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Changes in species and functional composition in the herb layer of sub-Mediterranean *Ostrya carpinifolia* abandoned coppices

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Abstract

In recent decades, the traditional management of woods has ceased in several parts of the Apennine ridge, with the result that some woods have not undergone forestry for 40-70 years. The research aim was to assess the variation of species and functional composition in the herb layer of *Ostrya carpinifolia* woods (central Italy), after cessation of the usual management (coppice-with-standards). Using a space-for-time substitution, we compared stands at the end of the usual rotation cycle (20-25 years) with stands not subjected to silvicultural treatments for about 40-45 years and collected environmental and structural data. The main drivers of the herb layer modification, assessed using Ellenberg indicator values analysis and redundancy analysis (RDA), were primarily related to time since the last coppicing and wood structure. Results of indicator species analyses (ISAs) and Wilcoxon rank sum tests indicated that in abandoned coppices, the regenerative processes proceed through the spread of late-successional species, while the light filtering through canopy fosters species usually considered of fringe habitats. The functional strategies revealed by ISA and RDA underlined still stressful conditions in stands at the end of the usual coppicing rotation cycle, which might be thought as a legacy of the post-logging condition, and processes of recovery/maturation of the forest systems in abandoned woods leading to a better spatial and temporal niche partitioning. The preferential distribution of species usually growing in the Apennine beech woods supports the hypothesis that the studied *O. carpinifolia* woods are secondary forest ecosystems originating from the degradation of mixed beech woods.

Keywords - Ancient forest species; Coppicing rotation cycle; European hop-hornbeam; Forestry; Management abandonment; Understory

Introduction

A long history of human land use created the European forests that we know today (e.g., Perlin 1988; Kelemen et al. 2014; Gilliam 2016). In Italy, where forests have been exploited over hundreds of years, secondary forests almost completely replaced the primeval ones (Motta 2002), and thus the current structure and composition of forests are a legacy of past and present management (Chiarucci et al. 2010). This is the case of woods dominated by European hop-hornbeam (*Ostrya carpinifolia* Scop.), which have been considered of secondary origin, likely being a degradation phase of sub-Mediterranean beech mixed woods (Catorci et al. 2003), as hypothesized for some other European beech forests managed for a long time (Piskernik 1985; Šercelj 1996).

O. carpinifolia needs a low amount of resources and has a great ability to re-sprout from stumps (agamic growth of suckers) after logging. These features facilitate its dominance in overexploited woods (Blasi et al. 2006). In fact, *O. carpinifolia* plays an important role in the forest vegetation of the Italian sub-Mediterranean context, at altitudes lower than 1,200 m a.s.l. (Bernetti 1995) on different substrates. These woods are usually managed as coppice-with-standards. In this kind of management, devoted to firewood and charcoal production, trees are usually cut down (coppiced) about every 20-25 years, to stimulate re-sprouting, except for some of them, called "standards" (about 100 items/ha), which are allowed to grow during two or more coppicing rotation cycles. This management system results in several even-aged stands with heterogeneous structure on a coarse scale.

Among the main ecological features of coppicing is a shifting mosaic of light and dark phases, which maintains viable populations of light demanding, but also shade-tolerant organisms (Hédl et al. 2017). In recent decades, the traditional coppicing rotation cycles have ceased in several sectors of the Apennines, due to the abandonment of mountain farming and settlements (Ciancio et al. 2006), with the result that some woods have not undergone forestry for 40-70 years, posing the question of how to manage these communities in the future from an economic and environmental

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point of view. It was stated that scenarios of conversion from coppicing to other types of management can provide diverging effects on diversity, cover and composition of the herb layer (Decocq et al. 2004; Van Calster et al. 2008). Studies on the effects of coppicing abandonment from central and western Europe mostly reported strong changes in species diversity and composition, often resulting in a decrease in species richness (Van Calster et al. 2007; Baeten et al. 2009; Hédl et al. 2010). Kopecký et al. (2013) demonstrated a shift from a species-rich assemblage to an impoverished flora dominated by a few shade-adapted species, leading to a taxonomic homogenization of the forest understory. Temporal species turnover evidenced to be only a minor component of the community change, and new assemblages are nested subsets of the former ones (Kopecký et al. 2013). Light-demanding species are considered the most prone to local extinction, while species with high specific leaf area substantially increase in frequency (Kopecký et al. 2013). Moreover, abandonment of the coppice-with-standards regime alters the seed bank characteristics, as well as its relation with vegetation (Van Calster et al. 2008). In particular, longer management cycles under high forest yield impoverish seed banks, while coppicing allows heliophilous species to persist in the seed bank and to reappear after the following coppice cut (Brown and Oosterhuis 1981). However, it was observed that coppicing or its re-introduction in a secondary forest leads to contrasting species patterns, also related to dominant tree species (Hédl et al. 2017).

In *O. carpinifolia*-dominated stands, Catorci et al. (2011, 2012a) found that temporal species turnover followed an ecological cyclic process, characterized by occurrence/disappearance of species groups throughout the coppicing cycle (1 to 25 years after the cut). In particular, light demanding species of dry conditions (mainly annual plants with low seed mass and drought stress tolerance) occur soon after canopy disturbance; partially shade-tolerant species peak in the central phases of the recovery process, while shade-tolerant plants spread out in the late phases of the coppicing rotation cycle. Ancient forest species (*sensu* Hermy et al. 1999) are restricted to shelter niches and have been deemed to have a poor ability to re-colonize the understory, due to the too short period of the coppicing rotation cycle. This species turnover reflects, at the community level, a

pattern of functional variation (Catorci et al. 2012a). In particular, Catorci et al. (2012a) found that young stands were differentiated by fast growing species with acquisitive strategies, which reproduce only sexually, with light seeds, summer green and overwintering green leaves, and a long-lasting flowering. Intermediate-aged and mature stands (9-16 and 17-24 years since the last coppicing, respectively) were characterized by traits associated with early leaf and flower production, high persistence in time, and showing retentive strategies aimed at resource storage (e.g., geophytes, spring green leaves, rhizomes, and mesomorphic/hygromorphic leaves).

