

Old coppice versus high forest: the impact of beech forest management on plant species diversity in central Apennines (Italy)

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Abstract

Aims

Silvicultural management plays a major role in shaping understory diversity through its action on stand structure. In many parts of Europe, recent socioeconomic changes have led to the progressive abandonment of coppicing in favor of high forest (HF) management. In order to examine how this change impacts understory species, we compared old coppice-with-standards and HF stands in terms of structural features and understory richness and composition, also taking into account the diagnostic species pool of the habitat. Since the management systems for coppices and HFs differ in cutting regime, we expect that they would cause different changes in floristic composition and richness.

Methods

The study area was the Montagne della Duchessa massif, in central Italy. Structural differences and floristic richness were compared, and the diagnostic species diversity was analyzed using rarefaction curves and Rényi diversity profiles. Differences in understory composition were analyzed through indicator species analysis.

Important Findings

Our results showed that, though the old coppices have a slightly higher number of understory species in general, the HF stands have

greater mean species richness in both understory and diagnostic species, the latter being more evenly distributed inside the community. These findings were related to the cut regime, which favor a constant canopy cover over time and thus the maintenance of more stable microclimatic conditions, promoting the higher abundance and evenness of shade-tolerant and vernal species. Conversely, the dense canopy of the old coppice appears to affect the understory richness by reducing the presence of light-demanding species, but still without a complete recolonization of the shade-tolerant species. Overall, our findings provide the first insights supporting that, in a Mediterranean montane context, old coppice conversion to HF could over time improve the species diversity in these habitats and help maintain good conservation status of the typical mature beech forests.

Keywords: diagnostic species, habitat directive 92/43 EEC, Mediterranean beech forests, rarefaction curves, Rényi diversity profiles, silviculture, understory diversity, understory richness

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INTRODUCTION

In forest communities, structural features play an important role in modulating floristic composition and ecosystem functions (Neumann and Starlinger 2001). Tree canopy and size, age, stem diameters and density all influence such environmental conditions as light, temperature and moisture in the understory and the nutrient flux, which in turn could have an impact on species composition and competition

processes (du Bus de Warnaffe and Lebrun 2004; Thimonier *et al.* 1992, 1994). Forest management modifies forest structure, and therefore may play an important role in shaping species diversity and promoting ecological stability (Decocq *et al.* 2004; Humphrey *et al.* 2000). The effects of forest management depend mainly on its intensity and extent, both of which induce a disturbance regime in the understory (Barbier *et al.* 2008; Durak 2012; Jiménez *et al.* 2015; Van Oijen *et al.* 2005).

European temperate forests have been exploited throughout human history. The most common management types already existed in the 19th century, when many forests were managed as single coppice or coppice-with-standards (CWS), and some as high forests (HF) harvested tree by tree (Oldeman 1990; Piussi 1994). In a CWS system, young shoots are cut down on short rotations and new shoots re-sprout from dormant buds on the cut stumps. Single-stemmed trees (standards) are retained in a sparse canopy for one or more rotations, in order to ensure genetic diversity and a certain amount of canopy cover. By contrast, HF systems are characterized by stands of single-stemmed trees that originate from seed; the rotation times for these systems are longer than those for CWS stands. Among the temperate broadleaved forests, those dominated by beech (*Fagus sylvatica*) are some of the most extensive and widespread throughout Europe, from Sweden and Norway to its southern limit in Italy, where beech dominates the Apennine chain and afford the most common woody resource, exploited for millennia. Traditionally, these forests have been managed for centuries as coppices or CWSs. However, in recent years changing economic and societal demands in many parts of Europe have led to a progressive decline in CWS management in favor of modern HF management regimes (Baeten *et al.* 2009; Van Calster *et al.* 2008a). These processes are also widespread in Italy, where the progressive depopulation and socioeconomic changes occurring over the last 60 years in the mountainous areas of the Apennine chain have led to a pronounced drop in local demand for small-sized timber, firewood and charcoal (Bracchetti *et al.* 2012; Falcucci *et al.* 2007; Sitzia *et al.* 2010). As a consequence, many CWSs have been almost completely abandoned and most of them have been converted to HFs (Ciancio *et al.* 2006; Coppini and Hermanin 2007).

Fagus sylvatica forests have been intensely studied from different points of view (Bartha *et al.* 2008; Canullo *et al.* 2011; Di Pietro 2006; Magri *et al.* 2006; Willner *et al.* 2009), and some authors have already addressed the conversion problem, most of them focusing on lowland deciduous forests in central Europe (Baeten *et al.* 2009; Decocq *et al.* 2004; Van Calster *et al.* 2008a; Vild *et al.* 2013); however, only a few have examined beech-dominated forests in mountainous areas of the Mediterranean region, in most cases using a structural approach (Ciancio *et al.* 2006). Moreover, up to our knowledge no study has compared old CWS and HF beech stands in terms of understory species diversity.

