoPhylo) in Qian and Jin (2016), using the R package V. PhyloMaker2 (Jin and Qian, 2022). The PhytoPhylo megaphylogeny allows to generate robust phylogenies for studies of community ecology and biogeography, particularly those analysing patterns of phylogenetic variation along environmental gradients (Qian and Jin, 2016). Based on this tree, phylogenetic α -diversity (PD) was determined for each plot as the total branch length joining the basal node (i.e. the spermatophyte node) to the branch tips of all species in the plot (Faith, 1992). The correlation between PD and SR was explored with a linear mixed model, using quadrat-level data (PD ~ SR + 1|macroplot). Although this relationship is usually positive, deviations suggesting unexpected patterns can occur (Karanth et al., 2019). Phylogenetic structure was then quantified using the two indices Mean Nearest Taxon Distance (MNTD) and Mean Phylogenetic Distance (MPD), based on presence/absence data. The former describes the phylogenetic relatedness among species, focusing on the level of branch-tip phylogenetic clustering of the species in the plot, while the latter is a measure of the relationships at the higher-level groups in the phylogenetic tree (Webb et al., 2002). For the three indices above, the standardised effect size (PD.ses, MPD.ses and MNTD.ses, respectively) was used to exclude the effect of species richness and assess whether the observed value deviates from the range expected by chance. Hence, positive values of PD.ses indicate higher phylogenetic diversity than expected based on species richness; likewise, both MPD.ses and MNTD.ses point to phylogenetic dispersion when >0 or clustering when <0. To compare MPD and MNTD to null community data we used a simple null model of randomly drawing species (phylogeny branch tips), holding plot species richness constant as suggested in the Phylocom software (Webb et al., 2008; Coppi et al., 2019). All phylogenetic metrics were obtained with the package Picante (Kembel et al., 2010).

Understorey functional responses to management were tested for five traits associated with the acquisition and conservation of resources (vegetative traits) and reproductive efficiency (Garnier et al., 2015): i) Specific Leaf Area (SLA), as a proxy of potential relative growth rate and mass-based maximum photosynthetic rate; ii) Leaf Dry Matter Content (LDMC), as a proxy of resistance to stress factors, resource conservation and leaf lifespan; iii) plant vegetative height (PH), associated with competitive ability, iv) plant reproductive height (RH), as a measure of seed dispersal ability, and v) seed mass (SM), related to the ability of seeds to persist in the soil and of seedlings to establish and survive. Trait values were obtained from TRY (Kattge et al., 2020). Trait values were available for at least 84 % of the species in our dataset. For each trait and plot, we calculated the Community Weighted Mean (CWM; Garnier et al., 2004) and Rao Quadratic index of functional diversity (Rao, 1982), using the dbFD function of the "FD" package (Laliberté and Legendre, 2010; Laliberté et al., 2014). Since random variation in species richness can have spurious effects on the Rao index that might affect the results obtained (Pavoine et al., 2013), we calculated the Standardised Effect Size of the same index. Positive values of the Standardised Effect Size indicate that the Rao index (functional diversity) of the community is higher than expected under the null model. The null

model was created by randomising (with 999 permutations) the abundances of the species in each plot, holding species richness and abundance in the plot constant (Mason et al., 2008).

Linear mixed models were built to relate understorey diversity indices (taxonomic, phylogenetic, and functional) with the type of management, which was used as a fixed explanatory variable. Concerning phylogenetic and functional diversity, only standardised indices were taken into account. “Macroplot” was included as a random factor to account for the nested structure of our experimental design (quadrats within macroplots). Modelling was carried out using the *lme* function (Bates et al., 2015). Poisson distribution was used for the count data (SR), whereas Gaussian distribution was used for all the other response variables.

