



DOCTORAL SCHOOL IN BIOLOGY
Section: Biodiversity and Ecosystems Analysis

XXVII Cycle
A.A. 2013/2014

***Floristic and structural variability of the
central Apennines beech forests in
relation to natural and anthropogenic
determinants***

***Variabilità floristica e strutturale delle faggete cen-
tro-appenniniche in relazione ai determinanti naturali
e antropogenici***

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Tutor: Dr. Maurizio Cutini



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appenniniche in relazione ai determinanti naturali e
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Abstract

Forests are complex ecosystems, in which the floristic composition is the result of the combined effect of several factors, acting at different levels. Climate, lithology, geomorphology act at a broader scale, driving the forest's communities differentiation while, at a finer scale, the understory species composition is shaped by the forest stand structure that directly influences the environmental conditions (light, temperature, moisture) at the ground level. *Fagus sylvatica* forests are the most abundant broadleaved communities in central and southern Europe; in Italy they represent the typical montane vegetation in the Apennine chain, where these coenoses reach the highest elevations of their whole distributional range. Beech forests have been managed for centuries, prevalently as coppice, or coppice-with-standards (CWS), and high forest (HF). However, in recent decades deep socio-economical changes have led to the progressive abandonment of coppice cut and its conversion to high forest management. These two systems differ in cut intensity and severity (both higher in CWS): given that forest management impacts upon overstory structure and therefore determines the understory composition, management changes are likely to affect understory species composition and diversity.

In this thesis I have analyzed the effect of the main environmental drivers on beech forests communities; I then focused on the management effects on understory species and 9210* Habitat diagnostic species richness and composition (*sensu* Habitat Directive 92/43 EEC), in order to understand the possible implications of the old CWS conversion on the floristic composition.

The study was conducted in central Apennines, on the Montagne della Duchessa massif, where beech forests occupy a surface of more than 1200 ha; these forests have ceased to be managed since '60s, so the CWS have become older, and are destined to be converted to the HF cut.

I studied the role of the environmental factors in differentiating the beech forests communities by using a dataset of 40 relevés randomly selected. The dataset obtained has been analyzed through a cluster analysis and a Indicator Species Analysis (ISA), in order to obtain groups of relevés and to characterize them in floristic terms; the groups obtained were then compared in terms of environmental and topographic variables, Ellenberg indicator values, life forms, Social Behaviour Types (SBT) and structural parameters. Results showed that the floristic and coenological variability is

shaped by a climatic and edaphic gradient, that both contribute to define two main communities: a microthermal one, placed at higher altitudes and cooler aspects (*Cardamino kitaibelii* - *Fagetum sylvaticae*), and a termophilous one, lying at lower altitudes and warmer aspects (*Lathyro veneti* - *Fagetum sylvaticae*). Social Behaviour Types and structural parameters were useful for detecting the effects of the progressive reforestation process occurring inside the microthermal community at higher elevation.

In order to investigate the differences between old CWS and HF stands in terms of understory richness and composition, I used 66 relevés, selected through a random-stratified method, so as to have a comparable number of relevés for each management category; old CWS and HF stands were compared in terms of structural attributes and floristic richness through a U Mann-Whitney test: the results showed how management is the main factor responsible for differences in the tree layer's spatial aggregation pattern and vertical layering, and that therefore determines the amount of surface available for understory species. HF stands showed a higher mean richness of both understory and diagnostic species, these latter being more evenly distributed (higher species equitability) inside the community. This leads to the consideration that in HF stands the cut regime provided a constant canopy cover over time, and then maintained more stable microclimatic conditions favoring a higher abundance and evenness of the shade-tolerant and vernal species. Conversely, in old CWS the dense canopy negatively affected the understory richness by reducing the light-demanding species pool, while the shade-tolerant species have not yet had time to spread.

In order to understand the implications of the old CWS conversion on beech forests ecosystem's ecological functions, the same dataset was analyzed through plant functional traits, by creating a relevés x traits matrix. A Redundancy Analysis (RDA) was performed to assess the relationship between traits states and management, while a U Mann-Whitney test was used to assess differences in traits states richness between the management types. The results were consistent with the previous findings based on habitat diagnostic species, as HF stands showed a higher affinity to traits typical of mature forests, while old CWS were more related to traits related to managed stands. Moreover, HF stands showed a higher abundance of those traits related to the natural forest's seasonal change, this indicating a good species distribution among the functional niches. Even in this case, old CWS was shown to be in a transitional stage, still represented by some traits related to management, where the mature forest traits are also present, but with lower abundance.

Finally, given that in a forest ecosystem understory represent more than 90% of species richness, and is the most sensitive to disturbance, the modern silvi-cultural strategies should take into account the management effects on forest biodiversity, and adopt sustainable interventions able to favor the typical biodiversity of the ecosystems we want to manage. This thesis provides useful information for management purposes, as our findings show that, in the forests studied, the old CWS conversion to HF could be a good management strategy if our aim is the conservation over time of the species typically related to mature forest conditions.

Riassunto

Le foreste sono ecosistemi complessi, la cui composizione floristica è il risultato dell'effetto combinato di diversi fattori, che agiscono a vari livelli. Il clima, la litologia e la geomorfologia agiscono a scala più ampia, determinando la differenziazione delle comunità forestali, mentre, a scala più fine, la composizione floristica del sottobosco è selezionata dalla struttura del popolamento forestale, che ha una influenza diretta sulle condizioni ambientali (luce, temperatura, umidità) a livello del suolo. Le foreste a *Fagus sylvatica* sono le più abbondanti comunità di latifoglie in Europa centrale e meridionale ed in Italia rappresentano la tipica vegetazione montana della catena appenninica, dove queste cenosi raggiungono le quote più elevate dell'intero areale. Le foreste di faggio sono state gestite per secoli, prevalentemente come cedui, o cedui matricinati, e come fustaie ma negli ultimi decenni, profondi cambiamenti socio-economici hanno portato al progressivo abbandono del taglio ceduo e al successivo avviamento all'altofusto. Questi due sistemi si differenziano sia per intensità che severità del taglio, entrambi di maggiore entità nel ceduo; dato che la gestione forestale agisce direttamente sulla struttura del popolamento forestale, cambiamenti nella gestione del taglio possono avere effetti sulla composizione e sulla diversità floristica del sottobosco.

In questa tesi ho analizzato gli effetti dei principali fattori ambientali sulle comunità di faggeta, concentrandomi poi sugli effetti della gestione forestale sulla composizione e ricchezza specifica sia delle specie del sottobosco che delle specie diagnostiche dell' Habitat 9210* (*sensu* Direttiva Habitat 92/43 CEE), al fine di comprendere le possibili implicazioni della conversione dei cedui invecchiati sulla composizione floristica. Lo studio è stato condotto in Appennino centrale, sul massiccio delle Montagne della Duchessa, dove le faggete occupano una superficie di più di 1200 ettari; queste foreste non sono state più gestite a partire dagli anni '60, quindi i cedui, ormai invecchiati, sono ora destinati all'avviamento all'altofusto.

Ho studiato il ruolo dei fattori ambientali nella differenziazione delle comunità di faggeta utilizzando 40 rilievi, selezionati in maniera casuale. Il set di dati ottenuto è stato analizzato attraverso una Cluster Analysis ed una Indicator Species Analysis (ISA) al fine di ottenere gruppi di rilievi, e di caratterizzarli in termini floristici; i gruppi ottenuti sono stati confrontati sulla base delle variabili ambientali e topografiche, dei valori di indicazione

di Ellenberg, forme biologiche, Social Behaviour Types (SBT) e parametri strutturali. I risultati hanno mostrato che la variabilità floristica e cenologica delle faggete studiate è modellata da due gradienti, uno climatico ed uno edafico, che contribuiscono entrambi nel definire due comunità principali: una microtermica, posta a quote maggiori ed esposizioni più fredde (*Cardamino kitaibelii* - *Fagetum sylvaticae*), ed una termofila, posta a quote più basse ed esposizioni più calde (*Lathyro Veneti* - *Fagetum sylvaticae*). L'utilizzo dei Social Behaviour Types, ed il loro incrocio con i dati sui parametri strutturali, ha permesso inoltre di rilevare gli effetti del processo di riforestazione che sta avvenendo all'interno della comunità microtermica, alle quote maggiori.

Al fine di indagare le differenze tra cedui invecchiati e fustaie in termini di ricchezza e composizione floristica del sottobosco, ho utilizzato 66 rilievi, selezionati attraverso un metodo random-stratificato in modo da avere un numero paragonabile di rilievi per ciascuna categoria di gestione. I cedui invecchiati e le fustaie sono state confrontate sia in termini di attributi strutturali che di ricchezza floristica attraverso un test U di Mann-Whitney. I risultati hanno mostrato come la gestione sia il principale responsabile delle differenze nella distribuzione spaziale e nella stratificazione verticale dello strato arboreo, che determinano quindi la quantità di superficie disponibile per le specie del sottobosco. Le fustaie hanno mostrato una maggiore ricchezza media per rilievo sia delle specie del sottobosco che di quelle diagnostiche, le quali hanno inoltre mostrato una maggiore eterogeneità ed equiripartizione all'interno della comunità. Questo porta a considerare che nelle fustaie il regime di taglio ha assicurato una copertura costante nel tempo, favorendo quindi il mantenimento di condizioni microclimatiche più stabili, che hanno determinato una maggiore abbondanza sia delle specie sciafile che primaverili. Al contrario, nei cedui invecchiati la densa copertura della volta arborea sembra avere influenzato negativamente la ricchezza del sottobosco riducendo le specie più eliofile, mentre le specie più sciafile, tipiche di foreste mature, sono presenti, ma con abbondanze minori.

Al fine di comprendere le implicazioni della conversione dei cedui invecchiati sulle funzioni ecologiche dell'ecosistema di faggeta, lo stesso gruppo di rilievi è stato analizzato sulla base dei plant functional traits, creando una matrice di rilievi x traits. Attraverso una Redundancy analysis (RDA) è stata valutata la relazione tra traits e gestione selvicolturale, mentre è stato utilizzato un test U di Mann-Whitney per analizzare le differenze in ricchezza dei traits tra i due sistemi selvicolturali. I risultati emersi sono coerenti con quelli precedentemente ottenuti, relativi alle specie

diagnostiche dell' Habitat; le fustaie hanno mostrato infatti una maggiore affinità per i traits tipici di foresta matura, mentre i cedui invecchiati si sono rivelati maggiormente legati a caratteri relativi a foreste gestite. Inoltre, nelle fustaie è stata rilevata una maggiore abbondanza di traits legati al naturale cambiamento stagionale delle foreste, indice di una migliore ripartizione delle specie tra le nicchie funzionali. Anche in questo caso, i cedui invecchiati hanno dimostrato di essere in una fase transitoria, ancora rappresentata da caratteri legati alla gestione, in cui i traits legati ad aspetti maturi sono comunque presenti, ma con minore abbondanza. In conclusione, considerando che in un ecosistema forestale il sottobosco rappresenta più del 90% della ricchezza specifica, le moderne strategie selvicolturali devono tenere in considerazione gli effetti della gestione sulla biodiversità forestale, in modo da adottare interventi sostenibili, in grado di favorire la biodiversità tipica degli ecosistemi che si vogliono gestire. Questa tesi fornisce indicazioni utili per la gestione in quanto i risultati ottenuti mostrano che, nelle foreste studiate, la conversione del ceduo invecchiato può essere una buona strategia di gestione, se il nostro obiettivo è la conservazione nel tempo delle specie tipicamente legate a condizioni di foresta matura.

Papers published or prepared in the course of the PhD

Paper 1

Scolastri A., Cancellieri L., Iocchi M., Cutini M., 2014. Patterns of floristic variation on a montane beech forest in the central Apennines (central Italy). *Plant Sociology* 51 (2): 69-82.

Paper 2

Scolastri A., Cancellieri L., Iocchi M., Cutini M. Old Coppice vs High Forest: the impact of beech forest management on plant species diversity in central Apennines (Italy). *Biodiversity & Conservation*, submitted.

Paper 3

Scolastri A., Bricca A., Cancellieri L., Cutini M. Old Coppice vs High Forest: effects of two management types on understory functional composition. *Plant Ecology*, submitted.

General introduction

Forests as complex biological systems

In broadleaved forest communities, the floristic composition is the result of the combined effect of several factors, acting at different levels: at a broader scale, environmental variables such as climate, lithology, geomorphology, and also successional dynamics, are great drivers of the forests' coenological differentiation (Van der Maarel, 2005). Moreover, at a finer scale, the major factor shaping the biotic and abiotic conditions is the forest stand, as it creates the specific microclimate and governs carbon and nutrient cycling, dictating habitat conditions for countless organisms (Durak, 2012). In fact, overstory structural features play an important role in modulating floristic composition and ecosystem functions (Neumann & Starlinger, 2001): tree canopy and size, age, stem diameters and density, have a direct influence on the environmental conditions (light, temperature, moisture) at the ground level, and can impact on understory species composition and competition processes (e.g. Thimonier *et al.*, 1992, 1994; Du Bus de Warnaffe and Lebrun, 2004). Growing under the trees canopy for most of the year, understory species are well adapted to the short light supply and show adaptations that are reflected into vegetative and reproductive strategies, that allow them to persist, compete, grow, and reproduce under shady conditions. Understory species represent more than 90% of the floristic diversity in forest ecosystems (Gilliam, 2007) and, by the reasons mentioned above, they are also the most sensible to changes in overstory structure and composition.

Beech forests: an overview

Among broadleaved forests, those dominated by *Fagus sylvatica* are the most abundant in central and southern Europe, thanks to the beech's physiological characteristics, allowing it to spread over a wide range of habitats, soil types and climatic conditions (Peters, 1997; Ellenberg, 1988). As well as in the Eastern Europe (Willner *et al.*, 2009), beech forests in Italy also represent the typical montane vegetation in the Apennine chain and, more generally, in the Mediterranean area (Di Pietro, 2009), as beech is found continuously throughout the whole Peninsula, from the southern Alps

to Sicily, with the exception of Sardinia and the smaller islands (Jalas & Suominen, 1972-1999); within this range, *Fagus sylvatica* dominates in deciduous forests, forming both pure and mixed communities from (400) 800 up to 2000 m a.s.l. Along the Apennine chain, it is the uppermost forest type, showing a pronounced aptitude for expansion in different environmental conditions, including those moderately altered by human activities. Given their key position, Apennine beech forests in many cases comprise a mixture of species belonging to different biogeographical districts; these biogeographical interrelations occur throughout the entire Apennine range, but are particularly represented in its central sector (Lazio and Abruzzo) where the central position, the higher altitude and the complex arrangement of the massifs, all contributed in creating a high degree of environmental heterogeneity (Di Pietro, 2009).

Forest management and its impact on understory

Italian beech forests, as well as other European broadleaved forests, have been managed for centuries, since they represent the most common woody resource. 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), prevalently on the basis of the product needed: firewood, charcoal or poles. Moreover, the consequent disturbance regime has probably modified over time the understory floristic composition, creating communities well adapted to the recurrent disturbance. In a CWS system, young shoots are cut down during 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 rotation, in order to ensure genetic diversity and a certain amount of canopy cover. By contrast, HF systems are characterized by single-stemmed trees stands which originate from seed and have prolonged rotation times. The tree stand is strongly affected by the forest management method, where the spatial structure of the forest is shaped by the management method implemented (Burton *et al.*, 2009; Scheller and Mladenoff, 2002); therefore it has a potential role in determining species diversity and ecological stability (Humphrey *et al.*, 2000; Decocq *et al.*, 2004). The effects of forest management depend mainly on its intensity and extent, both of which could induce a disturbance regime in the understory (Van Oijen *et al.*, 2005). Thus, the forest understory diversity and the ecosystem functioning are

likely to be affected not only by forest management/its lack, but also by the type of the forest management implemented (Decocq *et al.*, 2004, 2005; Schmidt, 2005).

Forest management: changes currently ongoing

One significant, though largely overlooked, environmental change that has occurred in recent decades is the large-scale abandonment of CWS management (Baeten, *et al.*, 2009): from '60s, the changing economical and societal demands, caused the progressive decline of CWS management in favor of modern HF management regimes in many parts of Europe (Van Calster *et al.*, 2008; Baeten *et al.*, 2009). These processes are also widespread in Italy, where progressive depopulation along the mountainous areas of the Apennine chain has led to a pronounced drop in local demand for small size timber, firewood and charcoal. As a consequence, many CWS have been almost completely abandoned and most of them are destined to HF conversion (Ciancio *et al.*, 2006; Coppini and Hermanin, 2007). CWS and HF management differ in cut frequency and severity (both higher in CWS): as vegetation composition is partially the result of the environmental conditions created by this management form, the conversion to HF is likely to have caused significant changes in the herb layer (e.g. Barkham 1992; Decocq *et al.*, 2004; Van Calster *et al.*, 2008). In the last decades, the conservation of forest biodiversity has become a key topic in the discussion on the conservation and sustainability of natural resources, given the forests' role as carbon sinks, and the effects of the intense exploitation by man. Even though *Fagus sylvatica* forests have been intensely studied from several viewpoints, such as ecological (Bartha *et al.*, 2008), functional (Campetella *et al.*, 2011; Canullo *et al.*, 2011), populational (Magri *et al.*, 2006), biogeographical (Willner *et al.*, 2009), we still know little about the effects of forest abandonment and coppice conversion on the understory plant communities. Modern management practices should also consider the forest ecosystem's diversity, favoring the conditions for the persistence and abundance of the habitat's species.