We compared old CWS and HF beech stands of the central Apennines (Italy), first characterizing the structure of both systems, then focusing on plant species diversity, with particular emphasis on beech forest diagnostic species (*sensu* Habitat Directive 92/43/EEC).

In particular, we sought to answer the following questions:

1. What are the differences between old CWS and HF in terms of understory species richness and composition?

2. Which are the differences between old CWS and HF in terms of the diversity of diagnostic species?

Since the progressive aging of coppices and the subsequent change in cut regime is likely to have an impact on the understory species, information about the differences in floristic composition and diversity between old CWS and HF stands can be particularly useful for conservation and management of beech forests.

MATERIALS AND METHODS

Study site

The study was carried out in the Montagne della Duchessa massif, located within the northern portion of the Velino-Sirente chain, between the Lazio and Abruzzo regions (central Italy, see Fig. 1). This mountainous site includes high altitude peaks such as Monte Morrone (2141 m a.s.l.), Monte Costone (2239 m a.s.l.) and Monte Murolungo (2184 m a.s.l.). The surrounding area is mainly mountainous and is characterized by a limestone substrate (Accordi *et al.* 1988) and a sub-Mediterranean climate. The vegetation consists mainly of microthermal *F. sylvatica* forests (belonging to *Cardamino kitaibelii-Fagetum sylvaticae*) at higher elevations and thermophilous *F. sylvatica* forests (belonging to *Lathyro veneti-Fagetum sylvaticae*) at lower elevations (Scolastri *et al.* 2014); both are recognized as priority habitat, falling into the 9210* code (Apennine beech forests with *Taxus* and *Ilex*) (Habitat Directive, 92/43 EEC). Beech forests occupy a surface of about 1200 ha, ranging approximately from 1000 m to 1900 m a.s.l.; the current extent is the result of local land use adopted over centuries, such as grazing (mainly sheep and cows, frequently at high altitude) and forest management. The stands are almost monospecific, as *F. sylvatica* dominates the tree layer, but there are also other woody species such as *Acer pseudoplatanus* and *Sorbus aucuparia* at higher elevations, and *A. opalus* ssp. *obtusatum* at lower elevations. These forests have been managed mainly as CWS and as HF, mainly following a patchy pattern. Historically, two main exploitation events happened: in 1915, beech forests were cut intensely, prevalently for charcoal and poles, while between the 1950s and 1960s, cuttings were broader and distributed over almost the entire area. During this time, CWSs were managed as clearcutting, while HF stands were managed as shelterwood with successive cuts, albeit often with a lack of intermediate treatments (e.g. liberation treatment) and in some cases this gave rise to stands formed by older trees and younger individuals derived from the natural regeneration after cut. Subsequently, in the 1970s, cuts were only occasional and very modest. Both HF and CWS stands have not been exploited since the 1960s, so the surveyed HFs are still in their cut cycle, while coppices are over their turn and have to be considered as old CWS (>38 years); moreover, none of them has been converted to HF yet. As these environmental conditions and land use history are regionally widespread throughout the central Apennines, the Montagne della Duchessa massif can be considered a highly representative

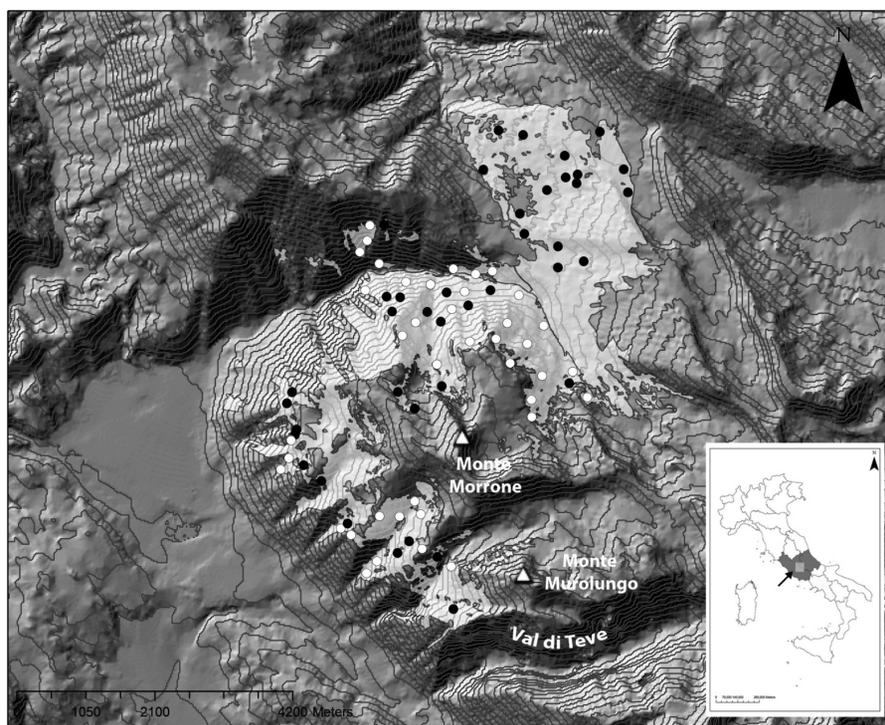


Figure 1: the study area. The forest areas surveyed are bounded and colored in light grey; old coppice-with-standards (CWS) plots are represented with white dots, high forest (HF) plots with black ones.