3. Results

3.1. Microclimate

The mean values in the daily Tmax were always significantly lower in the high forest than in the coppice stands except for the summer; despite the same trend, no significant differences were found in this season. High forest plots guaranteed a greater cooling effect (Fig. 2a). On average, the difference in Tmax cooling capacity between the high and the coppice forest was 2.37 and 0.68 °C in spring and summer, respectively; the same trend occurred in autumn and winter (respectively 1.63 and 1.37 °C greater in the high forest). The mean difference in Tmax cooling capacity between high and coppice forest across the four seasons was 1.45 °C. The cooling effect in the spring was positively related to basal area and tree density (*p*-values = 0.02). Daily Tmin mean values were significantly higher in the high than in the coppice forest only during summer, and the same trend occurred across all seasons. On average, the difference in Tmin warming capacity (higher Tmin values) was 0.65 and 0.77 °C in spring and summer, respectively; the same trend occurred in autumn and winter (0.55 and 0.44°C greater in the high forest). The mean difference in Tmin warming capacity between coppice and high forest across the four seasons was 0.62 °C (daily, monthly and seasonal averages are reported in Appendix A, Tables A.2, A.4 and A.3 respectively).

Concerning soil, seasonal differences in daily Tmax, Tmin and Tmean

between coppice and high forest were mostly non-significant and almost always greater in the high forest than in coppice (Fig. 2b, daily, monthly and seasonal averages are reported in Appendix A, Tables A.5, A.7 and A.6 respectively).

3.2. Understorey diversity and composition

Total vascular plant species richness in the 24 quadrats (79 species) was unevenly partitioned between the coppice plots (63 species, 79.75 %) and the high forest plots (55 species, 69.62 %) (the complete matrix of species presence is available in Appendix A, Tables A.8). At the plot level, differences between the two groups of plots were significant in

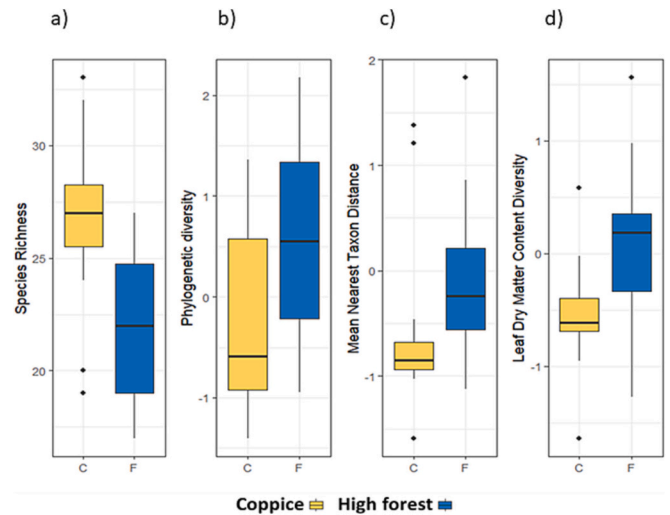


Fig. 3. Variation of selected indices of taxonomic, phylogenetic and functional diversity of the understorey in high and coppice forest quadrats; a) Species Richness; b) standardised phylogenetic diversity (PD.ses); c) standardised Mean Nearest Taxon Distance (MNTD.ses); d) standardised diversity in Leaf Dry Matter Content (Rao.ses). All indices are significantly influenced by type of management (*p* < 0.1) based on the linear mixed model ($y \sim \text{forest management} + 1 | \text{macroplot}$; see Table 4).

