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Effect of forest structure and management on the functional diversity and composition of understorey plant communities

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Abstract

Questions: Do forest structural parameters related to stand heterogeneity enhance functional diversity (FD) of understorey plant communities? Do FD and functional composition of understorey plant communities vary between high-forest (HF) and old coppices-with-standard (oldCWS) management types? Are HF stands characterized by a higher FD than oldCWS?

Location: Submediterranean beech forests of Montagne della Duchessa Reserve (central Italy).

Methods: We sampled 57 (20 m × 20 m) forest plots, 29 oldCWS and 28 HF stands, where we recorded plant species cover abundance. We used Leaf–Height–Seed and clonal traits, and run multiple separate linear models to quantify the effect of forest structural parameters and management types on FD and functional composition of understorey plant communities.

Results: We found that increasing lying deadwood enhanced FD of specific leaf area (SLA) through micro-environmental heterogeneity of soil fertility regardless of management type. We also found that increased horizontal stratification filtered the range of plant sizes, probably through light reduction. HF management enhanced FD of SLA and clonal traits through micro-environmental heterogeneity, while reducing the FD of plant size and seed mass. HF tended to select plant communities characterized by high resource acquisition strategies but lower persistence between ramets, possibly as an effect of more mature forest conditions.

Conclusion: Our study suggests that understorey plant community diversity and composition change in response to forest structure and management. Combining Leaf–Height–Seed with clonal traits offers a promising framework for understanding and predicting plant response to management practices.

KEYWORDS
clonal traits, community assembly, coppice, deadwood, forest management, forest structure, habitat filtering, plant traits, SLA

1 | INTRODUCTION

For millennia European temperate forests have been managed (Peters, 1997; Sabatini et al., 2018). In the last centuries, the most common management types in European forests have been coppices-with-standards (hereafter "CWS"; also named "low forests") and high forests (hereafter "HF"). CWS management involves the logging of almost all the trees over a short rotation period except for a small number of uncut trees (called "standards") to partially prevent soil erosion and to guarantee the maintenance of the forest genetic variability (Oldeman, 1990; Ciancio et al., 2006). After socio-economic changes by the end of the Second World War, the demand for small-sized timber in many European and Mediterranean mountain areas declined, and forest stands subjected to CWS were progressively abandoned (MacDonald et al., 2000; Kopecký et al., 2013). CWS stands that overcome their rotation length are called "old coppices-with-standards" (oldCWS), representing an interesting semi-natural system for investigating the effect of past land use on vegetation (Chelli et al., 2021). In contrast, HF management consists of selective tree cuts over longer rotation periods, so eventually resulting in timber larger in size. CWS and HF differ in the intensity and frequency of their disturbance regime, the former having higher disturbance levels compared to the latter. However, few studies have as yet addressed how these management types impact understorey plant diversity (Scolastri et al., 2017a, 2017b).

Plant traits (*sensu* Violle et al., 2007) are quantitative descriptors of species' ecological niches. Analysing their distribution within the communities can provide an excellent tool for developing models of vegetation response to changing environmental conditions (Laliberte et al., 2010; Funk et al., 2017; Bricca et al., 2022). The traditional way to describe biological communities from a functional point of view is through two complementary metrics, namely community-weighted mean (CWM) and functional diversity (FD). CWM reflects the abundance-weighted mean trait value in a given community and can be interpreted as a measure of functional composition, while FD quantifies the degree of functional dissimilarity between coexisting species, and is largely used to detect community assembly mechanisms (Garnier et al., 2004; de Bello et al., 2021a).

Despite the increasing scientific interest in forest ecology, we still lack a satisfactory understanding of how plant understories respond to management strategies. This is chiefly due to two reasons. First, forest studies using a trait-based approach have generally considered only a few traits, namely plant height (H), specific leaf area (SLA), and seed mass (SM). While these traits collectively capture fundamental axes of trait variation related to competitive ability (H), resource exploitation (SLA), or reproductive ability (SM) (L–H–S scheme; Westoby, 1998), they do not reflect other functional dimensions, like plant clonality (Klimešová et al., 2016). Clonality is linked to on-spot persistence and space occupancy and has traditionally received little attention in the scientific literature (Klimešová et al., 2017, 2021). Clonality increases the plant's capacity to spread across the space surrounding the parent plant, and in highly heterogeneous habitats it may give a competitive advantage (Oborny

et al., 2000; Yu et al., 2008). In forest ecosystems, clonality can represent a key strategy, as sexual reproduction is generally hindered because of the short time window for pollination and limited early-year sunny conditions (Canullo et al., 2011; Campetella et al., 2020; Tardella et al., 2022).