area. Moreover, most of the area considered in this study lies in the ‘Montagne della Duchessa’ Regional Natural Reserve, which recently has been recognized as a Special Protection Area (according to the European Directive 79/409/EEC), part of which has also been recognized as a Site of Community Importance (according to the European Directive 92/43/EEC). The area belongs also to the ‘Apennines high-elevation’ site of the international Long-Term Ecological Research network (LTER) (Cutini *et al.* 2012; Stanisci 2012).

Sample design and data collection

Only old CWS and HF stands were compared. Information about the management regime was obtained through the Reserve’s forest management plan and the book of cuts available at the Italian State Forestry Corps. In order to reduce the effect of the environmental variability and to analyze the management effect on understory richness and composition in old CWS and HF stands, the data obtained from old CWS and HF stands were put into a GIS environment (ArcGIS 9.2, ESRI) and a stratification procedure was performed by creating classes of aspect and slope (data were extracted by a Digital Elevation Model, 20 m resolution).

Altitude was not considered in the stratification procedure, as the distribution of the old CWS and HF stands along the altitudinal gradient proved to be comparable (more details on stratification procedure and data on environmental variables are provided in supplementary Appendix A). This stratification allowed us to have old CWS and HF plots with a comparable

environmental variability, and then to consider only the possible effects due to management differences. A total of 80 points were randomly placed inside the strata created using Hawth’s tool program (Beyer 2004) in the GIS environment, each one at a minimum distance of 200 m from the others, and at a minimum of 30 m from the forest borders, in order to reduce pseudoreplication and the edge effect. Sixty-six square plots (36-old CWS and 30 HF) were monitored during May–July in 2012 and 2013. Each plot (400 m²) was divided into 16 subplots (25 m²); inside each plot the vascular species abundance was quantified by subplot frequency (i.e. from 0 to 16). Plants were identified at species level using standard floras (Pignatti 1982; Tutin *et al.* 1964–1980, 1993); nomenclature was standardized according to Conti *et al.* (2005). The diagnostic species selected in this study were those adopted by the Habitat Directive Interpretation Manual (Biondi *et al.* 2009; European Commission 2013) as target for the 9210* Habitat (Apennine beech forests with *Taxus* and *Ilex*), which defines the central and southern Apennine beech forests (Biondi *et al.* 2009, 2012). In the Habitat Directive, the concept of diagnostic species is based on the plants’ fidelity towards specific vegetation units (Chytrý *et al.* 2002), so these species can be good indicators for conservation and management purposes (further information about the Habitat Directive, and the list of the diagnostic species found, are included in the supplementary Appendix B).

The following structural parameters were taken at plot level: canopy closure (taken using a spherical densiometer), diameter at breast height (DBH, 1.3 m above ground

level) for trees with dbh ≥ 2.5 cm, and tree height (every five sampled trees using a laser rangefinder). Trees were classified as dominant, co-dominant, dominated or shrubby and as individual, sucker or standard tree (Tabacchi *et al.* 2006).

Statistical analysis

Old CWS and HF stands were compared on the basis of structural and floristic differences. A Kolmogorov–Smirnov procedure was conducted for all the variables in order to test the normality. Because the data did not meet the assumption of a normal distribution, all the comparisons were made through the *U* Mann–Whitney non-parametric test ($P < 0.05$). A sequential Bonferroni correction was applied in order to adjust significance levels to control Type 1 error rates in multiple testing (Quinn and Keough 2002).

Structural diversity

Structural comparison was performed on the basis of canopy closure, basal area (m^2/ha), mean DBH (cm), mean tree height (m), the number of individual trees per plot and the ratio of sprouts on the total number of individuals. Differences in vertical structure were investigated using structural diversity indices. The Shannon index (SH_{DBH}) was applied to the proportion of trees in each size (DBH) class after dividing tree diameters in 10 cm DBH classes:

$$\text{SH}_{\text{dbh}} = \sum (-\log_2 p_i) p_i$$

where p_i is the relative abundance of trees in the i_{th} size class (Buongiorno *et al.* 1994; Fabbio *et al.* 2006).