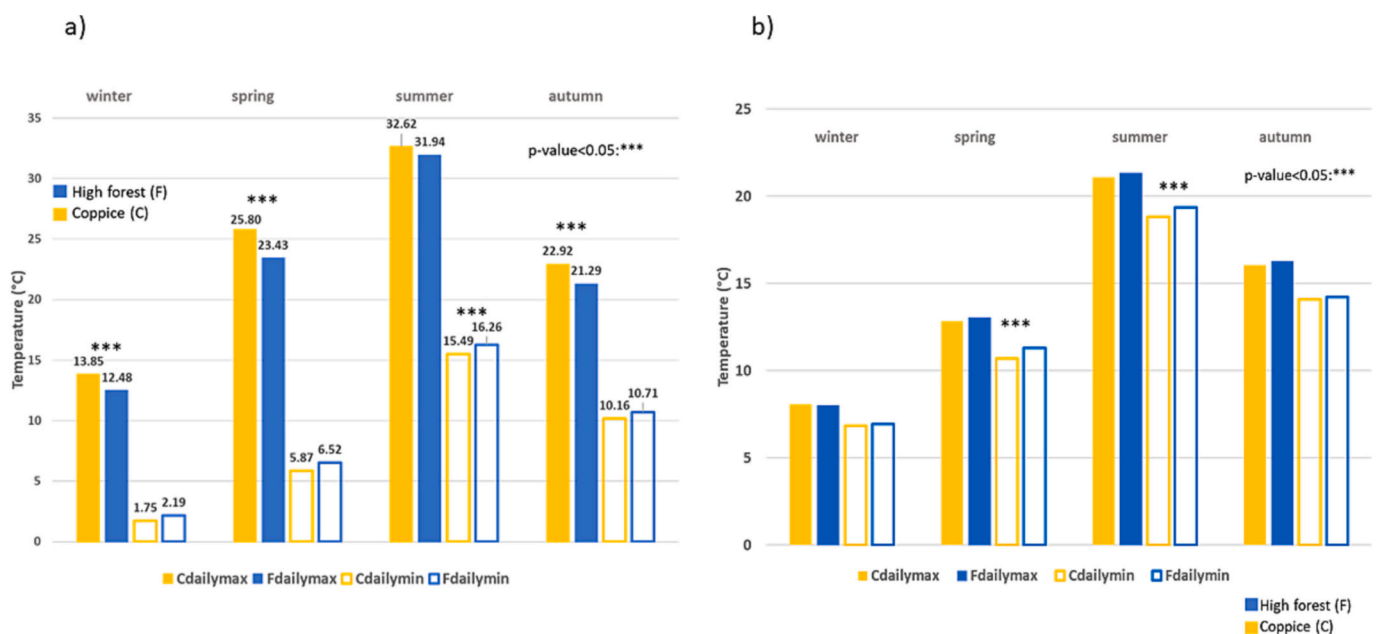


Fig. 2. a) Mean values of maximum and minimum air daily temperature (dailymax and dailymin, respectively) for each season in coppice and high forest; b) Soil daily maximum and minimum temperatures in coppice and high forest by season.

terms of mean species richness ($p < 0.01$), but not in terms of Shannon diversity and species evenness (Appendix A, Table A.10; Fig. 3). As expected, SR was higher in the coppice stands; model results confirmed this effect (Table 3, Fig. 3a).

Concerning composition, PERMANOVA results supported significant species shifts between the coppice and the high forest plots, as shown in the NMDS scattergram (Fig. 4; p -perm < 0.05 ; stress value: 0.18; Linear fit $R^2 = 0.84$; Non-metric fit $R^2 = 0.97$; p -disp = n.s.).

Based on Ellenberg values, the coppice understorey showed a more light-demanding (mean L = 5.75 ± 0.47 vs. 5.17 ± 0.49 in the high forest, $p < 0.01$) and acidophilous character ($R = 3.45 \pm 0.59$ vs. 4.41 ± 0.48 , $p < 0.001$). Analysis performed with the ClimPlant data revealed an increased proportion of species with higher T values in the coppice sites, pointing to a shift towards a more thermophilous understorey. Specifically, the Tmean and Tmax and Tmin values of the community thermal niche were higher in the coppice (Fig. 5), although only T mean was significantly different (Tmean = 19.07 ± 8.13 , vs. 13.81 ± 4.39 in high forest, $p = 0.06$; Tmax = 23.43 ± 6.86 in coppice vs. 19.93 ± 6.2 in high forest, p -value: n.s.; Tmin = 7.76 ± 2.38 in coppice vs. 6.81 ± 2.29 in the high forest, p -value: n.s.).