Secondly, many forest studies have focused only on chronosequences where light availability linked to canopy closure after logging represented the main ecological gradient affecting forest understories. These studies found that a decrease in the amount of light reaching the understories acted as a key driver in the selection of specialized forest floor species (Graae & Sunde, 2000; Bartha et al., 2008; Decocq et al., 2004; Campetella et al., 2011; Scolastri et al., 2017b). This process is in line with the habitat filtering theory (Keddy, 1992), which posits that specific environmental conditions select only those species that share more similar trait values close to the ecological optimum ("functional convergence"; Keddy, 1992; de Bello et al., 2013). For example, species growing in more mature stands that need to withstand limiting light conditions tend to be short, with larger seeds and higher SLA (Kenderes & Standovár, 2003; Verheyen et al., 2003; Campetella et al., 2011; Vanneste et al., 2019; Padullés Cubino et al., 2021). However, forest studies that investigate the role of changing structural parameters under closed-canopy stands as drivers of community assembly processes are still uncommon (but see Ottaviani et al., 2019). Structural parameters, like vertical and horizontal tree stratification, or the amount of lying deadwood, may promote a patchy distribution of resources within the forest stands which in turn can enhance the diversity of plant strategies. This micro-environmental resource heterogeneity allows functionally different species to occupy different environmental microhabitats within the site (i.e., "functional divergence"; de Bello et al., 2013). As such, the effect of structural parameters in closed forest stands through micro-environmental heterogeneity processes can contribute to explain their high understorey FD (e.g., Lelli et al., 2019; Vanneste et al., 2019; Closset-Kopp et al., 2019; de Pauw et al., 2021).

We considered H, SLA, SM, and clonal traits to study the role of structural parameters (i.e., vertical tree stratification, horizontal stratification, and amount of lying deadwood) and the effect of two forest management types (oldCWS and HF) on the understories of *Fagus sylvatica* forests of the central Apennines (Italy). Previous investigation performed in the same area showed that the HF management is characterized by a higher understorey species richness with functional strategies typical of more mature forest conditions in terms of leaf anatomy and phenology, flowering phenology, pollination, dispersal, and number of clonal species (Scolastri et al., 2017a, 2017b).

In this study, we hypothesize that: (H1) horizontal and vertical tree stratification and lying deadwood will promote functional divergence through a higher micro-environmental heterogeneity; (H2) HF stands will be characterized by plant adaptations typical of more mature forest conditions: shorter plant size, larger SM, SLA and lateral spread, higher number of clonal offspring and persistence of clonal organs compared to oldCWS; and that (H3) HF management will

lead to higher functional divergence compared to oldCWS through higher micro-environmental heterogeneity in more mature forest conditions.

2 | METHODS

2.1 | Study area

The study area is the Montagne della Duchessa Reserve, located in the western sector of the Velino-Sirente mountain chain (central Apennines, Italy). The area has a submediterranean climate (Cutini et al., 2021). The bedrock is largely calcareous. This mountainous area is characterized by beech forests of the order *Fagetalia sylvaticae* occupying about 1200 ha and belonging to the habitat of the 92/43/EEC Habitats Directive "Apennine beech forests with *Taxus* and *Ilex*" (code 9210*) growing on limestone substrates. They are classified as *Fagus* forests on non-acid soils (code T17) in the EUNIS habitat classification (Chytrý et al., 2020). Our study sites correspond to those described in Scolastri et al. (2017a, 2017b).

Traditionally, these beech forests have been managed as HF and CWS. HF consists of a uniform shelterwood system over longer rotation periods, based on continuous canopy cover, thuas eventually resulting in timber larger in size. In contrast, CWS involves the logging of almost all the trees over a shorter rotation period except for a small number of uncut trees (called "standards"; Ciancio et al., 2006; Nocentini, 2009). The material obtained from the CWS management is mainly small-sized timber, mostly used as firewood and charcoal. Like other European mountains, the central Apennines were affected by the depopulation phenomenon leading to a decrease in traditional land use (Malavasi et al., 2018). Starting from the 1960s, both HF and CWS forests have been left unexploited. Thus, while the surveyed HF are still in their cut cycle, CWS forests are over their turn and have to be considered as oldCWS (>38 years; Scolastri et al., 2017a).

Currently, forests of the study area are almost entirely characterized by monospecific stands of *F. sylvatica*, which largely dominates the tree layer. Forests at different elevations present a different composition: woody tree species such as *Acer pseudoplatanus* and *Sorbus aucuparia* at higher elevations, and *A. opalus* ssp. *obtusatum* at lower elevations. In terms of forest structure, oldCWS have a higher number of tree individuals, with lower height and smaller diameter compared to HF. Basal area between the two systems did not differ (Appendix S1). Finally, HF stands have been found to host higher species richness compared to oldCWS stands (Appendix S1). A detailed description of forest structure and species richness in response to management practices can be found in Scolastri et al. (2017a).

2.2 | Vegetation sampling and forest structural parameters

We used 57 forest vegetation plots of 400 m² represented by 29 oldCWS and 28 HF, recorded with an estimation of the species cover abundance according to the scale of Braun-Blanquet (1932; Appendix S2). These plots resulted from a stratification procedure aiming to minimize the potential effect of environmental variability on management types. Accordingly, they were randomly placed into classes of aspect (SW and NE) and slope (0–30° and 31–45°), with a minimum distance of 200 m among them to avoid pseudo-replication and 30 m buffer from the forest edge to avoid the edge effect (Scolastri et al., 2017a, 2017b). Finally, to have a homogeneous condition of canopy cover between oldCWS and HF, we excluded old-CWS plots with canopy cover values below 98%. We selected this threshold because it represents the minimal value of canopy cover for HF.