As far as we know, there are no data on the effect of coppicing cessation on sub-Mediterranean lowland communities, but studies performed in Apennine beech forests demonstrated that the forest specialist species doubled their relative abundance after about 40–60 years after coppicing at the stand scale, but the turnover between open and closed-canopy species might be lower than expected at the landscape scale (Bartha et al. 2008; Campetella et al. 2011). Moreover, different forest areas may display contrasting patterns, since the species number may be either higher or lower in the actively coppiced stands than in the abandoned ones (Bartha et al. 2008; Campetella et al. 2011). In addition, Burrascano et al. (2018) demonstrated that species composition, but not richness and beta-diversity, differed significantly between managed and unmanaged stands, and that species turnover was explained by different variables in distinct stands. These results do not seem to fully match with those of several studies that indicate a decrease in richness at the plot scale with increasing time since the last coppicing in other climatic conditions (Debussche et al. 2001; Manson and Macdonald 2002; Decocq et al. 2004; Gondard and Romane 2005; Bartha et al. 2008). This underlines the need to deepen our knowledge on how the herb layer changes after coppicing cessation in the unproductive and dry sub-Mediterranean context. This is particularly urgent in hilly forests, where strong summer drought stress severely influences the ecosystems and alternates with a long-lasting cold winter with several frost episodes (Orsomando et al. 2000). Learning more would be important, since the herb layer contributes to forest biodiversity (e.g. Hart and Chen 2006;

Gilliam 2007), ecosystem functioning (Nilsson and Wardle 2005), nutrient cycling (Muller 2014), biomass (Gonzalez et al. 2013), and seedling community (George and Bazzaz 2014).

The research aim was to assess the changes in species and functional composition of no longer managed sub-Mediterranean European hop-hornbeam coppiced woods. To this end, we compared stands at the end of the usual rotation cycle (20-25 years) with stands not subjected to any silvicultural treatment for about 40-45 years. We hypothesized that the recovery processes due to management cessation diversify the functional strategies by the spread of some groups of species different from the so-called forest specialist species. To test this hypothesis, we explored the following questions: i) what is the role of environmental variables and management cessation in driving species and functional variation in the herb layer? ii) what are the indicator species and trait states of unmanaged and managed stands? In addition, we aimed to understand whether the results emerging from the analysis of no longer managed coppiced stands could provide hints in support of the hypotheses that sub-Mediterranean and temperate abandoned coppiced woods have the same trends involving the decrease of light-demanding taxa and the homogenization of the herb layer composition, and that the studied *O. carpinifolia* woods could be considered as secondary forest ecosystems, originating from the degradation of mixed beech woods (Catorci et al. 2003, 2011).

Material and methods

Study area

The study area lies in the hilly calcareous sectors of the Umbria-Marche Apennines (central Italy) (Fig. 1), between the Temperate and Mediterranean macroclimatic regions (Pesaresi et al. 2014). The main climatic features are typical of the sub-Mediterranean landscapes: mean annual temperature of 12-13 °C; mean annual rainfall of 900-1,100 mm; 2-3 months (mainly January and February) with a mean minimum temperature below 0 °C; drought stress lasting from mid-July to the end of August; vegetative period of 180-210 days (Orsomando et al. 2000). The studied woods are generally characterized by the following tree species: *Ostrya carpinifolia* Scop. (dominant),

Fraxinus ornus L. subsp. *ornus*, *Acer opalus* Mill. subsp. *obtusatum* (Waldst. & Kit. *ex* Willd.) Gams, and *Quercus cerris* L. From a phytosociological point of view, these woods belong to the *Fraxino orni-Ostryion* Tomažič 1940 alliance (*Quercetalia pubescenti-petraeae* Klika 1933 order and the *Quercetea pubescentis* Doing-Kraft *ex* Scamoni *et* Passarge 1959 class).

Sampling design and data collection

As our goal was to assess the variation of the herb layer composition after coppicing cessation, we compared two different forest types selected on the basis of the time since the last coppicing using a "space-for-time substitution" approach (Pickett 1989). This approach has been used to infer many aspects of vegetation dynamics, providing significant insight into the patterns and mechanisms of regeneration and succession (Foster and Tilman 2000; Garnier et al. 2004). We identified two groups of stands: one at the end of the usual rotation cycle (20-25 years since the last coppicing event) according to Marche Region regulation (DGR 2585/2001) and one that has not been coppiced in the last 40-45 years. The latter stands are very infrequent in the Umbria-Marche Apennines due to the great suitability of the European hop-hornbeam for firewood (Urbinati 2009). Information on treatments were gathered from local woodcutters and the registers of the Italian Forest Service.

To reduce the number of environmental variables, we considered stands on limestone, north-facing slopes (from west to east clockwise), with elevations ranging from 650 to 900 m a.s.l. and slope angle of 20-40°. For each stand, we randomly selected the coordinates of the lower left-hand corner of one 20 m x 20 m plot. Plots with heterogeneous aspect and slope were discarded, as well as those crossed by roads/pathways or near the border (less than 100 m) of the wooded area. In total, we laid 38 plots (20-25 years old, 19 plots; 40-45 years old, 19 plots), in which we recorded: altitude (m a.s.l.), aspect angle (azimuth degrees), slope angle (vertical degrees), cover of outcropping rock and rock fragments (cover percentage, visually estimated). We visually estimated

cover values of the plant species in the tree (individuals taller than 5 m), shrub (individuals tall from

0.5 to 5 m), and herb layers using the Braun-Blanquet scale (Braun-Blanquet 1964).

