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Influence of Previous Coppice Management on Stand Structure and Vegetation Diversity of 9210* Habitat Beech Forests in the Central Apennines (Italy)

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Keywords: coppices | *Fagus sylvatica* | forest landscape | Natura 2000 | silvicultural options | sustainable forest management | understory plants

ABSTRACT

Aims: Forests classified as Natura 2000 priority Habitat 9210* (Apennine beech forests with *Taxus baccata* and *Ilex aquifolium*) cover most of the European beech distribution along the Italian peninsula. Most of these forests have been coppiced for centuries until 60–70 years ago, and today, some are lapsed coppices and others in conversion to high forests. In both cases there is a lack of knowledge on the ongoing ecological dynamics, especially with regard of species composition changes, that is a base for their sustainable management.

Location: Central Apennines (Italy).

Methods: We analyzed forest structure and their impact on plant diversity from 50 plots in three sites where forests have been differently managed also in relation to their private, common or public ownership. We assessed the relationships between forest structure and understory plant diversity, applying multivariate statistical analysis and running regression models for estimating the influence of forest structure variables on species richness.

Results: We appraised the heterogeneity of the 9210* Apennines beech forests featuring five floristic-vegetation groups with cluster analysis in four structure stand types: lapsed coppices (LPC), coppices in conversion (CCO), two-layer coppices (TLC) and recolonized stored coppices (RSC). The Non-metric multidimensional scaling ordination shows that CCO, the most common structural type investigated, is not clearly related to any specific variable. The best models suggested that the mean cambial age and tree height can positively predict all dependent richness variables.

Conclusions: The structural and compositional diversities of these forests require an innovative management approach integrating silvicultural options commonly considered divergent (coppice vs. high forests) for providing new ecosystem services and socioeconomic opportunities for local mountain communities, to support biodiversity, and to increase forest resilience to natural disturbances.

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1 | Introduction

The forest cover transition that occurred in Europe throughout the last 500 years can be mainly attributed to relevant socioeconomic changes and their effects on land management systems (Debussche, Lepart, and Dervieux 1999; Chauchard, Carcaillet, and Guibal 2007; McGrath et al. 2015; Malandra et al. 2019). Nowadays, European forests and other wooded lands cover approximately 225 million hectares, more than one-third of Europe's land surface (MCPFE 2020; Ferrara et al. 2021). Reliable statistics on forest management are not fully available for all EU member countries, but it is estimated that approximately 25–30 million ha (15%) of the productive forests of Europe are managed as coppices (sensu Schuck et al. 2002), especially in France, Italy, Spain, Turkey, Greece and other Balkan countries (Unrau et al. 2018). These are forests mainly composed of stool-shoots or root suckers with or without retention seed trees, called standards. Coppices, are a significant part of Europe's seminatural forests and in Italy they cover more than 3.7 million hectares (42% of total cover) according to the last National Forest Inventory (2015) (https://www.inventarioforestale.org/). Since Neolithic times, coppicing with its numerous local variants has been used for domestic needs as fuelwood, utensils, fodder and building materials, or in former industries producing iron ore, glass and tanbark (Bartha et al. 2008; Buckley and Mills 2015). Since the beginning of the XX century, but more intensively after the 1950s, populations of rural and mountainous areas migrated toward cities. Extensive portions of regularly coppiced forests were then abandoned and shifting toward lapsed coppiced, a preliminary stage of the conversion to even-aged high forest, generally resulting in a single storey forest (Schuck et al. 2002), especially in beech forests (Coppini and Hermanin 2007).

In the Central Apennines, coppicing has been largely applied for centuries to deciduous mixed forests dominated by *Quercus cerris*, *Ostrya carpinifolia, Fraxinus ornus*, *Quercus pubescens*, *Castanea sativa*, *Quercus ilex* and *Fagus sylvatica*, in decreasing order (Fabbio and Cutini 2017). Beech forests, due to their high-altitude distribution (from 1000 to 1800 m a.s.l.), were traditionally managed as multifunctional silvo-pastoral systems along their elevation gradient. There is still evidence of: (i) the release of permanent protection belts (portions of unmanaged forest) at the upper forestlines to hinder livestock access and rocks or debris sliding from upper slopes; (ii) coppicing with prolonged rotation periods at upper elevations and on steeper slopes to ensure the same productivity in harsher environments; (iii) coppicing with shorter rotations at intermediate elevations for firewood and mainly charcoal production; (iv) at lower elevations wood pastures and a few high forest stands for livestock grazing and some timber production (Urbinati et al. 2014). Today, this mosaic-structured mountain landscape has almost disappeared. Stand abandonment and widespread conversion of coppices toward even-aged high forests, encouraged by Rural Development Program directives, Natura 2000 guidelines, and also enforced by forest laws and regulations caused a clear standardization of forest structure.

Since the 1970s, nature conservation issues gained increasing attention in Italy, both at the national and regional scales (Lovari and Cassola 1975; Cassola and Lovari 1976; Romano et al. 2021). Today the Italian Natura 2000 network includes more than 2600 sites, covering about 19% of the total land surface (Trentanovi et al. 2018) and around 30% of that of Italian forests (European Commission 2014). In addition, a composite network of national and regional protected areas designated under the Italian National Law 1991/394, overlaps with over 50% of the surface area of the Natura 2000 sites (Marchetti, Cullotta, and Di Marzio 2005).

The 9210* *Apennine beech forests with Taxus baccata and Ilex aquifolium* is one of the more widespread forest habitats in Italy. Its extended cover along the entire peninsular distribution of beech generated controversial debate. The Italian Manual of Habitat Interpretation (Biondi et al. 2009) stated that all Apennine beech forests could be included in this habitat even if English yew (*Taxus baccata* L.) and holly (*Ilex aquifolium* L.) are only locally occurring and attributing this fact to forest overexploitation. However, according to *ad hoc* studies, the 9210* habitat in Central Apennines should be split in two distinct ones because *Taxus* and *Ilex* are fitting two different ecological niches (Scarnati et al. 2009), more mesic the former and more xeric the latter. In addition, these authors found structural differences in beech forests hosting respectively the two target species. Nonetheless, despite the unique habitat classification, the variable geomorphic and bioclimatic features of the Apennines reflect a complex vegetation structure and syntaxonomy of beech stands (Di Pietro 2009). Their wide latitude range (around 1000 km along the peninsula) and high elevation gradient (from 1000 to 1800 m a.s.l.), together with some differences in local forest management can explain the differing compositions of the forest layers, especially at the ground layer.

