

# Patterns of Clonal Growth Modes Along a Chronosequence of Post-Coppice Forest Regeneration in Beech Forests of Central Italy

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**Abstract** Forest coppicing leads to changes in composition of the herbaceous understory through soil disturbance and alteration of the light regime. While the role of seed dispersal traits at the start of succession after coppicing has been extensively studied, the role of persistence traits such as clonal growth and bud banks is not yet sufficiently understood. To gain better understanding of this role, we studied the patterns of clonal growth organs and related clonal traits of species in a series of coppiced beech forests of the Central Apennines (Marches region, Italy) in various stages of recovery after the last coppicing event. We conducted stratified random sampling and established a chronosequence of recovery stages based on stand age (reflecting the number of years since the last coppicing). The beech stands

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were classified into three age groups (Post-logged, Recovering, and Old-coppice stands) according to the characteristic stages of beech coppice dynamics. Clonal growth organs and the corresponding clonal traits of plants in the forest understory vegetation were assessed with the help of a CLO-PLA1 database. We found no significant change in the proportion of clonal species along the studied chronosequence. In contrast, most of the traits and about the half of the clonal growth organs showed correlation with stand age or preference for a certain habitat (i.e., stage of regeneration). Clonal and bud bank traits proved to play an important role in the persistence of species subjected to forest coppicing cycles in the studied area.

**Keywords** Adaptation · Clonality · Coppice rotation cycle · Forest succession · Persistence · Plant functional traits · Stand age · Understory vegetation · Vegetative mobility

### Abbreviations

CGO – Clonal growth organ · PCO – Principal coordinate analysis ·

DCA – Detrended correspondence analysis · RDA – Redundancy analysis

**Plant nomenclature** Pignatti (1982) except for *Cardamine bulbifera*, *Cyanus triumfettii*, *Drymochloa sylvatica*, *Koeleria lobata* and *Lactuca muralis*, the nomenclature of which follows the latest taxonomic findings

### Introduction

Silvicultural management interventions cause disturbance in forest ecosystems and alter such ecological parameters as light, temperature, air humidity and soil properties (Federer and Tanner 1966; Anderson et al. 1969; Gondard and Deconchat 2003; Rubio and Escudero 2003). Considering that the response of species to environmental conditions is determined by their biological traits (Reich et al. 2003; McIntyre and Lavorel 2007), study of life-history traits offers new possibilities for improving our understanding of ecological processes such as community assembly in space and time (Lavorel et al. 2007). Consequently the detection and prediction of species responses to environmental changes on a range of scales (Garnier et al. 2004; Aubin et al. 2009) is facilitated.

Recently, plant traits have been used in studies of the effects of disturbance in forests (Graae and Sunde 2000; Verheyen et al. 2003; Sammul et al. 2004; Aubin et al. 2009). It has been demonstrated that the diverse environmental conditions in coppiced forests act as filters on plant functional traits, especially those pertinent to dispersal and demands for light, i.e., seed and leaf traits (Mason and MacDonald 2002; Decocq et al. 2004; Bartha et al. 2008). Specifically, light demanding species with low SLA are replaced by low light tolerating species with high SLA, while species with persistent seed bank are replaced by species without seed bank during forest succession (Brown and Warr 1992; Dahlgren et al. 2006). The role of persistence traits such as clonality and bud bank, however, remain to be explored in depth.

There is evidence that clonal growth is generally less abundant in disturbed habitats (Silvertown 2008) and more abundant in shaded ones (van Groenendael et al. 1996). The guerilla strategy (*sensu* Lovett Doust and Lovett Doust 1982) was shown to be of importance in nutrient-rich, well-watered and/or shaded habitats (Lovett-Doust 1981), presumably due to foraging for light (Sammul et al. 2004). The trait syndromes related to phalanx-strategy (i.e., shorter spacers, large bud bank), however, are more important in heterogeneous, disturbed habitats characterized by nutrient-poor and water-stressed habitat conditions (Oborny 1994; Jónsdóttir and Watson 1997; Vesik and Westoby 2004; Halassy et al. 2005; Klimešová and Klimeš 2008). Song et al. (2002) showed that in different kinds of forests the species diversity was positively correlated with the relative importance of clonal plants, and with phalanx strategy in particular. Demographic investigations (Vandepitte et al. 2009) on the clonal species *Mercurialis perennis* in a forest succession context suggested that sexual reproduction is reduced under closed canopies of older succession stages where species persistence would mainly rely on clonal growth. This has further implications for the clonal diversity and spatial genetic structure of clonal species with respect to the degree of canopy closure (Vandepitte et al. 2009).

To cope with the complexity of clonal plant traits, Klimeš et al. (1997) introduced the concept of groups sharing the same Clonal Growth Organs (CGOs), pertinent to the patterns and dynamics of clonal growth. These groups are based on a combination of plant traits related to the origin of CGOs, such as stem, root, initial and final position of CGOs (above-ground or below-ground), presence of special storage organs (tubers and bulbs), length and longevity of spacers between ramets, presence of bud bank (small, large), and finally, patterns of bud protection and thickening (Klimeš et al. 1997). Recent developments in construction of databases of plant traits related to vegetative reproduction (van Groenendael et al. 1996; Klimeš et al. 1997; Klimeš and Klimešová 1999; Kull et al. 2000; Mucina et al. 2003; Klimešová and Klimeš 2008) offer new perspectives on comparative field studies, allowing to tackle multi-species systems at multiple spatiotemporal scales (Prach and Pyšek 1994; van Groenendael et al. 1996; Klimeš et al. 1997; Klimeš and Klimešová 1999; Liira et al. 2002; Song et al. 2002; Klimeš 2003; Sammul et al. 2003; Halassy et al. 2005; Canullo et al. 2006; Klimešová and Klimeš 2007; Wellstein and Kuss 2011 – this issue).

However, few papers have dealt with coppice woods, particularly in the Mediterranean (Decocq et al. 2004; Gondard and Romane 2005; Gondard et al. 2006), and there are no investigations focusing on community-level patterns of clonal traits along the regeneration chronosequences initiated after cessation of coppicing.