Indicator species were more numerous in coppice than in high forest plots (Table 1) and included light demanding shrubs such as *Rubus ulmifolius* and *Genista pilosa*, vs. shade tolerant herbs such *Anemone nemorosa* and *Physospermum cornubiense* in the high forest plots. In addition, the two management forms clearly influenced the ecological composition of the understorey, in terms of forest categories (Table 2). While forest specialists (category 1.1) were significantly more represented in the high forest plots, the coppice understorey included a higher proportion of taxa typical of edges and openings (1.2) as well a higher frequency of generalists of mainly open vegetation (2.2).

3.3. Phylogenetic structure and diversity

Plot-level PD was positively related with species richness ($R^2_m = 0.57$; $R^2_c = 0.58$; $p < 0.01$), ranging from 1644 to 2595 (mean 2266 ± 339) to 1785–2564 (mean 2119 ± 211) in the coppice and high forest plots, respectively, with no significant differences between the two groups. Conversely, PD.ses values were higher in the high forest than in coppice (mean 0.54 ± 0.96 vs. -0.19 ± 1.00 ; $p = 0.084$), and this was marginally significant in the models (Table 3, Fig. 3b). A more significant difference emerged in terms of phylogenetic structure. In fact, the MNTD.ses metrics based on presence/absence data pointed to phylogenetic clustering (negative values) only in the coppice stands, especially in the young and mid-stage plots (mean -0.48 ± 0.88 in coppice plots vs. 0.52 ± 0.94 in high forest plots; $p = 0.01$). The reduction of branch-tip phylogenetic evenness in the coppice understorey was also

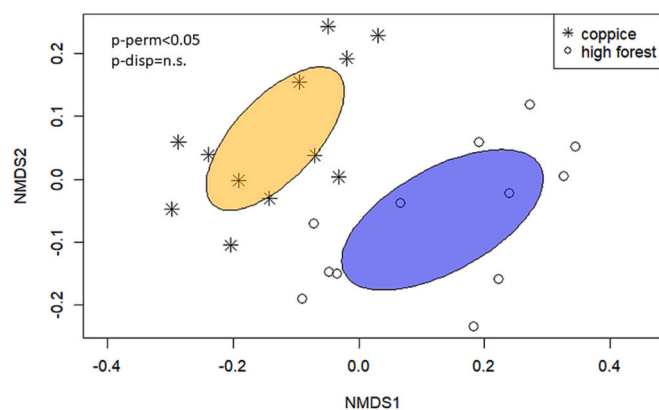


Fig. 4. Non-metric multidimensional scaling showing significant variation in understorey species composition between coppice and high forest plots. Stress value: 0.18; Linear fit $R^2 = 0.84$; Non-metric fit $R^2 = 0.97$.

supported by model results (Table 3, Fig. 3c). No phylogenetic clustering emerged in the high forest plots.

3.4. Functional traits

Among the examined traits, only LDMC showed significant differences between high and coppice forest plots when considering the standardised metrics of diversity (SES.Rao LDMC in coppice = -0.55 ± 0.52 and in high forest = 0.07 ± 0.76 , p -value < 0.05). Model results revealed a positive effect of high forest management on this metric (Table 3, Fig. 3d). Moreover, the CWM of LDMC was significantly lower in the high forest than in coppice plots ($p < 0.05$) (Appendix A, Tables A.10).

4. Discussion

4.1. Microclimate

Our results showed that coppicing significantly reduces the air temperature buffering capacity of the oak forest. Especially in the spring, the season of maximum plant growth in the Mediterranean, the Tmax cooling effect in coppice stands was considerably decreased compared to the high forest, by 2.37°C on average. Higher absorption and reflection of the incoming short-wave solar radiation, associated with increased evapotranspirative cooling and lower air turbulence, are the major factors for the cooling effect during clear and warm days (Ehbrecht et al., 2017; Davis et al., 2019). Evidence exists that this effect depends on forest structure and is weaker when stand density and tree stock are reduced (Greiser et al., 2018; Zellweger et al., 2019; Meeussen et al., 2021), which is here supported by the positive relationship between cooling effect, and both stand basal area and tree density. Although the increase in stand density and tree stock in the coppice due to re-growth after cutting allows a partial recovery of the buffering capacity, the short utilisation cycles stop this process at a given “buffering” point which remains far below that of the high forest.