We executed relevés from mid-May to mid-June 2015, to record both the spring and the summer

growing species. To better assess the environmental differences between the two groups of plots,

for each species we identified Ellenberg's Indicator Values (EIVs) (Ellenberg 1974; Ellenberg et al.

1991) adapted to the Italian flora (Pignatti 2005; Guarino et al. 2012).

To assess the trait-based response of plant communities of the herb layer to environmental

features and land use changes, we selected a set of traits involved in strategies related to resource

acquisition/retention, space occupation/competitive ability, and dispersion/reproduction (Grime et

al. 1997; Díaz et al. 2004; Lavorel et al. 2007): occurrence and type of storage organ and vegetative

propagation, leaf anatomy, leaf persistence, flowering phenology, and seed mass. A description of

each trait, with a list of the respective states and data sources, is reported in Online Resource 1.

All data generated or analysed during this study are included in this article and its supplementary

information files (Online Resource 2).

Data analysis

Preliminary data processing

We converted slope aspect angles measured in the field from the 0-360 compass scale to a 0-180

linear scale, giving north-north-east-facing slopes (i.e. the coldest aspect) the minimum value and

south-south-west slopes (i.e. the warmest aspect) the maximum value, so that slopes symmetrical

with respect to the north-north-east / south-south-west axis had the same values (e.g. east-south-east

and west-north-west correspond to 90°).

We expressed species abundances in percent values using the average cover values of Braun-

Blanquet classes: + (< 1%) – 0.5 %; 1 (1–5%) – 3 %; 2 (5–25%) – 15%; 3 (25–50%) – 37.5%; 4

212   (50–75%) – 62.5%; 5 (75–100%) – 87.5%. r (rare species) were attributed 0.1%. Species

213   nomenclature followed Conti et al. (2005).

214   For the herb layer of each plot, we calculated the community-weighted mean trait values

215   (CWMs) for each trait state, following the equation of Violle et al. (2007) and Ricotta and Moretti

216   (2011):

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$$CWM_j = \sum_{i=1}^{n} P_{ij} T_{ij}$$

218   where CWM_j is the community-weighted trait of the plot j, P_{ij} is the relative abundance of the

219   species i in the plot j, T_{ij} is the mean trait value of the species i in the plot j (which in this study

220   corresponds to 0 or 1, i.e. the presence/absence of the trait state, as we treated all traits as

221   categorical variables), and n is the number of species with the considered trait. The CWM

222   represents the average trait value in a community, weighted by relative abundance of the species

223   (Garnier et al. 2004). Being a direct extension of the biomass ratio hypothesis (Grime 1998), CWMs

224   are particularly useful to account for species abundances when analysing community functional

225   structure and to examine the shifts in single-trait values in response to environmental and

226   management changes (Garnier et al. 2004).

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228   *Drivers of herb layer assemblages*

229   We calculated the simple average EIVs (light intensity, air temperature, continentality, soil

230   moisture, and soil nitrogen content) in each plot as proxies of environmental variations (Diekmann

231   2003; Käfer and Witte 2004). Average EIVs are said to reflect the site conditions better than the

232   EIVs of individual species, because the occurrence of a species in a relevé may deviate from its

233   optimum due to ecological tolerance (Kowarik and Seidling 1989). Then, we calculated descriptive

234   statistics (mean, standard deviation, median, and interquartile range) of EIVs for each group of

235   stands.

236   To assess the effects of the explanatory variables (altitude, aspect angle, slope angle, outcropping

237   rock and rock fragments cover, tree, shrub and herb layer cover, time since the last coppicing) on

238   the herb layer species composition and CWMs of trait states, we performed two canonical

239   redundancy analyses (RDA) on the "relevés-by-herb species cover (%)" and "relevés-by-CWM"

240   matrices, constrained by the explanatory variables. Time since the last coppicing was treated as a

241   categorical variable with two categories: 20-25 years and 40-45 years. Prior to RDA, the herb

242   species cover matrix had been Hellinger-transformed. Adjusted R^2 values were calculated to

243   produce unbiased estimates of the contributions of the independent variables to the explanation of

244   the response variables (Peres-Neto et al. 2006).

245   We calculated the median values of altitude, aspect angle, slope angle, cover of outcropping

246   rock, rock fragments, tree, shrub and herb layers cover for the two groups of plots and performed

247   two-sided Wilcoxon rank sum tests (confidence interval 95%) to detect significant differences in

248   these variables between the two types of stand.

249   We used R software (version 3.1.1, R Foundation for Statistical Computing, Vienna, Austria

250   http://www.R-project.org) and the following R-packages: *vegan*, version 2.4-3, to transform species

251   data (decostand function) and to perform RDA (rda function); *FD*, version 1.0-12, to calculate

252   CWMs (functcomp function), and *exactRankTests*, version 0.8-29, to perform Wilcoxon rank sum

253   tests (wilcox.exact function).

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255   *Species and functional differences in the herb layer*

256   To detect species and trait states related to the different time since the last coppicing, we used

257   indicator species analysis (ISA), which makes it possible to discern those items that show

258   preferential distribution in a group of samples in comparison with other groups (Dufrêne and

259   Legendre 1997). ISA involves the calculation of an indicator value (IV), which is the product of

260   relative abundance and relative frequency, using the formula:

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$$IV_{gi} = RA_{gi} \times RF_{gi}$$

where *RA* is the relative abundance and *RF* is the relative frequency for each species/trait state *i* in each group *g* (Dufrêne and Legendre 1997). Once the IV is calculated, the group in which IV is at its maximum is identified (De Cáceres et al. 2010).