In this study we compared the composition of CGOs of plant species in a series of coppice beech forests in stages of recovery after the last coppicing event. Coppicing opens the tree canopy and perturbs the forest understory vegetation, bringing about changes in light, moisture and nutrient conditions and damaging the soil surface and forest-ground plant cover (Buckley 1992; Ciancio et al. 2006; Coppini and Hermanin 2007). Based on the assumption that these changes accompanying regeneration processes in forests act like filters that are selective for species with appropriate clonal traits, we wished to address the following hypotheses:

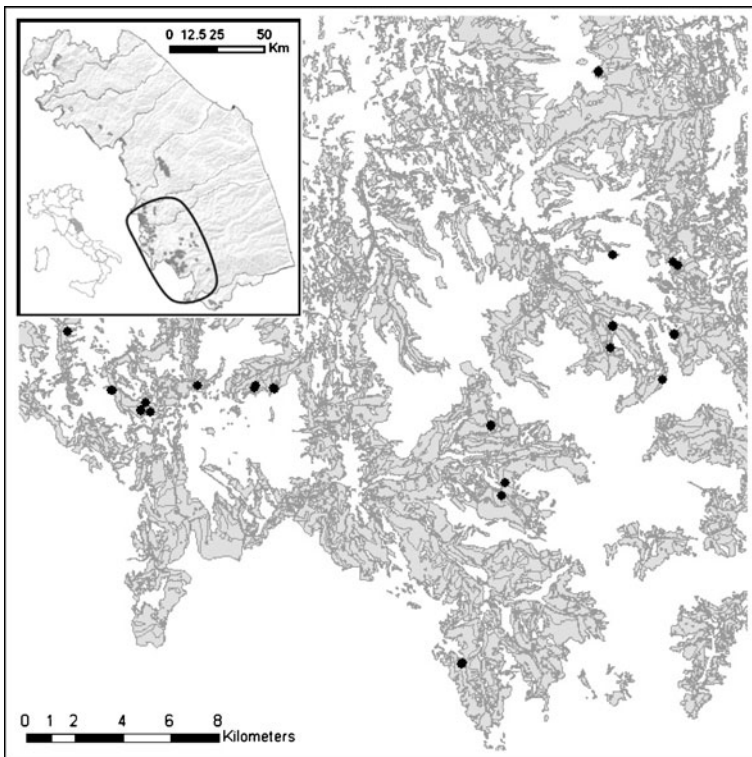
(H1) The proportion of clonal species increases during the recovery of a forest after the abandonment of coppicing because clonal growth in general is less prominent in disturbed conditions and more prominent in shady habitats.

(H2) Older stages of forest regeneration are characterized by a higher number of clonal species with longer spacers, short-lived connections (splitting clones), and small below-ground bud-banks because such species prefer shaded and moist habitat conditions.

## Material and Methods

### Study Area

The study area is located in the Central Apennines in the southern part of the Marche region, Italy (Fig. 1), a region with a temperate climate, annual precipitation ranging from 1,100 mm to 1,500 mm and mean annual temperatures of 8°C to 12°C (Amici and Spina 2002). The local bedrocks are mainly Mesozoic and Tertiary limestones, supporting soils classified Skeleti-Calcaric Phaeozems and Calcari-Humic Leptosols,



**Fig. 1** The location of the study area in the Central Apennines, Italy (southern Marche mountain range, outlined in the box). The beech stands are shown as shaded patches; full dots indicate the positions of sampled plots (modified from IPLA 2001)

having low water capacity, medium-high (10%–40%) content of carbonates, loamy texture, and pH ranging from neutral to sub-alkaline (ASSAM 2006).

The studied beech forests belong to the *Cardamino kitaibelii-Fagetum sylvaticae* and the *Lathyro veneti-Fagetum sylvaticae* (the *Geranio striati-Fagion*), according to the Zürich-Montpellier system (cfr. Di Pietro et al. 2004). The tree layer is dominated by *Fagus sylvatica*, with mixtures of *Acer obtusatum*, *Laburnum anagyroides*, *Fraxinus excelsior*, *Sorbus aria*, *Acer platanoides*, *A. pseudoplatanus*, *Corylus avellana*, *Taxus baccata* and *Ilex aquifolium*. The geomorphology is the major complex factor controlling the landscape-level distribution of the beech forests in the study area. Compact and larger patches of forests are present on the valley slopes, in contact with secondary grasslands at the upper elevation limit; they border mixed deciduous forests at their low elevation limit. Recent decreases of the human population density in the region due to urban-bound emigration and the resulting drop in firewood and charcoal demand brought about changes in traditional intensive coppice management (Ciancio et al. 2006). The beech forests in the study area today cover around 10,000 hectares, of which 90% are managed or abandoned coppices (IPLA 2001). In this silvicultural system, clear felling of stems is carried out in coppicing rotation cycles of 25–30 years. Some mature trees (so called “standards”) are retained through two or three normal coppicing rotation cycles, usually in a density of 80 to 150 trees per hectare (Coppini and Hermanin 2007). For further details on vegetation dynamics of the studied area see Bartha et al. (2008).

### **Sampling Design**

From a large pool of beech coppice forest stands identified by Bartha et al. (2008), 20 sites (0.5 to 35 ha large) were selected through a stratified procedure involving elevation (200 m classes, between 1,000 m and 1,600 m a.s.l.) and stand age (10 years classes, since the last coppicing) as the major stratifying criteria (Bartha et al. 2008). Elevation was used as a “proxy” variable accounting for the main beech forest types reported in the regional forest inventory (IPLA 2001). In the selected forest sites, 33 plots (20 m × 20 m each) were sampled (Fig. 1); two plots were placed in larger and heterogeneous sites. Relatively precise age estimation of each forest site was used to construct a chronosequence (space-for-time substitution system; Pickett 1989) starting at the time of the last coppicing. Hence, the chronosequence included 20 sites aged 4, 5, 6, 8, 8, 14, 15, 17, 22, 22, 24, 28, 29, 35, 45, 48, 48, 55, 64, 65 years, respectively. The pool of sites was classified into three age groups, including:

1. **Post-logged stands** coppiced within the last 14 years ( $n=9$ ), and encompassing all the stands where the canopy closure provided by sucker growth is still not complete; (In a coppiced beech stand canopy closure occurs 8–10 years after harvesting (Ash and Barkham 1976), but it can take longer in habitats with poor soils and low stem density (Barkham 1992), as noted for some of the study area sites. For this reason, the 14-year-old sites were also included.)
2. **Recovering stands** 15 to 30 years old ( $n=13$ ), where the main features of coppice forest structure are under recovery; these stands include the maximum extent of coppicing time rotation in the study area;
3. **Old coppice stands**, including sites left unexploited for at least 31 years ( $n=11$ ).