The assessment of land use legacy on forests has gained attention in vegetation science studies (Garbarino and Weisberg 2020), particularly the effects of stand management history on understory species composition (Bricca et al. 2023). Several studies have assessed the effects of past land-use on forest plant species composition and diversity using old maps, archive data, interviews and soil analyses, where the comparison between past and present cover was based on relative differences in forest species composition (Hermy and Verheyen 2007; Cervellini et al. 2017). Other studies, as in the southern Pyrenees, found that land use legacies and site variables are controlling the understory plant communities in beech-dominated forests (Fortuny, Carcaillet, and Chauchard 2014). The livestock type (e.g., cattle vs. sheep) and the past forest management were the two main factors affecting the vegetation changes, also influenced by macrosite environmental variables (i.e., slope, elevation, precipitation, temperature) and microsite features (i.e., soil moisture and LAI) (Fortuny, Carcaillet, and Chauchard 2014). In French Mediterranean mountain forests, land use legacies were assessed at the landscape scale, and stand diversity was explained by previous management and by recent land abandonment (Chauchard, Guibal, and Carcaillet 2013). The consequences of forest management withdrawal on understory plant diversity is another important and related topic. In Germany, Mölder, Streit, and Schmidt (2014) reported how forest management cessation results in decreasing herb-layer diversity and productivity in many Central European deciduous woodlands. In Switzerland and Czech Republic, the cessation of management, especially coppicing, decreased the species richness also at the tree layer (Heiri et al. 2009; Altman et al. 2013). The coppicing abandonment after centuries of practice can indeed trigger important ecological changes, mainly linked to the decreasing amount of available light below the canopy, on stand structure and understory species composition (Heiri et al. 2009; Kopecký, Hédl, and Szabó 2013; Mölder, Streit, and Schmidt 2014). In temperate broadleaf forests, Verheyen et al. (2012) reported that the increase in total canopy cover can facilitate litter decomposition due to a higher presence of species producing more easily decomposable litter, as well as an overall eutrophication caused by significantly increased nitrogen deposition rates. They called this accumulated nitrogen a "time bomb" capable of stimulating a flush of nutrients when the canopy opens again after thinning, felling or re-coppicing, and triggering a shift in vegetation type.

The presence/absence of each herbaceous species or their cover share variation within the stand can be indicators of ecological changes (Scolastri, Cancellieri, et al. 2017). Several studies proved how differently stand structures can affect the richness and diversity of understory vegetation (Garadnai et al. 2010; Müllerová, Hédl, and Szabó 2015; Horvat, Biurrun, and García-Mijangos 2017; Canullo et al. 2017; Tinya et al. 2023; Saulino et al. 2022) and how the occurrence of sporadic, non-dominant tree species could enhance understory plant richness (Tardella et al. 2017). The conservation of stand structure diversity is therefore a key issue of the Sustainable Forest Management (SFM) guidelines within the "conservation of biological diversity" criterion (Bertini et al. 2019). Stand structure attributes can be used as indicators of ecological diversity to assess the effects of different silvicultural options (Staudhammer and LeMay 2001; McElhinny et al. 2005).

In this study, we focused on Central Apennines 9210* beech forests of different ownership: public, shared and private. Besides some local difference in management objectives, all forests have been traditionally used to provide fuelwood and/or livestock pasture. This study aimed: (i) to detect the diversity of stand structures, (ii) to measure the vegetation heterogeneity associated to forest structure and former forest management, (iii) to assess the possible influence of forest structures on plant diversity, and (iv) to propose suitable and sustainable silvicultural approaches in Apennines beech forests, for improving their resilience to natural disturbances, also in relation to their important role in the mountainous landscapes.

2 | Material and Methods

2.1 | Study Sites

We selected European beech (*Fagus sylvatica* L.) forests of the Italian Central Apennines included in Habitat 9210* (Apennine beech forests with *Taxus* and *Ilex*). Two sites are in the Marche region (Mt. Acuto, ACU and Val di Castro, VDC) and one in the Umbria region (Mt. Coscerno, COS) (Figure 1). Each has a different property type that may have influenced the forest management practices and goals (Table 1). All surveyed forests grow within an elevation range of 800–1300 m a.s.l. and pertain to mountain landscapes largely shaped by millennia of human influence. Bedrocks are mostly calcareous as well as most soil types, and the climate is mainly oceanic-temperate (sensu Rivas-Martinez 2004), with average annual precipitation of about 1200 mm and annual mean temperature ranging from 7°C to 11°C (Table 1). We obtained topographic variables from the TINITALY DEM (Tarquini et al. 2023), and climate data from the free global CHELSA dataset (Karger et al. 2017). All study