Since there was no data on the crown projection area, as in the original calculation proposed by Neumann and Starlinger (2001), the Vertical Evenness (VE) was considered on the basis of its components: VE_N (the proportion of the number of trees in each layer) and VE_G (the proportion of the basal area in each layer). The latter two indices were calculated considering the number of trees in each social position, as proposed by Fabbio *et al.* (2006):

$$\text{VE}_N = \sum ((-\log_2 p_i) p_i / \log_2 3)$$

where p_i is the relative abundance of trees in each layer;

$$\text{VE}_G = \sum ((-\log_2 p_i) p_i / \log_2 3)$$

where p_i is the relative basal area in each layer.

The SH_{DBH} ranges from zero (lower DBH heterogeneity) to ∞ (higher DBH heterogeneity) while the VE assesses the multi-storied (higher values) or single-storied (lower values) stands (Fabbio *et al.* 2006). Both indices evaluate the vertical layering of the stand.

Floristic diversity and composition

Floristic differences between CWS and HF stands were investigated using two main layers on the basis of the life forms:

overstory (Phanerophytes) and understory (Nanophanerophytes, Chamaephytes, Hemipterophytes, Geophytes and Terophytes).

Old CWS and HF were compared through plot-based rarefaction curves (Gotelli and Colwell 2001) using the 9210* Habitat Directive understory diagnostic species, in order to give a qualitative meaning to the understory richness. Rarefaction curves were performed in EstimateS (Colwell 2013) using the analytical formula of Chiarucci *et al.* (2008). Samples were randomized without replacement, selected from $n = 1$ to S (where S is equal to the total number of samples) and the cumulative number of different species tabulated. The 95% confidence intervals of the rarefaction curves (\hat{S}_{MaoTao}) were assessed to determine whether species richness was significantly different among datasets (Colwell 2013). Heterogeneity, evenness and dominance of the habitat 9210* understory species pool inside the dataset were investigated using the diversity profiles, based on the Rényi's generalized entropy theory (Carranza *et al.* 2007; Rényi 1961; Ricotta and Avena 2003). In fact, for a distribution function characterized by its proportional abundance $p_i = (p_1, p_2, \dots, p_n)$. Rényi (1970) extended the concept of Shannon's information (entropy), defining a generalized entropy of order α as:

$$H_\alpha = \frac{1}{1-\alpha} \log \sum_{i=1}^N p_i^\alpha$$

where $0 \geq \alpha \geq \infty$ and p_i denotes the relative abundance of the i_{th} element in a system ($i = 1, 2, \dots, N$), and N is the total number of element types in a system.

In order to investigate the differences in understory composition, an Indicator Species Analysis (ISA; Dufrene and Legendre 1997) was performed on the species per plot matrix, after removing rare species, that is, low frequency species that appeared in only one plot. This analysis provided an indicator value for each species in each group (in our case, old CWS and HF) and identified the representative species (according to their occurrence and abundance) of each silvicultural system. The same analysis was also done using the Ellenberg Indicator Values (Ellenberg 1998; Pignatti 2005) for light and nutrients, in order to understand which conditions characterize the two silvicultural systems. The ISA values were tested for significance using a Monte Carlo test (4999 permutations, $\alpha = 0.05$).

The Rényi diversity profiles were performed using the 'BiodiversityR' package (version 2.3.6) (Kindt and Coe 2005) in the R-statistical framework (version 2.15.3; R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>), and the ISA was performed using the PC-ORD software (McCune and Mefford 1999).

RESULTS

Structural diversity: differences between beech management systems

Significant differences between old CWS and HF were found for almost all the considered parameters (mean DBH, mean

height, number of individuals and sprouts ratio) (Table 1). Old CWS stands had stems with lower DBH and lower mean height, but a higher number of individuals than in HF. As a direct consequence of the management method, old CWS also showed a higher ratio of sprouts, the proportion of stems which have regenerated from stumps. Canopy closure was quite high in both systems, and the lack of difference in the mean basal area is due to the fact that even though old CWS had the higher number of stems, they had lower DBH values than HFs.

Regarding structural diversity indices, only the SH_{dbh} and VE_G were significant: old CWSs were found to have lower values of the SH_{dbh} and higher VE_G values than HF, which, in turn, showed a higher DBH heterogeneity, but with a tendency to be single-storied.

Floristic diversity: the impact of beech forest management on the understory and diagnostic species diversity

Despite a higher total number of species (145 versus 118), old CWS showed a significantly lower mean number of both understory and diagnostic species per plot than HF (Table 1), while no significant difference was found for the overstory layer. Rarefaction curves, applied to 9210* understory diagnostic species (Fig. 2), showed that HF stands had higher species richness and higher steepness in the first part of the curve than old CWS. Moreover, the plotted proportion of the diagnostic species inside the total species pool showed that the contribution of the diagnostic species was higher in HF compared to old CWS stands.