The mean values of each ecological attribute used to describe three different forest age groups are depicted in Table 1.

### Data Collection

The field data collection was done in 2006, from late May to the end of July. In each sampled plot, six vertical strata were distinguished, including emergent tree layer, canopy tree layer, sub-canopy tree layer, upper shrub layer (2.5–5 m tall), lower shrub layer (0.5–2.5 m), and herb layer (below 0.5 cm). Cover (%) of each stratum and projection cover of each vascular species was estimated, in the latter case using the Braun-Blanquet (1964) scale. The height (m) of all tree layers was assessed using Vertex apparatus (Haglöf Sweden SA). The cover (%) of fallen deadwood, litter, and bare soil was also estimated visually.

Light condition, nutrient content, and soil moisture were calculated per plot using the indicator values of species (weighted by their mean % cover) found in the plots (Ellenberg 1974; Pignatti 2005).

The species groups sharing particular Clonal Growth Organs (CGOs), were derived from the concept of Clonal Growth Modes introduced by Klimeš et al. (1997) and implemented in CLO-PLA1 database (Klimešová and Klimeš 1998). They are defined according to a combination of plant traits related to the origin of a given clonal growth organ (CGO), such as stem, root, and others, the initial and final position of CGOs (above-ground or below-ground), the presence of special storage organs (tubers and bulbs), the length and longevity of spacers between ramets, the presence of a bud bank (small, large), the type of storage, and finally bud protection and thickening (Klimeš et al. 1997; see Electronic Supplementary Material 1). Approximately 70% of species in our data set were present in the CLO-PLA1

**Table 1** Mean values of selected structural, textural, and ecological characteristics between three regeneration stages (Post-logged stands (n=9), Recovering stands (n=13), Old coppice stands (n=12))

Groups	(I) Post-logged	(II) Recovering	(III) Old coppice	(Age) Spearman correlation ( <i>rho</i> )
Species number	<b>50.67<sup>a</sup></b>	31.85 <sup>ab</sup>	<b>30.82<sup>b</sup></b>	-0.449(**)
Herb layer cover (%)	<b>43.11<sup>a</sup></b>	29.08 <sup>b</sup>	30.45 <sup>b</sup>	-0.280
Herb layer height (cm)	<b>46.11<sup>a</sup></b>	38.00 <sup>ab</sup>	<b>33.64<sup>b</sup></b>	-0.444(**)
Tree layer cover (%)	<b>61.00<sup>a</sup></b>	89.08 <sup>b</sup>	89.55 <sup>b</sup>	0.588(**)
Emergent tree height (m)	14.67 <sup>a</sup>	16.85 <sup>a</sup>	<b>20.45<sup>b</sup></b>	0.447(**)
Dominant tree cover (%)	<b>37.22<sup>a</sup></b>	81.92 <sup>b</sup>	81.36 <sup>b</sup>	0.490(**)
Dominant tree height (m)	9.11 <sup>a</sup>	12.08 <sup>a</sup>	<b>19.18<sup>b</sup></b>	0.796(**)
Shrub layer cover(%)	51.56 <sup>a</sup>	46.77 <sup>a</sup>	<b>26.09<sup>b</sup></b>	-0.690(**)
Ellenberg Light	<b>5.83<sup>a</sup></b>	4.64 <sup>b</sup>	4.34 <sup>b</sup>	-0.711(**)
Ellenberg Nutrient	<b>4.70<sup>a</sup></b>	5.32 <sup>ab</sup>	<b>5.62<sup>b</sup></b>	0.748(**)
Ellenberg Moisture	<b>4.44<sup>a</sup></b>	4.78 <sup>b</sup>	4.95 <sup>b</sup>	0.563(**)

Significant differences ( $P \leq 0.05$ ) between the stages are indicated by letters (Mann-Whitney U-test). Significantly different groups are marked in bold. Spearman correlation *rho* of each attribute with respect to the stand age since the last coppicing is also reported. \*\* –  $P < 0.01$ .

database. We revised the classification of these species into CGO groups using our field observations (unpublished data) and on the basis of the relevant clonal traits (Klimeš et al. 1997; Halassy et al. 2005). For species found in the CLO-PLA1, all the assigned clonal traits were extracted from Klimeš et al. (1997: Table 2). We classified those species not found in the CLO-PLA1 database with CGOs using detailed field observations of the clonal traits according to Klimeš et al. (1997) (see Electronic Supplementary Material 1). Some species can be characterized by more than one type of CGO in the classification system of Klimeš et al. (1997). Only the dominating CGO (as established by our field observations) was considered in the analyses in the latter cases.

### ***Data Analyses***

For every trait and for every CGO, the number of species and the percentage number of species representing that trait or that CGO were calculated to express the importance of the traits or the importance of CGOs at plot scale, only considering the herb layer. Because the total number of species varied considerably between plots (cf. Bartha et al. 2008) and because we were interested in the relative importance of traits and CGOs along the chronosequence of the forest regeneration, the percentage number of species (proportion of species) with a certain trait or with a certain CGO was used in the comparative analyses.

Prior to analyses, the CGOs of low importance (fewer than five species in the sample) were omitted from the dataset. Some traits were complementary or dependent (e.g., CGO of above-ground origin or CGO of below-ground origin). In this case, only one of the traits was chosen (at random) and included in the dataset. This selection procedure resulted in two matrices (a matrix based on 13 CGOs, and the other based on 13 traits).

The correlations (Spearman's  $\rho$ ) between the stand age and selected structural and ecological characteristics of stands were calculated (Table 1). Differences in these characteristics between the three regeneration stages were tested as well (Mann-Whitney U-test). Differences in the importance of CGOs and related clonal traits between post-coppice regeneration stages were analyzed using a Kruskal-Wallis test, followed by Mann-Whitney U-test.

We ran a detrended correspondence analysis (DCA) first to decide (on the basis of the species turnover gradients depicted by axis 1 of DCA) whether the linear or unimodal model was more appropriate in the subsequent ordination analyses. Both gradients were short (1.225 S.D. and 0.442 S.D. for the CGO data and clonal-trait data, respectively), suggesting that an ordination technique based on the linear model could be used in the subsequent multivariate analyses.