Aims

Given these premises, in this thesis I aim to analyze differences in floristic richness and composition between old CWS and HF stands, trying to understand which management type most favors the abundance of the understory species typical of beech forest habitat. To do this, I have structured my project into three objectives:

1. To study the floristic and coenological variability of the beech forests in a district of central Apennines, in relation to the main environmental determinants (**chapter 1**).
2. To analyze the differences in structural features and floristic richness between old CWS and HF stands, focusing on understory species and 9210* Habitat indicator species (*sensu* Habitat Directive 92/43 EEC)(**chapter 2**).
3. To analyze the differences between old CWS and HF stands in terms of functional composition using plant functional traits, as they reflect the species' adaptations to the environment (**chapter 3**).

CHAPTER 1

Patterns of floristic variation on a montane beech forest in the central Apennines (central Italy)

Patterns of floristic variation on a montane beech forest in the central Apennines (central Italy)

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Abstract

Climate, history and human land use have a strong influence on the distribution and floristic composition of beech forest communities. In the last 50 years, the decrease in human activities has led to the resumption of reforestation dynamics, so a certain variability in floristic composition is expected. We aim to identify the causes of local floristic variability in different stands of beech forests, integrating floristic, structural and ecological analysis.

Cluster analysis and Indicator Species Analysis (ISA) were performed to highlight floristic differences; the clusters obtained were compared through environmental and topographic variables, Ellenberg indicator values, life forms, Social Behaviour Types (SBT) and structural parameters. The species heterogeneity derives from a climatic and edaphic gradient. Two main types of beech forests were recognized: a microthermal one, placed at higher altitudes and cooler aspects (*Cardamino kitabehlii* - *Fagetum sylvaticae*), and the termophilous one, lying at lower altitudes and warmer aspects (*Lathyro veneti* - *Fagetum sylvaticae*). SBT and structural parameters were useful for detecting the effects of dynamic processes of reforestation. The integration of the floristic, structural and ecological analysis led to an accurate coenological overview of the beech forest communities and to the detection of the natural reforestation processes currently ongoing.

Keywords: Ellenberg's Indicator Values, floristic composition, forest management, forest structure, Indicator Species Analysis, Social Behaviour Types.

Introduction

Fagus sylvatica is the most abundant broadleaved forest tree in central and southern Europe thanks to its physiological characteristics, and can form communities that dominate in a wide range of habitats, soil types and climatic conditions (Peters, 1997; Ellenberg, 1988). It represents the typical montane vegetation in the Apennine chain and, more generally, in the Mediterranean area (Di Pietro, 2009), as well as in Eastern Europe (Willner *et al.*, 2009). Beech is found continuously throughout the Italian Peninsula from the southern Alps to Sicily with the exception of Sardinia and the smaller islands (Jalas & Suominen, 1972–1999). Within this range, *Fagus sylvatica* dominates in deciduous forests forming both pure and mixed communities from (400) 800 up to 2000 m a.s.l.; in the Apennines it is the uppermost forest type, showing a pronounced aptitude for expansion in different environmental conditions, including those moderately altered by human activities.

Apenninic beech forests have been intensely managed for centuries; however the depopulation and changes in the socio-economic conditions in Italy over the last 60 years have both led to a progressive drop in local demand for small size timber, firewood and charcoal, as in other Mediterranean countries (Romero-Calcerrada & Perry, 2004; Mottet *et al.*, 2006; Geri *et al.*, 2010; Bracchetti *et al.*, 2012). As a consequence many areas have been almost completely abandoned

(Ciancio *et al.*, 2006; Sitzia *et al.*, 2010) with no monitoring of their natural evolution. There are many phytosociological studies and reviews describing the sinecology of different beech forests throughout both the European and Mediterranean regions (Dierschke, 1990; Marinček *et al.*, 1993; Bergmeier & Dimopoulos, 2001; Biondi *et al.*, 2002; Willner, 2002); recently some studies have also started to take into account forest structure when describing forest's floristic and coenological patterns (e.g. Bartha *et al.*, 2008; Burrascano *et al.*, 2008, 2011; Canullo *et al.*, 2011; Sabatini *et al.*, 2013).

By integrating both floristic, structural and ecological analysis, this study aims to identify the causes of the floristic variability of the Duchessa beech forests. We set out to test if there are different communities in the forests surveyed; in particular, we want to answer to the following questions: (i) Are there different species assemblages in the local *Fagus sylvatica*-dominated communities, and can we distinguish different types of forests? (ii) Which environmental parameters determine the constitution of these communities?

As the Duchessa beech forests are included in the priority habitat 9210* ('Apennine beech forests with *Taxus* and *Ilex*', *sensu* 92/43/EEC Directive; EEC, 1992), understanding their floristic differentiation and increasing the knowledge of their coenological peculiarities, could help to preserve these communities and improve their management strategies for a better habitat conservation.

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Methods

Study area

The study was carried out in the Montagne della Duchessa massif, which is located within the northern portion of the Velino-Sirente chain, between the regions of Lazio and Abruzzo (central Italy) (Fig. 1). This mountainous site includes high altitude peaks such as Monte Morrone (2,141 m a.s.l.), Monte Costone (2,239 m) and Monte Murolungo (2,184 m). The surrounding area is mainly mountainous, characterized by a limestone substrate (Accordi *et al.*, 1988) and can be referred to temperate region *sensu* Rivas-Martinez classification (Blasi, 2010). In particular, the bioclimate features, defined using rainfall and temperature data from Rosciolo (903 m a.s.l.) meteorological station (1971-2002) (Fig. 2), shows that the annual average rainfall is 838.7 mm, the wettest month is November (110.7 mm) and the driest July (32.8 mm). The annual average temperature is 11.4°C, the hottest month is August (28.7°C) and the coldest January (-1.2°C). The Rosciolo station belongs to the temperate bioclimate characterized by a lower supratemperate (mountain) thermotype and a subhumid ombrotpe (Rivas-Martinez, 2004).

In the study area, beech forests occupy about 1,200 ha, ranging from 1,100 to 1,800 m a.s.l. These forests have been managed for centuries mainly as coppice with standards and as high forest. Historically, two main exploitation events have occurred: in 1915, when beech forests were intensively cut, mainly for coal and poles, and between '50s and '60s when cuts were broader and distributed over almost the entire area. After this latter event, these forests have no longer been exploited and the progressive reduction of the sheep-farming over the past 50 years has led to spontaneous reforestation processes, mainly at high altitudes (Ave-

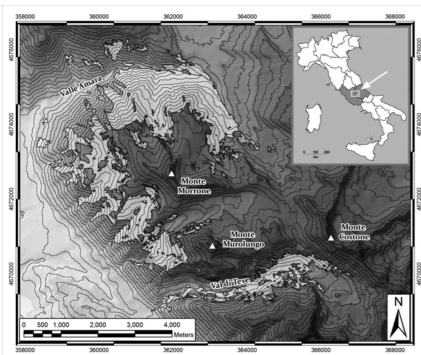


Fig. 1 – The study area, bounded and colored in light grey.

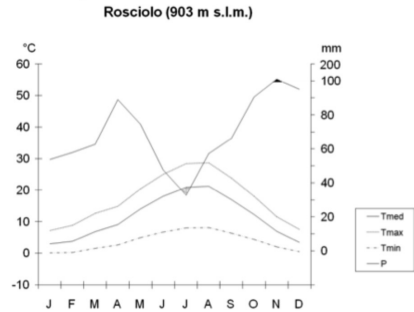


Fig. 2 - Thermopluviometric diagram (Rosciolo meteorological station [1971-2002; Data source: Ufficio Idrografico e Mareografico, Regione Lazio]).

na & Blasi, 1980; Petriccione, 1993).

The observed environmental conditions, bedrock composition and land-use history are regionally widespread in central Apennines; thus the Montagne della Duchessa massif could be considered a highly representative area for long-term environmental research (Theurillat *et al.*, 2007; Cutini *et al.*, 2012). Moreover, since the '90s, the Montagne della Duchessa site is a Regional Natural Reserve and, more recently, it has been recognized as a Special Protection Area (according to the European Directive 79/409/EEC). Part of it has also been recognized as a Site of Community Importance (European Directive 92/43/EEC).

Data collection

Forty square plots (400 m² each) were investigated during the May-July period of 2012. For each of them altitude (m), aspect (degrees) and slope (degrees) were measured. The sampling scheme included both vascular flora and forest structure surveys. Each plot was randomly selected throughout a stratified method, in GIS environment (ArcGIS 9.2, ESRI), on the basis of the main environmental parameters (altitude, aspect and slope) and the silvicultural management. The phytosociological relevés were made by following the methodology of the Sigmast Zurich-Montpellier school (Braun-Blanquet, 1932), while floristic nomenclature follows Conti *et al.* (2005). As structural parameters we recorded the diameter at breast height (DBH, 1.3 m above ground level) of each tree with a diameter ≥ 2.5 cm and the number of trees in each plot.

The micromorphology was evaluated using the Terrain Ruggedness Index (TRI, Riley *et al.*, 1999) calculated from the digital elevation model (20x20 m) using SAGA GIS software (Conrad, 2007). The TRI quantifies the topographic heterogeneity, and corresponds to

the average elevation change (from a digital elevation grid) between any point on a cell and its surrounding area.

To characterize the community types, the standard Ellenberg's indicator values (L, T, M, R, N) optimized for the Italian Flora and the life forms were used (Pignatti, 2005), calculated as weighted averages per relevé. The recorded species were classified into Social Behaviour Types (SBT, Borhidi, 1995) on the basis of the species preference for a definite habitat, i.e. based on their similar phytocoenological role (Moola & Vasseur, 2004; Bartha *et al.*, 2008). According to Bartha *et al.* (2008), five SBT categories were used: beech forest species (SBT1), forest generalist species (SBT2), non-forest species, i.e. species preferring open and sunny communities (SBT3), marginal species, i.e. exotic or members of ruderal or agricultural communities (SBT4) and gap species, linked to forest edges and gaps (SBT5). Each species was assigned to an SBT category according to its regional synecology, its main role in the local flora (Pignatti, 1982), and the field experience (a complete list of species distributed among the SBTs categories is shown in Tab. 1).

Data elaboration and analysis

The hierarchical arrangement of the surveyed communities was performed through a two way cluster analysis using a plot x species matrix in which cover values were transformed according to van der Maarel's cover-abundance scale (van der Maarel, 1979). A Relative Euclidean algorithm was used as a distance measure, and the Flexible Beta ($\beta = -0.25$) as linkage method. To test their ecological consistency, relevé groups derived from the dendrogram obtained through the cluster analysis were compared in terms of environmental parameters (altitude, aspect, slope and canopy closure), morphological features (rockiness, stoniness and TRI values), coenological indicators (Ellenberg Indicator Values, life forms and SBTs) and structural parameters (mean DBH, number of trees). Aspect values were transformed using the Heat Load Index formula (McCune *et al.*, 2002), in order to obtain a continuous variable, ranging from 0 (NE) to +1 (SW). Normality distribution and variance homogeneity were tested through Kolmogorov-Smirnoff test; as data did not show a normal distribution, we performed a Kruskal-Wallis non-parametric test to understand which groups were significantly different ($P < 0.05$) from each other in relation to the selected groups of parameters. An Indicator Species Analysis (ISA; Dufrière & Legendre, 1997) was carried out to identify the representative species (according to their occurrence and abundance) of each obtained cluster (McCune *et al.*, 2002). For each species, the strength of its association with a specific cluster was tested using a Monte Carlo test (4999 permutations, $\alpha 0.05$).

The same analysis was performed using a plot x Ellenberg Indicator Values matrix (L, T, M, R, N) and a plot x SBT classes matrix, in order to highlight the coenological descriptors that characterize each cluster.

To identify the main drivers that characterize the communities highlighted by the cluster analysis a constrained ordination method was performed and applied on a plot x species matrix, using the environmental, morphological and structural features that showed significance in the Kruskal-Wallis test as constrained variables. In order to choose the appropriate method, a Detrended Correspondance Analysis (DCA) was performed. Since the first axis length ranged between 3 and 4, an RDA was chosen as a constrained ordination method (Lepš & Šmilauer, 2003). Data were normalized using the Hellinger transformation method.

The Two Way Cluster Analysis and ISA were elaborated using PC-ORD software (McCune & Mefford, 1999), the Kruskal-Wallis test was performed using STATISTICA software (Anon, 2001), while the ordination methods and the Hellinger transformation were carried out using the R program (Package 'vegan', Oksanen *et al.*, 2012).

Results

The dendrogram obtained from the classification analysis (Fig. 3) shows two main clusters: the first includes 29 plots and is divided into two sub-clusters (1a and 1b); the second includes 11 plots with a higher level of similarity.

The ISA made using the species x plot matrix (Tab. 2) showed that sub-cluster 1a has 16 indicator species, of which those having higher indicator values are *Cardamine kitaibelii*, *Galium odoratum*, *Rubus hirtus* and

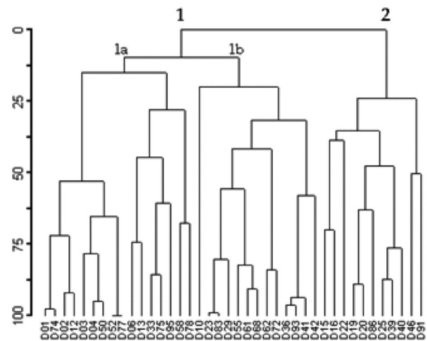


Fig. 3 - Cluster dendrogram.

Actaea spicata, while the sub-cluster 1b has no significant indicator species, even though it includes many exclusive species such as *Berberis vulgaris*, *Primula vulgaris*, *Silene nutans*, *Stellaria holostea*, *Ceterach officinarum*, *Cruciata laevipes*, *Cyanus triumfetti*, *Galium corrudifolium*, *Medicago lupulina*, *Poa trivialis*, *Stellaria montana*, *Trifolium pratense* and *Veronica officinalis*.

Cluster 2 showed the highest number (24) of significant indicator species, among which those with higher indicator values are *Acer opalus* subsp. *obtusatum*, *Brachypodium rupestre*, *Fraxinus ornus*, *Hepatica nobilis*, *Laburnum anagyroides*, *Lilium bulbiferum* and *Campanula trachelium*.

The Kruskal-Wallis test (Tab. 3) showed significant differences in terms of elevation, Ellenberg indicator values (L, T, C, R), life forms (P), and SBT (SBT1, SBT2 and SBT3) between sub-cluster 1a and 2. In addition there were some minor significant differences between sub-cluster 1a and 1b (G, DBH, number of trees) and between sub-cluster 1b and cluster 2 (L, C, R, P, SBT2, SBT3, SBT5).

The ISA made on the plot x Ellenberg indicator values matrix showed that sub-cluster 1 is associated to shade-tolerant species (L values = 2, 3, 4) typical of cold high mountain environment (T value = 2) on calcareous substrate (R value = 9), with high moisture levels (M value = 5) and humic soils (N value= 6). Cluster 2 is associated to species that cover a wider range of Ellenberg values: from partial shadow to full light (L values = 5, 6, 8), with temperature typical of lower mountain altitudes (T values = 5, 6, 7, 8) in both moderately acidophilous and calciphilous soils (R values= 3, 4, 7, 8), tendentially in more arid conditions (U values = 3, 6, 7) and with soils that range from scarce nutrient conditions to high levels (N values = 3, 4, 7, 8). Sub-cluster 1b did not show any association.

The ISA made on the plot x SBT matrix showed that the sub-cluster 1a is related to the beech forest specialist species (SBT1), while cluster 2 is related to forest generalist species (SBT2) and to open habitats (SBT3) and gaps (SBT5). No SBT were related to sub-cluster 1b.

The total explained variance for the dataset, constrained by environmental (altitude, aspect, slope), topographic (TRI) and structural variables (DBH, number of trees), was 16.5% (adj. R²). The RDA ordination showed a clear plots distribution within the space along the first axis (Fig. 4), highlighting a positive correlation between group 1a and higher altitudes (AL) and northern slopes (AS), while group 2 was found to be more related to higher steepness and rugged conditions of the ground. Group 1b showed a positive correlation to the number of trees (Nind) and negative correlation to DBH values (DBHm).

From a phytosociological point of view, on the ba-

sis of the occurrence of *Cardamine kitaibelii*, *Anemone nemorosa*, *Polystichum aculeatum* and *Epilobium montanum*, the microthermal beech forests (groups 1a and 1b) may be referred to the *Cardamino kitaibelii-Fagetum sylvaticae* association (see Tab. 4). This type of woodland is specifically present in the higher part of the montane belt in a wide part of the Central and Northern Apennine mountains on limestone substrate (Ubaldi et al., 1987; Biondi et al., 2002, 2013; Catorci et al., 2010). Our results confirm the microthermal characteristics of this forest type. The floristic composition of the thermophilous communities (group 2) includes characteristic and differential species of *Lathyro veneti-Fagetum sylvaticae* association (Biondi et al., 2002), such as *Lathyrus venetus*, *Cyclamen hederifolium*, *Sorbus aria* and *Viola alba* subsp. *denhardtii* (see Tab. 5). This association generally refers to coenoses on limestone substrates of the central Apennines and is often a transitional coenosis between hilly woods dominated by *Ostrya carpinifolia* and the montane beech woods (Biondi et al., 2002, 2013; Catorci et al., 2010).

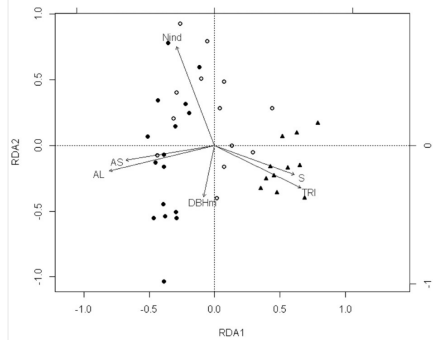


Fig. 4 - RDA plot. Filled and open circles represent the plots of clusters 1a and 1b, respectively, whereas triangles represent the plots of cluster 2. Vectors represent the association of the environmental and topographical parameters. Nind= number of trees; DBHm: mean diameter at breast height; AL= altitude; AS= aspect; S: slope; TRI= terrain ruggedness index.