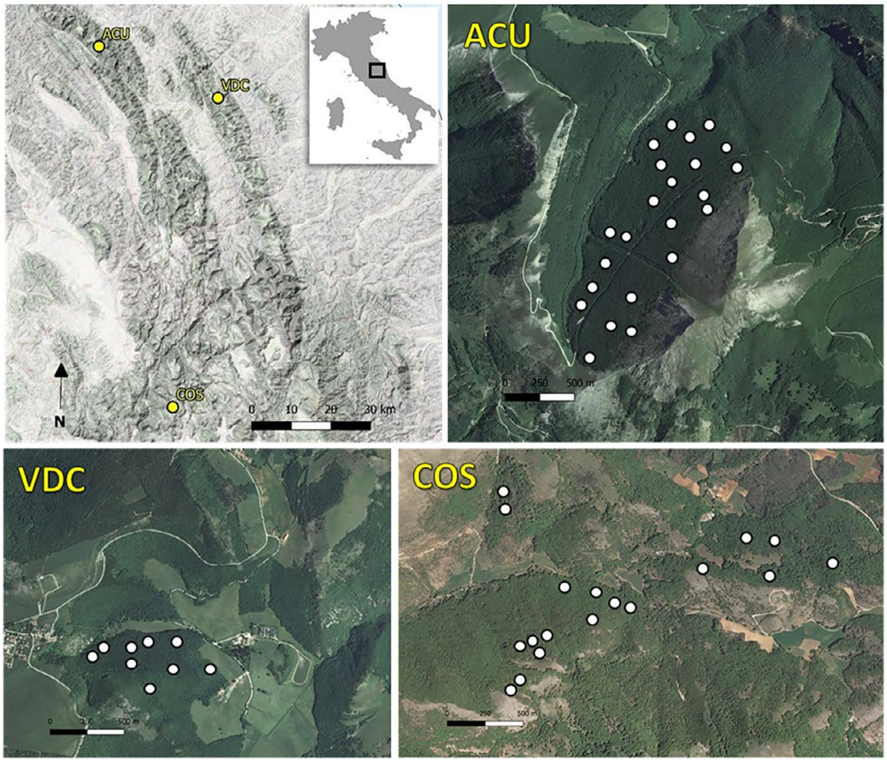

FIGURE 1 | Location of the three study sites (ACU, VDC, COS) (yellow dots in upper left image) and spatial distribution of the 50 forest sampled plots (white dots).

TABLE 1 | Main topographical and climatic variables of the three study sites.

Site	Forest ownership type	Lat [Dd]	Long [Dd]	Mean elevation [m a.s.l.]	Mean slope [°]	Main aspect	Mean annual temperature [°C]	Mean annual precipitation [mm]	SCI code	SPA code
ACU	Collective	43.477	12.671	1193	28	NW	7.2	1240	IT5210005	IT5310031
VDC	Private	43.364	13.040	808	23	NE	11.0	1243	IT5320012	IT5330025
COS	Public	42.671	12.902	1319	16	NW	7.7	1258	IT5210063	—

Abbreviations: SCI, Sites of Community Importance; SPA, Special Protection Areas.

sites belong to or border the Sites of Community Importance (SCIs) and Special Protection Areas (SPAs) of the Natura2000 network (Table 1).

2.2 | Data Collection

Forest structure data were collected in multiple field campaigns carried out between 2012 and 2014 at the three study sites (ACU, VDC and COS) within a total of 50 plots, mapped in the field with a sub-metric GNSS receiver. For the tree layer survey, following the national forest inventory protocol, we used circular plots of variable radius of 7–15 m according to stand density, to collect at least 20 individual stems (trees or coppice shoots) with a diameter at breast height (DBH) ≥ 5 cm. For each tree, we measured its DBH and total tree height (HGT). Two circular 2 m radius subplots were randomly located within each forest plot to survey natural seed regeneration. Within each larger plot, with a Pressler increment borer we cored 20% of the trees at 1.30 m selected according to the DBH distribution, to determine their cambial age and the mean age class distribution of each structural type. We mounted and glued the cores on wooden supports, polished them thoroughly with progressively finer sandpaper, counted tree rings and measured them with the semiautomatic LINTAB system. Within each plot, we also measured the size (diameter and height or length) of coarse woody debris (CWD) after individual classification of each specimen as stump, snag (standing deadwood) or log (laying deadwood), following the guidelines of the Italian National Forest Inventory INFC (Gasparini et al. 2021).

The centroid of the same 50 plots was used to delimit subplots of 400 m^2 where we carried out complete floristic-vegetational surveys on vascular plants. For each occurring species, we estimated their cover/abundance according to the Braun-Blanquet (1928) in three distinct layers according to life forms classification (Raunkiaer 1934; Pignatti 1982): tree layer (Phanerophytes, high > 5 m), shrub layer (Nanophanerophytes, Chamaephytes and Phanerophytes up to 5 m) and herbaceous layer (Therophytes, Geophytes, Hemicryptophytes and herbaceous Chamaephytes).

2.3 | Data Analysis

We assigned each sample plot to a forest structure type (STR) based on stand physiognomy, signs of former management (e.g., coppice stumps, large standards, seed trees), mean values of stand variables (DBH, tree height, total and beech basal area), volume and type of deadwood (snags, logs and stumps) and abundance of beech seedlings/saplings (Table S1). The forest structures found in the 50 plots could be assigned to four main types (Figure 2): (i) lapsed coppices (LPC) ($n = 15$); (ii) coppices in conversion to high forests (CCO) ($n = 25$); (iii) two-layer coppices (TLC) ($n = 5$) and (iv) recolonized stored coppices (RSC) ($n = 5$). LPCs are coppiced stands left to grow beyond their normal rotation length as a planned forestry practice or just as a result of abandoned management. CCO are former coppice stands shifting toward high forest through the practice of singling, where all but one of the regrowing stems are progressively cut, leaving the remaining one to grow as if it were a maiden (uncut) tree. According to the growth phase and the site conditions (e.g., canopy cover), some regeneration from either seeds or sprouts can occur in the understory. TLC are stands with a more stratified vertical structure than the previous ones, probably originated from compound coppices or coppices with standards. The trees of the two layers are very distinct in size and age, and regeneration (from both seeds and sprouts) can occur in the understory. The RSC are marginal stands featuring more irregular structures, located either at forest borders or in formerly less dense beech coppices, where suitable light conditions favored the occurrence of other tree species.

For each plot we assessed total and within layer (tree, shrub, herbaceous) species richness, calculated the Shannon diversity index (H) for the tree layer and, only for the herbaceous layer, we assessed the social behavior types [SBT1, beech forest specialist species; SBT2, forest generalist species; SBT3, non-forest species; SBT4, marginal species (weeds, exotic, ruderal or crop-related species); SBT5, gap species (linked to forest edges and gaps)] (Bartha et al. 2008) and the life forms [Therophytes (T); Geophytes (G); Hemicryptophytes (H), Chamaephytes (Ch)] (Raunkiaer 1934; Pignatti 1982) (Table S2). In addition, we considered as nemoral species the sum of SBT1 and SBT2 species, *sensu* Bartha et al. (2008) and the mean number of target species of 9210* habitat richness (on total species) following the Italian Manual of the Habitat Directive (Biondi et al. 2009). The taxonomic nomenclature of vascular plants follows the checklist of Italian flora (Bartolucci et al. 2018). For each STR, we calculated the specific mean number values of all the above listed variables. Furthermore, after transforming the matrix with the vegetation data according to the van der Maarel scale (van der Maarel 1979), in order to identify vegetation groups according to the species composition we performed a cluster analysis (CA) using 'vegan' package (Oksanen et al. 2022) for the R software (R Core Team 2020) and the 'Indicspecies' package (De Cáceres and Legendre 2009) to detect the indicator species (IS) of the vegetation groups identified through the CA (Table S3).