In each plot, we considered two forest stand parameters: the proportion (%) of lying deadwood (estimated visually from the projected cover on the ground within the plot) and tree diameter at breast height (DBH, cm), measured for all trees with a minimum DBH of 2.5 cm. Trees were classified as dominant, co-dominant, dominated, or shrubby (Scolastri et al., 2017a, 2017b).

2.3 | Plant functional traits

As an indicator of species' functional performances, we selected a set of three above-ground and three clonal traits (Table 1).

TABLE 1 List of the plant traits considered in this study, their abbreviations, definitions, and functions (Westoby, 1998; Klimešová et al., 2019)

	Trait (abbreviation)	Trait definition (units)
Leaf–height–seed traits	Plant height (H)	Distance between the upper boundary of the main photosynthetic tissue on a plant and the ground level (m)
	Specific leaf area (SLA)	One-sided area of a fresh leaf, divided by its oven-dry mass (mm²/mg)
	Seed mass (SM)	Oven-dry mass of an average seed of a species (mg)
Clonal traits	Lateral spread (LS)	Distance between parental and offspring shoots (cm/year)
	Persistence of clonal growth organs (PCGO)	Lifespan of the physical connection between mother and daughter shoots (year)
	Clonal offspring (CO)	Number of offspring shoots produced per parent shoot per year (n/year)

Specifically, for above-ground traits, we considered SLA, vegetative plant height (H), and SM, which correspond to Westoby's Leaf–Height–Seed scheme (Westoby, 1998). For clonal traits, we considered lateral spread (LS), the number of clonal offspring (CO), and persistent clonal growth organ (PCGO; Klimešová et al., 2015, 2017). These three clonal traits are informative of space occupancy, resource foraging and sharing, and species' ability to recover from disturbance (Klimešová et al., 2016). All selected traits play a key role in the ecological functioning of forest understories (Chelli et al., 2019; Burton et al., 2020; Padullés Cubino et al., 2021), resulting in independent axes of functional variation (Appendix S3).

We removed from our analysis tree seedlings and saplings from the understorey as assigning trait values of mature individuals from the database to tree seedlings and saplings would overestimate their functional role. Therefore, in this study, the understorey layer consisted of all woody and non-woody vascular plants, except for tree seedlings and saplings (Chelli et al., 2021). We obtained H, SLA, and SM data from the LEDA database (Kleyer et al., 2008). Clonal traits were retrieved from CLO-PLA (Klimešová et al., 2017). Trait data were available for all species whose relative cumulative cover was higher than at least 80% (Pakeman & Quested, 2007; Májeková et al., 2016). This threshold holds on the concept of the "biomass ratio hypothesis", stating that the most abundant species exert a key effect on ecosystem functioning (Grime, 1998).

2.4 | Forest structural indices

We considered a set of forest structural indices linked to environmental heterogeneity, namely entropy of diameter distribution (SH_{DBH}), vertical evenness of the basal area (VE_G), and the proportion of lying deadwood.

SH_{DBH} was calculated using the Shannon index applied to the proportion of trees in each size class after dividing tree diameters (DBH) into 10-cm classes (Scolastri et al., 2017a). The Shannon index values (SH_{DBH}) range from zero (absence of heterogeneity) to the logarithm of the possible number of categories, which is 2.58 (maximum heterogeneity). We considered this index as a proxy of horizontal stratification: values approaching zero represent low variability as trees share similar diameters (i.e., low horizontal stratification), whereas high values represent trees of different diameter classes (i.e., high horizontal stratification).

Since there was no data on the crown projection area, as in the original calculation proposed by Neumann and Starlinger (2001), the vertical evenness (VE_G) was calculated as the proportion of the basal area in each social position (i.e., dominant, co-dominant, dominated, or shrubby):

$$VE_G = \sum \left[\left(-\log_2 p_i \right) p_i / \log_2 3 \right] \quad (1)$$

where p_i is the relative basal area in each social position. VE_G is expressed as the vertical layering of the stand; lower values are linked to

single-storied layers, i.e., basal area stored in one or two layers (lower vertical stratification), and higher values are linked to the multistoried layers, i.e., basal area stored in more layers (higher vertical stratification; Scolastri et al., 2017a). SH_{DBH}, VE_G, and the proportion of lying deadwood were only weakly correlated (Appendix S4).

2.5 | Data analysis

We preliminarily checked trait distributions and $\log_{10}$-transformed H and SM, and square-root-transformed LS to improve the normal distribution of species trait values (Májeková et al., 2016). We quantified the FD of the understorey community with Rao's Quadratic Entropy (Botta-Dukát, 2005; de Bello et al., 2021a), which expresses the expected dissimilarity between two individuals of a given assemblage selected at random with replacement:

$$FD = \sum_{i,j}^{S} d_{ij} p_i p_j \quad (2)$$

where S is the number of species, d_{ij} is the distance or dissimilarity between the ith and jth species, and p_i and p_j are the relative coverage of the ith and jth species. The functional distance (d_{ij}) was computed with Gower distance, which standardize the functional distance between each pair of species (i.e., $d_{ij} = 0$ when two species assume the same trait values and $d_{ij} = 1$ when two species have exactly the opposite trait values; de Bello et al., 2021b). Finally, to remove the influence of species richness and composition and to shed light on community assembly pattern, we calculated the standardized effect size (SES) of the FD:

$$SES\,(FD) = \frac{(Observed\ FD - Mean\ Expected\ FD)}{SD\ Expected\ FD} \quad (3)$$

where SES values smaller than zero indicate FD being lower than expected by chance (functional convergence) and vice versa for SES values larger than zero (functional divergence), while values close to zero mean diversity does not deviate from the random expectation (Botta-Dukát & Czúcz, 2016). Random values were created by shuffling the trait values 999 times (Botta-Dukát & Czúcz, 2016). Before calculating the SES, we checked if the distribution of the 999 expected values followed a normal distribution (Botta-Dukát, 2018). For each SES-FD index, we performed a t-test to assess if the distribution of SES values in each management type (oldCWS and HF) differed from zero to assess patterns of functional convergence, divergence or random (de Bello et al., 2017).

As a measure of functional composition, we calculated (CWM; Garnier et al., 2004) for each trait and plot as follows:

$$CWM = \sum_{i=1}^{S} p_i x_i \quad (4)$$

where S is the number of species, p_i is the relative coverage of species i ($i = 1, 2, ..., S$), and x_i is the trait values for species i.

Before quantifying the effect of structural parameters (SH_{DBH}, VE_G, and the amount of lying deadwood) and forest management

types on SES-FD and CWM indices, we explored individual relationships between response and predictor factors. In particular, we used analysis of variance (ANOVA) to compare models following three types of relationships: linear, unimodal, and logarithmic (Appendixes S5 and S6). Then, we fitted multiple global linear models for SES-FD and CWM indices with the three structural parameters according to their best-fitting relationship. We scaled continuous predictors to a zero mean and unit variance to obtain comparable coefficients and improve model performances (Harrison et al., 2018). We also included management type as a categorical variable with two levels (oldCWS and HF) in the global models to accommodate the fact that FD can differ between HF and oldCWS as a consequence of different management or other unmeasured variables (e.g., legacy effect on local species pools). Thus, we did not use mixed models with management type as a random effect because we were interested in analyzing the direct effect of management type (Harrison et al., 2018).

We included interaction terms between the three structural parameters and management type to determine whether the structural parameters affected differently the diversity of the forest with contrasting management. Then, we used stepwise backward model selection to select the best model based on the Akaike information criterion (AIC). In the final model, we checked for multicollinearity among predictors by calculating the variance inflation factor of each predictor (VIF; Zuur et al., 2010). In the case of multicollinearity (VIF > 3), we removed the predictor showing the higher variance inflation factor and we re-ran the model (Zuur et al., 2010). We performed this approach until multicollinearity in the models was low (VIF < 3; Zuur et al., 2010). Lastly, we used diagnostic plots to check model assumptions (i.e., normally distributed errors with constant variance and lack of autocorrelation in the residuals of normality, homogeneity of variance, and independence of residuals; Zuur et al., 2010; Harrison et al., 2018). However, modeling CWM can lead to inflated Type I error rates (de Bello et al., 2021a; Zelený, 2018). A possible solution to avoid overestimation of the significant relationship is to combine linear models with a modified permutation test called "max test" (Zelený, 2018). Max test involves two independent permutation tests: the first one tests the species trait–species composition link ("column-based permutation") in which species trait values are shuffled randomly 999 times across species; the other permutation tests the link between plot attributes and species composition ("row-based permutation"), and it is performed by randomly shuffling plot attributes 999 times across plots (Zelený, 2018). A p-value for each permutation procedure (p_r, row-based permutation; p_c, column-based permutation) is estimated as the probability that the observed adjusted R^2 is significantly higher than those expected by chance according to a one-tailed t-test (α < 0.05). When the p-values of both modified permutations are smaller than 0.05, the variation of observed model is significant (Zelený, 2018).

We calculated all functional indices in R version 4.1.2. (R Core Team, 2021). Specifically, we calculated FD for each trait using the function "RaoRel" in R the *cati* package, while random values used to calculate standardized effect size were obtained with the "replicate" function in the *base* R package. Finally, we used the "cwm" function

in the *weimea* R package (Zelený, 2020) to calculate the CWM for each single trait. Standardization of predictors was done with the "decostand" function ("standardize") in the *vegan* R package. Linear models were performed with the "lm" function in the *stats* R package. Model selection was done with the "step" function in the *stats* R package. Multicollinearity was checked with the "vif" function in the *car* R package.

3 | RESULTS

3.1 | Effect of structural variables and management types

We found significant effects of structural parameters and management type on FD and composition of understorey plant communities (Tables 2 and 3). Specifically, for structural parameters, horizontal stratification (SH_{DBH}) negatively affected SES-FD$_H$, promoting a shift from divergence (SES > 0) to convergence strategies (SES < 0; Figure 1c; Table 2). The proportion of lying deadwood was positively related to SES-FD$_{SLA}$, highlighting a change at 10% of deadwood values from functional convergence (SES < 0) to functional divergence (SES > 0; Figure 1a, Table 2). Also, lying deadwood was negatively related to CWM$_{CO}$ (Figure 1b; Table 3). Management type affected significantly SES-FD indices, with higher values found in HF compared to oldCWS for SLA, LS, PCGO, and CO. Moreover, CWM$_{PCGO}$ was higher in HF than in oldCWS. Finally, management type affected CWM$_{SLA}$ with higher values found in HF than in oldCWS (model close to significance after permutation approach; Table 3). We did not find any significant effect of any interaction between management type and structural parameters on functional indices (SES-FD and CWM). Also, functional indices (SES-FD and CWM) for both SM and LS were not significantly affected by any predictors.