Principal coordinate analysis (PCO) was used to analyze the patterns of changes in both the CGO and trait compositions. The original age of the stands and the original importance values (relative frequency of trait or of CGO for each species present in a plot) were then correlated (using Spearman's  $\rho$ ) with sample scores along the PCO axes. As the first axes of both trait-based and CGO-based ordinations showed significant correlations with the stand age (cf. the Results section for details), we report the related correlations only (i.e., correlations with the first PCO axis). To test whether the stand age alone is sufficient to explain the compositional

**Table 2** Mean number and percentage of clonal species sharing the same clonal trait in three regeneration stages (Post-logged stands (n=9), Recovering stands (n=13), Old coppice stands (n=12))

TRAITS	Mean SPECIES NUMBER			Mean SPECIES %		
	Post-Logged	Recovering	Old coppice	Post-Logged	Recovering	Old coppice
CGO root	<b>8.55<sup>a</sup></b> (3.84)	2.92 <sup>b</sup> (2.01)	2.00 <sup>b</sup> (0.89)	<b>24.17<sup>a</sup></b> (4.87)	11.53 <sup>b</sup> (7.47)	9.22 <sup>b</sup> (4.13)
CGO stem	28.00 <sup>a</sup> (14.07)	20.00 <sup>a</sup> (6.36)	20.09 <sup>a</sup> (3.85)	<b>75.82<sup>a</sup></b> (4.87)	88.46 <sup>b</sup> (7.47)	90.77 <sup>b</sup> (4.13)
CGO above ground	<b>2.77<sup>a</sup></b> (2.22)	0.92 <sup>b</sup> (0.86)	0.90 <sup>b</sup> (0.83)	<b>7.03<sup>a</sup></b> (3.34)	<b>3.93<sup>a</sup></b> (4.38)	3.79 <sup>ab</sup> (3.21)
CGO below ground	<b>33.77<sup>a</sup></b> (15.73)	22.00 <sup>ab</sup> (7.58)	<b>21.18<sup>a</sup></b> (3.18)	<b>92.96<sup>a</sup></b> (3.34)	<b>96.06<sup>a</sup></b> (4.38)	96.20 <sup>ab</sup> (3.21)
Spacer Long	10.77 <sup>a</sup> (4.73)	7.61 <sup>a</sup> (2.18)	8.18 <sup>a</sup> (2.04)	<b>30.06<sup>a</sup></b> (4.73)	35.03 <sup>ab</sup> (9.18)	<b>37.17<sup>b</sup></b> (7.56)
Spacer Short	<b>22.11<sup>a</sup></b> (11.40)	13.38 <sup>b</sup> (5.69)	12.81 <sup>b</sup> (3.06)	60.06 <sup>a</sup> (5.42)	56.12 <sup>a</sup> (12.63)	57.86 <sup>a</sup> (8.69)
No Spacer	3.66 <sup>a</sup> (2.34)	1.92 <sup>a</sup> (1.18)	<b>1.09<sup>b</sup></b> (0.53)	9.86 <sup>a</sup> (5.11)	8.83 <sup>a</sup> (5.61)	<b>4.95<sup>b</sup></b> (2.63)
Connection Long	<b>31.33<sup>a</sup></b> (15.97)	16.88 <sup>b</sup> (5.02)	16.27 <sup>b</sup> (15.97)	<b>84.73<sup>a</sup></b> (5.39)	72.24 <sup>a</sup> (11.54)	73.78 <sup>b</sup> (6.13)
Connection Short	5.33 <sup>a</sup> (2.39)	6.07 <sup>a</sup> (2.72)	5.81 <sup>a</sup> (1.94)	<b>15.26<sup>a</sup></b> (5.39)	27.75 <sup>b</sup> (11.53)	26.21 <sup>b</sup> (6.13)
Fast Spread	<b>15.44<sup>a</sup></b> (6.40)	9.23 <sup>b</sup> (3.32)	8.54 <sup>b</sup> (1.91)	43.32 <sup>a</sup> (8.36)	41.69 <sup>a</sup> (14.37)	38.97 <sup>a</sup> (8.34)
Insignificant Spread	21.11 <sup>a</sup> (11.77)	13.69 <sup>a</sup> (6.66)	13.45 <sup>a</sup> (3.26)	56.67 <sup>a</sup> (8.36)	58.30 <sup>a</sup> (14.37)	60.54 <sup>a</sup> (8.02)
Rare Spread	0.00 (0.00)	0.00 (0.00)	0.09 (0.30)	0.00 (0.00)	0.00 (0.00)	0.47 (1.58)
Storage	<b>34.55<sup>a</sup></b> (15.89)	22.61 <sup>ab</sup> (7.73)	<b>21.90<sup>b</sup></b> (3.61)	<b>95.08<sup>a</sup></b> (1.84)	98.65 <sup>b</sup> (2.15)	99.28 <sup>b</sup> (1.39)
CGO Storage	0.77 <sup>a</sup> (0.83)	0.38 <sup>a</sup> (0.65)	0.45 <sup>a</sup> (0.52)	2.54 <sup>a</sup> (2.79)	1.24 <sup>a</sup> (2.09)	2.00 <sup>a</sup> (2.35)
No-CGO Storage	<b>0.22<sup>a</sup></b> (0.44)	<b>1.00<sup>b</sup></b> (0.57)	0.81 <sup>ab</sup> (0.87)	<b>0.52<sup>a</sup></b> (1.12)	<b>5.63<sup>b</sup></b> (6.07)	3.94 <sup>ab</sup> (4.27)
Bud Protection	2.44 <sup>a</sup> (1.58)	1.46 <sup>a</sup> (0.87)	1.63 <sup>a</sup> (0.80)	7.04 <sup>a</sup> (4.84)	7.39 <sup>a</sup> (6.05)	7.24 <sup>a</sup> (3.38)
Large Bud Bank	<b>29.33<sup>a</sup></b> (14.19)	16.92 <sup>b</sup> (5.96)	17.09 <sup>b</sup> (3.01)	80.06 <sup>a</sup> (4.78)	72.88 <sup>a</sup> (12.85)	77.37 <sup>a</sup> (4.70)
Small Bud Bank	4.00 <sup>a</sup> (1.73)	5.46 <sup>a</sup> (2.78)	4.90 <sup>a</sup> (1.44)	<b>11.30<sup>a</sup></b> (3.46)	25.16 <sup>b</sup> (13.11)	22.28 <sup>b</sup> (5.14)
Extensive Perennial Root	<b>31.44<sup>a</sup></b> (15.88)	17.15 <sup>b</sup> (6.53)	16.45 <sup>b</sup> (3.04)	<b>85.43<sup>a</sup></b> (4.73)	73.16 <sup>b</sup> (11.76)	74.46 <sup>b</sup> (5.13)
Multiplication Frequent	<b>32.11<sup>a</sup></b> (14.22)	21.53 <sup>ab</sup> (7.05)	<b>20.90<sup>b</sup></b> (3.85)	<b>88.88<sup>a</sup></b> (5.94)	94.08 <sup>ab</sup> (3.87)	<b>94.53<sup>b</sup></b> (3.91)
Multiplication Infrequent	<b>4.33<sup>a</sup></b> (3.39)	1.15 <sup>b</sup> (1.21)	0.72 <sup>b</sup> (0.46)	10.95 <sup>a</sup> (5.75)	4.17 <sup>b</sup> (3.83)	3.19 <sup>b</sup> (2.13)
No Multiplication	0.11 (0.33)	0.23 (0.43)	0.45 (0.52)	0.16 <sup>a</sup> (0.49)	1.73 <sup>a</sup> (3.58)	2.26 <sup>a</sup> (2.60)
Thickening	<b>29.00<sup>a</sup></b> (15.12)	16.38 <sup>b</sup> (5.85)	15.45 <sup>b</sup> (2.42)	<b>78.21<sup>a</sup></b> (6.39)	70.48 <sup>ab</sup> (11.94)	<b>70.48<sup>b</sup></b> (7.63)
Long Longevity spacer	23.77 <sup>a</sup> (13.61)	14.53 <sup>a</sup> (5.02)	14.90 <sup>a</sup> (2.91)	62.88 <sup>a</sup> (5.55)	62.93 <sup>a</sup> (7.82)	67.42a (6.20)
Short Longevity spacer	<b>9.11<sup>a</sup></b> (2.47)	6.46 <sup>b</sup> (2.63)	6.09 <sup>b</sup> (1.81)	27.25 <sup>a</sup> (8.13)	28.22 <sup>a</sup> (6.14)	27.61 <sup>a</sup> (7.15)
No Longevity	3.66 <sup>a</sup> (2.34)	1.92 <sup>a</sup> (1.18)	<b>1.09<sup>b</sup></b> (0.53)	9.86 <sup>a</sup> (5.11)	8.83 <sup>a</sup> (5.61)	<b>4.95<sup>b</sup></b> (2.63)