The stronger buffering capacity of the high forest also resulted from the higher Tmin values of both air and soil, compared with the coppice stands. This warming effect is likely explained by increased understorey heat retention, especially at night, through the shielding of the outgoing long-wave radiation by the dense tree canopy (De Frenne et al., 2019, 2021; Geiger et al., 2009). This implies that coppice stands could help more than the high forest to cool the microclimate at night, guaranteeing a buffering against hot weather during summer. Further studies would be helpful to better understand the role of the shrub and subdominant tree layers in microclimate regulation in thermophilous deciduous forests.

4.2. Understorey diversity and composition

Taxonomic, phylogenetic, and functional metrics provided complementary information about understorey vegetation response under contrasting management, pointing to the importance of considering different facets of diversity to better understand the impact of disturbances (Bricca et al., 2020). Recent evidence from European temperate forests showed that these metrics can respond differently to anthropic factors and environmental conditions (De Pauw et al., 2021; Erdős et al., 2023).

In our study, the disturbance regime caused by active coppice-with-standards management maintained a higher SR and an overall different species composition in the understorey. Increase in SR, however, was not paralleled by Shannon diversity and evenness, as coppicing increased the species abundance imbalance by altering interspecific competition relationships. Increased species richness emerged from other studies on European oak and beech coppice-with-standards forests abandoned since decades, subject to conversion to high forest or to low intensity selective cuttings (Decocq et al., 2004; Baeten et al., 2009;

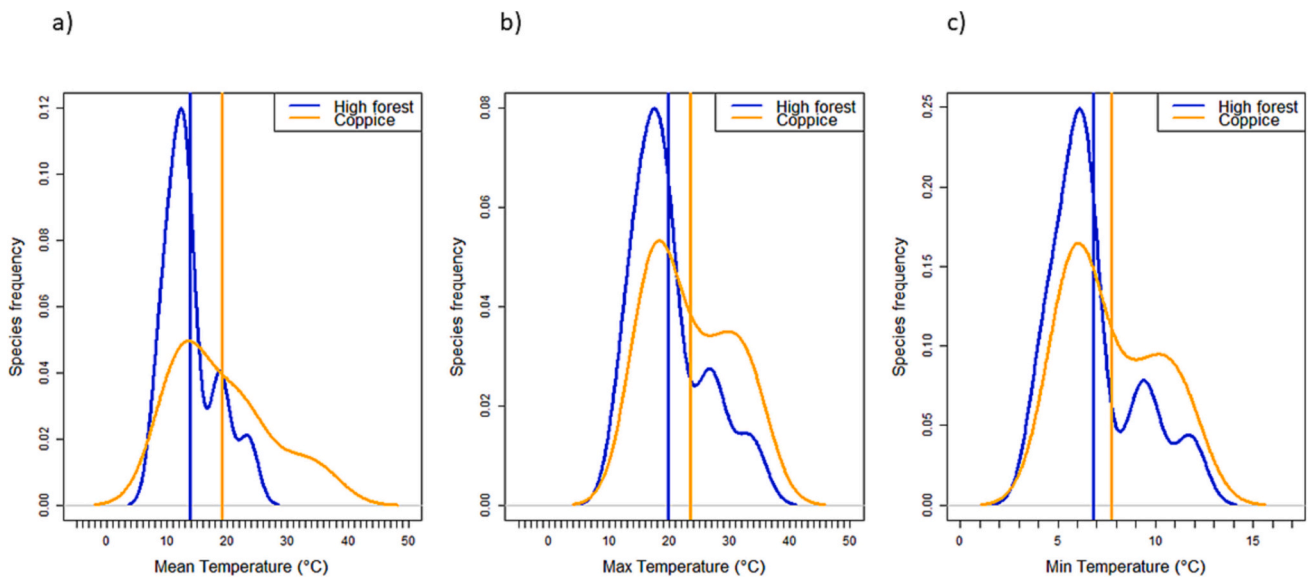


Fig. 5. Density curves showing understory species frequency of: a) Tmean, and b) Tmax and c) Tmin in coppice and high forest, considering their abundance-weighted average values in each quadrat; floristic temperature data were retrieved from the ClimPlant database (Vangansbeke et al., 2021).