Discussion

Our results showed that altitude is the most significant environmental factor and, by creating a climatic gradient together with aspect, has a major effect in shaping the species composition of the forest communities. At the same time, the slope and micromorphology (terrain ruggedness) contribute to the creation of an edaphic pattern, mainly opposed to the climatic

Tab. 1 - Social Behaviour Types: 1 - Beech forest specialists 2 - Forest generalists 3 - Non forest species (preferring open sites) 4 - Ruderal species 5 - Gap species (linked to forest edges and gaps).

SBT 1		<i>Viola alba</i>	<i>Veronica chamaedrys</i>
<i>Acer opalus obtusatum</i>	<i>Doronicum columnae</i>	SBT 3	SBT 4
<i>Acer pseudoplatanus</i>	<i>Dryopteris filix-mas</i>	<i>Acinos alpinus</i>	<i>Arisarum vulgare</i>
<i>Actaea spicata</i>	<i>Emerus majus</i>	<i>Ajuga reptans</i>	<i>Cirsium eriophorum</i>
<i>Adoxa moschatellina</i>	<i>Epipactis helleborine</i>	<i>Arabis alpina</i>	<i>Prunus avium avium</i>
<i>Anemone nemorosa</i>	<i>Euonymus latifolius</i>	<i>Arabis collina</i>	<i>Rumex obtusifolius</i>
<i>Arenonia agrimonoides</i>	<i>Festuca exaltata</i>	<i>Asphodelus macrocarpus</i>	<i>Scrophularia scopoli</i>
<i>Cardamine bulbifera</i>	<i>Festuca heterophylla</i>	<i>Berberis vulgaris</i>	<i>Senecio vulgaris</i>
<i>Cardamine enneaphyllos</i>	<i>Fragaria vesca</i>	<i>Brachypodium rupestre</i>	<i>Silene dioica</i>
<i>Cardamine kitaibelii</i>	<i>Fraxinus ornus</i>	<i>Bunium bulbocastanum</i>	<i>Silene vulgaris</i>
<i>Carex pilosa</i>	<i>Galanthus nivalis</i>	<i>Campanula glomerata</i>	<i>Stellaria media</i>
<i>Cephalanthera damasonium</i>	<i>Geranium robertianum</i>	<i>Campanula micrantha</i>	<i>Tanacetum parthenium</i>
<i>Corydalis cava cava</i>	<i>Geum urbanum</i>	<i>Carex humilis</i>	SBT 5
<i>Epilobium montanum</i>	<i>Hepatica nobilis</i>	<i>Carex macrolepis</i>	<i>Alliaria petiolata</i>
<i>Fagus sylvatica</i>	<i>Laburnum anagyroides</i>	<i>Ceterach officinarum</i>	<i>Arabis turrita</i>
<i>Galium odoratum</i>	<i>Lactuca muralis</i>	<i>Cotoneaster integerrimus</i>	<i>Chaerophyllum hirsutum</i>
<i>Lucula sylvatica</i>	<i>Lathyrus venetus</i>	<i>Crocus vernus</i>	<i>Clematis vitalba</i>
<i>Mercurialis perennis</i>	<i>Lathyrus vernus</i>	<i>Cyanus triumfetti</i>	<i>Crataegus monogyna</i>
<i>Moehringia muscosa</i>	<i>Melica uniflora</i>	<i>Cymbalaria muralis</i>	<i>Cruciatia laevipes</i>
<i>Polystichum aculeatum</i>	<i>Melittis melissophyllum</i>	<i>Cytisophyllum sessilifolium</i>	<i>Digitalis lutea australis</i>
<i>Polystichum setiferum</i>	<i>Milium effusum</i>	<i>Dactylis glomerata</i>	<i>Helleborus foetidus</i>
<i>Prenanthes purpurea</i>	<i>Moehringia trinervia</i>	<i>Epipactis microphylla</i>	<i>Lamium gargaricum</i>
<i>Ribes uva-crispa</i>	<i>Monotropa hypopogea</i>	<i>Euphorbia cyparissias</i>	<i>Lonicera alpinica</i>
<i>Sanicula europaea</i>	<i>Neottia nidus-avis</i>	<i>Fallopia convolvulus</i>	<i>Opopanax chironium</i>
<i>Scilla bifolia</i>	<i>Ostrya carpinifolia</i>	<i>Festuca circummediterranea</i>	<i>Peucedanum oreoselinum</i>
<i>Sorbus aucuparia</i>	<i>Peucedanum austriacum</i>	<i>Galium aparine</i>	<i>Potentilla micrantha</i>
<i>Stellaria nemorum</i>	<i>Poa nemoralis</i>	<i>Galium corrudifolium</i>	<i>Rubus hirtus</i>
<i>Viola reichenbachiana</i>	<i>Poa sylvicola</i>	<i>Hieracium piloselloides</i>	<i>Rubus idaeus</i>
SBT 2	<i>Polygonatum multiflorum</i>	<i>Hieracium species</i>	<i>Sorbus aria</i>
<i>Adenostyles glabra</i>	<i>Polygonatum odoratum</i>	<i>Juniperus communis</i>	<i>Vicia villosa</i>
<i>Anemone apennina</i>	<i>Primula vulgaris</i>	<i>Laserpitium latifolium</i>	
<i>Aquilegia vulgaris</i>	<i>Pulmonaria apennina</i>	<i>Lilium bulbiferum</i>	
<i>Aristolochia lutea</i>	<i>Quercus cerris</i>	<i>Lilium martagon</i>	
<i>Asperula laevigata</i>	<i>Ranunculus lanuginosus</i>	<i>Medicago lupulina</i>	
<i>Brachypodium sylvaticum</i>	<i>Rosa arvensis</i>	<i>Medicago species</i>	
<i>Calamintha grandiflora</i>	<i>Saxifraga rotundifolia</i>	<i>Poa compressa</i>	
<i>Campanula persicifolia</i>	<i>Scutellaria columnae</i>	<i>Poa trivialis</i>	
<i>Campanula trachelium</i>	<i>Senecio ovatus</i>	<i>Primula veris</i>	
<i>Cephalanthera longifolia</i>	<i>Senecio squalidus</i>	<i>Pteridium aquilinum</i>	
<i>Clinopodium vulgare</i>	<i>Silene nutans</i>	<i>Rhamnus alpina</i>	
<i>Corylus avellana</i>	<i>Solidago virgaurea</i>	<i>Sedum album</i>	
<i>Cyclamen hederifolium</i>	<i>Stellaria holostea</i>	<i>Sesleria nitida</i>	
<i>Cyclamen repandum</i>	<i>Tamus communis</i>	<i>Silene italica</i>	
<i>Cystopteris fragilis</i>	<i>Tilia platyphyllos</i>	<i>Tanacetum corymbosum</i>	
<i>Daphne laureola</i>	<i>Veronica officinalis</i>	<i>Trifolium pratense</i>	
<i>Daphne mezereum</i>	<i>Vicia peregrina</i>	<i>Veratrum nigrum</i>	

one, that indicates the degree of soil erosion. These two factors are able to modulate landscape patterns because they are strictly correlated to the resources availability (e.g. light, temperature), and can affect vegetation growth and distribution (Ellenberg, 1988; Franklin, 1998; Baeza *et al.*, 2007). At the cooler end of the climatic gradient lies sub-cluster 1a, in which *Fagus sylvatica* is the dominant overstory species and the contribution of other phanerophytes is significantly lower (*Acer pseudoplatanus* and *Sorbus aucuparia* in the top layer and *Juniperus communis* in the shrub layer). Understory has a great abundance of species such as *Actaea spicata*, *Cardamine kitaibelii* and *Galium odoratum*. The coenological indicators demonstrate

that this group can be considered as the microthermal forest, characterized by an understory that grows in shady, cool and moisty conditions. The soil is calcareous, humic, generally deep and less eroded: these are the environmental conditions in which beech forest species (SBT1) grow better (e.g. *Acer pseudoplatanus*, *Arenonia agrimonoides*, *Cardamine kitaibelii*, *Galium odoratum*, *Sorbus aucuparia*, *Stellaria nemorum*, *Viola reichenbachiana*, see also tab. 3). Moreover, species such as *Actaea spicata*, *Cardamine kitaibelii*, *Euphorbia amygdaloides*, *Lathyrus vernus* and *Viola reichenbachiana* are also beech forest diagnostic species (*sensu* 92/43/EEC Directive) (Biondi *et al.*, 2009; Biondi *et al.*, 2012) and are related to less fragmented

Tab. 2 - Indicator species list for the three clusters obtained by ISA; α values are shown only when significant ($P < 0.05$).

Classification group	1a			1b			2		
	Frequency class	Indicator value	α^*	Frequency class	Indicator value	α^*	Frequency class	Indicator value	α^*
Acer pseudoplatanus L.	II	31	0.015
Actaea spicata L.	III	50	0.000
Adenostyles glabra Miller (DC)	III	46	0.003	I
Anemone apennina L.	III	34	0.025	.	.	II	.	.	.
Aremonia agrimonoides (L.) Neck.	IV	48	0.001	II
Cardamine bulbifera (L.) Crantz	IV	49	0.002	I	.	II	.	.	.
Cardamine kitaibelii Bech.	IV	69	0.000
Dryopteris filix-mas (L.) Schott	III	44	0.001
Galium odoratum (L.) Scop.	V	74	0.000	II
Lactuca muralis (L.) Gaertn.	IV	41	0.009	II	.	I	.	.	.
Lathyrus vernus (L.) Bernh.	III	36	0.029	II	.	I	.	.	.
Pulmonaria apennina Cristof. & Puppi	III	38	0.008	I
Rubus hirtus Waldst. & Kit.	III	50	0.000
Sorbus aucuparia L.	II	25	0.035
Stellaria nemorum L.	II	25	0.033
Viola reichenbachiana Jord. ex Boreau	IV	45	0.004	II	.	I	.	.	.
Berberis vulgaris L.	.	.	.	I
Cardamine enneaphylos (L.) Crantz	II	.	.	II	.	II	.	.	.
Ceterach officinarum Willd.	.	.	.	I
Clinopodium vulgare L.	I	.	.	I
Cruciata laevipes Opiz	.	.	.	I
Cyanus triumfetti (All.) Dostál ex A. & D.Löve	.	.	.	I
Cymbalaria muralis Gaertn., Mey. & Scherb.	I	.	.	I
Daphne mezereum L.	I	.	.	II
Epipactis microphylla (Ehrh.) Sw.	I	.	.	II	.	.	I	.	.
Festuca exaltata C. Presl	I	.	.	I
Festuca heterophylla Lam.	I	.	.	II	.	.	I	.	.
Galium corradifolium Vill.	.	.	.	I
Geranium robertianum L.	I	.	.	II
Juniperus communis L.	.	.	.	I	.	.	I	.	.
Lamium gargaricum L.	I	.	.	I
Medicago lupulina L.	.	.	.	I
Moehringia muscosa L.	I	.	.	II	.	.	I	.	.
Poa nemoralis L.	I	.	.	II	.	.	I	.	.
Poa sylvicola Guss.	I	.	.	I
Poa trivialis L.	.	.	.	I
Polystichum aculeatum (L.) Roth	I	.	.	II
Primula vulgaris Huds.	.	.	.	I
Silene nutans L.	.	.	.	I
Stellaria holostea L.	.	.	.	I
Stellaria media (L.) Vill.	I	.	.	I
Stellaria montana Pierrat	.	.	.	I
Trifolium pratense L.	.	.	.	I
Veronica officinalis L.	.	.	.	I
Acer opalus Mill. subsp. obtusatum (Waldst. & Kit. ex Willd.) Gams.	I	.	.	II	.	.	V	82	0.000
Arabis turrata L.	II	36	0.002
Brachypodium rupestre (Host) Roem. & Schult.	.	.	.	I	.	.	IV	51	0.001
Campanula trachelium L.	I	IV	58	0.000
Cephalanthera damasonium (Mill.) Druce	I	III	41	0.005
Corylus avellana L.	II	27	0.018
Cyclamen hederifolium (Aiton.) Daphne laureola L.	I	.	.	I	.	.	III	37	0.017
Fraxinus ornus L.	IV	73	0.000
Hepatica nobilis Schreb.	.	.	.	I	.	.	IV	52	0.001
Laburnum anagyroides Medik.	I	IV	68	0.000
Laserpitium latifolium L.	II	31	0.023
Lilium bulbiferum L.	I	IV	58	0.001
Melittis melissophyllum L.	II	36	0.002
Neottia nidus-avis (L.) Rich.	II	III	37	0.010
polygonatum odoratum Mill.	I	.	.	I	.	.	IV	45	0.003
Primula veris L.	II	27	0.015
Quercus cerris L.	II	27	0.018
Rosa arvensis Huds.	.	.	.	I	.	.	III	32	0.029
Scutellaria columinae All.	III	46	0.001
Sesleria nitida Ten.	I	.	.	I	.	.	II	26	0.043
Solidago virgaurea L.	I	II	27	0.026
Sorbus aria (L.) Crantz	III	44	0.002
Viola alba Besser	II	III	34	0.034

forests (Carranza *et al.*, 2012). *Actaea spicata*, *Dryopteris filix-mas*, *Lathyrus vernus*, *Stellaria nemorum* and *Viola reichenbachiana* are also species linked to 'ancient forest' conditions on the basis of their dispersal capacity and ecology (Hermý *et al.*, 1999).

At the warmer end of the climatic gradient (lower altitude), and in steeper slopes we found group 2; this is the termophilous community, where the overstory is richer and characterized by the presence of different woody species (higher phanerophytes contribution including *Acer opalus* subsp. *obtusatum*, *Fraxinus ornus*, *Laburnum anagyroides*, *Quercus cerris* and *Ostrya carpinifolia*). Understory is generally rich and composed by species that show an heterogeneous habitat preference but are also mainly related to lighter, warmer and drier conditions, and to thinner and eroded soils. The species more correlated to these conditions are the forest generalists and the open habitats species (e.g. *Campanula trachelium*, *Cyclamen hederifolium*, *Hepatica nobilis*, *Brachypodium rupestre*, *Sesleria nitida*). The high frequency of these species groups can be also interpreted as an effect of the spatial heterogeneity due to the existence of morphological discontinuities and rocky outcrops and to a higher degree of human activities at lower altitudes, such as farming and forestry. In particular, intense exploitation in the past (Nocentini, 2009; Carranza *et al.*, 2012) favored this floristic pattern, characterized by the presence of species linked to open and disturbed habitats. Group 1b shows intermediate conditions between microthermal and termophilous communities. Unlike the microthermal community (group 1a), this group shows a lower species richness, geophytes and beech forest

species. Moreover, it seems not to be associated to any particular coenological indicator. This is consistent with the fact that this group includes plots at lower altitudes but lying in the bottom of valleys where some climatic traits resemble plots at higher elevations. The diversification of this group is mainly related to structural features (see RDA analysis). In forests that have not been managed for decades, a higher number of trees with lower DBH can be seen as an indirect evidence of a dynamic process of spontaneous reforestation, but other structural analyses will be necessary for an adequate and more complete interpretation. Over the past 50 years, the progressive abandonment of both forestry and grazing among the upper-montane belt has led to a natural reforestation of secondary grasslands. Therefore the maximum degree of dynamic transformations is mainly found at relatively higher elevations where soil erosion degree is lower. In the reported case study, the observed natural reforestation process is conducted by *Fagus sylvatica*. This species shows a pronounced aptitude for expansion in many environmental conditions, both at high altitudes by natural reforestation and occupancy of 'open spaces' (grassland and shrub/grassland mosaics) and at low altitudes, this also being thanks to infiltration into mixed woodland, similar to what was observed in other districts of the Apennines (Peroni *et al.*, 2000; Sizzia *et al.*, 2010; Bracchetti *et al.*, 2012). As geophytes are generally related to mature forest stands (Decocq *et al.*, 2004; Hermý *et al.*, 1999), their scarcity in this particular group (1b) contributes to its being considered as a developmental stage derived from the forest advancement.

Tab. 3 - Explanatory variables of the three clusters (means, \pm S.D. and S.E.). Ellenberg indicator values, life forms and chorotypes are used under weighted mean form. Different superscript letters indicate significant differences in the Kruskal-Wallis test ($p < 0.05$). Only the significant parameters are shown.