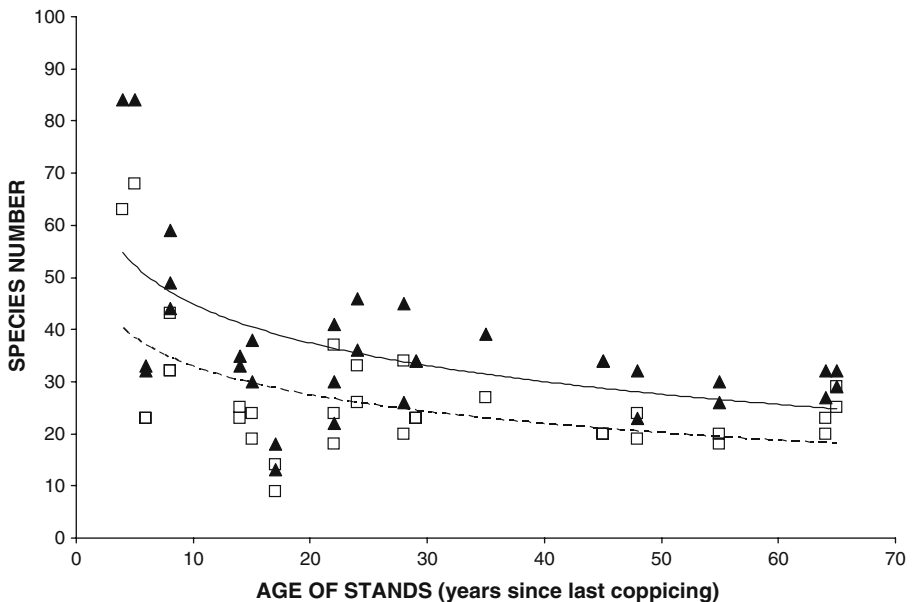
The standard deviation values are given in parentheses. Mean values sharing the same letters within a row mean that groups of stands are not significantly different at  $P=0.05$  based on Mann-Whitney U-test. Significantly different traits values are highlighted in bold.

variation in clonal traits and in CGOs, a partial redundancy analysis (partial RDA) was used. The stand age was set as covariable, while selected forest structural characteristics (tree layer cover, emergent tree height, dominant tree cover, dominant tree height, shrub layer cover, herb layer cover, herb layer height; Table 1) served as variables of interest. The potential effects of light, soil nutrients and soil moisture (expressed as cover-weighted Ellenberg indicator values of species per plots) were evaluated using a similar partial RDA design. Significance of the axes was assessed using Monte Carlo permutation tests ( $n=1,000$ ).

The SYN-TAX 5.0 software package (Podani 1993) was used to execute the PCO ordinations. Product moment correlation was used as the resemblance measure in the PCO analyses. CANOCO 4.5 (ter Braak and Šmilauer 2002) was used to perform the DCA and RDA analyses. The non-parametric tests were performed using Statistica 7.0 (StatSoft 2005).

## Results

We found 261 vascular plant species, of which approximately 74% were clonal, in the pool of our sampling plots. The number of species decreased along the chronosequence (Fig. 2). The number of clonal species showed a logarithmic negative regression with age ( $S=-7.9307 * \ln(\text{Age}) + 51.162$ ,  $R^2=0.291$ ,  $P<0.01$ ). Non-clonal species followed a similar non-linear function ( $S=-2.803 * \ln(\text{Age}) + 18.435$ ,  $R^2=0.266$ ,  $P<0.01$ ). In contrast with the considerable variation in the species richness, we found no significant change in the proportion of clonal species (Fig. 2).