Table 1

Indicator species associated with coppice and high forest in terms of frequency and cover. The analysis was performed with the function *multipatt* in *Indicspecies* package (Caceres and Legendre, 2009).

Management type	Indicator species	p-Value	
Coppice	<i>Rubus ulmifolius</i>	***	
	<i>Poa nemoralis</i>	***	
	<i>Genista pilosa</i>	***	
	<i>Viola alba</i>	***	
	<i>Carex pallescens</i>	**	
	<i>Cruciata glabra</i>	*	
	<i>Crataegus monogyna</i>	*	
	<i>Lonicera caprifolium</i>	*	
	<i>Calluna vulgaris</i>	*	
	High Forest	<i>Anemone nemorosa</i>	***
		<i>Physospermum cornubiense</i>	*
<i>Malus florentina</i>		*	
<i>Fraxinus ornus</i>		***	
<i>Rusos aculeatus</i>		*	
<i>Pyrus pyrastrer</i>		*	
<i>Carpinus betulus</i>		*	

* p < 0.05.

** p < 0.01.

*** p < 0.001.

Bartha, 2008; Campetella et al., 2016; Cervellini et al., 2017; Bricca et al., 2020; Chelli et al., 2023). The interaction between changes in microclimate (discussed above) and light regime in the coppice plots can easily explain such differences. Shading by the tree and shrub layers is a well-known mechanism limiting herb layer species richness in dense temperate forests (Axmanová et al., 2012; Landuyt et al., 2019; Dormann et al., 2020). Higher light availability in the coppice stands can thus account for the increased species richness due to the spread of light-demanding and mostly acidophilus taxa, as reflected in the higher light and lower acidity indicator values. Although measured soil pH was actually lower in the high forest plots (Appendix A, Table A.13), acidophilus understory species were less represented here, likely due to unsuitable light conditions. An increase in soil acidity after the conversion of coppice to high forest was already found in central Europe (Baeten et al., 2009) and is likely an additional factor for the shifts in species composition and lower diversity observed in our high forest plots. Species richness in European forests is in fact usually positively associated with soil pH, possibly due to an impoverishment of calcifuge

Table 2

Relative frequency (species number per quadrat) and abundance (percentage of ground cover) of forest guilds in coppice and high forest; guilds are according to Heinken et al. (2021). 1.1: species that can be mainly found in closed forests; 1.2: species that occur typically along forest edges and in forest openings; 2.1: species that can be found in both forest and open vegetation; 2.2: species that can be found partly in forest, mainly in open vegetation; O: typical open habitat species. The relative frequency and abundance of each guild was calculated for each plot and compared in coppice vs. high forest using a Wilcoxon/t-test.

Forest guilds	Frequency			Abundance		
	Coppice	High forest	p-value	Coppice	High forest	p-value
1.1	0.16 ± 0.04	0.29 ± 0.1	0.0003	0.1 ± 0.04	0.23 ± 0.15	0.02
1.2	0.11 ± 0.03	0.02 ± 0.04	0.0003	0.08 ± 0.03	0.03 ± 0.05	0.01
2.1	0.5 ± 0.08	0.53 ± 0.08	n.s	0.63 ± 0.14	0.63 ± 0.15	n.s
2.2	0.21 ± 0.07	0.13 ± 0.05	0.003	0.18 ± 0.11	0.09 ± 0.04	n.s
O	0.02 ± 0.02	0.02 ± 0.03	n.s	0.01 ± 0.02	0.02 ± 0.02	n.s

species pools occurred during the Pleistocene and early Holocene (Chytrý et al., 2003; Verstraeten et al., 2013).