To identify the indicator species and trait states of each group, we performed two ISAs on the matrices "relevés-by-herbs species cover (%)" and "relevés-by-trait states cover" (sums of the absolute abundances of species with a trait state), where relevés were grouped on the basis of the years since the last coppicing. We tested the statistical significance ($P < 0.05$) of the observed maximum IVs using permutation tests with 999 runs, and considered species/trait states with significant IVs. We discarded species/trait states whose component of relative abundance was lower than 0.6 or whose component of relative frequency was lower than 0.25 (De Cáceres et al. 2012). To perform ISA, we used the *indicspecies* R-package, version 1.7.6 (multipatt function).

Results

Drivers of herb layer assemblages

Tree layer cover was the only explanatory variable displaying significant differences ($P = 0.029$) between plots included in stands coppiced 20-25 and 40-45 years before the survey (median values 100% vs. 90%, respectively, see Online Resource 3). Soil moisture and nitrogen EIVs were greater in no longer managed stands in comparison to stands at the end of the coppice rotation cycle, while light intensity values slightly decreased (Tab. 1). The RDA models explained 35.64% and 35.66% (*adj.-R²*, $P = 0.001$) of the herb species cover and traits' CWMs variability, respectively. Axis 1, accounting for 31.87% of the constrained variance ($P = 0.001$) of the species data set, was mainly related to time after coppicing. Axis 2 explained 20.46% ($P = 0.001$) of the constrained variance and was chiefly correlated with shrub and herb layers cover (Fig. 2). Axes 3 and 4 explained 17.93% and 12.40% ($P = 0.001$) of the constrained variance and were mainly linked to altitude and rock fragments cover, respectively.

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287   Axis 1 of the RDA performed on the traits' CWMs data set, accounting for 49.42% of the

288   constrained variance, was mainly related to time after coppicing. Axis 2 explained 23.88% of

289   variance ($P = 0.001$) and was correlated with shrub and herb layers cover, as well as to the time

290   since the last coppicing (Fig. 3); axis 3, mainly linked to rock fragments cover, explained 11.72% of

291   variance ($P = 0.007$).

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293   *Species and functional differences in the herb layer*

294   Indicator species of the 20-25 years old stands were *Hepatica nobilis* Schreb., *Sesleria nitida*

295   Ten., *Primula vulgaris* Huds. subsp. *vulgaris*, *Carex digitata* L., *Melittis melissophyllum* L. subsp.

296   *melissophyllum*, and *Pulmonaria apennina* Cristof. *et* Puppi (Tab. 2). This group includes

297   xerophilous light-demanding species, as well as shade-tolerant species growing on deep and moist

298   soils. Indicator species of the 40-45 years old stands were: *Melica uniflora* Retz., *Brachypodium*

299   *sylvaticum* (Huds.) P. Beauv. subsp. *sylvaticum*, *Ajuga reptans* L., *Lactuca muralis* (L.) Gaertn.,

300   *Helleborus foetidus* L. subsp. *foetidus*, *Digitalis lutea* L. subsp. *australis* (Ten.) Arcang., and

301   *Euphorbia amygdaloides* L. subsp. *amygdaloides* (Tab. 2). These species are generally shade-

302   tolerant and grow on moist soils well supplied with nitrogen.

303   From a functional point of view, vegetative propagation by fragmentation (observed indicator

304   value 0.664, $P = 0.001$), absence of storage organs (0.752, $P = 0.006$), and persistent green leaves

305   (0.679, $P = 0.001$) were indicator trait states of the herb layer of the 20-25 years old stands, while

306   tap root (0.731, $P = 0.030$), summer green leaves (0.787, $P = 0.001$), and seed mass greater than

307   10.00 mg (0.643, $P = 0.046$) were indicator trait states of the 40-45 years old stands.

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309   **Discussion**

310   Time since the last coppicing was the main factor explaining the variability of the species and

311   trait data sets. As indicated by EIVs analysis, some environmental conditions (soil moisture and

312   nitrogen) changed as a result of coppicing cessation and regeneration processes, even if, according

to Franklin et al. (2002), the studied woods, still in a phase of biomass accumulation and competitive exclusion, should be considered ecologically young. In the oldest stands, we recorded a certain degree of opening in the tree canopy, in agreement with Baeten et al. (2009) and Hédl et al. (2010). Actually, several structural trends may contribute to the foliage clumping and the decrease of canopy cover during the regeneration processes (Neufeld and Young 2014), leading to forest recovery (Brown and Parker 1994). For instance, the tree crown becomes progressively taller, allowing a higher lateral penetration of light, stems and suckers perish, and thus the amount of light filtered through the canopy is likely greater. Variation in the canopy structure could be a key factor in influencing the understory composition (Tardella et al. 2017), since it affects light availability in the understory (Tinya et al. 2009; Lochhead and Comeau 2012) and several edaphic features (Barbier et al. 2008; Bartels and Chen 2010; Neufeld and Young 2014). However, despite the appreciable canopy openings, EIVs assessment indicated a modest decrease in mean light value. This is probably due to the reduction of xerophilous species, which are often also heliophilous, with high light EIV (e.g. *Sesleria nitida*); this might confound the interpretation of the real variation of light conditions in the understory.