Cluster	1a		1b		2	
Number of relevés	16		13		11	
	Mean \pm S.D.	S.E.	Mean \pm S.D.	S.E.	Mean \pm S.D.	S.E.
Altitude	1590.19 \pm 147.84 ^a	\pm 36.96	1561.92 \pm 190.42 ^{ab}	\pm 52.81	1375.91 \pm 108.59 ^b	\pm 32.74
Ellenberg L	4.01 \pm 0.48 ^a	\pm 0.12	4.26 \pm 0.65 ^a	\pm 0.18	4.79 \pm 0.3 ^b	\pm 0.09
Ellenberg T	4.41 \pm 0.46 ^a	\pm 0.11	4.77 \pm 0.55 ^{ab}	\pm 0.15	5.28 \pm 0.5 ^b	\pm 0.15
Ellenberg C	4.3 \pm 0.17 ^a	\pm 0.04	4.33 \pm 0.27 ^a	\pm 0.08	4.62 \pm 0.17 ^b	\pm 0.05
Ellenberg R	4.14 \pm 0.45 ^a	\pm 0.11	3.53 \pm 1.19 ^a	\pm 0.33	5.1 \pm 0.23 ^b	\pm 0.07
Phanerophytes	89.88 \pm 2.19 ^a	\pm 0.55	89.77 \pm 4.26 ^a	\pm 1.18	109.45 \pm 14.36 ^b	\pm 4.33
Geophytes	5.97 \pm 2.81 ^a	\pm 0.70	1.81 \pm 1.71 ^b	\pm 0.48	7.41 \pm 5.45 ^a	\pm 1.64
Richness	20.75 \pm 8.84 ^a	\pm 2.21	11.15 \pm 5.54 ^b	\pm 1.54	24.45 \pm 9.98 ^a	\pm 3.01
DBH	13.32 \pm 6.27 ^a	\pm 1.57	9.14 \pm 2.34 ^b	\pm 0.65	11.46 \pm 2.38 ^a	\pm 0.72
Number of trees	42.31 \pm 21.72 ^a	\pm 5.43	52.08 \pm 29.44 ^b	\pm 8.17	61.69 \pm 30 ^a	\pm 9.05
SBT1	0.44 \pm 0.12 ^a	\pm 0.03	0.38 \pm 0.15 ^b	\pm 0.04	0.14 \pm 0.07 ^b	\pm 0.02
SBT2	0.43 \pm 0.11 ^a	\pm 0.03	0.43 \pm 0.15 ^a	\pm 0.04	0.56 \pm 0.11 ^b	\pm 0.03
SBT3	0.02 \pm 0.04 ^a	\pm 0.01	0.09 \pm 0.17 ^a	\pm 0.05	0.1 \pm 0.06 ^b	\pm 0.02
SBT5	0.09 \pm 0.1 ^{ab}	\pm 0.02	0.08 \pm 0.1 ^a	\pm 0.03	0.18 \pm 0.09 ^b	\pm 0.03

Tab. 5 - *Lathyro veneti-Fagetum sylvaticae* Biondi, Casavecchia, Pinzi, Allegrezza et Baldoni 2002 ex Biondi, Casavecchia, Pinzi, Allegrezza et Baldoni 2013 in Biondi, Allegrezza, Casavecchia, Galdenzi, Gigante, Pesaresi 2013.

Relevé number from dendrogram Fig. 3	1	2	3	4	5	6	7	8	9	10	11
Altitude (m)	D15	D16	D22	D19	D20	D86	D25	D39	D40	D46	D91
Aspect	SSW	SW	SWW	NNE	SWW	NNE	EES	SW	S	SSE	NNE
Slope (degrees)	30	28	28	30	28	45	40	45	41	35	43
Area (m2)	400	400	400	400	400	400	400	400	400	400	400
Cover total (%)	100	100	97	99	98	98	100	95	99	100	99
<i>Lathyro veneti-Fagetum sylvaticae</i> Biondi, Casavecchia, Pinzi, Allegrezza et Baldoni 2002 ex Biondi, Casavecchia, Pinzi, Allegrezza et Baldoni 2013 in Biondi, Allegrezza, Casavecchia, Galdenzi, Gigante, Pesaresi 2013											
<i>Geranio versicoloris-Fagion sylvaticae</i> Gentile 1969*											
Acer opalus Mill. subsp. obtusatum (Waldst. & Kit. ex Willd.) Gams*	1	1	2	2	2	1	2	1	2	2	2
Daphne laureola L.*	+	+	.	+	.	+	.	.	.	+	1
Sorbus aria (L.) Crantz subsp. aria	.	.	+	.	.	+	+	1	1	1	.
Anemone apennina L. subsp. apennina	.	.	1	1	1
Viola alba Besser subsp. dehnhardtii (Ten.) W. Becker	+	.	+	.	+	+	+	.	.	+	.
Lathyrus venetus (Mill.) Wohlf.	.	.	+	+	+	+	.	.	+	.	.
Cyclamen hederifolium Aiton subsp. hederifolium	.	.	+	.	+	+
Galanthus nivalis L.	.	.	+
Scilla bifolia L.	.	.	.	+
Polygonatum multiflorum (L.) All.	+
<i>Fagatelia sylvaticae</i> Pawlowski in Pawlowski, Sokolowski & Wallisch 1928											
Fagus sylvatica L. subsp. sylvatica	5	5	5	5	5	5	5	5	5	3	5
Rosa arvensis Huds.	+	+	+	.	+	+
Cephalanthera damasonium (Mill.) Druce	+	+	+	.	+	.	.	+	+	.	.
Neottia nidus-avis (L.) Rich.	+	.	+	+	+	.	.	+	+	.	.
Campanula trachelium L. subsp. trachelium	+	+	+	.	+	.	+	+	+	+	.
Hepatica nobilis Schreb.	+	+	+	+	+	1
Lathyrus vernus (L.) Bernh. s.l.	.	+
Euphorbia amygdaloides L. subsp. amygdaloides
Cardamine bulbifera (L.) Crantz	.	.	+	+	+	+	+	.	.	.	+
Solidago virgaurea L. subsp. virgaurea	+	+	+	.	.
Milium effusum L.	.	.	+
Festuca heterophylla Lam.	+
Prunus avium L. subsp. avium	.	.	+
Aodoxa moschatellina L. s.l.
Moehringia trinervia (L.) Clairv.	+
Cardamine enneaphylos (L.) Crantz	1	.	.	1	.	1
Mercurialis perennis L.	+	+	1
Lactuca muralis (L.) Gaertn.
Euonymus latifolius (L.) Mill.	+	.
Melica uniflora Retz.	+
Saxifraga rotundifolia L. subsp. rotundifolia	+
Trasgressive species from the order <i>Quercetalia pubescenti-petraeae</i> Klika 1933 corr. Moravec in Beguin & Theurillat 1984											
Fraxinus ornus L. subsp. ornus	1	.	1	.	1	.	2	1	1	3	2
Laburnum anagyroides Medik. s.l.	.	1	+	+	+	.	+	1	+	+	.
Ostrya carpinifolia Scop.	1	2	1
Lilium bulbiferum L. subsp. eroceum (Chaix) Jan	+	.	+	+	+	+	.	+	.	.	+
Melittis melissophyllum L. subsp. melissophyllum	.	.	1	.	+	.	.	+	+	.	.
Cephalanthera longifolia (L.) Fritsch	+	+	+	.	.	.
Epipactis helleborine (L.) Crantz s.l.	.	.	.	+	+	+	.	.	+	.	+
Helieborus foetidus L. subsp. foetidus	+	.	.	.
Quercus cerris L.	1	.	2	1
Campanula persicifolia L. subsp. persicifolia	.	.	+
Emerus majus Mill. s.l.	+	.	.
Silene italica (L.) Pers. s.l.	.	.	+	+	.	.
<i>Quercus-Fagetea</i> Br.-Bl. & Vlieger in Vlieger 1937											
Corylus avellana L.	+	.	+	2	.
Brachypodium rupestre (Host) Roem. & Schult.	+	.	+	+	.	+	+	+	.	.	.
Poa nemoralis L. s.l.	+	+
Potentilla micrantha Ramond ex DC.	+	+	+	.	.	+
Tamus communis L.	+	.	.	+	.
Luzula sylvatica (Huds.) Gaudin subsp. sylvatica	+	+	+	+	.	.
Viola reichenbachiana Jord. ex Boreau	.	.	+
Brachypodium sylvaticum (Huds.) P. Beauv. subsp. sylvaticum	.	.	+
Fragaria vesca L. subsp. vesca	.	.	+
Tilia platyphyllos Scop. subsp. platyphyllos	2
Sporadic species	5	9	19	2	8	5	3	16	5	2	6

Conclusions

The climatic and spatial patterns expressed along the altitudinal gradient, together with the effect of the progressive land use abandonment in the Duchessa area, has led to a marked diversification in species composition of the local beech forest. The selected environmental parameters defined a climatic and edaphic 'gradient' that were found to be the main driving factors underlying the variations in species composition within these communities. The spatial patterns of these two main environmental gradients seem to be mainly driven by morphology.

Two main beech forests were recognized: i) microthermal communities, that show a high degree of structural heterogeneity caused by dynamic processes (spontaneous reforestation); ii) termophilous communities, that show a relatively lower degree of structural heterogeneity but a higher degree of floristic heterogeneity caused by the occurrence of species coming from the adjacent termophilous mixed forests and from open, disturbed areas. Within the microthermal

communities, two subtypes were recognized: i-I) communities with a relatively higher occurrence of typical beech forest shade-tolerant species (like *Cardamine kitaibelii*, *Galium odoratum*, *Actaea spicata* and *Stellaria holostea*); i-II) communities showing a juvenile canopy and a relatively higher occurrence of some generalist non-forest species (like *Brachypodium rupestre* and *Campanula trachelium*).

In conclusion, our results confirm that, as the silvicultural exploitation (clearcutting in particular) may have negative effects on soil erosion, particular attention should be paid to forest stands that lie on steeper slopes; in these cases a decrease in the intensity of thinning could reduce the negative effects of the canopy opening on soil, as also confirmed by other studies (Ciancio *et al.*, 2006). Finally, this study highlights this kind of research's importance, taking into account forest management so as to better understand the floristic patterns and its dynamics in different silvicultural conditions. This could, in turn, improve understanding the relation between forest management and conservation goals.

Syntaxonomical scheme

QUERCUS-FAGETEA Br.-Bl. & Vlieger in Vlieger 1937

FAGETALIA SYLVATICAE Pawlowski in Pawlowski, Sokolowski & Wallisch 1928

Aremonio-Fagion sylvaticae (Horvat 1938) Torok, Podani & Borhidi 1989

Cardamino kitaibelii-Fagenion sylvaticae Biondi *et al.* ex Biondi, Casavecchia, Pinzi, Allegrezza, Baldoni 2013

Cardamino kitaibelii-Fagetum sylvaticae Ubaldi *et al.* ex Ubaldi 1995

Geranio versicoloris-Fagion sylvaticae Gentile 1969

Doronico orientalis-Fagenion sylvaticae (Ubaldi, Zanotti, Puppi, Speranza & Corbetta ex Ubaldi 1995) Di Pietro, Izco & Blasi 2004

Lathyro veneti-Fagetum sylvaticae Biondi *et al.* ex Biondi, Casavecchia, Pinzi, Allegrezza, Baldoni 2013

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Appendix 1: dates and localities

Tab. 4: Rel.1: 2012.06.21, loc. Mandria di Stefanella; Rel.2: 2012.07.03, loc. Iaccio fonte dell'Avena; Rel.3: 2012.07.02, loc. Fonte dell'Avena; Rel.4, Rel.7: 2012.06.27, loc. Mandria di Stefanella; Rel.5: 2012.06.26, loc. Valle dell'Asino; Rel.6: 2012.07.03, loc. Fonte dell'Avena; Rel.8: 2012.06.21, loc. Bosco di Cartore; Rel.9: 2012.06.26, loc. Mandria di Stefanella; Rel.10: 2012.07.12, loc. Mercaturo; Rel.11: 2012.07.14, loc. Iaccio Fonte dell'Avena; Rel.12: 2012.07.13, loc. Monte Ginepro; Rel. 13: 2012.07.04, loc. Iaccio Fonte dell'Avena; Rel.14: 2012.06.07, loc. Vallone del Cieco; Rel. 15: 2012.07.13, loc. Iaccio Fonte dell'Avena; Rel.16: 2012.07.11, loc. Iaccio Fonte dell'Avena; Rel.17: 2012.07.13, loc. Mercaturo; Rel.18: 2012.07.26, loc. Bosco di Cartore; Rel.19: 2012.06.27, loc. Vallone del Cieco; Rel.20: 2012.07.22, loc. Mandria di Stefanella; Rel.21, Rel.23: 2012.07.20, loc. Praticchio del Tordo; Rel.22: 2012.05.15, loc. Pietra Grossa; Rel.24: 2012.07.26, loc. Pietra Grossa; Rel.25: 2012.07.21, loc. Pratone della Cesa; Rel.26: 2012.05.26, loc. Mandria di Stefanella; Rel.27: 2012.08.01, loc. Valle Amara; Rel.28: 2012.05.30, loc. Bosco di Cartore; Rel.29: 2012.05.24, loc. Vallone della Cesa.

Tab 5: Rel.1, Rel.2: 2012.08.01, loc. Valle dell'Asino; Rel.3, Rel.8: 2012.06.14, loc. Prime Prata; Rel.4: 2012.05. 29, loc. Piè di Monte; Rel.5: 2012.06.13 loc. Prime Prata; Rel.6: 2012.05.28, loc. Piè di Monte; Rel.7: 2012.07.25, loc. Pietra Incacchiata; Rel.9: 2012.06.20, loc. Piè di Monte; Rel.10: 2012.07.04, loc. Pietra Incacchiata; Rel.11: 2012.06.05, loc. Valle Amara.

Appendix 2: sporadic species

Tab. 4: Rel. 5: *Ribes uva-crispa* L. +; Rel. 10: *Digitalis lutea* L. subsp. *australis* (Ten.) Arcang. +, *Scrophularia scopolii* Hoppe ex Pers. +; Rel. 11: *Prenanthes purpurea* L. +; Rel. 12: *Cirsium eriophorum* gr. +, *Monotropa hypopogea* Wallr. +, *Silene italica* (L.) Pers. s.l. +, *Cymbalaria muralis* Gaertn., B. Mey. & Scherb s.l. +, *Prenanthes purpurea* L. +; Rel. 13: *Senecio ovatus* (P. Gaertn., B. Mey. & Scherb.) Willd. s.l. +; Rel. 14: *Crocus vernus* (L.) Hill s.l. +; Rel. 15: *Acinos alpinus* (L.) Moench s.l. +, *Arisarum vulgare* Targ. Tozz. +, *Campanula micrantha* Bertol. +, *Laserpitium latifolium* L. +, *Sedum album* L. +, *Senecio vulgaris* L. +, *Veronica chamaedrys* L. subsp. *chamaedrys* +, *Poa sylvicola* Guss. +, *Carex macrolepis* DC. +, *Aquilegia vulgaris* auct. Fl. Ital. +, *Chaerophyllum hirsutum* L. s.l. +, *Poa compressa* L. +, *Rubus idaeus* L. +, *Silene dioica* (L.) Clairv. +, *Prenanthes purpurea* L. +; Rel. 16: *Arabis alpina* L. s.l. +, *Rosa pendulina* L. +, *Rumex obtusifolius* L. subsp. *obtusifolius* +, *Senecio squalidus* L. s.l. +, *Tanacetum parthenium* (L.) Sch. Bip. +, *Sesleria nitida* Ten. +, *Bunium bulbocastanum* L. +, *Aquilegia vulgaris* auct. Fl. Ital. +, *Chaerophyllum hirsutum* L. s.l. +, *Poa compressa* L. +, *Rubus idaeus* L. +, *Silene dioica* (L.) Clairv. +; Rel. 17: *Juniperus communis* L. 1, *Arabis collina* Ten. s.l. +, *Campanula glomerata* L. +, *Cyanus triumfetti* (All.) Dostál ex Á. & D. Löve +, *Euphorbia cyparissias* L. +, *Galium corrudifolium* Vill. +, *Medicago lupulina* L. +, *Poa trivialis* L. +, *Silene vulgaris* (Moench) Garcke s.l. +, *Trifolium pratense* L. s.l. +, *Vicia villosa* Roth subsp. *varia* (Host) Corb. +, *Dactylis glomerata* L. s.l. +, *Bunium bulbocastanum* L. +; Rel. 19: *Sesleria nitida* Ten. +; Rel. 20: *Berberis vulgaris* L. subsp. *vulgaris* +, *Carex macrolepis* DC. +; Rel. 24: *Silene nutans* L. s.l. +, *Veronica officinalis* L. +, *Poa sylvicola* Guss. +; Rel. 25: *Cruciata laevipes* Opiz +, *Dactylis glomerata* L. s.l. +; Rel. 28: *Ceterach officinarum* Willd. s.l. +, *Poa sylvicola* Guss. +, *Cymbalaria muralis* Gaertn., B. Mey. & Scherb s.l. +; Rel. 29: *Galium aparine* L. +.