3.2 | Assembly rules across management types

In HF plots, SES-FD$_H$, SES-FD$_{SM}$, and SES-FD$_{LS}$ tended to functional convergence (i.e., average values significantly lower than zero), while SES-FD$_{SLA}$ and SES-FD$_{PCGO}$ tended to functional divergence (i.e., average values significantly higher than zero; Figure 2). SES-FD$_{CO}$ showed a random pattern. In contrast, in oldCWS plots, most SES-FD indices showed a random pattern, while SES-FD$_{LS}$ and SES-FD$_{CO}$ tended to functional convergence (Figure 2).

4 | DISCUSSION

We studied the effects of stand structural parameters and management type on the FD and composition of Leaf–Height–Seed and clonal traits of understorey communities in beech forests. Partially in contrast with our first hypothesis, we found lying deadwood and horizontal stratification affected different functional strategies of

TABLE 2 Results of final (multiple) linear models predicting the standardized effect sizes of functional diversity (SES-FD) for single traits (H, vegetative height; SLA, specific leaf area; SM, seed mass; LS lateral spread; PCGO, persistent of clonal growth organ; CO, number of clonal offspring) from structural parameters (SH_{DBH}, entropy of diameter distribution; VE_G, vertical evenness of basal area; lying deadwood), and management type (oldCWS and HF, with oldCWS as baseline)

Index	SH_{DBH}	VE_G	Deadwood	Management type (reference level:oldCWS)	Interaction (reference level:oldCWS) Deadwood	Adj R^2	AIC
[+]SES-FD$_H$	**−0.30**	–	–	–	–	**9**	152.50
SES-FD$_{SLA}$	–	0.24	**0.26**	**−0.77**	–	**18**	136.51
[+]SES-FD$_{SM}$	–	–	−0.05	–	0.03	3	151.48
[++]SES-FD$_{LS}$	−0.12	–	−0.02	**−0.30**	–	**7**	71.72
SES-FD$_{PCGO}$	–	–	–	**−0.83**	–	**17**	155.10
SES-FD$_{CO}$	–	–	–	**−0.72**	–	**19**	130.50

Note: We report the coefficient values of the predictors, the adjusted (Adj) R^2 (in percentage), and Akaike information criterion (AIC) for each model. Significant predictors and models ($p < 0.05$) are reported in bold. [+], log$_{10}$-transformed species traits; [++], square-root-transformed species traits.

TABLE 3 Results of final (multiple) linear models predicting the community-weighted mean (CWM) for each single trait (H, vegetative height; SLA, specific leaf area; SM, seed mass; LS lateral spread; PCGO, persistent of clonal growth organ; CO, number of clonal offspring) with the structural parameters (SH_{DBH}, Shannon diversity for tree diameters; VE_G, vertical evenness of basal area; lying deadwood), and management types (oldCWS and HF with oldCWS as baseline)

Index	SH_{DBH}	VE_G	Deadwood	Management type (reference level:oldCWS)	Interaction (reference level:oldCWS) SH_{DBH}	Deadwood	Adj R^2	p_c	p_r	AIC
[+]CWM$_H$	–	0.01	–	0.001	–	–	<1	–	–	−105.3
CWM$_{SLA}$	–	–	1.12	**−3.49**	–	–	18	**<0.001**	0.07	341.0
[+]CWM$_{SM}$	−0.07	−0.4/**−0.9**	0.1	−0.03	0.14	−0.18	<1	–	–	70.03
[++]CWM$_{LS}$	–	–	**0.25**	–	–	−0.25	**7**	–	–	80.00
CWM$_{PCGO}$	–	–	–	**0.25**	–	–	25	**<0.001**	**0.04**	−5.60
CWM$_{CO}$	–	–	**−0.29**	–	–	–	25	**<0.001**	**0.04**	84.50

Note: We report the coefficient values of the predictors, the adjusted (Adj) R^2 (in percentage), the significance (in bold) of the row-based permutation (p_r) and column-based permutation (p_c), and the Akaike information criterion (AIC) for each model. [+], log10-transformed species traits; [++], square-root-transformed species traits. Unimodal relationships were used for SM with VE_G (linear and unimodal terms are separated by a slash).

plant understories, specifically resource exploitation through micro-environmental heterogeneity and plant size through habitat filtering (H1); HF stands hosted fast-growing plant communities but with shorter-lived connections between ramets than oldCWS (H2); overall, we observed a shift from functional convergence/randomness in oldCWS to functional divergence/randomness in HF for most traits, except for H and SM (H3). We did not find any effect of vertical stratification on the selected traits. Finally, the variation in SM seems to play a smaller role in structuring forest plant communities than leaf, plant size, and clonal traits in terms of forest structure and management.