Most importantly, high forest management favoured a higher proportion of specialists adapted to cool and shady conditions (guild 1.1 of Heinken et al., 2022) such as *Anemone nemorosa*, *Physospermum cornubiense* and *Carpinus betulus*, while coppicing was associated with a significant increase of understory species typical of edges and gaps, as well as of generalists of mainly open habitats, in line with recent evidence by Chelli et al. (2023). Although Ellenberg T did not provide any signal of thermophilization in the understory, the warmer microclimate in the coppice stands in spring and summer was reflected in the higher annual Tmean values of the understory (+5.26 °C) detected with the thermal niche data from ClimPlant (Vangansbeke et al., 2021). Understory thermophilization in temperate forests has been documented since the last decade due to the interaction of climate warming, forest management and disturbance (De Frenne et al., 2013; Stevens et al., 2015; Govaert et al., 2021). This process is likely context-dependent and influenced by the biogeographical region, the macroclimate, the forest type and the local floristic assemblages, suggesting more studies across

Table 3

Results of the linear mixed models for the diversity metrics with management type as independent variable ($y \sim \text{forest management} + 1 | \text{macroplot}$). Model fit was evaluated based on the proportion of variance explained by fixed factors alone (R^2_m : marginal R^2) and the proportion of variance explained both by the fixed and random factors (R^2_c : conditional R^2) (Nakagawa and Schielzeth, 2013).

Response variable	High Forest	R^2_m	R^2_c
Species Richness (SR)	-4.583*	0.24	0.56
Shannon index (H')	-0.205	0.08	0.79
Evenness (J)	-0.018	0.01	0.59
Standardised phylogenetic distance (PD.ses)	0.725*	0.12	0.12
Standardised Mean Phylogenetic Distance (MPD.ses)	0.409	0.03	0.06
Standardised Mean Nearest Taxon Distance (MNTD.ses)	0.991***	0.24	0.24
Community weighted mean (CWM) of Specific Leaf Area	-0.962	0.02	0.79
Standardised RAO index (Rao.ses) of Specific Leaf Area	-0.232	0.05	0.05
CWM of Leaf Dry Matter Content	-12.32	0.16	0.35
Rao.ses of Leaf Dry Matter Content	0.624**	0.19	0.21
CWM of Vegetative height	1.741	0.13	0.55
Rao.ses of Vegetative height	-0.624	0.08	0.16
CWM of Reproductive height	0.22	0.02	0.71
Rao.ses of Reproductive height	-0.64	0.09	0.28
CWM of Seed mass	10.693	0.07	0.90
Rao.ses of Seed mass	0.037	0.00	0.46

* $p < 0.1$.

** $p < 0.05$.

*** $p < 0.01$.

the Mediterranean to better understand its incidence in relation to different management approaches. Our findings suggest that coppicing can accelerate and exacerbate understory thermophilization by reducing the cooling capacity of the forest system. On the other hand, the development of warm-adapted, light-demanding and drought-resistant understories can also be seen as an adaptive process that will lead to the shaping of species assemblages more able to cope with the effects of climate change. Embedding coppicing in landscapes with also denser forest management types may therefore represent a suitable strategy to accommodate both cold-adapted species with contracting range and warm-adapted species with expanding range (Hylander et al., 2022).

Remarkably, active coppice-with-standards management had an effect also on the phylogenetic structure of the understory. Converging evidence was provided by the PD.ses and MNTD.ses indices which pointed to a decrease of phylogenetic diversity and evenness in the coppice understory. Phylogenetic clustering in forest plant communities often results from the pressure of environmental filters that select related species adapted to the local constraints (Selvi et al., 2016; Aldana et al., 2017; Ottaviani et al., 2019; Lazzaro et al., 2020; Lanta et al., 2023). If adaptations to selective environments involve complex traits, these are more likely to be shared by related co-occurring species than expected under neutral evolution, leading to a phylogenetic signal of these traits (Crisp and Cook, 2012). The severe and continued disturbance regime to the natural forest dynamics caused by coppicing is thus likely to favour in the long-term a few groups of related species in the regional flora, well adapted to constraints such as high temperatures, large seasonal and daily offsets, dryer air and soil conditions, and stronger solar radiation during spring and summer. Mechanical impacts on soil properties and understory plants caused by harvesting operations at each coppicing cycle (Marchi et al., 2016) can also contribute to this process of directional selection of species with pre-adaptive traits such as thick leaves, deep root system, bud bank, clonality, resprouting capacity and lateral spread.