Tab. 5: Rel. 1: *Epipactis microphylla* (Ehrh.) Sw. +, *Dactylis glomerata* L. s.l. +, *Polygonatum odoratum* (Mill.) Druce +, *Galium aparine* L. +, *Arabis collina* Ten. s.l. +; Rel. 2: *Galium aparine* L. +, *Arabis collina* Ten. s.l. +, *Carex humilis* Leyss. +, *Clematis vitalba* L. +, *Hieracium piloselloides* Vill. +, *Juniperus communis* L. +, *Lonicera alpigena* L. subsp. *alpigena* +, *Vicia villosa* Roth subsp. *varia* (Host) Corb. +, *Di-*

gitalis lutea L. subsp. *australis* (Ten.) Arcang. +; Rel. 3: *Asphodelus macrocarpus* Parl. subsp. *macrocarpus* 1, *Veratrum nigrum* L. 1, *Dactylis glomerata* L. s.l. +, *Polygonatum odoratum* (Mill.) Druce +, *Asperula laevigata* L. +, *Campanula glomerata* L. +, *Cyclamen repandum* Sm. subsp. *repandum* +, *Peucedanum austriacum* (Jacq.) W.D.J. Koch s.l. +, *Pteridium aquilinum* (L.) Kuhn subsp. *aquilinum* +, *Silene vulgaris* (Moench) Garcke s.l. +, *Tanacetum corymbosum* (L.) Sch. Bip. subsp. *achilleae* (L.) Greuter +, *Aquilegia vulgaris* auct. Fl. Ital. +, *Scutellaria columnae* All. subsp. *columnae* +, *Aristolochia lutea* Desf. +, *Primula veris* L. subsp. *suaveolens* (Bertol.) Gutermann & Ehrend. +, *Arabis turrata* L. +, *Bunium bulbocastanum* L. +, *Alliaria petiolata* (M. Bieb.) Cavara & Grande +, *Digitalis lutea* L. subsp. *australis* (Ten.) Arcang. +; Rel. 4: *Bunium bulbocastanum* L. +, *Alliaria petiolata* (M. Bieb.) Cavara & Grande +; Rel. 5: *Veratrum nigrum* L. +, *Fallopia convolvulus* (L.) Á. Löve +, *Aristolochia lutea* Desf. +, *Primula veris* L. subsp. *suaveolens* (Bertol.) Gutermann & Ehrend. +, *Arabis turrata* L. +, *Bunium bulbocastanum* L. +, *Alliaria petiolata* (M. Bieb.) Cavara & Grande +, *Vicia villosa* Roth subsp. *varia* (Host) Corb. +; Rel. 6: *Crataegus monogyna* Jacq. +, *Laserpitium latifolium* L. +, *Sesleria nitida* Ten. +, *Aquilegia vulgaris* auct. Fl. Ital. +, *Scutellaria columnae* All. subsp. *columnae* +; Rel. 7: *Polygonatum odoratum* (Mill.) Druce +, *Sesleria nitida* Ten. +, *Scutellaria columnae* All. subsp. *columnae* +; Rel. 8: *Polygonatum odoratum* (Mill.) Druce +, *Arabis collina* Ten. s.l. +, *Carex macrolepis* DC. +, *Cytisophyllum sessilifolium* (L.) O. Lang +, *Euphorbia cyparissias* L. +, *Monotropa hypopogea* Wallr. +, *Opopanax chironium* (L.) W.D.J. Koch +, *Peucedanum oreoselinum* (L.) Moench +, *Vicia peregrina* L. +, *Moehringia muscosa* L. +, *Laserpitium latifolium* L. +, *Sesleria nitida* Ten. +, *Scutellaria columnae* All. subsp. *columnae* +, *Arabis turrata* L. +, *Vicia villosa* Roth subsp. *varia* (Host) Corb. +, *Digitalis lutea* L. subsp. *australis* (Ten.) Arcang. +; Rel. 9: *Polygonatum odoratum* (Mill.) Druce +, *Moehringia muscosa* L. +, *Laserpitium latifolium* L. +, *Primula veris* L. subsp. *suaveolens* (Bertol.) Gutermann & Ehrend. +, *Alliaria petiolata* (M. Bieb.) Cavara & Grande +; Rel. 10: *Polygonatum odoratum* (Mill.) Druce +, *Arabis turrata* L. +; Rel. 11: *Cotoneaster integerrimus* Medik. 1, *Polygonatum odoratum* (Mill.) Druce +, *Rhamnus alpina* L. s.l. +, *Laserpitium latifolium* L. +, *Sesleria nitida* Ten. +, *Scutellaria columnae* All. subsp. *columnae* +.

CHAPTER 2

Old Coppice vs High Forest: the impact of beech forest management on plant species diversity in central Apennines (Italy)

Old Coppice vs High Forest: the impact of beech forest management on plant species diversity in central Apennines (Italy)

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Abstract

Silvicultural management, acting on stand structure, have a role in shaping understory diversity. Recent socio-economical changes have led to the progressive coppice abandonment and its conversion to high forest management in many parts of Europe, raising question about the impact on understory species. In this work we compare old coppice-with-standards and high forest stands in terms of structural features and understory richness and composition, taking also into account the habitat's diagnostic species pool. These two systems differ in cut regime, therefore changes in floristic composition and richness are expected. The study area was the Montagne della Duchessa massif, in central Italy, using a dataset of 66 plots. Structural differences and floristic richness were analyzed through the U Mann-Whitney; the diagnostic species diversity was further analyzed using rarefaction curves and Rényi diversity profiles. Differences in understory composition were analyzed through a Indicator Species Analysis. High forest stands showed a higher mean richness of both understory and diagnostic species, these latter being more evenly distributed inside the community; this is related to the cut regime that, providing a constant canopy cover over time, maintained more stable microclimatic conditions that in high forests determined the higher abundance and evenness of shade-tolerants and vernal species. Conversely, in old coppice, seems that the dense canopy affected the understory richness by reducing the light-demanding species, while the shade-tolerant species have not yet had the time to spread. Our findings showed that old coppice conversion can improve the typical mature beech forest's species conservation over time.

1. Introduction

In forest communities, structural features play an important role in modulating floristic composition and ecosystem functions (Neumann & Starlinger, 2001): tree canopy and size, age, stem diameters and density, influence environmental conditions (light, temperature, moisture) of the understory and the nutrient flux, which could also impact on species composition and competition processes (e.g. Thimonier *et al.*, 1992, 1994; Du Bus de Warnaffe and Lebrun, 2004). Forest management modify forest structure; therefore it could have a potential role in shaping species diversity and ecological stability (Humphrey *et al.*, 2000; Decocq, 2004). The effects of forest management depend mainly on its intensity and extent, both of which could induce a disturbance regime in the understory (Van Oijen *et al.*, 2005).

European temperate forests have been managed throughout human history. We know that 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 during 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 rotation, in order to ensure genetic diversity and a certain amount of canopy cover. By contrast, HF systems are characterized by single-stemmed trees stands which originate from seed and have prolonged rotation times. Among the temperate broadleaved forests, those dominated by beech (*Fagus sylvatica*) are the most extensive and widespread throughout Europe (mainly in the central and Western part of the continent), from Sweden and Norway to its southern limit in Italy, where beech dominate the Apennine chain and represent the most common woody resource, exploited for millennia. Traditionally, these forests have been managed for centuries as coppices or CWS. However, because of changing economical and societal demands, in recent years CWS management has undergone a progressive decline in favor of modern HF management regimes in many parts of Europe (Van Calster *et al.*, 2008; Baeten *et al.*, 2009). These processes are also widespread in Italy, where the progressive depopulation and socio-economical changes occurring over the last 60 years along the mountainous areas of the Apennine chain have led to a pronounced drop in local demand for small size timber, firewood and charcoal. As a consequence, many CWS have been almost completely abandoned and most of them are destined to HF conversion (Ciancio *et al.*,

2006; Coppini and Hermanin, 2007). *Fagus sylvatica* forests have been intensely studied from several different points of view (e.g. Bartha *et al.*, 2008; Canullo *et al.*, 2011; Magri *et al.*, 2006; Willner *et al.*, 2009), and some authors have already faced the conversion problem, most of them focusing on lowland deciduous forests in central Europe (Decocq *et al.*, 2004; Van Calster *et al.*, 2008; Baeten *et al.*, 2009; Vild *et al.*, 2013), but only few have addressed mountain beech-dominated mediterranean forests, often using a structural approach (Ciancio *et al.*, 2006). In particular, to our knowledge no old CWS and HF comparison in terms of understory species has yet been made.

On this basis, in this work we compare old CWS and HF beech forest stands of the central Apennines. First of all we characterize both systems from the structural point of view; then we focus on plant species diversity, with a particular interest in beech forests' diagnostic species (Habitat Directive 92/43/EEC).

In particular, we try to answer to the following questions:

- 1) Which 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 term of habitat's diagnostic species diversity?
- 3) Which system retains most of the diagnostic beech forest species pool?

CWS and HF are systems that differ mainly in cut intensity and severity (both higher in CWS): the progressive aging of coppice, and the subsequent change in cut regime, is likely to have an impact on the understory species more adapted to the beech forest, as their composition is shaped by the stand's structural features, that modulate the environmental factors. Therefore, understanding the differences in floristic composition and diversity between old CWS and HF stands can provide useful information for conservation and management purposes.

2. Materials and methods

2.1. 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 it is characterized by a limestone substrate (Accordi *et al.*, 1988), and a sub-Mediterranean climate. The vegetation consists mainly of microthermal *Fagus sylvatica* forests (belonging to *Cardamino kitaibelii-Fagetum sylvaticae*) at higher elevations and termophilous *Fagus sylvatica* forests (belonging to *Lathyro veneti-Fagetum sylvaticae*) at lower elevations (Scolastri *et al.*, 2014); both are recognized as prior 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 achieved 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 mono-specific, as *Fagus sylvatica* dominate the tree layer, but there is also the presence of other woody species like *Acer pseudoplatanus*, *Sorbus aucuparia* at higher elevation, and *Acer opalus* ssp. *obtusatum* at lower elevation. These forests have been managed mainly as Coppice-with -standards (CWS) and as High Forest (HF) but the stands have not been exploited since the 1960s, so the surveyed coppices have to be considered as old CWS (> 38 years) and currently, none of them has been converted to HF yet. Historically, two main exploitation events happened: in 1915, when beech forests have been intensely cut prevalently for carbon and poles, and between '50s and '60s, when cuttings were broader and distributed over almost the entire area. During this time, HF stands were managed as shelterwood with successive cuts, albeit often with a lack of intermediate treatments (for example, liberation treatment); in some cases, this gave rise to stands formed by older trees and younger individuals derived from the natural regeneration after cut. Subsequently, in '70s, cuts were only occasional and very modest. As these environmental conditions and land use history are regionally widespread in the central Apennines, the Montagne della Duchessa massif can be considered an highly representative area. Moreover, most of the area considered in this study lies in the

‘Montagne della Duchessa’ Regional Natural Reserve, more recently, the Reserve has been recognized as a Special Protection Area (according to the European Directive 79/409/EEC) and lately part of it 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 (LTER) network (Stanisci, 2012; Cutini *et al.*, 2012).

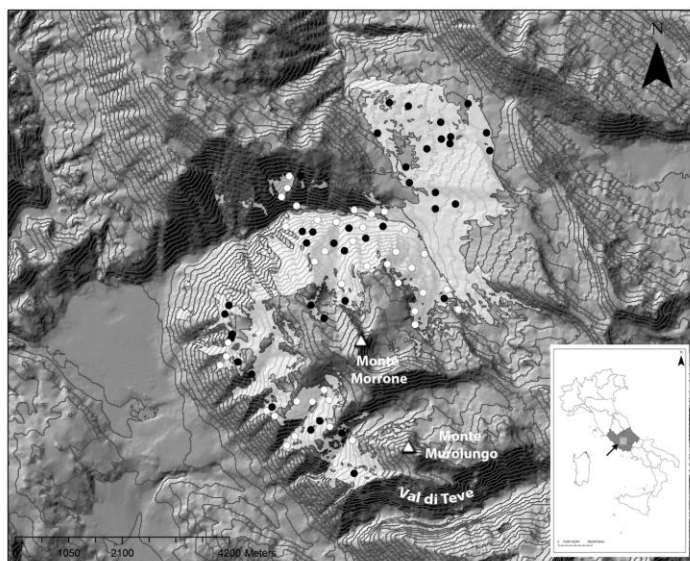


Fig. 1 - The study area. The forest areas surveyed are bounded and colored in light grey; old Coppice-with-standards (CWS) plots are represented by white dots, while High Forest (HF) plots are the black ones.

2.2. 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 Corp. The

data achieved on old CWS and HF stands were spatialized in the 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 meters resolution). Altitude was not considered into the stratification procedure, as the old CWS and HF stands distribution along the altitudinal gradient was comparable (in appendix A is provided a more detailed description of the stratification method, together with a plot x environmental variables table). 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 differences in management. 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 pseudo-replication and the edge effect. 80 square plots (400 m² each) were carried out during the May-July period (2012-2013); the dataset was then restricted to 66 plots (36 old CWS and 30 HF) in order to select only the plots that were representative of the two management systems, excluding mixed situations.

Each plot was divided into 16 sub-plots (25 m²); inside each plot the vascular species abundance was quantified by sub-plot frequency (i.e. from 0-16). Plants were identified at species level using standard floras (Tutin *et al.*, 1964-1980, 1993; Pignatti, 1982); nomenclature was standardized according to Conti *et al.* (2005). In this study, diagnostic species were considered as they are the habitat's species pool indicated by the UE as conservation target for the NATURA2000 Network sites, identified according to the Habitat Directive Interpretation Manual (Biondi *et al.*, 2009; EU 2007). Since diagnostic species are generally species that preferably occur in a single or a few vegetation types, they are useful for the identification of vegetation types in field surveys (Chytrý *et al.*, 2002), and also can be good indicators for conservation and management purposes. The following structural parameters were registered 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 \geq 2.5 cm and tree height (every 5 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).

2.3. Statistical analysis

Old CWS and HF stands were compared on the basis of structural and floristic differences. A Kolmogorov-Smirnoff 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).

2.3.1. 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 trees 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).

Data on the crown projection area, as in the original calculation proposed by Neumann and Starlinger (2001), being missing, the Vertical Evenness (VE) was considered on the basis of its components: VE_N (the proportion of number of trees into each layer) and VE_G (proportion of the basal area into each layer). These two latter indices were calculated considering the number of trees into 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;

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

where p_j is the relative basal area in each layer.

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

2.3.2. 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, Hemicriptophytes, Geophytes and Terophytes). Old CWS and HF were compared through plot-based rarefaction curves (Gotelli & 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}_{MacTao}) 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 (Rényi, 1961; Ricotta & Avena, 2003; Carranza *et al.*, 2007). 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 denote 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; Dufrêne & Legendre, 1997) was performed on the species per plot matrix, after removing rare species (i.e., low frequency species that appeared in only one plot). This analysis

provides an indicator value for each species in each group (in our case, old CWS and HF) and identify the representative species (according to their occurrence and abundance) of each silvicultural system. The values are tested for significance using a Monte Carlo test (4999 permutations, α 0.05). The Rényi diversity profiles were performed using the 'BiodiversityR' package (version 2.3.6)(Kindt & 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 & Mefford, 1999).

3. Results

3.1. 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)(Tab. 1); old CWS stands showed to have stems with lower DBH and lower mean height, but have an higher number of individuals than HF. Old CWS, as a direct consequence of the management method, showed also a higher sprouts ratio, that represent 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 suggest a comparable individuals density level. Regarding to structural diversity indices, only the SH_{dbh} and VE_G were significant: old CWS 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.

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

Despite a higher total number of species (145 vs 118), old CWS showed a significant lower mean number of both understory and diagnostic species per plot than HF (Tab. 1), while no significant difference was found for the overstory layer.

	CWS		HF		P value
	Mean	S.D.	Mean	S.D.	
Canopy closure	99.03	±1.61	99.57	±1.01	0.102 <i>n.s.</i>
Basal area	1.33	±0.24	1.46	±0.32	0.122 <i>n.s.</i>
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
VEN	0.72	±0.09	0.67	±0.21	0.425 <i>n.s.</i>
VEG	0.73	±0.2	0.36	±0.26	0.000
Understorey richness	14.86	±7.11	20.57	±7.83	0.002
9210* species richness	7.03	±3.54	12.30	±4.15	0.000

Tab. 1 - U Mann-Whitney test results for structural parameters and species richness. 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 VEN and VEG are both indicators of vertical differentiation; in particular, VEN is the proportion of trees into each layer, and VEG is the proportion of the basal area into each layer. The p-values after sequential Bonferroni correction are showed; *n.s.* means not significant.

Rarefaction curves, applied to 9210* understory diagnostic species (Fig. 2), showed a higher species richness and a higher steepness among the first part of the curve for HF stands respect to old CWS. Moreover, the plotted proportion of the diagnostic species inside the total species pool shows that the contribution of the diagnostic species is higher in high forests with respect to coppice stands.

The Rényi diversity profiles (Fig. 3) applied to the diagnostic species showed that, as the alpha value increases, in HF stands the floristic heterogeneity and evenness increased (higher values of Shannon and Simpson indices and higher values of the reciprocal of the Berger-Parker index) with respect to old CWS.

On the basis of the ISA results (Tab. 2), HF stands showed high association with 15 species (13% of the understory species), 10 of these (67%) being 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 into the Habitat diagnostic species list.

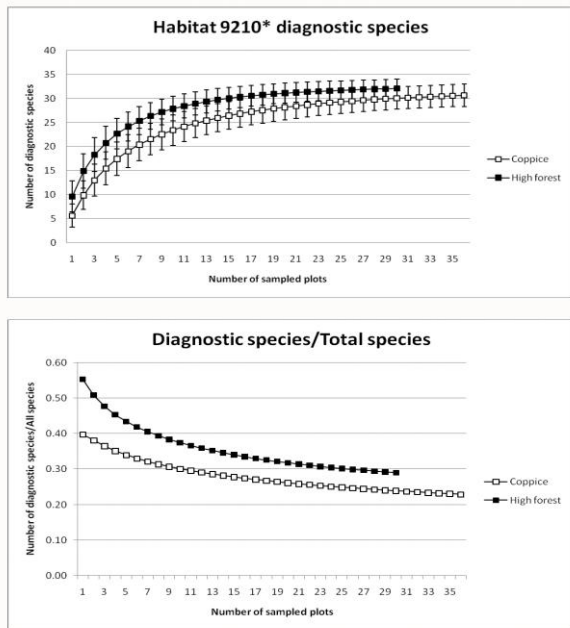


Fig. 2 - Rarefaction curves for the 9210* Habitat (92/43 EEC) diagnostic species and the proportion of diagnostic species on the total species pool in old Coppice-with-standards (CWS) and High Forest (HF) stands. Black squares are HF plots, while white squares are old CWS plots. In figure, for each plot the confidence intervals shown. The first graph show a higher steepness and a higher diagnostic species richness in HF during the first part of the curve. The second graph show a higher proportion of diagnostic species on the entire species pool in HF stands.