The stands at the end of the usual coppicing rotation cycle, i.e. after 20-25 years from the last cut, were characterized by shade-tolerant and to some extent drought-tolerant species (*Hepatica nobilis*, *Primula vulgaris*, *Carex digitata*, and *Melittis melissophyllum*), mainly belonging to *Quercetalia pubescenti-petraeae* order and *Quercetea pubescentis* class (Tab. 2). These plants may be considered generalist forest species (Decocq et al. 2005; Chiarucci et al. 2010), fostered by centuries-old coppicing activities (the so-called "true forest species", *sensu* Honnay et al. 1998), which in the final phases of the coppicing rotation cycle lowered and/or marginalized other groups of species, such as the light-demanding ones typical of dry conditions. These species, as evidenced by Catorci et al. (2011), quickly spread in the understory after logging, thanks to proper traits (e.g. small seeds, mainly annual and biennial life cycle) and, as stated by Rackham (2006), may be considered "plants that appear or especially flourish every time a wood is cut down". *Sesleria*

nitida, an early-successional competitive clonal species, which chiefly grows in abandoned pastures, may be included in this group of species, but can persist in the forest stands until the end of the coppicing rotation. In fact, dense tussocks of competitive species may persist for long time in forests with strongly altered soil conditions (Hermy 1994; Verheyen and Hermy 2001) and in the understory of coppiced woods (Wellstein et al. 2014).

Some trait states showed preferential distribution in stands at the end of the coppicing rotation cycle, underlining still stressful conditions, which might be thought as a legacy of the post-logging condition. In fact, vegetative propagation by rhizome fragmentation is supposed to be linked to the high stress/disturbance regimes (e.g. van Groenendael et al. 1996; Klimeš 2008); absence of storage organs has been related to the canopy openings right after the coppicing activities (Catorci et al. 2012a), whereas persistent green leaves, a particularly efficient resource acquisition strategy, allow plants to exploit a wider temporal niche, under thick tree canopies like those of the final phases of the coppicing rotation cycle.

Stands beyond the end of the usual coppicing rotation cycle (40-45 years after logging) were characterized by drought intolerant species, which grow on quite deep and moist soils, well supplied with nitrogen, and mostly belong to the *Carpino-Fagetea* class (Catorci et al. 2011; Mucina et al. 2016). These species, reflecting the ongoing processes of forest maturation, might be considered as "ancient forest species" (*sensu* Hermy et al. 1999), which are late-successional species associated with moist and nutrient-rich soils (Peterken and Game 1984). These species, which have a low colonization potential because of poor seed dispersal capacities and high sensitivity to disturbance (Peterken and Game 1984), may take several years to recolonize secondary forests (e.g. Whitney and Foster 1988; Motzkin et al. 1996). Moreover, this kind of species has been found to strongly react to small, favourable changes in light conditions (Plue et al. 2013).

The increase of such species (*Brachypodium sylvaticum*, *Lactuca muralis*, *Euphorbia amygdaloides*), usually growing in the Apennine beech woods and diagnostic of *Carpino-Fagetea* class (Mucina et al. 2016), seems to give further support to the hypothesis that the studied *O.*

carpinifolia woods are secondary forest ecosystems that originated from the degradation of mixed

beech woods, caused by forestry, a process hypothesized for other European managed beech woods

(Piskernik 1985; Šercelj 1996).

Other species (i.e. *Helleborus foetidus* and *Digitalis lutea* subsp. *australis*) increased their

frequency/abundance in no longer managed woods. These species usually grow in fringe vegetation

(Čarni 2005; Mucina et al. 2016), where the extent and pattern of solar radiation differ from that of

the coppiced woods interior and the soil is quite rich in nutrients. Moreover, the partially shadowed

conditions reduce the daily light irradiance, lowering the water evaporation and, thus, the drought

stress (Pausas and Austin 2001). Because of this, these species differ from the light-demanding taxa

(mostly typical of dry, poor environments) that characterize the coppiced woods in the first years

after logging (see Catorci et al. 2011).

The functional strategies revealed by ISA and RDA for no longer managed stands (tap root,

summer green leaves, and seeds of the highest seed mass class) seem to underlie the process of

recovery/maturation of the forest systems, since these indicator trait states are likely devoted to a

better partitioning of the spatial and temporal niches. In fact, tap roots, as well as summer green

leaves, have been associated to a late flowering strategy (Catorci et al. 2012b, 2013). Plants with

high seed mass have an early flowering strategy (in fact, most of species with high seed mass in our

dataset bloom in spring, see Online Resource 2), allowing for a longer time for seed maturation,

dispersal, germination, and juvenile production (Moles et al. 2004; Moles and Westoby 2006;

Bolmgren and Cowan 2008; Du and Qi 2010). Seedlings from large seeds are better than seedlings

from small seeds in their ability to tolerate long periods of low light during seedling establishment

(Hewitt 1998; Kitajima 2002) and to emerge from burial under deep litter or soil (see Moles and

Westoby 2006 and references therein), conditions associated with mature forest regeneration stages.

General model and conclusion

As previously stated by Catorci et al. (2011, 2012a), in sub-Mediterranean climate, during the coppicing rotation cycle, namely from 1 to 25 years after logging, the variations of environmental conditions in the understory lead to a non-random decline of light-demanding and drought tolerant taxa, which are substituted by the so-called generalist forest species (see Bengtsson et al. 2000) and to impoverished assemblages of the herb layer, reflecting the mechanisms proposed by Kopecký et al. (2013) for European lowland closed-canopy forests. Variations occurred after the end of the usual rotation cycle (abandoned woods) largely follow the statements of Verheyen et al. (2012), who suggested that after abandonment, species composition shifted towards more shade-adapted and nutrient-demanding species, which in the study case might be considered as "ancient forest species". However, our results seem to indicate that in sub-Mediterranean highly exploited secondary coppiced woods, the trends are a bit more complex than in temperate regions. In fact, a new phase of herb layer coenological diversification seems to start by the spread of a group of species coming from the forest edges, where they likely had been segregated during the usual coppicing rotation cycle.