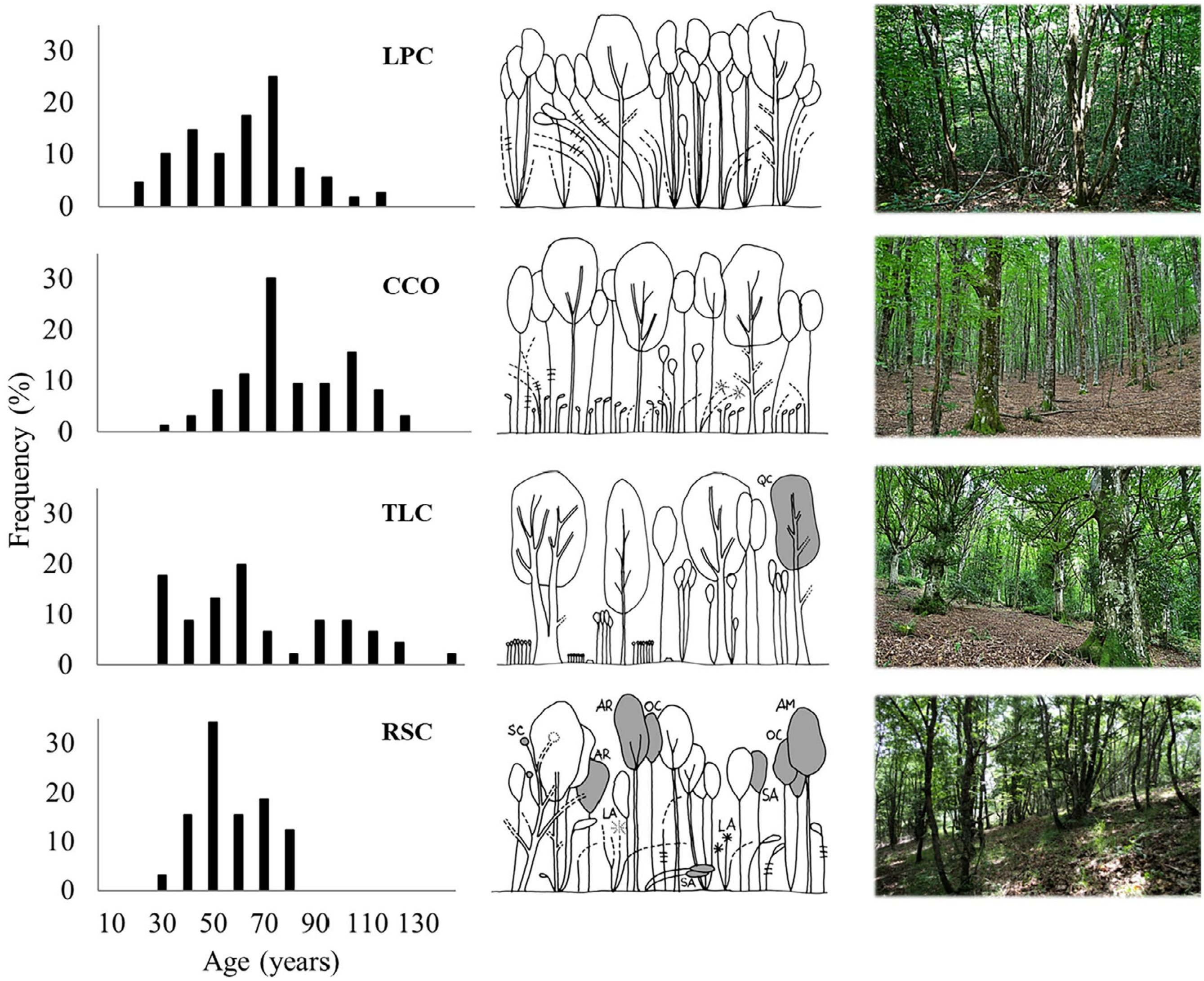

FIGURE 2 | Mean cambial age distributions (left column), original sketches (central column) and field pictures (right column) of the four structural types: Lapsed coppices (LPC), coppices in conversion (CCO), two-layer coppices (TLC) and recolonized stored coppices (RSC). AM, *Acer pseudoplatanus*; AR, *Acer platanoides*; LA, *Laburnum anagyroides*; OC, *Ostrya carpinifolia*; QC, *Quercus cerris*; SA, *Sorbus aria*; SC, *Salix caprea*. Trees with no label are *Fagus sylvatica* (drawings by coauthor G. Iorio).

Aiming to detect the effects of the stand structure on the understory species composition, we applied generalized linear mixed-effects models (GLMMs) using the *glmer* function of the 'lme4' package (Bates et al. 2015), with the Poisson error distribution and the sites as random effects. We used richness, nemoral species and SBT1 as dependent variables and structural features as fixed independent terms. We excluded the DBH as fixed effect in order to avoid multi-collinearity (highly correlated with HGT). We selected the best-fitted models showing the lowest Akaike information criterion (AIC) values (Burnham and Anderson 2002) using the *dredge* function of the 'MuMln' package (Barton 2013). We calculated the marginal and conditional R^2 (Nakagawa and Schielzeth 2013) using the *r.squaredGLMM* function of the 'MuMln' package (Barton 2013), to represent respectively the variance explained by the fixed effects and by the entire model, including both fixed and random effects. All statistical analyses were run using R software (R Core Team 2020). Finally, we performed a Non-metric multidimensional scaling (NMDS) analysis on the forest structure variables with Gower function as distance measure, using the statistical software 'PCORD v7' (McCune and Grace 2002). The significance was tested using a Monte Carlo permutation method based on 250 runs with randomized data. We overlaid understory vegetation groups as centroids and on-field forest structure classification as convex hull polygons on the ordination biplot, to explore the correlation pattern among STR and VEG. Additionally, we overlaid the significant correlation of topographic features (elevation, slope and north-eastness index) derived by a digital elevation model (ASTER GDEM2) with a spatial resolution of 30 m (Tachikawa et al. 2011).