The Rényi diversity profiles (Fig. 3) applied to the diagnostic species showed that as the alpha value increased, the

Table 1: U Mann–Whitney test results for structural parameters and species richness

	CWS	HF	P value
	Mean ± SD	Mean ± SD	
Canopy closure	99.03 ± 1.61	99.57 ± 1.01	0.102 n.s.
Basal area	1.33 ± 0.24	1.46 ± 0.32	0.122 n.s.
Mean DBH	9.30 ± 1.61	20.36 ± 5.53	0.000
Mean height	9.27 ± 1.56	14.00 ± 3.24	0.000
Number of individuals	55.78 ± 24.09	28.53 ± 9.08	0.000
Sprouts ratio	0.82 ± 0.09	0.32 ± 0.25	0.000
SHDBH	1.73 ± 0.17	2.00 ± 0.39	0.000
VE_N	0.72 ± 0.09	0.67 ± 0.21	0.425 n.s.
VE_G	0.73 ± 0.2	0.36 ± 0.26	0.000
Understory richness	14.86 ± 7.11	20.57 ± 7.83	0.002
9210* species richness	7.03 ± 3.54	12.30 ± 4.15	0.000

DBH refers to the diameter at breast height, and is a measure of density, SHDBH is the Shannon diversity index applied to the DBH classes, while VE_N and VE_G are both indicators of vertical differentiation; in particular, VE_N is the proportion of trees in each layer, and VE_G is the proportion of the basal area in each layer. n.s., means not significant.

The P values after sequential Bonferroni correction are shown.

floristic heterogeneity and evenness increased in HF stands (higher values of Shannon and Simpson indices and higher values of the reciprocal of the Berger–Parker index) compared to old CWSs.

On the basis of the ISA results (Table 2), HF stands showed high association with 15 species (13% of the understory species), 10 of which (67%) were also habitat diagnostic species (*Anemone apennina*, *Aremonia agrimonoides*, *Cardamine bulbifera*, *Galium odoratum*, *Lactuca muralis*, *Lathyrus vernus*, *Potentilla micrantha*, *Ranunculus lanuginosus*, *Rubus hirtus* and *Viola reichenbachiana*). Old CWS were represented by only one species, *Lilium bulbiferum*, not included in the Habitat diagnostic species list. The ISA calculated using the Ellenberg indicator values for light and nutrients (Table 3) showed that the HF were characterized by shaded conditions (L2, L3 and L4) and a moderate to high nutrient availability (N4, N5 and N6). Instead, these results did not relate old CWS to any particular condition. Moreover, a further comparison of the most common species found in both systems (Table 4), showed that the most frequent species in old CWS and HF stands are almost the same, but with different frequencies (higher in HF stands).

DISCUSSION

Our results highlighted differences not only in structural features, but also in species richness between old CWS and HF.

In terms of structural features, as expected, the main differences were due to the management type and were reflected by a different spatial aggregation pattern and vertical layering. In old CWSs, stems were aggregated in stumps (high sprouts ratio), while in HF they were not aggregated and were more spaced; this spatial pattern could cause differences in space occupancy and therefore can determine differences in the amount of surface available for understory plants. Regarding the vertical layering, as suggested by Fabbio et al. (2006), the higher density in old CWS probably favored the stems' competition for light and space, leading over time to greater vertical evenness compared to that of HF stands.

In terms of species richness, old CWS showed a higher total species number with respect to HF stands. This fact can be the consequence of the differences in cut frequency and severity between the two management systems: in CWSs, clearcutting allows more light to reach the forest ground. Canopy openings and gaps modify the understory environmental conditions by allowing greater energy and water influx and this, combined with higher soil temperature, increases the litter decomposition rate (Barbier et al. 2008; Hobbie et al. 2006). This process limits the abundance of shade-tolerant species and favors the spread of light-demanding species, which in turn leads to higher overall species richness.

This is consistent with Vild et al. (2013), who suggested that these differences may depend on the light regime, which could be considered the most important factor promoting species diversity and variability and therefore used as a single