Such partial dissimilarity from what emerged in central Europe seems to indicate that the effects of coppicing cessation on biodiversity should be assessed under different climatic conditions and land use legacies. Moreover, our findings suggest that the landscape structure and metrics should be as important as stand management for biodiversity conservation, since stand-scale survival of light-demanding species and their coexistence with shade-tolerant species are ensured by the shifting mosaic of differently aged patches created by coppicing (Decocq et al. 2004), but also by the presence of fringe vegetation and unmanaged stands.

Finally, our results emphasize the question on what a "true forest species" really is; in fact, some authors (Decocq et al. 2005; Chiarucci et al. 2010) suggested that the so-called "true forest species" are mostly stress-tolerant species that could rather be considered coppice-woodland species, developed through centuries of traditional management that favoured the dominance of species linked to the shaded conditions of late-successional phases of this type of management. More

research is needed to elucidate this question, but our results seem to indicate that the pattern of plant

species typical of mature hilly forests in the sub-Mediterranean context could be more complex than

what would have been expected and the species pool typical of such forest conditions could be

composed of a higher number of functional strategies. It remains an open question if our findings

indicate a temporary step of the forest recovery processes, due to a particular phase of the overstory

evolution, or rather the prelude of a new coenological composition of the understory.

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631 **Table 1** Descriptive statistics of Ellenberg Indicator Values calculated on species' presence/absence

632 matrix for stands at the end of the usual rotation cycle, i.e. 20-25 years since last coppicing and

633 stands where silvicultural treatments had not been performed for 40-45 years.

634

	Years since last coppicing	Mean $\pm$ SD	Median (IQR)
Light intensity	20-25	5.0 $\pm$ 0.3	5.0 (0.4)
	40-45	4.8 $\pm$ 0.4	4.8 (0.5)
Air temperature	20-25	5.6 $\pm$ 0.2	5.6 (0.2)
	40-45	5.7 $\pm$ 0.3	5.6 (0.3)
Continentality	20-25	4.6 $\pm$ 0.1	4.6 (0.1)
	40-45	4.6 $\pm$ 0.1	4.6 (0.1)
Soil moisture	20-25	4.6 $\pm$ 0.1	4.6 (0.1)
	40-45	4.8 $\pm$ 0.2	4.8 (0.4)
Soil reaction	20-25	6.5 $\pm$ 0.1	6.4 (0.1)
	40-45	6.4 $\pm$ 0.2	6.4 (0.3)
Soil nitrogen	20-25	4.9 $\pm$ 0.3	4.8 (0.4)
	40-45	5.3 $\pm$ 0.3	5.3 (0.5)

635 SD – Standard deviation. IQR – Interquartile range

636 **Table 2** Indicator species of stands at the end of the usual coppicing rotation cycle (20-25 years

637 since the last coppicing) and of no longer managed stands (40-45 years since the last coppicing), as

638 performed using indicator species analysis, and respective observed indicator values (IV) and

639 significance values (*P*).

640

Group of stands	Indicators species	Observed maximum IV	*P*
20-25 yr old stands	*Hepatica nobilis* Schreb.	0.828	0.001
	Sesleria nitida Ten.	0.787	0.001
	Primula vulgaris Huds. subsp. *vulgaris*	0.787	0.001
	Carex digitata L.	0.664	0.001
	Melittis melissophyllum L. subsp. *melissophyllum*	0.593	0.008
	Pulmonaria apennina Cristof. *et* Puppi	0.421	0.002
40-45 yr old stands	*Melica uniflora* Retz.	0.733	0.009
	Brachypodium sylvaticum (Huds.) P. Beauv. subsp. *sylvaticum*	0.594	0.025
	Ajuga reptans L.	0.555	0.020
	Lactuca muralis (L.) Gaertn.	0.536	0.014
	Helleborus foetidus L. subsp. *foetidus*	0.529	0.004
	Digitalis lutea L. subsp. *australis* (Ten.) Arcang.	0.517	0.005
	Euphorbia amygdaloides L. subsp. *amygdaloides*	0.408	0.022

641

Fig. 1 Location of the study area (Umbria-Marche Apennines). The small square in the map on the upper right corner indicates the position of the study area in Italy. Circles identify stands at the end of the usual coppicing rotation cycle, i.e. 20-25 years since last cut; triangles indicate stands where silvicultural treatments had not been performed for 40-45 years.