3 | Results

3.1 | Forest Structure Diversity

Despite some physiognomic differences, the mean age distributions of the four structural types are all bell-shaped (Figure 2). The mean age varies between 58 and 101 years, but all the modes range between 50 and 70 years. CCO and TLC have a bimodal curve (70 and 100 years) suggesting two cohorts of trees. Lapsed coppices in average have the lowest mean size (DBH = 9 cm, height = 9 m) and age (58 years) and the highest deadwood volume, especially stumps (STU = 13.3 $m^3 ha^{-1}$) (Table 2). Coppices in conversion show the highest mean beech share (94%) and natural regeneration density (31,188 n ha^{-1}) and the lowest mean tree species diversity (mean Shannon diversity index H = 0.7). Two-layer coppices are the oldest stands (mean age 101 years) and have the largest mean size (DBH = 26 cm; tree height = 19 m) and basal area (45 $m^2 ha^{-1}$). The recolonized coppices have the highest mean tree species diversity (mean H = 1.6) (Figure 2) and CWD volume (snags 18.5 $m^3 ha^{-1}$; logs 4 m^3 ha^{-1}) but the lowest basal area (BAS = 27 $m^2 ha^{-1}$), beech share (60%) and beech regeneration (1415 n ha^{-1}) (Table 2).

3.2 | Structural Types and Vegetation Variables

The mean value of total species richness varies between 33.0 in RSC and 15.8 in TLC, whereas CCO and LPC have intermediate values (23.2 and 26.5, respectively) (Table 2). The mean richness of single layers is not very different in the tree and shrub layers of the four types but varies in the herb layer, with 23.0 species in RSC, 9.2 in TLC,19.1 in LPC and 17.9 in CCO. However, the share of nemoral herbaceous species (SBT1 + SBT2) is very similar (between 14.9 and 17.6) in the CCO, LCP and RSC structure types. The exception is the TLC forest structure, which has the lowest average number of nemoral species, but this should be regarded in relation to a very low total species richness. The beech forest specialist

TABLE 2 | Mean and standard deviations (in bracket) values of the variables measured in the 50 plots divided into the four structural types (STR): LPC, Lapsed Coppices; CCO, Coppices in conversion to high forest; TLC, Two-Layered Coppices; RSC, Recolonized Stored Coppices.

	Forest structural type			
Variable	**LPC**	**CCO**	**TLC**	**RSC**
N. plots (ACU-VDC-COS)	15 (10-3-2)	25 (12-6-7)	5 (1-0-4)	5 (0-0-5)
Diameter at breast height (DBH) [cm]	9 (1)	22 (7)	26 (12)	13 (2)
Total basal area (BAS) [$m^2 ha^{-1}$]	38 (6)	40 (9)	45 (6)	27 (4)
Beech relative basal area (FAG) [%]	84	96	89	60
Tree height (HGT) [m]	9 (2)	16 (3)	19 (5)	12 (1)
Cambial age (AGE) [years]	58 (17)	80 (18)	101 (25)	69 (11)
Beech regeneration (REG) [n ha^{-1}]	10,399 (10783)	31,188 (46753)	5901 (6350)	1415 (2399)
Snag volume (SNA) [$m^3 ha^{-1}$]	0.2 (0.5)	1.3 (3.8)	0.0 (0.0)	18.5 (28.0)
Log volume (LOG) [$m^3 ha^{-1}$]	2.6 (3.6)	2.8 (4.0)	1.0 (1.5)	4.0 (2.1)
Stump volume (STU) [$m^3 ha^{-1}$]	13.3 (19.5)	3.3 (3.8)	3.3 (4.3)	0.0 (0.1)
Tree layer Shannon diversity index (H)	1.2 (0.5)	0.7 (0.5)	1.1 (0.6)	1.6 (0.4)
Total richness [*n*]	26.4 (12)	23.2 (10.6)	15.8 (14.1)	33.0 (13.0)
Trees layer richness [*n*]	3.7 (1.8)	2.44 (1.4)	3.8 (2.5)	5.2 (1.8)
Shrubs layer richness [*n*]	3.8 (2.3)	2.9 (1.9)	2.8 (2.5)	4.8 (2.8)
Herbs layer richness [*n*]	19.1 (10.7)	17.9 (9.2)	9.2 (9.5)	23.0 (10.0)
Nemoral species richness [*n*]	15.3 (8.0)	14.9 (9.9)	7.6 (7.0)	17.6 (5.4)
Beech forest specialist species (SBT1) [*n*]	5.0 (3.0)	6.6 (3.6)	2.4 (2.2)	4.8 (1.1)
Generalist forest species (SBT2) [*n*]	10.3 (5.7)	8.3 (4.7)	4.8 (5.1)	12.8 (5.6)
Non-forest species (SBT3) [*n*]	2.1 (1.9)	1.6 (1.9)	0.8 (1.1)	4.4 (4.8)
Margin species (SBT4) [*n*]	0.3 (0.8)	0.3 (0.6)	0.0 (0.0)	0.2 (0.4)
Gap species (SBT5) [*n*]	1.3 (1.2)	1.0 (1.1)	0.8 (1.8)	0.8 (1.1)
Chamaephytes (Ch) [*n*]	0.4 (0.5)	0.8 (0.7)	0.0 (0.0)	0.6 (0.5)
Geophytes (G) [*n*]	6.4 (3.6)	8.2 (4)	4.4 (3.4)	5.6 (1.5)
Hemicryptophytes (H) [*n*]	10.8 (6.2)	7.8 (5.4)	3.8 (5)	15.2 (7.7)
Therophytes (T) [*n*]	1.5 (1.6)	1.0 (1.1)	1.0 (1.4)	1.6 (0.9)
Target species 9210* richness [*n*]	5.4 (3.3)	7.3 (3.6)	4.4 (2.3)	7.0 (2.1)

Note: The number of plots is reported as total number and, in bracket as divided for each site (respectively ACU-VDC-COS). Nemoral, Social Behavior Type (SBT), Raunkiaer's and target species are specifically referred to the herbaceous layer.