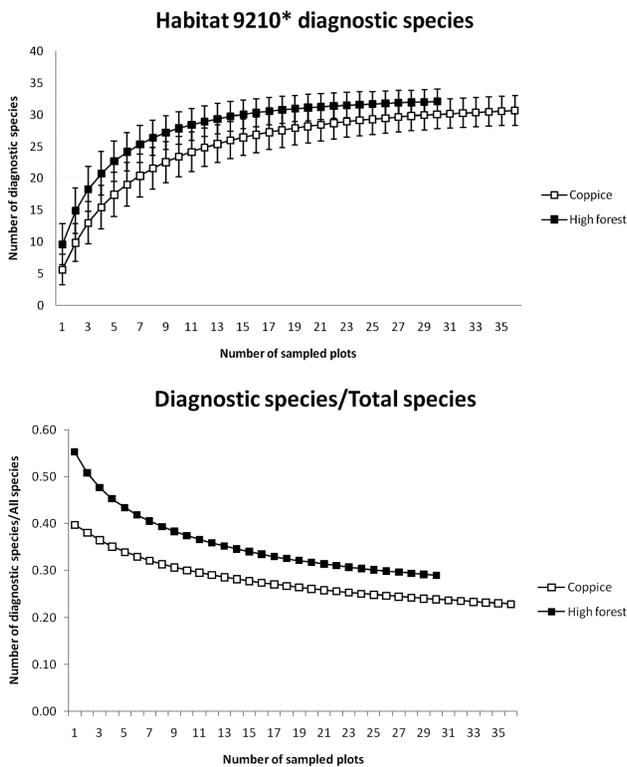


Figure 2: rarefaction curves for the 9210* Habitat (92/43 EEC) diagnostic species and the proportion of diagnostic species in the total species pool in old coppice-with-standards (CWS) and high forest (HF) stands. Black squares are high forest plots, while white squares are old CWS plots. The first graph shows higher steepness and higher diagnostic species richness in high forests in the first part of the curve. The second graph shows a higher proportion of diagnostic species in the entire species pool in high forest stands.

summary factor grouping less apparent microclimatic variations (Barkham 1992).

Previous studies conducted in lowland broadleaved forests indicated that coppice conversion had a generally negative impact on understory richness and diversity (Decocq *et al.* 2004; Vild *et al.* 2013), but Van Calster *et al.* (2008a) found a variable effect, mostly depending on the conversion type and, in particular, observed an increase in richness per plot in the situations of uneven-aged HF conversion. Our results showed that HF stands had higher mean understory richness per plot and higher diagnostic understory species richness per plot, the latter species being more evenly distributed (higher species equitability) inside the community. These differences may be explained by the management regime: HF contributed to a constant canopy cover over time (longer rotation times, shelterwood cut), which maintained more stable microclimatic conditions (Durak 2012) which, as mentioned above, may have favored higher abundance and more even distribution of shade-tolerant and vernal species such as *Cardamine kitabelii*, *Anemone apennina* and *Viola reichenbachiana*. This result is consistent with other studies conducted on other broadleaved forest types (Baeten *et al.* 2009; Brunet *et al.* 2010), which reported that areas with shelterwood cutting provide relatively undisturbed microsites where sensitive true forest species could survive (Godefroid *et al.* 2005). In fact, HF stands proved to be related to shaded habitat conditions and defined by species with a light response ranging between strictly shade tolerant (e.g. *Galium odoratum*, *Cardamine bulbifera*, *Ranunculus lanuginosus*) to semi-heliophilous (*Vicia sepium*, *Veronica chamaedrys*, *Rubus hirtus*). The slight variation in the light penetration pattern is related to canopy gaps caused by the past cut regime or by stochastic events such as falling

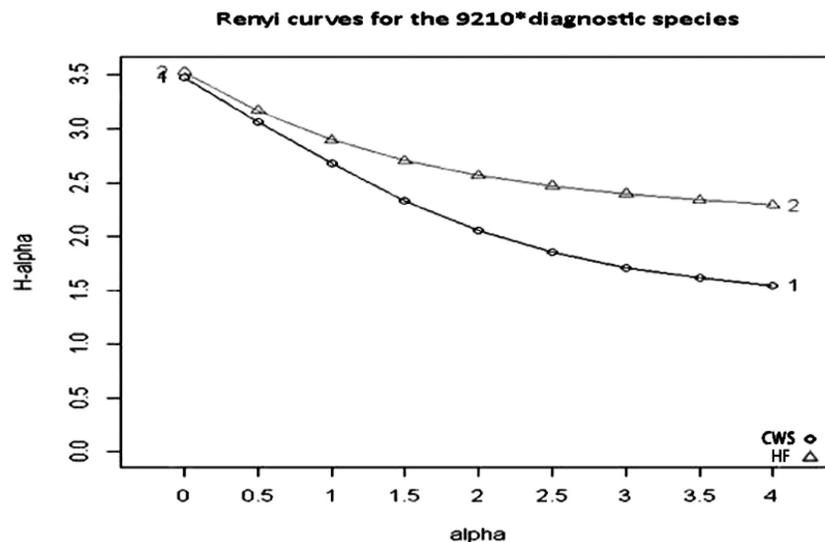


Figure 3: Rényi diversity profiles for the 9210* Habitat diagnostic species. Old coppice-with-standards (CWS, dots) are represented in curve number one (black), while high forest stands (HF, triangles) are represented in curve number two (grey). When alpha approaches 0, the diversity profile indicates differences in species number; when alpha approaches 1, it represents the Shannon diversity index; when alpha approaches 2, it represents the Simpson index; when alpha ≥ 4 it represents the reciprocal of the Berger–Parker index. High forests (HF) showed higher diagnostic species diversity and equitability.