**Fig. 2** Trends in species richness along the studied chronosequence. Black triangles represent total species number, with the relevant regression curve (Species =  $-7.9307 * \ln(\text{Age}) + 51.162$ ,  $R^2=0.291$ ;  $P<0.01$  – solid line); empty squares represent clonal species, with the related regression curve (Species =  $-10.734 * \ln(\text{Age}) + 69.596$ ,  $R^2=0.337$ ;  $P<0.01$  – dashed line)

The Mann-Whitney U-test revealed significant differences in the relative importance of clonal growth traits along the chronosequence (Table 2). The proportion of species with CGOs of root origin, and the proportion of species with above-ground CGOs, long connection between ramets, and extensive perennial primary roots was the highest in the post-logged stage (the early stage of the regenerative post-coppice succession). The relative number of clonal species without spacers was higher in the post-logged and in the recovering stages than in the old coppice stage. The proportion of species with CGOs of stem origin, and the proportion of species with below-ground CGOs, short connection between ramets, small bud bank and with specialized storage capacity were higher in older post-coppice developmental stages. However, the relative importance of these clonal traits did not differ between the recovering and old stages of the post-coppice succession. The relative contribution of species with long spacers, frequent multiplications, and storage capacity not located in specialized clonal organs increased gradually along the chronosequence. The proportion of species endowed with the ability of secondary growth or thickening, however, showed the opposite trend. There were three traits (bud protection, spacer longevity, and the speed of spatial spread) that did not show any significant trends during the post-coppice regeneration.

Seven CGOs showed significant changes among the stages of the regenerative post-coppice succession (Table 3). The relative participation (expressed as % of present species assigned to a given CGO) of *Root-splitters* (K1), *Spreading root sprouters* (K3), *Long-lived stolons* (K5) and *Turf graminoids* (K6) was the highest in the post-logged stage, whereas *Short epigeogenous rhizome* (K7) and *Short-lived hypogeogenous rhizome* (K13) showed the opposite trend. The CGOs with trends of preference for the stages of post-coppice regeneration is approximately 40%–50% of the present species (Fig. 2). Approximately 30% of clonal species belonged to CGO groups (K2, K8, K10, K11, K12) the relative success of which did not change along the studied regeneration chronosequence.

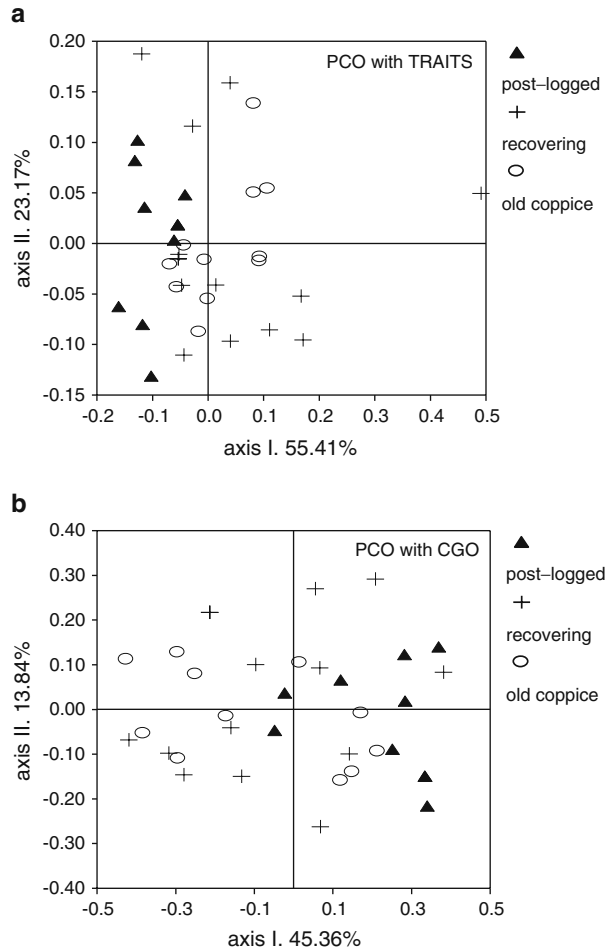
Multivariate analyses of plots, using 13 CGOs or 13 individual clonal plant traits as attributes, respectively, showed similar results. Both ordinations revealed a slight tendency to differentiation between the post-logged and the other two stages of the post-coppice regeneration (Fig. 3a,b). Both ordinations revealed significant correlations between the ordination scores of the first axes and the age of plots ( $-0.547$ ,  $P < 0.01$  in case of ordination based on CGOs;  $0.558$ ,  $P < 0.05$  for ordination based on clonal traits). There were significant correlations found between the ordination scores and the individual CGOs or between the ordination scores and the individual clonal traits (Tables 4 and 5). These correlations were consistent with the results suggested by the Mann-Whitney U-tests (see Tables 2 and 3). After removing the effect of plot age (by partial RDA analysis), no significant effects of the variables representing forest stand structure were detected on the compositional variability of CGO ( $P = 0.116$ ) or on the compositional variability of clonal traits ( $P = 0.413$ ). However, the analyses involving Ellenberg indicator values as variables and plot age as a covariate, revealed that the additional information provided by local light, soil moisture and soil nutrient conditions (represented by the cumulative % variance of the first three partial RDA axes) explained 15.7% of the compositional variability of CGOs ( $P = 0.044$ ) and 28.3% of the compositional variability of clonal traits ( $P = 0.004$ ).

**Table 3** Mean number and percentage of clonal species sharing the same Clonal Growth Organs (reported by codes, K1–K13, and labels) in the three groups of stands (Post-logged stands (n=9), Recovering stands (n=13), Old coppice stands (n=12))