4.1 | The effect of structural parameters on understorey species

As expected, increased lying deadwood promoted functional divergence in terms of resource exploitation strategies (SLA) (H1).

This pattern is in line with previous investigations that found a similar effect of deadwood on the FD of SLA (Chelli et al., 2021). Our results strengthen previous findings suggesting that strategies related to resource exploitation represent key functions of community assembly (Chelli et al., 2021). Lying deadwood cover is overall related to soil fertility (Fravolini et al., 2018; Appendix S7). Higher cover of lying deadwood may increase the micro-environmental heterogeneity by creating a patchy distribution of soil resources (Burrascano et al., 2018). This pattern may, in turn, select species having contrasting SLA strategies within the plots (Conti et al., 2017). Furthermore, the negative effect of deadwood on CO seems to be in contrast with the concept that richer-resource environments should favor species with a higher number of clonal offspring (Vojtkó et al., 2017). However, ecological studies have shown that heterogeneous and homogeneous environments select for opposite integrated clonal strategies having different clonal offspring, i.e., "guerrilla" and "phalanx" strategies
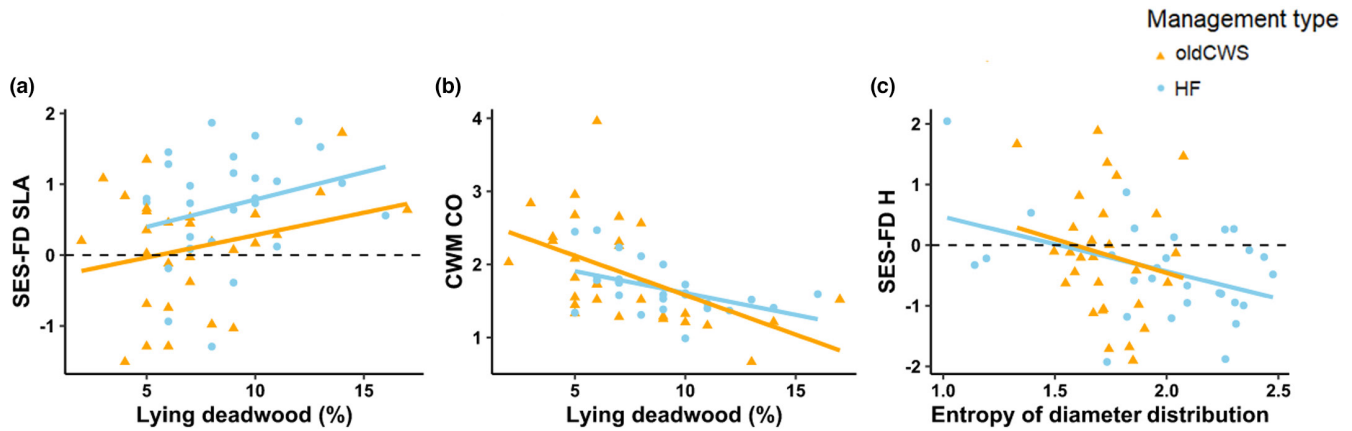
FIGURE 1 Relationship between the amount of lying deadwood (percentage values) and (a) the standardized effect size of functional diversity (SES-FD) for specific leaf area (SLA); (b) community weighted mean (CWM) for number of clonal offspring (CO). (c) Relationship between entropy of diameter distribution and SES-FD for height (H). Blue lines and circles represent high forests (HF), while orange lines and triangles represent old coppice-with-standards (oldCWS).

respectively (Doust & Doust, 1982; Whitlock et al., 2010). Such considerations are in line with our results as we detected a variation from species with a phalanx strategy and high offspring under more homogeneous environmental conditions (e.g., 4.3–6 clones per year for *Dactylis glomerata*, *Festuca circummediterranea*, and *Poa nemoralis*), to species with a guerrilla strategy and low clonal offspring under more heterogeneous soil conditions (e.g., one clone per year for *Adenostyles glabra*, *Cardamine enneaphyllos*, and *Lathyrus vernus*; Whitlock et al., 2010).

However, contrary to our first hypothesis (H1), horizontal stratification (SH$_{DBH}$) played a key role in narrowing the range of functional strategies for plant height. Variation of this structural feature is coupled (negatively) with the variation of light reaching the ground (Appendix S7). Light limitation may filter for specialized understorey plants sharing similar functional strategies (e.g., Campetella et al., 2011). Nonetheless, using direct measures of light transmission in forest understories, that is, the photosynthetically active radiation reaching the ground layer, or site-specific measurements of nutrient concentrations, could help refine the relationship between structural features and ecological conditions (Horvat et al., 2017).

4.2 | Relationships between management type and functional strategies

Management type differently affects some dominant functional strategies with HF stands characterized by higher CWM$_{SLA}$ and lower CWM$_{PCGO}$, and oldCWS with lower CWM$_{SLA}$ and higher CWM$_{PCGO}$ (H2). Species with large SLA are fast-growing, have a higher plastic response to light patchiness, and have a high capacity to maintain high photosynthetic ability under shadow conditions (Poorter et al., 2009). Therefore, high SLA values appear particularly profitable in a later-succession forest ecosystem (Campetella et al., 2011). However, we did not consider intraspecific trait variation. Thus, the

functional difference between HF and oldCWS is driven exclusively by the variation in species composition, meaning that HF are characterized by a higher number and abundance of forest generalist and beech specialist species with large SLA than oldCWS (Campetella et al., 2011; Scolastri et al., 2017b).