Table 2: ISA results: shown here are the indicator value and the *P* value for each species and its association to the management type (old coppice: CWS; high forest: HF)

Species	System	IndVal	<i>P</i> value
<i>Lilium bulbiferum</i>	CWS	22.3	0.0418
<i>Cardamine bulbifera</i> *	HF	64	0.0002
<i>Galium odoratum</i> *	HF	61.2	0.0004
<i>Rubus hirtus</i> *	HF	53.7	0.0002
<i>Aremonia agrimonoides</i> *	HF	53.4	0.0014
<i>Viola reichenbachiana</i> *	HF	53.4	0.0022
<i>Anemone apennina</i> *	HF	48	0.0078
<i>Lathyrus vernus</i> *	HF	42.6	0.0348
<i>Lactuca muralis</i> *	HF	42.2	0.045
<i>Pulmonaria apennina</i>	HF	41.2	0.0076
<i>Ranunculus lanuginosus</i> *	HF	33.3	0.0002
<i>Ajuga reptans</i>	HF	30.6	0.0078
<i>Geranium robertianum</i>	HF	30.3	0.0058
<i>Potentilla micrantha</i> *	HF	29.9	0.034
<i>Veronica chamaedrys</i>	HF	13.3	0.0424
<i>Vicia sepium</i>	HF	13.3	0.034

Asterisks mark the species belonging to the 9210* Habitat list. Old coppices (CWS) are represented by only one indicator species (*Lilium bulbiferum*), while high forests (HF) are related to 15 indicator species, 10 of which are also representative of the 9210* priority Habitat (92/43/EEC).

Only species with a significant *P* value are shown.

trees; past studies have demonstrated that the relationship between light and vegetation is better explained by past light regimes than by current light conditions, because of the slowness of species pool variations (Thomas *et al.* 1999). Moreover, most of the species were also related to high availability of nutrients, and therefore to deeper soils (e.g. *Lactuca muralis*, *Viola reichenbachiana*, *Ranunculus lanuginosus*, *Aremonia agrimonoides*) (Pignatti 2005; Rameau *et al.* 1989–2008). Being well adapted to a specific habitat, diagnostic species are generally sensitive to habitat variations and share characteristics such as lower dispersal ability or limited seedling recruitment, along with the need for long-term undisturbed habitats for colonization (Brunet and von Oheimb 1998; Hermy *et al.* 1999). The ISA results, together with Rényi diversity profiles applied to the Habitat diagnostic species seem to indicate that HF stands favored the persistence of mesophilous species strictly related to mature forest habitats. Moreover, the understory species in HF stands, in particular those that characterize the 9210* beech forests, showed higher equitability values. Studying similar forest communities in other central Apennine areas, Bartha *et al.* (2008) considered old coppices as the mature stage along a chronosequence from the last cut, where canopy cover is mainly high and the environmental conditions could be related to the most stable stage. As stated by previous studies on lowland thermophilous woods of central Europe, the high canopy cover conditions that develop after coppice abandonment lead to a progressive decline in typical thermophilous

Table 3: ISA results for the Ellenberg indicator values: shown here are the indicator value and the *P* value for each light and nutrient value, and its association to the management type (old coppice: CWS; high forest: HF)

	Ellenberg values	System	IndVal	<i>P</i> value	
Light	L2	HF	63	0.0012	
	L3	HF	62.5	0.0016	
	L4	HF	60.6	0.0036	
	L5	HF	59.2	0.0752	
	L6	HF	49.9	0.2104	
	L7	HF	54.7	0.0614	
	L8	CWS	22.2	0.1388	
	L9	HF	13	0.1104	
	L11	CWS	16.1	0.9594	
	Nutrients	N0	HF	12.7	0.8186
		N1	HF	28.1	0.1278
N2		CWS	33.8	0.229	
N3		CWS	35.3	0.9126	
N4		HF	55.9	0.0314	
N5		HF	61.7	0.0016	
N6		HF	68.8	0.0002	
N7		HF	59	0.0102	
N8		HF	24.8	0.3301	
N9	HF	13.2	0.5769		

The light values range between L1 (deep shadow) and L12 (full light); in particular, the significant categories are: L2: intermediate conditions between deep shadow and shadow (5% of light radiation); L3: shadow conditions, 5% of light radiation; L4: intermediate conditions between shadow and semi-shadow (10% of light radiation). The nutrient values range between N0 (oligotrophic soil, with few nutrients) and N9 (high nitrate and phosphate concentrations). In particular, the significant categories are: N4: intermediate conditions between humic and less humic soils; N5: humic soils, nutrient rich; N6: intermediate conditions between humic and nutrient concentration in soils; N7: concentration of nutrients in soils. Significant *P* values are shown in bold.