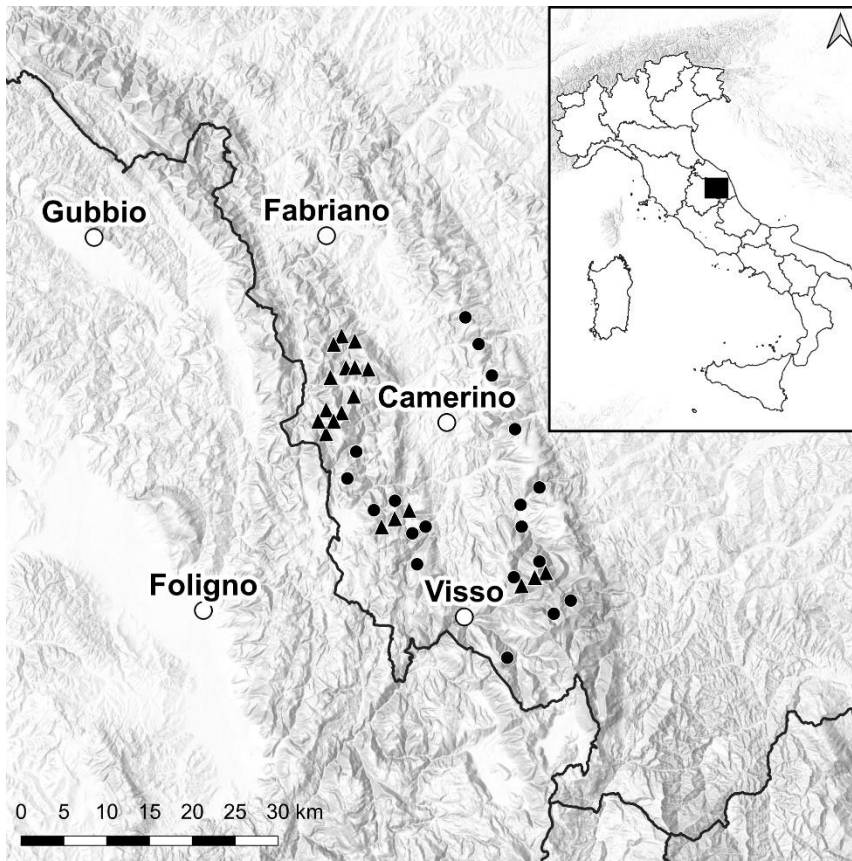**Fig. 2** Redundancy analysis ordination graph of the Hellinger-transformed "relevés-by-species" matrix, constrained by the explanatory variables altitude, aspect, slope angle, outcropping rock cover, rock fragments cover, tree, shrub and herb layer cover, time since the last coppicing. Labels of species falling next to the axes origin have been omitted (Ajre *Ajuga reptans*; Brru *Brachypodium rupestre*; Brsy *Brachypodium sylvaticum*; Cadi *Carex digitata*; Cyre *Cyclamen repandum*; Euam *Euphorbia amygdaloides*; Heno *Hepatica nobilis*; Lufo *Luzula forsteri*; Lusy *Luzula sylvatica*; Mepe *Mercurialis perennis*; Meun *Melica uniflora*; Saeu *Sanicula europaea*; Siit *Silene italica*; Seni *Sesleria nitida*; Taco *Tamus communis*; Vire *Viola reichenbachiana*)
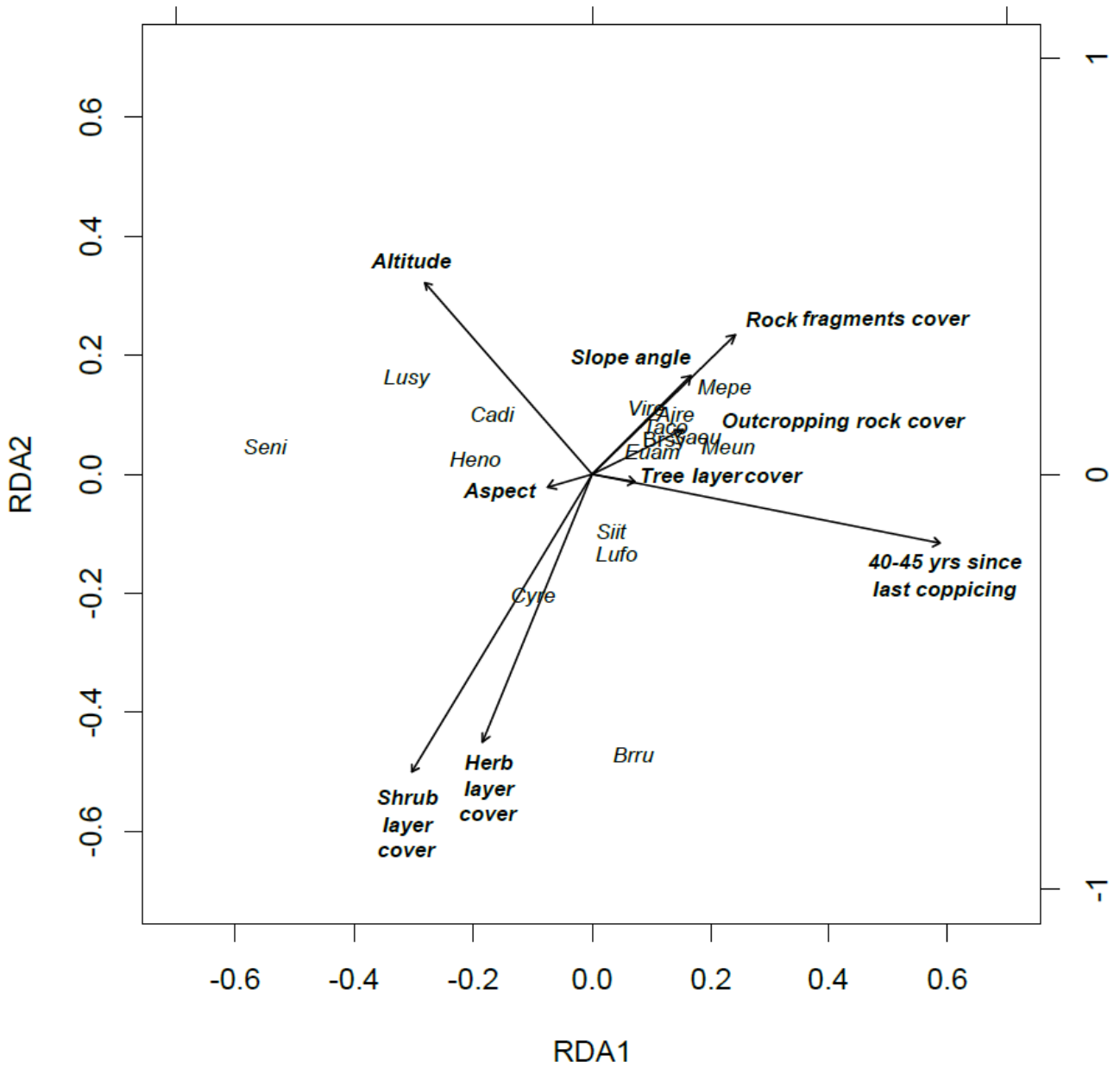