Some of the leaf functional adaptations of coppice understory species are likely associated with the overall higher CWM of LDMC found here. Leaf dry matter content mainly depends on the degree of thickening of the epidermal cell walls and of the cuticle with waxes and cutin,

which protects against excessive light radiation and water losses thanks to their hydrophobic nature (Yeats and Rose, 2013). This trait is associated with a resource conservative strategy, enhancing drought-tolerance and hydraulic safety (Garnier et al., 2015; Kramp et al., 2022). Compared with high forest, therefore, coppice management seems to promote more xerotolerant and resource-conservative understory plants, also reducing LDMC interspecific variation (diversity) through selection of species with converging values for this trait. The stronger microclimatic buffering of the high forest shown in this study creates more favourable conditions and can explain the lower CWM value of LDMC. This finding is in line with Cubino et al. (2021), who found that conservative leaf traits of European understory species increase in forest sites with more extreme annual temperatures and more open canopies. The higher LDMC variation within and between plots, was probably due to the stronger proportion of understory specialists with more resource-acquisitive strategies. This is also consistent with the finding that LDMC decreases with increasing maturity of the forest (Chelli et al., 2021).

5. Conclusions

This study provides the first evidence about the effects of coppice-with-standards vs. high forest management on microclimate and understory community dynamics of an ancient oak forest of the Mediterranean region. We showed that air temperature buffering capacity is reduced in coppiced forest, due to a lower tree stock and canopy cover, especially during the spring season and in the younger stands. Such reduced capacity will likely exacerbate the effects of warming and drought, with consequences on forest biodiversity and functioning. As expected from our hypothesis ii), coppicing increased understory species richness, though this was not matched by other taxonomic diversity metrics incorporating species abundance (H' and J) due to a reduction of species evenness. Increase in SR was largely due to more numerous light-demanding plants, but this was coupled with a reduction in the relative proportion of shade-tolerant forest specialists. With respect to high forest, coppicing also caused a significant shift in the thermal niche of the understory of +5.26 °C, on average. Even more remarkable was the loss of phylogenetic evenness (phylogenetic clustering) found in the coppice understory, which is likely the result of habitat filtering processes driven by the severe and repeated disturbance caused by forest utilisations. The increased LDMC and lower diversity of this trait in the coppiced stands are also likely related to both filtering and acclimation in favour of taxa with drought-tolerance traits, such as leaf epidermal cells with thickened walls, and thicker cuticles and wax layers. These changes provided support to our hypothesis iii). Coppice management is returning mainly for economic reasons in many regions of the world, but our findings underpin the potential negative impacts on forest buffering capacity and understory vegetation. Hence, while coppicing embedded in landscapes with high forest can accommodate both cold-adapted and warm-adapted species, large-scale adoption of this traditional management form is probably no longer warranted because of the effects on forest biodiversity and functioning under the current threats and drivers of global change.

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CRediT authorship contribution statement

Ilaria Santi: Writing – original draft, Methodology, Investigation,

Formal analysis, Conceptualization. **Elisa Carrari**: Writing – review & editing, Methodology, Investigation. **Pieter De Frenne**: Writing – review & editing. **Mercedes Valerio**: Investigation. **Cristina Gasperini**: Writing – review & editing, Investigation. **Marco Cabrucci**: Investigation. **Federico Selvi**: Writing – original draft, Supervision, Resources, Methodology, Investigation, Conceptualization.

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.

Data availability

Data will be made available on request.

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