understory species and the consequent increase of mesic, shade-tolerant species (Hédél *et al.* 2010). Despite the differences between the communities studied, these findings are consistent with our results; the lower contribution of diagnostic species to the species pool, and the lower mean understory richness per plot compared to that of HF stands, indicate old CWS as a stage in which the dense canopy negatively affects the species richness by reducing the light-demanding species pool, while the shade-tolerant species have not yet had enough time to spread. This trend is also highlighted by the lack of significant values for light and nutrients in the ISA. Moreover, the most common species found in old CWS are mostly the same as those found in HF stands, but with lower frequency in the former (Table 4). In addition, the diagnostic species are frequent in old CWS, although they are not yet evenly distributed throughout the understory layer. The management patchy pattern (CWS stands close to HF ones) could have favored the persistence over time of species with

Table 4: list of species that have the higher frequency in old coppice (old CWS) and high forest (HF) stands, respectively

Old CWS		HF	
Species	Frequency (%)	Species	Frequency (%)
<i>Viola reichenbachiana</i>	10.76	<i>Pulmonaria apennina</i>	14.79
<i>Cardamine kitaibelii</i>	11.28	<i>Cardamine enneaphyllos</i>	18.13
<i>Carex pilosa</i>	13.02	<i>Cardamine kitaibelii</i>	20.42
<i>Epipactis helleborine</i>	13.72	<i>Rubus hirtus</i>	21.25
<i>Euphorbia amygdaloides</i>	15.10	<i>Euphorbia amygdaloides</i>	21.67
<i>Aremonia agrimonoides</i>	16.84	<i>Anemone apennina</i>	33.96
<i>Lathyrus vernus</i>	17.19	<i>Viola reichenbachiana</i>	34.58
<i>Anemone apennina</i>	17.88	<i>Lathyrus vernus</i>	35.21
<i>Cardamine bulbifera</i>	18.23	<i>Aremonia agrimonoides</i>	45.00
<i>Galium odoratum</i>	21.53	<i>Galium odoratum</i>	59.58
<i>Cardamine enneaphyllos</i>	25.52	<i>Cardamine bulbifera</i>	60.21

The species are almost the same in both management types, but they differ greatly in frequency.

low dispersal ability (Carranza *et al.* 2012; Vellend 2003). On the other hand, the slightly higher number of species found in old CWS (145 versus 118 species) could indicate that understory maintained 'a memory' of the past management regime and as, after 50 years some heliophilous open-habitat species (such as *Brachypodium rupestre* and *Pteridium aquilinum*) grow together with more shade tolerant shrubby species (such as *Rosa pendulina* and *Cotoneaster integerrimus*).

CONCLUSIONS

Beech forests have been exploited for centuries, and their current species composition is also the result of the past forest management. Given the progressive transformation in land use that has been taking place in recent decades in mountainous areas and the trend to convert old CWS into HF in beech forest stands, concerns have arisen about how this change might impact beech understory composition. Some studies addressing this problem (Van Calster *et al.* 2008b; Vild *et al.* 2013) have considered conversion as a serious threat for species biodiversity in broadleaved forests. In this sense, we should note that if we consider biodiversity only a matter of species number, old coppices are of great value, as they showed a higher total number of species. Moreover, if we consider that biodiversity is also a matter of 'quality', we also need to pay attention to those species that characterize the habitat we are studying. We compared old coppices and HFs to understand whether conversion can have effects on the understory species, and if so, in what way. Our findings highlighted not only which system has the higher species richness or diversity, but also which was able to preserve the most typical understory species of the beech forest. HF management, by maintaining more stable microclimatic conditions over time, allowed higher abundance of species related to mature beech

forests (9210* Habitat diagnostic species). On the other hand, old coppices, having almost the same diagnostic species (even with lower frequency and abundance) showed high resilience. Beech coppices that overlap their cut cycle are destined to conversion to HF or to be completely abandoned, because of their progressive loss of capacity to issue shoots. Given the fact that over time, both choices (conversion or natural evolution) will favor the habitat species, it is only a matter of forest management. In this Mediterranean context, the conversion of the beech stands to HF can promote periodical overstory renovation, accelerate stand dynamics and reduce the risk of damage caused by windthrows and parasites (Ciancio *et al.* 2006). Moreover, in steeper sites, common in mountains of the Mediterranean area, conversion would mitigate hydrogeological risk and slope instability. At the same time, less frequent and less severe cuts would help maintain good conservation status of the mature beech forest species.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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