Concerning PCGO, mature forests were characterized by communities with short-lived connections between ramets. Interestingly, our results support an ecological trade-off between the persistence of clonal individuals and the rate of resource acquisition strategies along a stress gradient consistent also in forest ecosystems (Klimešová & Herben, 2015; Chelli et al., 2019; Campetella et al., 2020). On the one hand, plant communities either displayed expensive leaf tissues (low SLA) and a long-lived connection (high PCGO) or produced cheaper leaves (high SLA) with a short-lived connection (low PCGO). Similar findings have been previously detected in old-growth beech forests along climatic gradients (Campetella et al., 2020). However, we extended this consideration also in relation to disturbance: more mature forest stands that are less disturbed, HF in our case, are characterized by plant communities with a higher SLA and lower PCGO (i.e., maternal plant does not forage daughter), while younger and more disturbed forest stands are characterized by understorey plant communities with lower SLA and longer-lived connections.

4.3 | Management type affects community assembly

We found an overall higher SES-FD in HF than in oldCWS (H3). Specifically, SLA and PCGO showed functional divergence (higher FD than expected by chance) in HF stands, while LS and CO showed a higher degree of functional convergence (lower FD than expected by chance) in oldCWS stands. Contrary to this overall shift, H and SM increased their convergence in HF forest. Such results are in line with recent studies that supported high
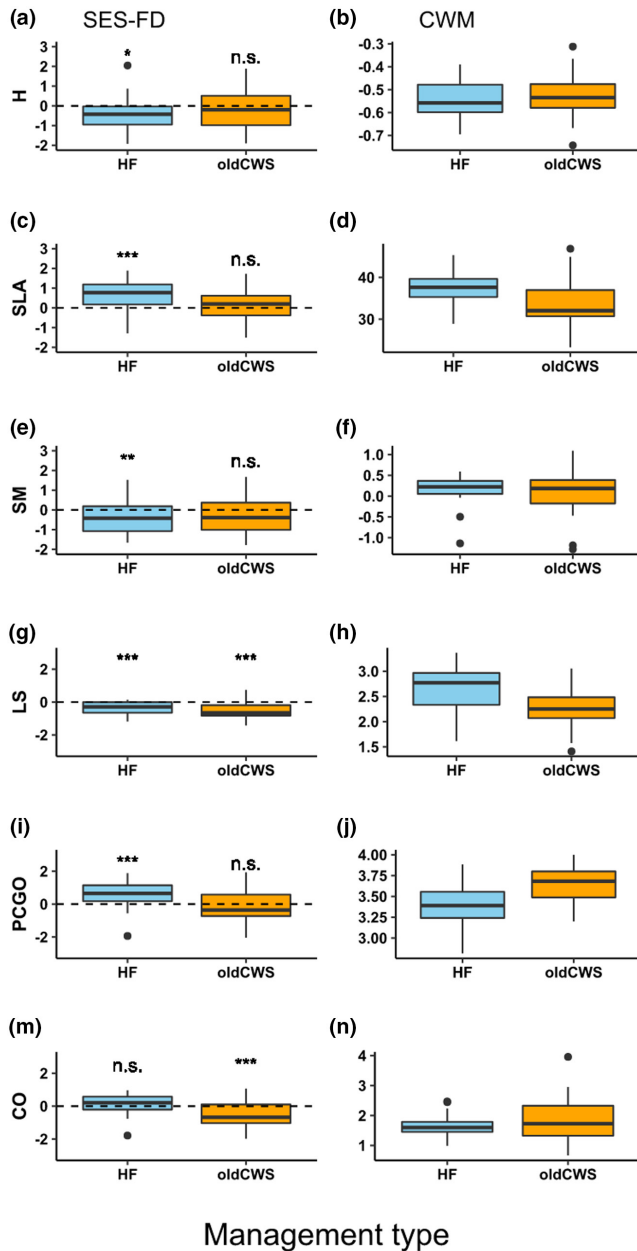
FIGURE 2 Relationship between management types (oldCWS, old coppice-with-standards in orange; HF, high forest in blue) and the standardized effect size of functional diversity (SES-FD) and community weighted mean (CWM) for (a, b) plant height (H, m); (c, d) specific leaf area (SLA, mm²/mg); (e, f) seed mass (SM, mg); (g, h) lateral spread (LS, cm/year); (i, l) persistence of clonal growth organ (PCGO, year); and (m, n) number of clonal offspring (CO, n/year). For SES-FD indices, significant differences between average values and zero according to the two-tailed t-test are reported ($*$, $p < 0.05$; $**$, $p < 0.01$; $***$, $p < 0.001$; n.s., not significant).