Fig. 3 Redundancy analysis ordination graph of the "relevés-by- community-weighted mean trait values" matrix, constrained by the explanatory variables altitude, aspect, slope angle, outcropping rock cover, rock fragments cover, tree, shrub and herb layer cover, time since the last coppicing. Labels of trait states falling next to the axes origin have been omitted (esp - early spring flowering; fra - rhizome fragmentation; hyg - hygromorphic leaves; mes - mesomorphic leaves; mls - mid-late summer flowering; nso - absence of storage organs; nvp - absence of vegetative propagation; per - persistent green leaves; rhi - rhizome; run - runner; s2 - seed mass 0.21-0.50 mg; s3 - seed mass 0.51-1.00 mg; s4 - seed mass 1.01-2.00 mg; s5 - seed mass 2.01-4.00 mg; s6 - seed mass 4.01-10.00 mg; s7 - seed mass > 10.00 mg; sum - summer green leaves; tr - tap root).
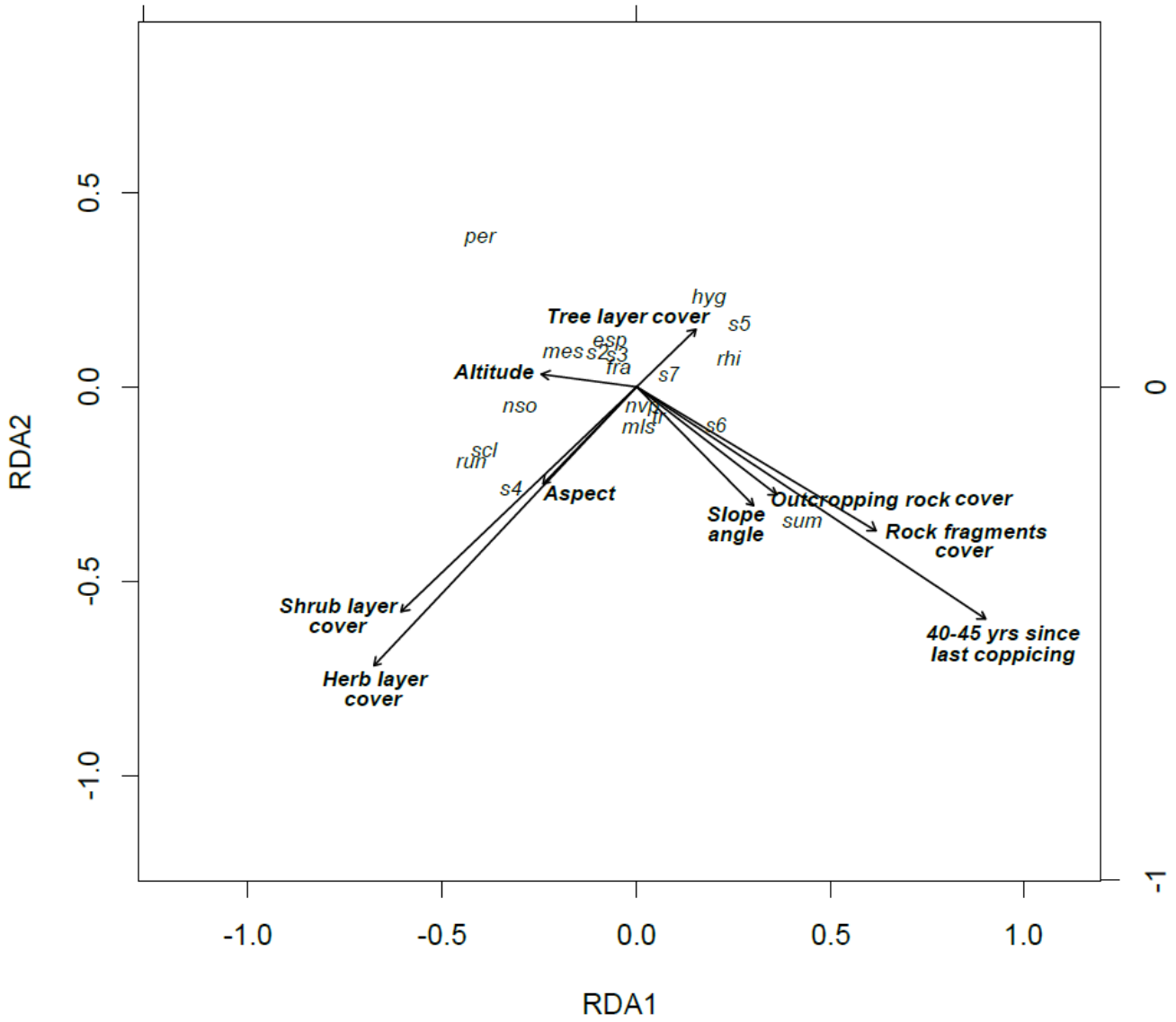
665 **Fig. 1**

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667   **Fig. 2**

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670   **Fig. 3**

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