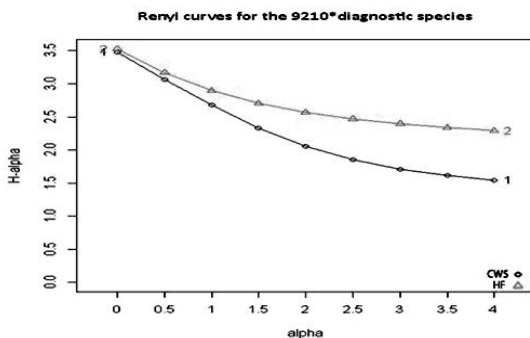


Fig. 3 - Rényi diversity profiles for the 9210* Habitat diagnostic species. Old coppice-with-standards (CWS, dots) are represented in curve number one (black), while High Forest stands (HF, triangles) are represented in curve number two (grey). When alpha approaches 0, the diversity profile indicate differences in species number; when alpha approaches 1, it represent the Shannon diversity index; when alpha approaches 2, it represent the Simpson index; when $\alpha \geq 4$ it represent the reciprocal of Berger-Parker index. HF showed a higher diagnostic species diversity and equitability.

Species	System	IndVal	p-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

Tab. 2 – Indicator Species Analysis results: here is showed the indicator value and the p-value for each species and its association to the management type (old coppice: CWS; high forest: HF). Only species with a significant p-value are shown. Asterisks are used to 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 them being also representative of the 9210* priority Habitat (92/43/EEC).

4. 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 are due to the management and are reflected by a different spatial aggregation pattern and vertical layering. In old CWS stems are aggregated (high sprouts ratio) in stumps, while in HF they are not aggregated and 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 to 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 a greater vertical evenness with respect to HF stands.

In terms of species richness, old CWS showed a higher total species number (gamma diversity) with respect to HF stands. This fact can be the consequence of the differences in cut frequency and severity between the two management systems: clearcutting, providing a higher amount of light that reach the forest ground, limit the abundance of shade-tolerant species and favor the spread of light-demanding species, then leading to a higher species richness. This is consistent with Vild *et al.* (2013), that suggested that these differences may depend on the light regime, which could be considered the most important factor able to promote species diversity and variability. Previous studies, conducted in lowland broadleaved forests, highlighted a generally negative impact of coppice conversion on understory richness and diversity (Decocq *et al.*, 2004; Vild *et al.*, 2013) but Van Calster *et al.*(2008) found a variable effect, mostly depending on the conversion type and, in particular, they found an increase in richness per plot in case of uneven-aged HF conversion. Our results showed a higher mean understory richness per plot in HF stands and a higher diagnostic understory species richness per plot, these latter species being more evenly distributed (higher species equitability) inside the community. These differences may be explained in relation to the management regime: HF contributed to a constant canopy cover over time (longer rotation times, shelterwood cut), this maintaining more stable microclimatic conditions (Durak, 2012) that may have favor as above a higher abundance and more even distribution of shade-tolerants and vernal species, such as *Cardamine kitaibelii*, *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), reporting that areas with

shelterwood cutting provide relatively undisturbed microsites where sensitive true forest species could survive (Godefroid *et al.*, 2005). The ISA analysis highlighted that the species more related to HF stands showed 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*), this showing a variation in light penetration pattern that could be an indicator of canopy gaps due to stochastic events, like falling trees, or be related to the past cut regime. Moreover, most of the species are also related to deep carbonatic soils with acidic reaction, nutrient rich (Mull)(e.g. *Lactuca muralis*, *Viola reichenbachiana*, *Ranunculus lanuginosus*, *Aremonia agrimonoides*)(Rameau *et al.*, 1989- 2008; Pignatti, 2005), this suggesting that the continuous cover guaranteed over time a lower soil erosion even in steeper sites, with respect to CWS cut type. Being well adapted to a particular habitat, diagnostic species are generally sensitive to habitat variations and share characteristics like lower dispersal ability or limited seedling recruitment, along with the need for long-term undisturbed habitats for colonization (Brunet & Von Oheimb, 1998; Hermy *et al.*, 1999); the ISA results, together with Rényi diversity profiles applied to the Habitat diagnostic species lead to consider that HF stand favored the persistence of mesophilous species strictly related to mature forest habitats, maintaining also a greater ecological niche differentiation, that allowed a better understory species equitability, in particular to those that characterize the 9210* beech forests. Studying similar forest communities in other central Apennine's areas, Bartha *et al.* (2008), consider old coppices as the mature stage along a chronosequence from the last cut, where canopy cover is mainly high and the environmental conditions are now close to a stable habitat. As stated by previous studies on lowland termophilous woods of central Europe, the high canopy cover condition that occur after coppice abandonment lead to a progressive decline in typical termophilous understory species and the consequent increase of mesic, shade-tolerant species (Hedl *et al.*, 2010). Despite the species composition differences between the communities studied, this is consistent with our results, as the lower contribution of diagnostic species on the species pool, and the lower mean understory richness per plot with respect to HF stands, indicate old CWS as a stage in which the dense canopy negatively affect the understory richness by reducing the light-demanding species pool, while the shade-tolerant species have not yet had time to spread over. Moreover in old CWS, the diagnostic species that characterize HF stands are also frequent, but still not well evenly distributed inside the understory layer. The

management patchy pattern (CWS stands near to the HF ones) could have favored the persistence of low dispersal ability species over time (Vellend, 2003; Carranza *et al.*, 2012) but, on the other hand, the slightly higher number of species found in old CWS (145 vs 118 species) could indicate that understory maintained ‘a memory’ of the past management regime and that, after 50 years some heliophilous open-habitat related species such as *Ajuga reptans*, *Brachypodium rupestre*, *Pteridium aquilinum* still remained together with shrubby species such as *Rosa pendulina* and *Cotoneaster integerrimus*.

5. Conclusions

Beech forests have been exploited for centuries, the current species composition being the result of past forest management. The progressive abandonment of the land use that has taken place in recent decades in mountainous areas and the trend to convert old CWS into HF stands raise questions about the effects that this change could have on the beech understory composition. Other studies faced this problem (Van Calster *et al.*, 2008b, Vild *et al.*, 2013), often considering conversion to be a threat for the broadleaved forests' biodiversity, as the dense canopy modify over time the understory composition by selecting for shade-tolerant and nutrient-demanding species. In this study our intent was not only to define which system showed the higher species richness or diversity, but also to understand which was the one able to preserve the typical beech forests' understory. HF management, by maintaining more stable microclimatic conditions over time, allowed a higher diversity of species related to mature beech forests (9210* Habitat diagnostic species) and therefore, the old CWS conversion can improve the persistence and abundance of these species.

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APPENDIX A

Here we provide information on the stratification procedure used to select the relevés points, and the stational parameters of the 66 plot that have been selected and used for the analysis.

System	Number of plots	Aspect		Slope (°)	
		Warmer (SW)	Cooler (NE)	Lower (0-30)	Higher (31-45)
old CWS	10	•		•	
	10	•			•
	10		•	•	
	10		•		•
HF	10	•		•	
	10	•			•
	10		•	•	
	10		•		•

Tab. A1- Additional information on the stratification procedure. Old CWS are old coppice-with-standards, while HF are high forest stands. Classes of aspect and slope were created considering warmer (SW) and cooler (NE) aspect, and lower (0-30°) and higher (31-45°) slope. Random points were selected on the basis of this stratification, in order to have an equal representation of the above-mentioned classes inside the two management categories.

Plot code	System	Altitude (m)	Aspect (°)	Slope (°)	Rockiness (%)	Stoniness (%)	Canopy closure (%)
D01	Old CWS	1417	360	30	2	2	97
D02	Old CWS	1694	60	22	0	1	100
D03	Old CWS	1449	10	18	2	5	100
D04	Old CWS	1590	45	12	0	0	99
D05	Old CWS	1514	50	15	0	7	100
D06	Old CWS	1799	50	18	2	9	100
D10	Old CWS	1811	100	30	0	4	99
D11	Old CWS	1586	310	10	0	5	100
D12	Old CWS	1522	360	30	0	7	97
D13	Old CWS	1639	270	30	0	8	100
D15	Old CWS	1329	210	30	1	4	100
D19	Old CWS	1523	23	30	11	1	99
D22	Old CWS	1375	240	28	0	2	98
D23	Old CWS	1696	120	22	1	4	99
D25	Old CWS	1347	120	40	2	3	98
D27	Old CWS	1711	40	34	0	3	100
D28	Old CWS	1671	45	33	0	9	100
D29	Old CWS	1333	40	35	0	15	100
D30	Old CWS	1830	90	33	0	12	99
D31	Old CWS	1688	45	32	0	8	93
D32	Old CWS	1866	40	33	0	17	99
D33	Old CWS	1773	340	38	0	4	100
D35	Old CWS	1692	60	38	0	2	99
D36	Old CWS	1319	320	32	5	4	100
D37	Old CWS	1436	210	36	0	6	100
D40	Old CWS	1448	180	41	0	2	100
D42	Old CWS	1408	290	40	4	15	100
D44	Old CWS	1579	175	36	2	7	100
D46	Old CWS	1196	150	35	0	12	100
D55	Old CWS	1762	350	28	1	7	100
D62	Old CWS	1631	170	25	1	5	100
D68	Old CWS	1681	310	18	0	4	99
D72	Old CWS	1677	160	18	0	9	96
D91	Old CWS	1239	29	43	9	2	100
D93	Old CWS	1312	160	36	0	10	99
D95	Old CWS	1649	290	33	2	2	95
D100	HF	1485	285	40	0	4	98
D101	HF	1624	130	40	0	6	100
D50	HF	1422	10	20	0	2	100
D58	HF	1713	330	20	0	9	100
D74	HF	1485	40	38	0	5	100
D75	HF	1553	330	35	0	2	95
D77	HF	1503	340	38	0	32	100
D78	HF	1857	80	35	11	10	99
D80	HF	1826	30	31	0	27	99
D84	HF	1533	350	40	1	5	100
D85	HF	1512	250	40	0	5	99
D87	HF	1510	280	47	0	6	100
D88	HF	1518	245	35	0	3	100
D96	HF	1468	306	45	2	23	99
DF05	HF	1520	210	3	0	19	99
DF06	HF	1556	50	6	0	3	100
DF07	HF	1481	20	20	0	3	100
DF10	HF	1482	220	10	0	12	100
DF11	HF	1499	280	10	0	2	100
DF12	HF	1565	270	10	0	7	100
DF13	HF	1525	240	15	0	9	100
DF14	HF	1527	222	18	0	13	100
DF16	HF	1564	20	15	0	5	99
DF17	HF	1623	70	15	0	6	100
DF18	HF	1624	20	10	0	34	100
DF19	HF	1448	275	5	0	1	100
DF20	HF	1414	210	10	0	2	100
DF21	HF	1574	290	20	0	31	100
DF24	HF	1582	250	10	0	13	100
DT01	HF	1544	190	20	0	4	100

Tab. A2 - List of the parameters recorded for each of the 66 plot used for the analysis. Old CWS are old coppice-with-standards, while HF are high forest stands. Altitude was recorded using a GPS, while aspect and slope were recorded using a compass with clinometer. Canopy closure was recorded using a spherical densiometer.

CHAPTER 3

Old Coppice vs High Forest: effects of two management types on understory functional composition

Old Coppice vs High Forest: effects of two management types on understory functional composition

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Abstract

The aim of this paper was to study the understory's functional composition of beech forest stands managed in two different ways. In particular, we wanted to analyze the differences in traits richness and association between old coppice-with-standards and high forests. The study area was the Montagne della Duchessa massif, in central Italy, which lies at the center of the Apennine's chain. 66 plots were made, and species abundances and structural parameters were recorded. Data on plant functional traits were collected using both European databases and the literature available. A redundancy analysis was made to assess the relationship between traits states and management, and a forward selection was used to select only the structural parameters with a significant effect on traits variability. A U Mann-Whitney test was used to assess differences in traits states richness between the management types. High forests showed to be more related to traits typical of mature forest conditions with respect to old coppices, the latter turning out to be more closely related to traits generally more frequent in disturbed stands, and also the differences in traits richness confirmed these findings. Our results suggest that, in case of abandoned coppices, their conversion to high forest management could be an appropriate strategy for allowing the persistence and abundance of species more adapted to mature forest conditions.

1. Introduction

Silvicultural management affects forest ecosystems by altering ecological parameters such as light, temperature, humidity and soil properties (Federer

and Tanner, 1966; Anderson *et al.*, 1969; Gondard and Deconchat, 2003; Rubio and Escudero, 2003); this induces a disturbance regime that expected to impact on understory species composition and competition processes (e.g. Thimonier *et al.*, 1992, 1994; Du Bus de Warnaffe and Lebrun, 2004; Van Oijen *et al.*, 2005). Biodiversity is generally considered as a structural community attribute, and it is often evaluated through species richness and its derived indices (Samuels & Drake, 1997). Being scale dependent (Palmer, 1994), these indices consider all species as equivalent, reducing their ability to assess the ecological mechanisms affecting biodiversity (Huston, 1994). Therefore, to allow generalizations and comparisons, several authors began to emphasize functional traits, rather than taxonomic differences, as biodiversity attributes (Noss, 1990; McCarthy, 2003; Moffatt & McLachlan, 2004). Plant functional traits are based on the fact that species differ in their susceptibility to disturbances, depending on particular life-history traits and strategies, such as regeneration, growth or dispersal (Grime, 1979; Grubb, 1985; Lavorel *et al.*, 1997; McIntyre *et al.*, 1999b). In its broadest sense, functional diversity can be defined as the distribution of trait values in a community (Díaz & Cabido, 2001; Tilman, 2001); these traits are used to create emergent groups of plant species sharing similar functioning at the organismic level, similar response to environmental factors and/or similar roles in ecosystems (McIntyre *et al.*, 1999a; McIntyre *et al.*, 1999b; Semanova and Van der Maarel, 2000; Grime, 2001; Lavorel and Garnier, 2002). These similarities are in fact based on their tendency to share a set of key functional traits (e.g. Diaz and Cabido, 1997; Grime *et al.*, 1997; Westoby, 1998; Weiher *et al.*, 1999; Lavorel and Garnier, 2002; Pausas and Lavorel, 2003). Trait-based approaches have improved the understanding of how forest ecosystems respond to environmental constraints and human impact (e.g. Nagaike *et al.* 2003; Verheyen *et al.* 2003; Decocq *et al.*, 2004; Catorci *et al.*, 2012; Catorci *et al.*, 2013). Beech forests are widespread throughout Europe (mainly in the central and Western part of the continent), from Sweden and Norway, to its southern limit in Italy where beech dominate the Apennine chain and represent the most common woody resource, exploited for millennia. Traditionally, these forests have been managed for centuries as coppices, or coppice-with-standards (CWS), and as high forest (HF) harvested tree by tree (Oldeman, 1990; Piusi, 1994). In Italy, as in many parts of Europe (Van Calster *et al.*, 2008; Baeten *et al.*, 2009), the progressive mountain depopulation and socio-economic changes occurring in recent decades have led to a pronounced drop in local demand for small size timber, firewood and charcoal. As a consequence, along the mountainous areas of the Apennines

chain, many CWS have been almost completely abandoned and most of them are destined to HF conversion (Ciancio *et al.*, 2006; Coppini and Hermanin, 2007). Previous works have focused on differences between managed and unmanaged stands, providing a good basis for the specific trait states association with stable and mature forest conditions (Graae & Sunde, 2000; Kenderes & Standovár, 2003; Kelemen *et al.*, 2014), and on functional traits changes along chronosequences in Mediterranean forests (Campetella *et al.*, 2011; Catorci *et al.*, 2013); other studies dealing with the conversion problem focused prevalently on floristic diversity of mixed deciduous forests (van Calster *et al.*, 2008; Baeten *et al.*, 2009; Vild *et al.*, 2013), while beech forests (Scolastri *et al.*, unpublished), while the functional approach has been rarely taken into account (Decocq *et al.*, 2004).

This study aims to compare old coppice-with-standards (CWS) and high forests (HF) in terms of understory functional composition; we concentrate on the understory layer since it plays an important role in beech forests' ecosystem functioning, supporting about 90% of the plant species richness, providing habitat and forage for many wildlife species (Gilliam, 2007; Campetella *et al.*, 2011).

In particular, we want to answer the following questions:

- 1) Which are the differences between old CWS and HF in terms of traits states richness?
- 2) Which traits are related to old CWS, and which characterize HF stands?

2. Materials and methods

2.1. Study area

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 area is characterized by a limestone substrate (Accordi *et al.*, 1988), and a sub-

Mediterranean climate. Beech forests occupy a surface of about 1200 ha, and ranges approximately from 1000 to 1900 m a.s.l., belonging to *Cardamino kitaibelii-Fagetum sylvaticae* association at higher elevations, and to *Lathyro veneti-Fagetum sylvaticae* association at lower elevations (Scolastri *et al.*, 2014); these beech forests are recognized as prior habitat, falling into the 9210* code (Apennine beech forests with *Taxus* and *Ilex*)(Habitat Directive, 92/43 EEC). In this site, as in many other Apennine's areas, human land use such as grazing (mainly sheep and cows, frequently at high altitude) and forest management affected the forest structure and extent over centuries. These forests have been managed mainly as Coppice With Standards (CWS) and as High Forest (HF); historically there have been two main exploitation events: in 1915 beech forests were intensively cut prevalently for carbon and poles, while between '50s and '60s cuttings were broader and distributed over almost the entire area. During both periods, HF stands were managed as shelterwood with successive cuts, albeit often with a lack of intermediate treatments (for example, liberation treatment). In many cases, this gave rise to stands formed by older trees and younger individuals derived from the natural regeneration after cut. Subsequently, in '70s, cuts were only occasional and very modest. As these stands have not been exploited since the 1960s, the surveyed coppice has to be considered as old CWS (> 38 years), none of them having yet been converted to HF. As these environmental conditions and land use history are regionally widespread in the central Apennines, the Montagne della Duchessa massif can be considered a highly representative area. Moreover, most of the area considered in this study lies in the 'Montagne della Duchessa' Regional Natural Reserve. More recently, the Reserve has been recognized as a Special Protection Area (according to the European Directive 79/409/EEC); part of it has also been recognized as a Site of Community Importance (according to the European Directive 92/43/EEC). The territory belongs also to the "Apennines high-elevation" site of the international Long-Term Ecological Research (LTER) network (Stanisci, 2012; Cutini *et al.*, 2012).