herbaceous species (SBT1) had the highest shares in CCO (6.6) and lower ones in TLC (2.4). Generalist species (SBT2), such as *Melica uniflora* and *Festuca heterophylla*, are rather common within the 4 types, with the maximum values in RSC (12.8) and minimum in TLC (4.8). The relative occurrence of non-forest species (SBT3) is higher in RSC (4.4) compared to the others (between 0.8 and 1.6), showing a legacy with the grassland origin of these newly formed forest stands. Marginal species (SBT4) are infrequent (0–0.3), and gap species (SBT5) are also not very common (0.8–1.3) (Table 2). Regarding Raunkiaer's life forms of the herbaceous species, geophytes (G) and hemicryptophytes (H) make up approximately 90% of the total species. The former had maximum values in CCO (8.2), and the latter had maximum values in RSC (15.2). Therophytes (T) are scarcely represented in general (1–1.6), with maximum in RSC, and Chamaephytes (Ch) are infrequent (0–0.8). Finally, 9210* habitat target species ranged between 7.3 (CCO) and 4.2 (TLC) (Table 2).

3.3 | Relations Between Forest Structural Types and Vegetation Groups

The cluster analysis applied to floristic-vegetational data detected five vegetation types (*Cardamine kitaibelii* group, *Luzula forsteri* group, *Neottia nidus-avis* group, *Saxifraga rotundifolia* group *and Lonicera alpigena* group) each characterized by a group of species identified through the ISA (Table S3).

The NMDS ordination (Figure 3) shows that CCO, the most common structural type found, featuring a widespread distribution over 50% of the plots ($n=25$) (Table 2), is not clearly related to any specific variable. The partial eccentricity of the CCO convex hull is negatively associated with H of the tree layer, CWD volume and slope (SLO). Positive relationships occur with the relative dominance of *Fagus sylvatica*, the total basal area and the beech regeneration density. *Cardamine kitaibelii*, *Luzula forsteri* and partially *Neottia nidus-avis* vegetation groups are included in the same convex hull. The second largest structure type is that of LPC, occurring in over 33% of the plots ($n=15$) and negatively influenced by AGE, HGT and DBH but positively associated with H and a larger deadwood (LOG and STU) share. LPC occur mainly on steeper slopes, and they contain the centroid of the *Saxifraga rotundifolia* group. The RSC convex hull indicates a clustered and limited distribution within the plots. This type has the largest share of SNA, and it is partially associated with the *Lonicera alpigena* group. Finally, TLC is slightly positively associated with AGE, HGT and DBH and with the *Neottia nidus-avis* vegetation group.

3.4 | Modeling the Influence of Forest Structure on Species Richness

The best models for estimating the influence of forest structure variables on species richness suggested that AGE and H can positively predict all dependent variables except for SBT1 species, whereas HGT is positively related only to SBT1 species occurrence. Conversely, BAS is a negative predictor of total and herbaceous species richness and of nemoral and SBT1 species occurrence (Table 3). FAG has a negative influence on total and herbaceous species richness. The contribution of the SITE as random effect was proved by the conditional R^2 calculated, but the standard deviations among sites were very low for all models.

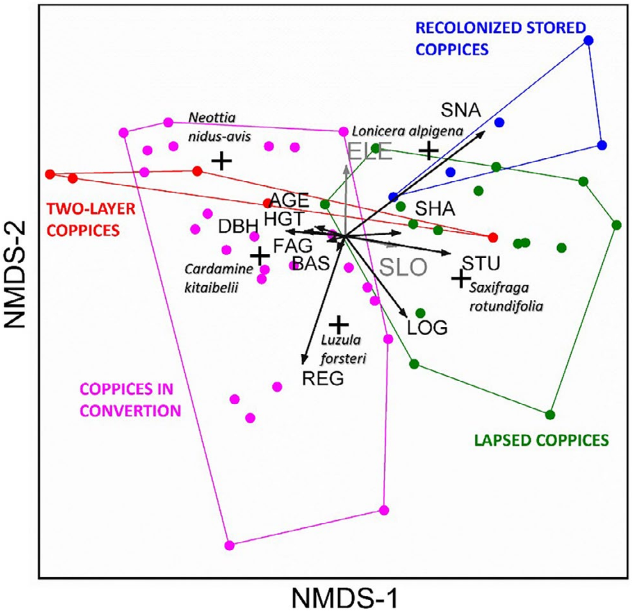

FIGURE 3 | Non-metric multidimensional scaling (NMDS) analysis with forest structure variables (black arrows). The five floristic-vegetation groups (VEG) are overlaid as centroids (black crosses), and the four structural types (STR) are outlined by convex hull polygons with the relative plot distribution ($n=50$ colored dots). The gray arrows indicate the only significant correlations of topographic variables. AGE, Age (years); BAS, Mean basal area (m^2); DBH, Mean dbh (cm); ELE, Average elevation (m a.s.l.); FAG, Portion of *Fagus sylvatica* (%); H, Shannon's diversity index of tree layer; HGT, Height (m); LOG, Log portion of deadwood volume (m^3); REG, Mean regeneration density (n ha^{-1}); SLO, Average slope (%); SNA, Snag portion of deadwood volume (m^3); STU, Stump portion of deadwood volume (m^3).

4 | Discussion

4.1 | The Effects of Past Management on Current Stand Structure and Vegetation Composition

The widespread occurrence of Apennine beech-dominated forests is the synergistic result of long-term intensive land use, that in most cases, outweighed by far the effects of macroecological constraints (Brown et al. 2013), and late Holocene cooling and moistening, which caused the decline in species-rich mixed silver fir forests (Morales-Molino et al. 2021). In the last centuries and up to 1950s, local populations heavily shaped the structure and composition of these forests for their subsistence needs (production of charcoal, fuelwood, forest litter, construction timber, pasture, etc.) (Nocentini 2009). The management options applied were calibrated to forest productivity (soil fertility), available cutting tools (from axes, handsaws to chainsaws) and traditional harvesting practices. Furthermore, the different forest ownership (public in COS, private in VDC and shared in ACU) influenced the

TABLE 3 | Results of the best GLMM models applied with the *glmer* function (with Poisson error distribution) and selected with the *dredge* function.