CLONAL GROWTH ORGANS	Mean SPECIES NUMBER			Mean SPECIES %		
	Post-logged	Recovering	Old coppice	Post-logged	Recovering	Old coppice
K1-Root-splitters	<b>3.22<sup>a</sup></b> (2.33)	0.53 <sup>b</sup> (0.87)	0.09 <sup>b</sup> (0.30)	8.63 <sup>a</sup> (5.58)	1.95 <sup>a</sup> (3.15)	<b>0.33<sup>b</sup></b> (1.11)
K2-Non-spreading root sprouter	0.88 <sup>a</sup> (1.36)	0.30 <sup>a</sup> (0.48)	0.45 <sup>a</sup> (0.52)	1.61 <sup>a</sup> (2.13)	1.31 <sup>a</sup> (2.11)	2.18 <sup>a</sup> (2.53)
K3-Spreading root sprouter	<b>4.22<sup>a</sup></b> (2.10)	1.76 <sup>b</sup> (1.53)	1.27 <sup>b</sup> (1.10)	<b>13.21<sup>a</sup></b> (7.61)	7.35 <sup>ab</sup> (6.91)	<b>6.02<sup>b</sup></b> (5.30)
K5-Long-lived stolon	<b>2.00<sup>a</sup></b> (1.73)	0.30 <sup>b</sup> (0.48)	0.18 <sup>b</sup> (0.40)	<b>4.91<sup>a</sup></b> (1.84)	1.34 <sup>b</sup> (2.15)	0.71 <sup>b</sup> (1.60)
K6-Turf graminoid	<b>2.22<sup>a</sup></b> (1.56)	0.46 <sup>b</sup> (0.66)	0.81 <sup>b</sup> (1.07)	<b>6.52<sup>a</sup></b> (5.26)	1.75 <sup>b</sup> (2.43)	3.30 <sup>b</sup> (4.10)
K7-Short epigeogenous rhizome	10.00 <sup>a</sup> (6.42)	7.15 <sup>a</sup> (3.64)	7.72 <sup>a</sup> (1.27)	<b>25.91<sup>a</sup></b> (5.84)	30.37 <sup>ab</sup> (8.95)	<b>35.27<sup>b</sup></b> (5.00)
K8-Long epigeogenous rhizome	2.00 <sup>a</sup> (1.00)	1.76 <sup>a</sup> (1.16)	1.63 <sup>a</sup> (0.80)	5.62 <sup>a</sup> (1.86)	7.70 <sup>a</sup> (4.00)	7.40 <sup>a</sup> (3.25)
K9-Short hypogeogenous rhizome	2.44 <sup>ab</sup> (2.40)	<b>1.61<sup>a</sup></b> (1.12)	<b>0.84<sup>b</sup></b> (0.64)	5.65 <sup>ab</sup> (4.17)	<b>7.00<sup>a</sup></b> (5.29)	<b>3.17<sup>b</sup></b> (2.85)
K10-Long hypogeogenous rhizome	<b>4.22<sup>a</sup></b> (1.20)	<b>2.92<sup>b</sup></b> (1.25)	3.36 <sup>ab</sup> (0.92)	12.64 <sup>a</sup> (3.83)	13.43 <sup>a</sup> (5.90)	15.37 <sup>a</sup> (4.08)
K11-Short-lived stolon	0.77 <sup>a</sup> (0.97)	0.61 <sup>a</sup> (0.65)	0.72 <sup>a</sup> (0.78)	2.12 <sup>a</sup> (2.47)	2.58 <sup>a</sup> (3.03)	3.07 <sup>a</sup> (3.14)
K12-Short-lived epigeogenous rhizome	2.33 <sup>a</sup> (0.86)	2.07 <sup>a</sup> (1.55)	1.72 <sup>a</sup> (1.42)	7.14 <sup>a</sup> (3.14)	8.31 <sup>a</sup> (5.55)	7.42 <sup>a</sup> (5.53)
K13-Short-lived hypogeogenous rhizome	1.22 <sup>a</sup> (1.20)	2.00 <sup>a</sup> (1.35)	2.09 <sup>a</sup> (0.94)	<b>2.93<sup>a</sup></b> (2.48)	9.96 <sup>b</sup> (8.54)	9.75 <sup>b</sup> (4.84)

The mean values are followed by standard deviation in brackets. The mean values sharing the same letters within a row mean that groups of stands are not significantly different at  $P=0.05$  based on Mann-Whitney U-test. Significantly different CGO values are marked in bold.

**Fig. 3** Multivariate analysis (PCO) where herb layer on sample plots differing by time since last coppicing (0–13 years – post logged, 14–30 years – recovering, 30–80 years – old coppice) were characterized (a) by 13 clonal and bud-bank traits and (b) by 13 clonal growth organs (CGO). The percentage of explained variance by each axis is shown



## Discussion

The estimated average proportion of clonal plants occurring in forest habitats in our study was 74%. This general feature suggests that clonal and bud bank traits play an important role in persistence of species under coppicing cycles of the forests in the studied area. We found no significant change in the proportion of clonal species along the studied chronosequence. Thus, clonal species were prominent in disturbed conditions as well as in shady habitats, leading us to reject our first hypothesis (H1). Focusing on specific clonal traits, most of them and about the half of the clonal growth organs showed correlation with stand age or showed preference for a certain habitat (i.e., stage of regeneration). We found that older stages of forest regeneration were characterized by more clonal species with longer spacers, short-lived connections (splitting clones), and small below-ground bud banks, confirming our second hypothesis (H2).

The prevalence of vegetative regeneration in forest vegetation is in line with the results of other studies reporting low dispersal ability and slow recovery of species of the

**Table 4** Correlation (Spearman  $\rho$ ) between the PCO axis 1 (age gradient, where the scores of the first PCO axis correlate positively with the forest stand age) and 13 selected clonal traits

Clonal traits	Axis (I)
Clonal organs are stems	0.808 (**)
Clonal organ below-ground	0.497 (**)
Spacer length long	0.651 (**)
Connection long time	-0.915 (**)
Vegetative spreading fast	0.261
Storage	0.665 (**)
Specialized clonal storage organs	0.016
Bud protection specialized leaves	0.019
Bud bank large	-0.723 (**)
Extensive perennial roots	-0.923 (**)
Multiplication frequent	0.092
Secondary thickening	-0.757 (**)
Spacer longevity long	-0.195

\*\* –  $P < 0.01$ .

forest herb layer (Moola and Vasseur 2004; Godefroid et al. 2005; Moora et al. 2009). Furthermore, the contribution of weedy and invasive species is negligible in the mountainous landscape of the Apennines (Bartha et al. 2008).