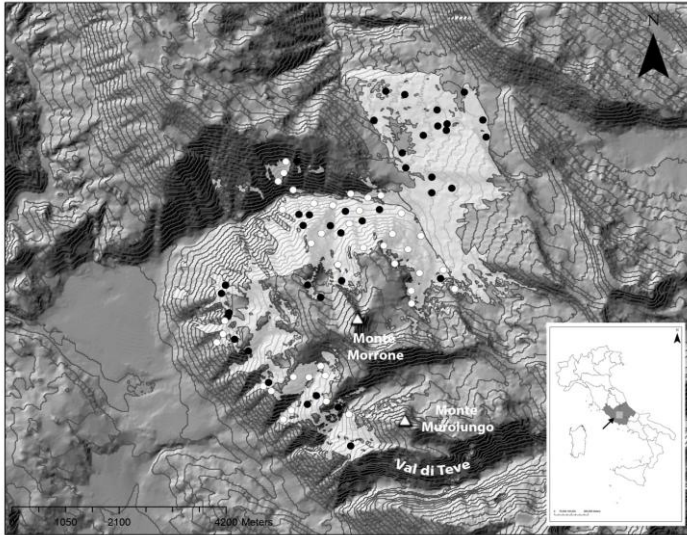


Fig. 1 - The study area. The forest areas surveyed are bounded and colored in light grey; coppice-with-standards plots are represented by white dots, while high forest plots are the black ones.

2.2. Sample design and data collection

Information about management was collected using the Reserve's forest management plan and the book of cuts available at the Italian State Forestry Corp. The data achieved on old CWS and HF stands were spatialized in the GIS environment (ArcGIS 9.2, ESRI). Aspect and slope data were extracted by a digital elevation model (DEM, 20 meters resolution) and each variable was divided into two categories: SW and NE for the aspect, and 0-30° and 31-45° for slope. Subsequently, the management types (old CWS and HF) and environmental categories were merged in order to select old CWS and HF stands which shared similar environmental conditions. This stratification and the subsequent selection were made in order to have old CWS and HF plots with a comparable environmental variability, and then to consider only the possible effects due to differences in management (Appendix A provides a more detailed description of the stratification method, together with a plot x environmental variables table). 80 points were randomly placed inside the strata created using Hawth's tool program (Beyer, 2004) in the GIS environment. The points were at a minimum

distance of 200 m from each other and at a minimum of 30 m from the forest borders, in order to reduce pseudo-replication and the edge effect. 80 square plots (400 m² each) were carried out during the May-July period (2012-2013); the dataset was then restricted to 66 plots (36 CWS and 30 HF) to avoid mixed situations and to include only the plots representative of the two management systems. Each plot was divided into 16 sub-plots (25 m²); inside each plot the vascular species abundance was quantified by sub-plot frequency (i.e. from 0-16). Plants were identified at species level using standard floras (Tutin *et al.*, 1964-1980, 1993; Pignatti, 1982); nomenclature was standardized according to Conti *et al.* (2005). The following structural parameters were registered 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 \geq 2.5 cm and tree height (every 5 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). Since the purpose of the study is to compare old CWS and HF in terms of functional composition, we selected a set of plant functional traits (Violle, 2007), taking into account both vegetative and reproductive strategies: life form, leaf anatomy, leaf phenology, earliest flowering period, flowering duration, diaspore, dispersion, pollination and clonality. Traits information were collected using online databases and the literature available (Pignatti, 1982, 2005; Klotz *et al.*, 2002; Klimešová & Klimeš, Clo-Pla3). We also considered the Social Behaviour Types (SBT, Borhidi, 1995; Bartha *et al.*, 2008), which are categories represented by species sharing the same habitat preference, since they provide a useful and simple method for assessing the forest ecosystem status (Bartha *et al.*, 2008; Scolastri *et al.*, 2014). Tab. 1 reports a description of each trait and the Social Behaviour Types categories, together with a list of the respective traits states and data sources.

Traits (Source)	Trait State	Details
Life form (Pignatti, 2005)	NP	Nanophanerophytes
	Ch	Chamaephytes
	H	Hemicryptophytes
	G	Geophytes
	T	Therophytes
Leaf anatomy (Klotz et al., 2002)	LA_1	Succulent
	LA_2	Scleromorphic
	LA_3	Mesomorphic
	LA_4	Higomorphic
Leaf phenology (Klotz et al., 2002)	LP_1	Spring green
	LP_2	Summer green
	LP_3	Overwintering green
	LP_4	Persistent
Flowering duration (Pignatti, 1982)	FD_2	Two months
	FD_3	Three months
	FD_4	Four months
	FD_5	Five months
	FD_6+	Six or more months
	Earliest flowering period (Pignatti, 1982)	EFP_II
EFP_III		March
EFP_IV		April
EFP_V		May
EFP_VI		June
EFP_VII+		July or later
Diaspora (Klotz et al., 2002)		DIASPO_1
	DIASPO_2	Spore
	DIASPO_3	Seed
	DIASPO_4	Fruit
	DIASPO_5	Fruit with appendage
	DIASPO_6	Fruit with appendage/mericaip
	DIASPO_7	Aggregate fruit (syncarpous)
Dispersion (Pignatti, 1982)	DISP_aut	Autochory
	DISP_ane	Anemochory
	DISP_zoo	Zoochory
	DISP_my	Myrmecochory
Pollination (Klotz et al., 2002)	IMP_ento	Entomophilous
	IMP_anem	Anemophilous
	IMP_ento1	Ento/anemophilous
	IMP_anem1	Anemophilous/self
	IMP_ento2	Entomophilous/self
Clonality (Klimešová & Klimeš, Clo-Pla3)	CLO_0	Not clonal
	CLO_1	Clonal
Social Behaviour Type (Bartha et al, 2008)	SBT 1	Beech forest specialist species
	SBT 2	Forest generalist species
	SBT 3	Non-forest species
	SBT 4	Ruderal species
	SBT 5	Gap species

Tab. 1 - Detailed traits list with traits codes, data sources and traits description.

2.3. Statistical analysis

Functional differences between CWS and HF stands were investigated considering only the understory layer, that include herb and shrub species that grow on the forest floor (height up to 1.5 meters). A quantitative “relevés x trait states abundances” matrix (T_a , absolute weighted abundances), was obtained multiplying “relevés x species abundances” with the binary “species x trait states” matrix (Catorci *et al.*, 2013). A Kolmogorov-Smirnoff 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 statistical comparisons were made using 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). To analyze the association between traits and silvicultural system, we chose to use a constrained multivariate analysis. A DCA was performed to choose the appropriate constrained ordination method: as the length of the first gradient was < 4 S.D., we decided to use a linear ordination method (RDA; Borcard *et al.*, 2011). Prior to RDA, a forward selection between T_a matrix and structural data matrix was made to select only the structural parameters that have a significant effect on traits variability; the T_a was used as a response variables matrix, where the selected structural features were used as explanatory variables. Prior to DCA, forward selection and RDA, the T_a matrix has been Hellinger-transformed to avoid the horseshoe effect, in which double zero (absence) are considered as a resemblance between sites (Borcard *et al.*, 2011). Adjusted R -square values were calculated to produce unbiased estimates of the independent variables' contributions to the explanation of the response variables (Peres-Neto *et al.*, 2006). The “relevés x trait states abundances” matrix was made using PCORD 5.0 software (McCune and Mefford, 2006). The Mann-Whitney U-test was computed with STATISTICA 8 software (Anon, 2001), while the DCA, forward selection and RDA were computed using ‘Vegan’ and ‘Packfor’ packages in R-Studio software (version 3.0.3, R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>).

3. Results

Mann-Whitney U-test results are shown in Tab. 2. After the sequential Bonferroni p-value adjustment, two SBT categories and 9 traits gave significant results. Among the traits tested, differences were found for life forms, leaf anatomy and phenology, flowering duration and flowering period, clonality, diaspora, pollination and dispersion. The analysis of SBT categories showed a higher number of forest habitat related species (SBT1, SBT2) in HF stands with respect to old CWS. Among the life forms, geophytes and hemicriptophytes (G, H) showed a higher abundance in HF stands, while the other life forms proved to be better distributed between the two systems. Regarding vegetative traits, the analysis showed a higher number of species with a mesomorphic and higromorphic leaves (LA3, LA4) in HF, together with summer green (LP 2) and persistent green (LP 4). In terms of reproductive traits, HF showed a higher amount of species which start flowering in may (EFP 5), and species with short flowering duration (FD 2, FD 3). Differences in pollination strategies showed higher frequency of entomophilous (ImpEnto) and entomophilous/selfish (ImpEnto/Self) species in HF. Dispersal unit comparison resulted in significant differences only for species with mericarps (DIASPO 1), which were higher in HF, while other categories showed a comparable distribution. In terms of dispersal strategy, there was a higher contribution of species which use animals as dispersal vehicle (DISP ZOO) in HF, together with species with autochorous dispersion (DISP AUTO). Both clonal (CLO 1) and non clonal (CLO 0) species showed higher abundance in HF.

Of all the structural parameters tested through the forward selection, only the mean height and the number of individuals turned out to be significant explanatory variables of the whole traits variability. RDA analysis graph results are shown in Fig. 2. The total explained variance for dataset resulting from RDA ordination, constrained by these two structural parameters was 4,3 % (adjusted *R*-squares) with 0.006 and 0.002 for the eigenvalues of the first two axes. The first axis explains the structural differences and provided a clear separation between the two silvicultural systems. Old CWS stands were concentrated toward the negative part of the first axis and the positive part of the second axis, while HF stands were concentrated toward the positive part of the first axis and the negative part of the second axis. The distribution of the relevés along the second axis did not clearly depend on the silvicultural system but, on the basis of the traits dispersion, may be considered as a gradient between dense to more open forests: in the positive

part there are traits related to open environment strategies as anemochory and zoochory, wind/self-pollination, terophytes, late flowering period (flowering in June, July, or later), seeds and fruit with appendages, long flowering duration, scleromorphic leaf anatomy and non-forest, ruderal (SBT 4) and gap (SBT 5) species as social behavior types. Conversely, at the bottom of the second axis, traits are mainly related to shady environment: short flowering duration, mesomorphic and higromorphic leaf anatomy, chamaephytes, hemicryptophytes, geophytes and nanophanerophytes, spring and summer leaf phenology, early flowering (flowering started in February and May), autochory, spores as diaspores, entomophilous/self-pollination and forest generalist species (SBT 2) as social behavior types. On the basis of their position in the RDA space, only 4 traits were associated with old CWS, while 16 traits were associated to HF stands. Among the vegetative traits, old CWS showed association only with scleromorphic leaves (LA 2) while, in terms of reproductive traits, showed to be associated to anemophilous pollination (IMP ANEM), zoochory (ZOO DISP), and fruit with appendages as dispersal unit (DIASPO 5). Old CWS showed no particular association with specific life form and to specific SBT category. Among the traits states related to old CWS stands, those represented by a higher species number were the zoochorous dispersion (62 species) and fruits with appendages (26 species). Among the vegetative traits, HF stands were found to be associated with chamaephytes and geophytes (Ch and G, respectively). HF were also characterized by species with higromorphic leaves (LA 4), that green on spring and summer (LP 1 and LP 2). In terms of reproductive traits, HF stands showed association with species with an early flowering period ranging between February, March and May (EFP II, EFP III and EFP V, respectively) and with both short (FD 3) and long (FD 5 and FD 6+) flowering duration. Pollination is mainly vehiculated by insects (ENTO 2), even there is also an incidence of self-pollination, and the associated dispersal units are mericarps (DIASPO 1), spores (DIASPO 2) and fruits (DIASPO 4), while there is no specific association with a particular dispersion trait. In terms of SBTs, HF was found to be related to generalist forest species (SBT 2). Among the traits states related to HF stands, those with a higher species number were spring leaf phenology (62 species), three months flowering duration (55 species), entomophilous/self-pollination (41 species), SBT 2 (38 species) and geophytes (35 species).

Trait state code	Description	Rank sum CWS	Rank sum HF	p-level
G	Geophytes	954	1258	0.001148
H	Hemipterophytes	953	1259	0.001097
SBT1	Beech forest specialists	941	1270	0.000644
SBT2	Forest generalists	912	1299	0.000153
LA3	Mesomorphic leaves	921	1291	0.000236
LA4	highromorphic leaves	919	1293	0.000214
LP4	Persistent green leaves	926	1286	0.000304
LP2	Summer green leaves	962	1250	0.001641
FD2	Two months flowering	893	1318	0.000056
FD3	Three months flowering	915	1297	0.000174
EFP5	Earliest flowering in may	884	1328	0.000033
clon0	Not clonal species	934	1277	0.000461
clon1	Clonal species	902	1310	0.000088
DIASPO1	Mericarps	901	1310	0.000086
dispauto	Autochory	886	1325	0.000038
dispzoo	Zoochory	953	1259	0.001097
Impento	Entomophilous pollination	943	1269	0.000691
impento/self	Ento/Selfish pollination	839	1372	0.000002

Tab. 2 - U Mann-Whitney test results. In table are reported only the significant trait states, their detailed description, the the rank-sum values for each system and the p-level values.

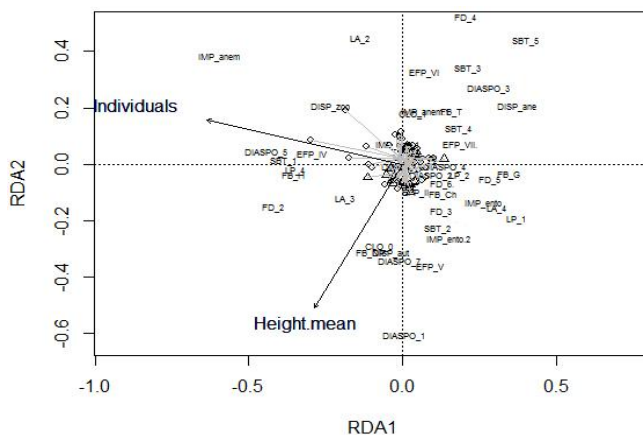


Fig. 2 -Redundancy Analysis ordination graph. Number of individuals (Individuals) and mean height (height.mean) were used as constraining variables. Old coppice-with-standards (old CWS) plots are diamonds, while high forest stands (HF) plots are triangles; traits are written in black. On the upper left part of the diagram lies the old CWS centroid, while on the lower right part lies the HF centroid.

4. Discussion

Plant functional traits have been widely used to describe ancient woodland species characteristics (Hermy, 1999), differences between managed and unmanaged forests (Graae & Sunde, 2000; Kenderes & Standovár, 2003) and between different management types (Decocq *et al.*, 2004) from a functional viewpoint. Findings provided a good basis for analyzing and discussing differences in traits composition between old CWS and HF stands. Previous studies conducted in the same site showed that the HF management, by maintaining more stable microclimatic conditions over time, in HF stands allowed a higher richness and heterogeneity of species typical of mature beech forest conditions (Scolastri *et al.*, unpublished); these differences in species diversity and composition are also reflected in functional differences. In terms of vegetative traits, HF stands proved to be associated with geophytes (e.g. *Cardamine sp. pl.*, *Galium odoratum*, *Lathyrus vernus*, *Anemone apennina*) and chamaephytes (e.g. *Euphorbia amygdaloides*, *Ajuga reptans*, *Stellaria holostea*), together with species with meso-higromorphic leaves that are prevalently summer or persistent green (e.g. *Alliaria petiolata*, *Geranium robertianum*, *Lathyrus sp. pl.*, *Sanicula europaea*), even if there was also good correlation to spring green species (*Anemone sp. pl.*, *Cardamine sp. pl.*). Some of these trait states demonstrate an adaptation of mature forest conditions (Graae & Sunde, 2000; Aubin *et al.*, 2007), where the dense canopy affects negatively the amount of light reaching the forest floor, acting as a selective filter for species. Consequently, species have developed several strategies to exploit solar radiation: the geophytes' growing period is condensed mainly from late winter to spring, before the tree canopy expands. Spring green leaves are considered one of the main traits state for light acquisition in woods (Catorci *et al.*, 2013). Conversely, species with summer green strategy (e.g. *Aremonia agrimonoides*, *Lathyrus sp. pl.*, *Pulmonaria apennina*, *Viola reichenbachiana*) are frequent when canopy closure is high; in such conditions, leaves are prevalently adapted to shady and moist conditions (meso-higromorphic leaves such as *Cardamine sp. pl.*, *Anemone sp. pl.*)(Thomas & Packham, 2007). Most of the chamaephytes found in HF stands showed a persistent green strategy, allowing them to photosynthesize throughout the year without seasonal tissue regrowth. These species are also found to be related to ecosystems where water stress is not particularly severe (Chabot & Hicks, 1982). The higher abundance of hemicriptophytes, that include both forest species (e.g. *Aremonia agrimonoides*, *Carex pilosa*, *Luzula sylvatica*, *Sanicula europaea*) and open habitat related species (e.g.

Brachypodium genuense, *B. rupestre*, *Sesleria nitida*), can be the result of both environmental conditions (e.g. cold stress), and of land use history (e.g. management) that created canopy apertures in the past. Old CWS showed association only with scleromorphic leaves (e.g. *Hepatica nobilis*, *Festuca drymeia*, *Sesleria nitida*, *Asphodelus macrocarpus*, *Poa nemoralis*), these latter being an adaptation related to more open habitat conditions; in fact, scleromorphy become useful as solar radiation increase, thus it can be seen as an indicator of disturbed habitat (i.e. SBT 3, Bartha *et al.*, 2008; Catorci *et al.*, 2012).