Independent variables	Total richness	Herbaceous richness	Nemorals	SBT1	Target 9210*
BAS	−0.10**	−0.11**	−0.10*		
FAG	−0.07*	−0.09*			
HGT				+0.13ns	
AGE	+0.11*	+0.13**	+0.10.		+0.12*
H	+0.22***	+0.13**	+0.15***		+0.17**
REG					
SNA					
LOG					
STU					
Marginal R^2	0.49	0.31	0.23	0.04	0.20
Conditional R^2	0.75	0.69	0.56	0.45	0.20
SD of random effect (SITE)	0.21	0.27	0.23	0.38	0.00

Note: +/− intercept values indicate a positive or negative significant effect of fixed terms. The variable SITE was considered as a random effect in all models. BAS, total basal area [$m^2 ha^{-1}$]; FAG, beech relative basal area [%]; HGT, height [m]; AGE, cambial age [years]; H, Shannon index of tree layer; REG, beech regeneration [n ha^{-1}]; SNA, snag volume [$m^3 ha^{-1}$]; LOG, logs volume [$m^3 ha^{-1}$]; STU, stumps volume [$m^3 ha^{-1}$]. Empty cells indicate variables excluded from the automated model selection procedure. Significant code *p values* are reported (not significant 'ns'): 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1.

management and the harvesting intensity (Urbinati et al. 2014). Our results are consistent with specific studies (Chelli et al. 2023; Chiarucci et al. 2019; Scolastri, Cancellieri, et al. 2017) highlighting the link between structure and vegetation diversity of central Apennines beech forests, as indicated by the detection of four types and five groups respectively.

We can envisage a forest maturity gradient from RSC to CCO due to structure and vegetation diversity as a result of combined natural and anthropogenic dynamics in formerly coppiced stands. The CCO stands are among the oldest ones and have a high basal area (lower only to TLC) together with the highest number of beech forest specialist species (SBT1), geophytes and habitat 9210* target species (e.g., *Cardamine kitaibelii, Actaea spicata, Corydalis cava*). This suggests that this structural type is the closest to the typical mature conditions of natural unmanaged and/or ancient forests (Hermy et al. 1999; Scolastri, Bricca, et al. 2017). The long-term withdrawal of coppice periodic harvesting is driving these stands toward a mainly even-aged high forest with homogeneous structure and density that limits the entrance of solar radiation at ground level. Nonetheless variability within the CCO stands is probably related to their higher plot frequency and some diversity in site conditions (e.g., altitude and slope) as indicated also by some vegetation differences. The three prevailing types (*Cardamine kitaibelii*, *Luzula forsteri* and the *Neottia nidus-avis* groups) express the different CCO ecological and structural features but could also be referred to the different ownership existing between the stands. On the other hand, the RSC stands are the least evolved forests from a successional perspective. In fact, the highest species richness of tree and shrub layers and the lowest BAS suggest a legacy to past coppicing of sparse forests. This is supported also by the higher richness of non-forest species (SBT3), typical of semi-natural open communities (Bartha et al. 2008), and of hemicryptophytes (e.g., *Thalictrum aquilegiifolium* and *Gentiana lutea*). The occurrence of non-forest species and the higher herbaceous species richness, may confirm the ecotonal position of RSC stands where the reduced canopy cover increase understory light availability and may reduce the microclimatic buffering (De Pauw et al. 2021).

Moreover, the higher amount of deadwood and tree species diversity indicate ongoing forest dynamics caused by abiotic disturbances and recent forest succession under canopy gaps (Hilmers et al. 2018). LPC are stands of intermediate successional maturity according to the heterogeneous values of structural and vegetation variables between plots, that could be influenced by the geomorphological features of the study sites, and by the past coppicing. This could favor the coexistence of disturbance related species with the ones typical of more mature habitats (Scolastri, Bricca, et al. 2017). The high scores of nemoral and generalist forest species (SBT2) can be related to a shifting successional stage toward more mature forests (Campetella et al. 2016). The stand structure of TLC is anthropogenic and quite uncommon in the central Apennines. Detailed literature on their species richness is also unavailable. TLC have a diversified tree layer with large and isolated standard seeding trees, legacy of former wood pasturing, mainly practiced on warmer and mild slopes. The lowest herbaceous species richness seems related to a more pronounced soil erosion caused by an intensive and prolonged pastoral use, which hampered the grass species recolonization.

The applied GLMMs estimated how forest structure could influence the forest species richness. Tree age is positively correlated with total richness and that of herb layer, nemoral and 9210* habitat target species. This outcome may seem controversial: on one hand several studies have shown that the understory species richness is decreasing with tree age due to light limitation at the forest floor (Bartha et al. 2008; Storch et al. 2023); on the other, same studies indicate that older trees can also increase the heterogeneity of the canopy and therefore the number of species (Hilmers et al. 2018).

The same richness indices were also positively correlated with the tree layer Shannon index. Overstory tree species diversity can increase understory species diversity (Mölder, Bernhardt-Römermann, and Schmidt 2008; Vockenhuber et al. 2011; Durak 2012; Ampoorter et al. 2020). According to a recent study with multi-taxa approach in mixed forests, the most influential drivers of forest biodiversity are under the direct control of the current silvicultural management. Heterogeneous stand structure and tree species composition promote the different organism groups in various ways (Tinya et al. 2023). In particular tree species can influence the herb layer by changing resource availability and environmental conditions in lower forest layers (Barbier, Gosselin, and Balandier 2008; Ampoorter et al. 2016). For example, the litter depth can induce the formation of a thick humus layer, a physical barrier for the herbaceous species germination. Therefore, a high tree species diversity with different degrees of litter decomposition can affect the depth of the organic layer (Vockenhuber et al. 2011). Therefore, stands with a low tree diversity or full beech dominance forming a thicker organic layer than other broadleaved tree species (Jacob et al. 2010), could reduce herbaceous species richness. Indeed we found a negative correlation between the beech basal area and the total and herbaceous layer richness. In addition, the basal area is also negatively related to species richness (total, herbaceous and nemoral) (Chiarucci and Bonini 2005; Campetella et al. 2016; Scolastri, Cancellieri, et al. 2017; Lelli et al. 2019; Ampoorter et al. 2020). A higher basal area, in our study, means denser and darker stands, lowering the understory diversity (Ampoorter et al. 2020), since light is the main limiting factor for ground forest cover (Barbier, Gosselin, and Balandier 2008). Vockenhuber et al. (2011) confirmed that increased light availability promotes the coexistence of plant species in forest and grassland ecosystems, without specific adaptations to the low light conditions of the forest understory. The light conditions within forest stands are largely influenced by the tree crown architecture and canopy density. Specifically, the dense canopies of *Fagus sylvatica* reduce light transmission compared to those of other broadleaved (Ellenberg and Leuschner 2010).