The detected relative constancy of clonality along the studied chronosequence might also suggest a high level of resilience of the forest vegetation by using the

**Table 5** Correlation (Spearman  $\rho$ ) between the PCO axis 1 (age gradient, where the decreasing scores of the first PCO axis represent the increasing time from the last coppicing) and 13 CGOs (reported by codes, K1–K13, and labels)

Clonal growth organ	Axis I
K1 Root-splitters	0.483 (**)
K2 Non-spreading root sprouter	-0.379 (*)
K3 Spreading root sprouter	0.682 (**)
K5 Long-lived stolon	0.396 (*)
K6 Turf graminoid	0.175
K7 Short epigeogenous rhizome	-0.528 (**)
K8 Long epigeogenous rhizome	-0.347 (*)
K9 Short hypogeogenous rhizome	0.019
K10 Long hypogeogenous rhizome	0.169
K11 Short-lived stolon	0.255
K12 Short-lived epigeogenous rhizome	-0.072
K13 Short-lived hypogeogenous rhizome	-0.645 (**)
NC Non-clonal species	0.864 (**)

\* –  $P < 0.05$ ; \*\* –  $P < 0.01$ .

clonal mode as the major tool for speedy recovery after cessation of disturbance. It is likely that rather than employing risky seedling recruitment, the post-disturbance forest recovery processes exploit functional redundancy of CGOs (especially their ability to acquire space and resources, and ability to persist) by using various rearrangements of CGOs, but still showing in summary rather balanced (constant) patterns of clonality along the time recovery axis.

The significant differences between the habitat conditions and the preference of certain clonal traits and clonal growth organs for a certain habitat support earlier findings by Vesk and Westoby (2004), Halassy et al. (2005), Canullo et al. (2006) and Klimešová and Klimeš (2008). Clonal plants with a large bud bank were most frequent in the initial stage. Disturbance, such as erosion and animal browsing, is typical in the early stages of post-coppice regeneration. The large bud banks help plants effectively regenerate after a disturbance event. Similar studies (Moola and Vasseur 2009) showed that forest clonal species tolerate clear-cut logging through their “release growth” strategy of new vegetative stems originating from persistent bud banks. In habitats where the above-ground parts of plants can be completely removed, resprouting relates to below-ground buds (Klimešová and Klimeš 2003, 2008; Vesk and Westoby 2004).

During the subsequent post-coppice forest regeneration, the available light decreased, while soil fertility and soil moisture increased. Parallel with these changes in the environment, the relative importance of species with long spacers and short longevity of connections increased. However, it appears that this trend can be attributed to a single CGO – *Short-lived hypogeogenous rhizome* (K13) the relative abundance of which increased during the chronosequence. In the old coppices this CGO accounted for approximately 25% of the cover of the herb layer and made up 10% of the present species. The other CGO with increasing contribution was *Short epigeogenous rhizome* (K7). This group was the most abundant in all stages of the post-coppice regeneration and accounted for 25%–35% of the present species. This CGO is characterized by short spacers, long connection between ramets, and slow spread – a trait syndrome contrasting the one of *Short-lived hypogeogenous rhizome* (K13). The trait-level analyses revealed that the relative frequency of species with short-connection permanency and long spacers increased during the post-coppice succession. Therefore we believe that the increasing contribution of species with high mobility (*Short-lived hypogeogenous rhizome*) is an indication of the habitat filtering for this CGO. In contrast, the relative increase of *Short epigeogenous rhizome* (K7) is only a statistical consequence of the decrease of other CGOs (K1, K3, K5 and K6). This argument is also supported by the fact that the absolute cover and the absolute number of species in *Short epigeogenous rhizome* (K7) did not change, while there was a significant increase in the absolute cover of *Short-lived hypogeogenous rhizome* (K13) (from 1.83 to 24.71,  $P < 0.05$ ) along the chronosequence. This CGO group comprises *Galium odoratum*, *Cardamine bulbifera*, *C. enneaphyllos*, *C. kitaibelii* and *Epilobium montanum* (characterized by high mobility and low integration), known to be closed-canopy beech forest specialists in the region (Bartha et al. 2008).

There were four CGOs (K1, K3, K5 and K6) with decreasing importance along the chronosequence. Traits common to *Root-splitters* (K1), *Spreading root sprouter* (K3, e.g. *Rubus idaeus*, *Hypericum perforatum*), *Long-lived stolon* (K5), and *Turf*

*graminoid* (K6) underpin highly integrated genets with high persistence and low mobility. The three latter CGOs are also related to a large bud bank. These features might explain the success of these CGOs in the post-logged open (dry and nutrient-poor) habitats. This is supported by Callaghan (1988) and van Groenendael et al. (1996), who report tightly packed modules (short spacers, potential for frequent multiplication, prolonged period of physical connection among ramets) to be advantageous in open, nutrient-poor habitats.

Using clonal traits and clonal trait syndromes (CGOs) instead of species provided the opportunity to address functional aspects of the compositional variation of vegetation along a regeneration chronosequence. Principal coordinate analyses revealed strong patterns in both clonal trait and CGO matrices. The first ordination axes in two different PCO analyses accounted for 55% and 45% of variance, respectively, and in both ordinations the first axes appeared to be correlated with the age of the plots since the last coppicing. Forest stand structure changed considerably along the coppice regeneration chronosequence, implying significant changes in light conditions, soil moisture, and soil nutrients. Our results present evidence that all these characteristics are correlated with the plot age. Yet, the partial RDA analyses revealed that after removing the effect of plot age, the pattern of clonal traits and CGOs remained correlated with the Ellenberg indicator values for light, moisture and nutrient conditions. This suggests that the environmental conditions related to light, moisture and nutrient conditions vary across the landscape and might be determined by factors other than plot age, e.g., topography, land-use history and elevation. This aspect merits further attention in a separate study.

The variable proportion of clonal species (importance of clonality) in plant communities can be expressed at the level of plant traits or at the level of clonal growth organs. Trait level patterns are easier to link to theory. Therefore it is easier to formulate hypotheses about the individual traits and the related interpretations might become more convincing. However, traits may appear and evolve in a concerted manner (as trait combinations or trait syndromes, such as CGOs), and therefore we believe that CGOs are more natural units and more suited to explain community-level patterns.

In our particular research context, the trait spectrums appeared to be more predictable and more characteristic of a habitat than the related CGO (as frequency distributions of specially organized combinations of traits). On the contrary, the functional group approach demonstrated suitability in other studies at the community level (e.g., Lavorel and Garnier 2002) and the landscape (e.g., Steinmann et al. 2009). However, in a comparative study of the trait-based and the group-based approaches conceived on a wider array of traits related to dispersal, establishment and persistence, a combination of the two approaches was found to be most useful for exploring species responses to a gradient of old-field forest succession (Aubin et al. 2009).

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