The HF stands' similarity to more mature and stable forest conditions is also reflected by reproductive traits; HF were mainly represented by early flowering species (from late winter to early spring, such as *Anemone apennina*, *A. nemorosa*, *Aremonia agrimonoides*, *Corydalis cava*, *Euphorbia amygdaloides*, *Galanthus nivalis*, *Galium odoratum*, *Melica uniflora*, *Potentilla micrantha*, *Rubus hirtus*, *Viola reichenbachiana*), that take advantage from an higher intake of solar radiation available at the ground level. As stated by Graae & Sunde (2000), short and/or earliest flowering period is typical of mature forest, while Kenderes & Standovár (2003) found a higher proportion of May flowering species in managed stands. This mixed situation is consistent if we consider that HF stands were also been managed over time and then were subjected to a recurrent cut disturbance. Our results also show a higher association of HF stands to species with a short flowering duration (three months for *Alliaria petiolata*, *Anemone apennina*, *Cardamine sp. pl.*, *Galium odoratum*, *Hepatica nobilis*, *Rubus hirtus*), with a greater frequency of species having a three months flowering duration. Species with long flowering duration are also present, even if with lower frequency; some of them are related to stoniness (e.g. *Arabis alpina*, *Geranium robertianum*) and to disturbed habitat conditions (*Arisarum vulgare*, *Poa trivialis*, *Stellaria media*). The temporal flowering pattern is also associated with the pollination type: anemophilous pollination (*Brachypodium sp. pl.*, *Carex sp. pl.*, *Poa sp. pl.*) can be a winning strategy in early spring, when trees are still leafless while, in the case of high canopy cover, other strategies should be employed. Nevertheless, even HF stands showed high association to early flowering period. These stands were more represented by species pollinated by insects (*Galium odoratum*, *Rubus hirtus*, *Viola reichenbachiana*). Entomophilous pollination is frequent during the summer season, since canopy forest negatively affects the wind penetration. Anemophilous pollination is also considered an increasing strategy in disturbed forest stands, where the cut frequency and severity create wide clearings; wind-pollinated species

proved to be related to old CWS stands, this indicating an higher management impact with respect to HF stands. Plants' ability to disperse seeds is another critical factor to ensure the species' persistence over time; Zoochory and anemochory are both long distance seed dispersion strategies, and (epi- and endo-) zoochorous dispersion is vehiculated by animals that may potentially travel many kilometers before releasing seeds into the environment (e.g. boars, deers, birds)(Matlack, 1994). Long distance dispersion strategies are considered the most effective colonizers of disturbed habitat (McLachlan & Bazely, 2001; Mabry *et al.*, 2000; Dzwonko & Loster, 1992). Zoochory gave contrasting results: despite being related to old CWS stands, zoochorous species (*Calamintha grandiflora*, *Carex pilosa*, *Corydalis cava*, *Festuca heterophylla*, *Galium odoratum*, *Lilium bulbiferum*, *Mercurialis perennis*, *Polygonatum odoratum*) showed higher frequency into HF stands, this showing this dispersion strategy' importance in both systems. Nevertheless, in HF stands it may be also the result of zoochorous species' ability to persist through vegetative propagation, as most of these species keep rhizomes. By contrast, species with short dispersal strategy characterize only HF stands: autochory and dispersions by invertebrates (slugs, ants) are considered as typically related to mature forest conditions and seems strongly dependent on the forest floor's microenvironment, this reflected by more shady and humid conditions (Matlack, 1994; Bossuyt *et al.*, 1999; Aubin *et al.*, 2007, 2009). However myrmecochory, despite being often regarded as typical dispersal trait in nemoral deciduous forests (Hermy *et al.*, 1999), showed no significant difference. This is consistent with Kenderes & Standovár (2003), who justified the comparable amount of species in managed stands, with the fact that these species are often also capable of vegetative spread. Other authors (Türke *et al.*, 2010; 2012) have also raised questions about ants as preferential dispersal vehicle in mature forests, since anthills are generally placed on the forest edges, while the shady and moisty conditions typical of closed forests are more suitable for slugs. Nevertheless Campetella *et al.* (2011) report an increasing importance of short distance seed dispersal along the forest recolonization process, from the last cut to close canopy conditions. In fact, species with this ability are usually shade-tolerant, and spring and summer flowering. In HF stands the diaspora type results mainly reflect the dispersion pattern, as the most represented dispersule types are mericarps, related to both autochorous (glabrous seeds) and zoochorous dispersion (thorny seeds), and fruits. Fruit with appendages, associated with old CWS, have structures useful for attachment to animals' fur and are related to epizoochory. As seed dispersal is considered crucial for

recolonization, the presence of clonal organs is strictly related to the species persistence in stable environments, when sexual reproduction is hindered (Silvertown, 2008). Some studies indicate that clonal growth is more related to shaded habitats (van Groenendael *et al.*, 1996) and therefore less abundant in disturbed ones. As time since the last disturbance elapses, opportunities for further colonization from seed diminish, and the clonal plants contribution increase (Silvertown, 2008). HF stands showed high association with both clonal and not clonal species. This is consistent with Canullo *et al.* (2011), who found no substantial difference in clonality traits between younger and mature forest stages, and Catorci *et al.* (2013) who indicate that clonality is not an alternative to sexual reproduction, but a complementary strategy for improving the species' persistence over time. Principal clonal strategies aim in fact to accumulate resources in below ground structures such as bulbils or rhizomes, that can also act as vegetative spread to explore the environment, since the resource aren't homogeneous (Catorci *et al.*, 2013). Finally, HF stands also showed a high association with forest habitat species (SBT 2), by containing a higher number of beech forest related species (SBT 1).

5. Conclusion

Our findings show a certain differentiation between old CWS and HF stands in terms of plant traits; in particular, there is a higher HF affinity to some traits generally more abundant in mature forests, like geophytes, spring green species, early flowering species, with entomophilous pollination strategy; old CWS, on the other hand, were more related to typical traits of managed stands (scleromorphic leaves, zoochorous dispersion). However, since we were comparing two managed stands, even HF showed the disturbance effects, expressed by the higher abundance of hemicriptophytes and zoochorous species, along with the lack of significance of myrmecochorous dispersion. Being old CWS and HF two management types that differ in cut severity and frequency, it seems that the continuous cover, provided over time by the shelterwood cut, allowed the maintaining of favorable habitat conditions for the abundance and persistence of the species better adapted to mature forest's understory conditions. Finally, the plant traits approach proved to be a useful and precise tool, able to give a clear ecological meaning to the floristic differences found between the two systems, and our findings provide interesting informations for management and conservation strategies.

Indeed, old CWS conversion to HF could be a good management strategy if our aim is the conservation over time of the typical species related to mature forest conditions.

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APPENDIX A

Here we provide information on the stratification procedure used to select the relevés points, and the stational parameters of the 66 plot that have been selected and used for the analysis.

System	Number of plots	Aspect		Slope (°)	
		Warmer (SW)	Cooler (NE)	Lower (0-30)	Higher (31-45)
old CWS	10	•		•	
	10	•			•
	10		•	•	
	10		•		•
HF	10	•		•	
	10	•			•
	10		•	•	
	10		•		•

Tab. A1- Additional information on the stratification procedure. Old CWS are old coppice-with-standards, while HF are high forest stands. Classes of aspect and slope were created considering warmer (SW) and cooler (NE) aspect, and lower (0-30°) and higher (31-45°) slope. Random points were selected on the basis of this stratification, in order to have an equal representation of the above-mentioned classes inside the two management categories.

Plot code	System	Altitude (m)	Aspect (°)	Slope (°)	Rockiness (%)	Stoniness (%)	Canopy closure (%)
D01	Old CWS	1417	360	30	2	2	97
D02	Old CWS	1694	60	22	0	1	100
D03	Old CWS	1449	10	18	2	5	100
D04	Old CWS	1590	45	12	0	0	99
D05	Old CWS	1514	50	15	0	7	100
D06	Old CWS	1799	50	18	2	9	100
D10	Old CWS	1811	100	30	0	4	99
D11	Old CWS	1586	310	10	0	5	100
D12	Old CWS	1522	360	30	0	7	97
D13	Old CWS	1639	270	30	0	8	100
D15	Old CWS	1329	210	30	1	4	100
D19	Old CWS	1523	23	30	11	1	99
D22	Old CWS	1375	240	28	0	2	98
D23	Old CWS	1696	120	22	1	4	99
D25	Old CWS	1347	120	40	2	3	98
D27	Old CWS	1711	40	34	0	3	100
D28	Old CWS	1671	45	33	0	9	100
D29	Old CWS	1333	40	35	0	15	100
D30	Old CWS	1830	90	33	0	12	99
D31	Old CWS	1688	45	32	0	8	93
D32	Old CWS	1866	40	33	0	17	99
D33	Old CWS	1773	340	38	0	4	100
D35	Old CWS	1692	60	38	0	2	99
D36	Old CWS	1319	320	32	5	4	100
D37	Old CWS	1436	210	36	0	6	100
D40	Old CWS	1448	180	41	0	2	100
D42	Old CWS	1408	290	40	4	15	100
D44	Old CWS	1579	175	36	2	7	100
D46	Old CWS	1196	150	35	0	12	100
D55	Old CWS	1762	350	28	1	7	100
D62	Old CWS	1631	170	25	1	5	100
D68	Old CWS	1681	310	18	0	4	99
D72	Old CWS	1677	160	18	0	9	96
D91	Old CWS	1239	29	43	9	2	100
D93	Old CWS	1312	160	36	0	10	99
D95	Old CWS	1649	290	33	2	2	95
D100	HF	1485	285	40	0	4	98
D101	HF	1624	130	40	0	6	100
D50	HF	1422	10	20	0	2	100
D58	HF	1713	330	20	0	9	100
D74	HF	1485	40	38	0	5	100
D75	HF	1553	330	35	0	2	95
D77	HF	1503	340	38	0	32	100
D78	HF	1857	80	35	11	10	99
D80	HF	1826	30	31	0	27	99
D84	HF	1533	350	40	1	5	100
D85	HF	1512	250	40	0	5	99
D87	HF	1510	280	47	0	6	100
D88	HF	1518	245	35	0	3	100
D96	HF	1468	306	45	2	23	99
DF05	HF	1520	210	3	0	19	99
DF06	HF	1556	50	6	0	3	100
DF07	HF	1481	20	20	0	3	100
DF10	HF	1482	220	10	0	12	100
DF11	HF	1499	280	10	0	2	100
DF12	HF	1565	270	10	0	7	100
DF13	HF	1525	240	15	0	9	100
DF14	HF	1527	222	18	0	13	100
DF16	HF	1564	20	15	0	5	99
DF17	HF	1623	70	15	0	6	100
DF18	HF	1624	20	10	0	34	100
DF19	HF	1448	275	5	0	1	100
DF20	HF	1414	210	10	0	2	100
DF21	HF	1574	290	20	0	31	100
DF24	HF	1582	250	10	0	13	100
DT01	HF	1544	190	20	0	4	100

Tab. A2 - List of the parameters recorded for each of the 66 plot used for the analysis. Old CWS are old coppice-with-standards, while HF are high forest stands. Altitude was recorded using a GPS, while aspect and slope were recorded using a compass with clinometer. Canopy closure was recorded using a spherical densiometer.

General conclusions

The aim of this thesis was to study the floristic composition and diversity of the central Apennines beech forests in relation to environmental factors and management strategies. I found that both have a strong influence on beech forest communities' distribution and composition at different levels.

The effect of the environmental features on beech forest communities

In order to analyze the effect of the management on the beech forests studied, first of all I needed to characterize these plant communities and understand how environmental parameters were responsible of the co-enological differentiation. Results showed that the floristic variability was mainly determined by altitude which, together with aspect, create a climatic gradient. Slope and soil micromorphology, even with lower impact, also contribute to the communities' diversification, by creating an edaphic pattern that also indicates the degree of soil erosion. Being strictly related to the availability of resources such as light, temperature, nutrients and soil depth (Ellenberg, 1988; Franklin, 1998; Baeza *et al.*, 2007), these two gradients drive the differentiation of two main communities that occur between 1400 and 1500 m a.s.l.. At higher elevations lies the microthermal community, characterized by lower light and temperature conditions (*sensu* Ellenberg 1988); in this community, the tree layer is almost beech-dominated, with the sporadic presence of *Acer pseudoplatanus* and *Sorbus aucuparia*, while understory layer is richer in beech forest-related species (e.g. *Aremonia agrimonioides*, *Cardamine kitaibelii*, *Galium odoratum*). Conversely, at lower elevations lies the thermophilous community. This, being in contact and continuity with the lowland mixed forests, is characterized by higher light and temperature conditions, and shows a higher tree layer richness (e.g. *Acer opalus* subsp. *obtusatum*, *Fraxinus ornus*, *Laburnum anagyroides*), together with a higher amount of forest understory generalist species (e.g. *Campanula trachelium*, *Cyclamen hederifolium*, *Hepatica nobilis*). The integration of floristic data with structural measures has also led to the detection of another process currently ongoing in mountain areas: results highlighted some floristic variability inside the microthermal community and also a structural features heterogeneity which may be the effect of the forest regeneration and recolonization, due to the progressive land use abandonment that has led

over time to reforestation processes occurring at the expense of the higher elevation meadows.

The management effects on understory composition and diversity

I investigated the effect of two management types on overstory structural features and on understory species richness, also analyzing differences in 9210* habitat diagnostic species (*sensu* Habitat Directive 92/43/EEC) diversity, with the intention not only of defining which system had the higher species richness, but to understand which was able to preserve the abundance and diversity of the typical beech forests' understory species. The results highlighted both structural and floristic differences between old CWS and HF stands. The management type proved to be the main factor responsible for the structural differences, reflected in a different spatial aggregation pattern and vertical layering which cause differences in space occupancy, and therefore affects the amount of surface available for understory species. The results also showed a higher mean understory richness per plot in HF stands, together with a higher diagnostic understory species richness per plot, these latter species being more evenly distributed (higher species equitability) inside the community. These differences are due the management regime, which in HF stands guaranteed a constant canopy cover over time (longer rotation times and shelterwood cut), this maintaining more stable microclimatic conditions (Durak, 2012) that may have favor, as above, a higher abundance and a more even distribution of shade-tolerants and vernal species (e.g. *Aremonia agrimonoides*, *Cardamine bulbifera* and *Lathyrus vernus*). Conversely, old CWS seemed to be at a stage in which the dense canopy negatively affect the understory richness by reducing the light-demanding species pool (Bartha *et al.*, 2008; Hedl *et al.*, 2010), while the shade-tolerant species have not yet had time to spread; in fact, the diagnostic species that characterize HF stands are also frequent, but still not evenly distributed inside the understory layer.

The management effect on species' functional traits

Given the differences between old CWS and HF stands in terms of diagnostic species, I further tested these two management systems on the basis of plant functional traits. Plant traits are used to create emergent

groups of plant species sharing similar functioning at the organismic level, similar response to environmental factors and/or similar roles in ecosystems (McIntyre *et al.*, 1999a; McIntyre *et al.*, 1999b; Semenova and Van der Maarel, 2000; Grime, 2001; Lavorel and Garnier, 2002); previous authors have used the functional traits approach on forest's ecosystems for several purposes, highlighting the functional characteristics of “ancient forest” species (Hermy *et al.*, 1999), making comparisons between managed and unmanaged forests (Graae & Sunde, 2000; Kenderes & Standovár, 2003), and studying beech coppice chronosequences (Campetella *et al.*, 2011; Canullo *et al.*, 2011) All this provides a good informational basis for plant response to shaded conditions of dense and mature forest, allowing me to face the possible conversion effects on understory from a functional point of view. The plant traits analysis showed results that are consistent with my previous findings based on habitat diagnostic species, as HF stands showed a higher affinity to vegetative and reproductive traits generally related to mature forests (e.g. geophytes, spring green species, early flowering species and entomophilous pollination); on the other hand, old CWS were more related to traits related to managed stands (e.g. scleromorphic leaves, zoochorous dispersion). Moreover, HF stands showed higher abundance of several traits that follow the natural forest's seasonal changes, this indicating a good species distribution among the functional niches. Conversely, old CWS proved once again to be in a transitional stage, as they are more represented by traits related to managed stands, while the mature forest related traits show lower abundance than in HF stands.

Final overview and management implications

In this thesis I have tackled the effects of environmental factors and forest management on beech forests of central Apennines. In particular, I studied the possible effect of a change in management regime on understory richness and composition, providing a good informational basis for further management strategies. Coppice and high forest have two different cut regimes, and differences on understory composition are expected. The conversion effect on understory species is a current topic among forest managers as, also in silviculture, there is a need for sustainable strategies to guarantee and improve the persistence of the managed ecosystems' typical biodiversity. Other authors, facing the coppice abandonment and conversion (Van Calster *et al.*, 2008b; Hedl *et al.*, 2010; Vild *et al.*, 2013) in lowland mixed deciduous forests of central Europe, consider this change in

management as a threat to biodiversity, because the progressive canopy closure negatively affects light demanding species and favor shade-tolerant species. This also occurs in mountain beech forests (Bartha *et al.*, 2008), although in these systems a dense canopy and low light amount should be the mature forest's typical conditions, where understory is composed mainly of species adapted to deep shade. Our results, showing old coppice as an intermediate stage with lower richness and abundance of the species better adapted to the natural beech forest habitat's disturbance cycle, suggests that in case of abandoned coppices, their conversion to high forest management could be a good strategy if the aim is the conservation over time of the typical species related to mature forest conditions.

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