At a landscape scale, a marked variation in understory species communities can be related to previous impacts occurred even a century or more ago (Foster et al. 2003). In general, the understory herbaceous species richness is lower in unmanaged than in managed deciduous forests, suggesting that disturbances caused by management usually increase plant species richness. Therefore, total plant species richness is not always a suitable indicator of forest conservation quality, but it can better signal previous disturbances (Boch et al. 2013).

4.2 | Sustainable Silviculture in Apennine Coppiced Beech Forests

Besides its general decline, coppicing is still currently practiced in southern Europe, whereas in central and eastern Europe it has been almost completely replaced by high forest management (Kozdasová et al. 2024). Especially in these regions there is an increasing interest, where possible, to restore or reintroduce coppice management for conservation purposes (Buckley 2020; Johann 2021; Vollmuth 2022). Differently, in central Apennines regions coppicing is still practiced mainly for energy wood production. On the other hand, as we try to demonstrate here, Central Apennines beech forests today, are largely over-aged coppices whose rotation cuts are now prohibited. The regional forest laws and regulations, Rural Development Program directives and Natura 2000 guidelines have enforced high forest conversion, but almost exclusively toward even-aged structures, at the risk of an extensive standardization of forest structures. We found that habitat target tree species such as *Abies alba*, *Taxus baccata*, *Ilex aquifolium*, or other broadleaves are rare and occurring with few individuals or clusters. Closed canopy cover, high competition with beech sprouts and ungulate browsing hamper their regeneration and growth (Miozzo, Ducci, and Montini 2014). The structural features and vegetation types of these forests, suggest that *ad hoc* and diversified management options should be implemented to maintain this diversity and increase their uneven-aged traits. Landscape-scale conventional coppice conversion should be reduced in favor of diversified options, ensuring a longer-term conservation of floristic diversity (Gartner and Reif 2005), a more heterogeneous structure and the provision of multiple ecosystem services. At landscape scale the importance of forest diversity with co-occurrence of differently managed forests including coppice systems in their multiple forms has been suggested for decades (Rackham 1976) and recently reiterated to enhance the provision of multiple ecosystem services and the resilience to climate change effects (Coppini and Hermanin 2007; Johann 2021; Slach, Volařík, and Maděra 2021). In some cases hotspots of remaining, active coppice systems are of special interest because they are managed as socioecological systems by close-knit village communities (Kamp 2022). Different structures can guarantee fluctuating open phases and their functional diversity by providing habitats for a suite of early-successional and cosmopolitan species and creating structural and composition mosaics at local and regional scales, increasing the value of forest conservation and biodiversity (Buckley 2020). Small-scale sylvicultural options are widely available and include: (i) “single tree orientated silviculture” (Larrieu et al. 2016, 2019; Manetti et al. 2016), based on the retention of some target trees selected by frequent and diversified thinning to become valuable timber or conservation trees; (ii) coppice with “clustered standards” embedded within the coppice to enhance the growth of selected retention trees (Mairota et al. 2016); (iii) group or individual selective thinning or cuts, (iv) retention of deadwood, senescent trees or islands, veteran trees with dendrothelms and/or microhabitats. Several biodiversity indices, such as those of saproxylic and non-saproxylic beetle communities, could benefit from deadwood retention, habitat heterogeneity and canopy openness (Parisi et al. 2021). Unfortunately, these treatments are often economically unsustainable unless funded by specific programs adapted to such general objectives (Cutini et al. 2021).

5 | Conclusions

This study on forest structure and vegetation diversity of 9210* habitat beech forests in Central Apennines (Italy) confirmed what several studies have recently underlined: the importance of the co-occurrence of differently managed forests, where coppices, in its multiple forms, should have renewed recognition given their ecosystem values and resilience to climate change effects (Johann 2021; Slach, Volařík, and Maděra 2021). Hotspots of remaining, active coppice systems are often under the radar of national and international forest and conservation authorities because they can also have a socioecological value (Kamp 2022). The effects of such forest management can be monitored using also herbaceous layer diversity as an indicator of environmental changes (Horvat, Biurrun, and García-Mijangos 2017). The coexistence of diverse management options, calibrated with the specific environmental conditions and the socioeconomic context, can be very beneficial, at local or regional scales. Forest complexity at all operational scales requires an increasingly interdisciplinary approach to provide the diverse ecosystem services of Apennine forests (Cutini et al. 2021).

Finally, forest laws, classification and management regulations should foster the appreciation of heterogeneous forest structures and understory diversity. At regional scale forest planning is very useful to set conservation priorities especially in Natura 2000 Network sites (Trentanovi et al. 2018). Nonetheless, we are aware that herb-layer species and structural complexity cannot always be effective surrogates of multitaxa biodiversity in European beech forests (Sabatini et al. 2016). Other taxonomic groups, such as bryophytes and lichens, should also be included in further studies for a better understanding of the management effect on plant diversity. Additionally, the impacts of multiple environmental change drivers on the growth of European beech should be accounted for when evaluating current and future changes in forest ecosystem functioning, given the differences in management history (Mausolf et al. 2020).

Author Contributions

A.V. and G.T. wrote the original draft; A.V., G.T., M.G., M.A. and C.U. conceived of the research idea and methodology; G.T., M.A., G.I. and C.U. collected data; A.V. with contributions from G.T. and M.G. performed statistical analyses; A.V. and G.T. curated data; M.A., G.I. and C.U supervised the research; C.U. acquired the funds; all authors discussed the results and commented on the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.