FD in undisturbed temperate deciduous forests (Closset-Kopp et al., 2019; Lelli et al., 2019; de Pauw et al., 2021). This pattern is probably an effect of higher heterogeneity within older stands (Burrascano et al., 2018; Vanneste et al., 2019). Further, HF also provides relatively undisturbed microhabitats, which may support a higher environmental heterogeneity in these forest stands

(Scolastri et al., 2017a). Such heterogeneity may explain the presence of species with different light-capturing strategies, from shade-tolerant (e.g., *Anemone apennina*, *Cardamine bulbifera*, *Galium odoratum*) to shade-avoidant (e.g., *Galanthus nivalis*), other than to non-forest species with semi-heliophilous strategies (e.g., *Vicia sepium*; Scolastri et al., 2017a, 2017b). Similarly, the presence of environmental heterogeneity and species with contrasting SLA may explain the higher diversity of PCGO strategies. While the pattern of PCGO was in line with our expectation, CO seems to not have played a deterministic role in shaping community assembly in more mature forest conditions like in HF. Accordingly, CO seems more importantly affected by habitat filtering in oldCWS. Possibly, nutrient-poor soils and more disturbed conditions in oldCWS compared to more fertile soils and less disturbed conditions in HF acted as filters for selecting species with a phalanx strategy (i.e. short LS with high CO; Canullo et al., 2011; Scolastri et al., 2017a; Closset-Kopp et al., 2019). Finally, the tendency toward higher convergence of H and SM in HF also supports the hypothesis that clonal traits may be the main driver of plant coexistence under more mature conditions (Canullo et al., 2011; Chelli et al., 2019).

4.4 | Management implications

The proportion of lying deadwood can alter the distribution of plant resource exploitation strategies regardless of forest management type. Specifically, an increase in lying deadwood promotes a shift from functional convergence (i.e., species having similar resource exploitation strategies) to divergence (i.e., species having dissimilar resource exploitation strategies). This is in line with a previous investigation performed only in oldCWS beech forests of the central Apennines (Chelli et al., 2021), though in our study we also considered the effect of different management types (oldCWS vs HF). We suggest that the amount of lying deadwood should be considered by local forest managers as an important factor to reduce the functional homogenization of forest stands regardless of the management type. Moreover, as lying deadwood contributes to soil fertility and soil water, it can also have a positive effect on forest species diversity (Fravolini et al., 2018; Appendix S7). Also, the degree of horizontal stratification can affect functional strategies across management types. Less stratified forest stands have been mostly associated with simplified structures with few resources available for understorey plants. However, we highlighted how these forests host more dissimilar species in terms of plant height. By leaving more lying deadwood on the ground and supporting the presence of trees with dissimilar diameters, functional homogenization of plant understorey for both SLA and H can be avoided.

Finally, our results indicate that despite the high initial disturbance pressure, once abandoned, forest understories in CWS stands tend to develop more mature forest functional conditions, as highlighted by the lack of significant differences in most CWMs between the two management types. Nevertheless, a 30-year absence of logging is not enough time for the development of understories with

functional conditions similar to those present in mature forests. This was indicated by the significant differences in most SES-FD indices between the two management types, which tended toward functional convergence in oldCWS. Moreover, considering that the recovery of understories in terms of forest specialist species requires at least 50–80 years from the last logging (Decocq et al., 2004), it is not surprising that understories of oldCWS share functional strategies typical of post-logged forests. Thus, when restoring CWS, a longer rotation period can help in promoting species with typical traits of more mature forest conditions. Forest managers, policymakers, and landscape planners could benefit from prioritizing the restoration of HF, as this forest management type displays functional divergence patterns for traits playing a key role in the forest understorey and therefore potentially having higher resilience to global environmental changes (Mori et al., 2013).

5 | CONCLUSIONS

Our study suggests that understorey plant community diversity and composition change in response to forest structure and management. We found that understorey plant recolonization after logging occurs in a two-step process. Firstly, during the closure of the canopy after logging, plant diversity is filtered as a consequence of a decrease of light reaching the ground according to a habitat filtering process. Secondly, under closed stands, more mature forest conditions with increased abiotic heterogeneity allow the establishment of species having different resource exploitation and clonal strategies, but similar plant size and seed mass. Our work strengthened the concept that in forest ecosystems resource acquisition strategies and clonal functions may play a key role in species coexistence. Thus, integrating clonal traits with LHS is a promising framework for understanding and predicting plant responses to forest structural change and management. Researchers and forest planners should consider the effects of forest structure and the degree of forest maturity after canopy cover restoration to enhance conservation and multiple ecosystem functions.

DATA AVAILABILITY STATEMENT

Species cover, species trait, functional indices and structural variables used in the analysis are available in Appendix S8.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Descriptive statistics of structural parameters and species richness of old coppices-with-standards (oldCWS) and high-forest (HF) stands.

Appendix S2. Location of the study area.

Appendix S3. Pairwise Pearson's correlation coefficients between species traits.

Appendix S4. Pairwise Pearson's correlation coefficients between structural features.

Appendix S5. Relationship between SES-FD indices and structural parameters.

Appendix S6. Relationship between CWM indices and structural parameters.

Appendix S7. Pearson's correlation coefficients between Ellenberg Indicator Values and structural features.

Appendix S8. Species cover, species trait, functional indices, and structural variables used in the analysis.