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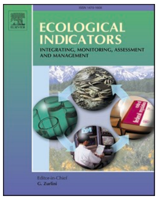

Forest structure and understory functional diversity at multiple scales: The importance of median tree height

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ABSTRACT

The understorey holds most of the vascular plant diversity in temperate forests. Functional diversity is a key aspect, commonly linked to forest age and management practices, but its relationship to specific structural features such as tree height and canopy cover is understudied.

We studied 28 beech forest plots in an Italian National Park encompassing coppice, high forest and unmanaged old-growth stands. Using a novel multiscale approach (increasing grain size by combining adjacent sampling units), we assessed functional diversity at plot scale (γ), in small-scale subunits (α), between subunits (β), further decomposing β into functional redundancy, uniqueness and clustering. Forest structural features and canopy cover were quantified via terrestrial laser scanning and digital cover photography and related to understorey functional diversity across scales.

We found that higher median tree height at the plot scale—though not canopy cover—is associated with increased functional diversity at scales up to ~10 m. This is accompanied by greater redundancy and functional clustering. However, no changes in functional diversity or redundancy were observed at the plot scale, meaning that small scales host a greater portion of trait diversity.

Our findings highlight the ecological relevance of median tree height, often overlooked in favour of canopy cover as a structural indicator of understorey functional diversity, for monitoring and management. Furthermore, our sampling design enabled the detection of scale-specific relationships that may have been missed by conventional plot-level vegetation surveys, i.e., an increase in diversity at the α level that does not translate to the plot level.

1. Introduction

Forest biodiversity is under increasing threat due to global changes, including climate change, land-use change, and pollution. While trees constitute the vast majority of forest ecosystem biomass, the understorey generally accounts for 82–87% of vascular plant richness in temperate forests, despite comprising less than 1% of the total biomass (Gilliam, 2014; Spicer et al., 2020). The understorey plays a crucial role in influencing biogeochemical cycles and forest regeneration (Andreetta et al., 2023; Landuyt et al., 2019). Still, few policies are open to consider it in indicators of sustainable forest management (Blondeel et al., 2021; Cutini et al., 2021; Frati et al., 2022).

European policies and regulations have begun to recognize the importance of forest biodiversity (European Commission, 2020; European Commission, 2021), however the biodiversity indicators they promote are based on total species richness (Directive (EU), 2016/

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2284), or limited to tree species (Criterion 4, Forest Europe, 2021). Species diversity is only one possible view on biodiversity: when the goal is to understand the processes underlying diversity patterns, or to maintain ecosystem functioning and services, it is necessary to consider different aspects of biodiversity rather than to preserve species for their intrinsic value (Pavoine and Ricotta, 2024). Functional traits can reflect adaptations to environmental factors (Lavorel and Garnier, 2002), providing a means to quantify the distinctness of species (Funk et al., 2017). The inclusion of functional diversity as a complement to taxonomic diversity is increasingly advocated to strengthen conservation and management strategies, since management choices can have consequences that go beyond a change in taxonomic diversity (Cadotte, 2011; Lelli et al., 2019).

European forests have been managed for many centuries (Aszalós et al., 2022). Different management strategies can impact stand diversity, often simplifying structural and biological complexity, with detrimental effects on the understorey (Landuyt et al., 2024). Coppicing, once a dominant practice (Buckley, 2020), has declined with falling demand for small-sized timber and charcoal (Kopecký et al., 2013). Abandoned coppices are often being converted, passively or actively, to high forest systems (Ciancio et al., 2006), which are valued for their low disturbance frequency and the large timber size (Chianucci et al., 2016). A trait-based approach has shown how the understorey of high forest has features closely resembling more mature and stable forest conditions (Scolastri et al., 2017). Old-growth forests, featuring no human intervention, represent a type of management aimed at conservation promoted by European policies, characterized by large living trees, high diameters and large amounts of aboveground biomass and deadwood (Burrascano et al., 2013). The understorey of old-growth forests features lower functional diversity, compared to that of mature even-aged high forests, but lacks the associations with trait syndromes typical of low-light conditions (Sabatini et al., 2014).

Structural parameters, like vertical and horizontal tree stratification, or the amount of lying deadwood, may promote a patchy distribution of resources within forest stands (Bricca et al., 2023; Chelli et al., 2021). Spatial scale influences the perception of the predominant processes (Chase, 2014), highlighting the need for a spatially explicit approach; different spatial scales can correspond to different ecological scales, each mostly driven by abiotic or biotic factors (De Bello et al., 2013). Biodiversity at nested ecological scales (α, γ) and between them (β) has been assessed for a long time (Whittaker, 1972), allowing the identification of different critical biodiversity patterns, such as for ecosystem multifunctionality (Pasari et al., 2013). Still, β diversity has been considered not nearly as often, despite its value in quantifying the variability and change inherent in ecosystems (Mori et al., 2018); this is particularly interesting for forest understorey, where resources are heterogeneously distributed (Chelli et al., 2021). In this study small-scale sampling units (α) are nested within a plot (γ), allowing for the quantification of within-plot heterogeneity (β).

Measuring β diversity is challenging because it is a complex, multidimensional concept which relies on the explicit consideration of space to define at least two distinct ecological scales, α and γ, which are often chosen arbitrarily, even with proper ecological reasoning. Our approach mitigates this issue by considering multiple spatial scales in the identification of relevant ecological scales. A further challenge is that unlike α and γ, which share similar definitions and formulas, β has often been defined differently or derived from the other two components. To compare all three components meaningfully, we require a unified framework in which β can vary independently (Pavoine and Ricotta, 2024). Rao's quadratic entropy provides such a framework: it treats β diversity consistently with α and γ and meets all the above criteria. Furthermore, this framework allows deriving components of redundancy (or uniqueness, 1 / redundancy) at both α and γ scales, and of functional clustering. Redundancy reflects functional similarity (dissimilarity, for uniqueness) between different species. Clustering reflects functional similarity within communities with respect to other communities; in this particular case, this is disentangled by the effects of species clustering.

Forest understorey communities are affected by complex relationships involving resource availability, soil pH, macro- and microclimate, with most of these factors being influenced by the overstory (Landuyt et al., 2018). In particular, the amount and heterogeneity of light and soil nutrient conditions determined by forest canopy and structure are fundamental (Chelli et al., 2021; Govaert et al., 2021), and sensitive to management practices (Decocq et al., 2004; Müllerová et al., 2015). Canopy cover mediates the effect of climate on aboveground traits related to plant size and resource economics (Díaz et al., 2016; Padullés Cubino et al., 2021). Belowground traits linked to plant capacity of harvesting soil nutrients and sharing resources between ramets (Chelli et al., 2024b) are also of particular interest (Campetella et al., 2020) and can have a different response from the aboveground ones (Canullo et al., 2011; Chelli et al., 2024a).

The relationships between forest stand features and environmental factors—such as local climate, age, canopy cover, structure and management—with plant traits, have been studied both in terms of diversity (Bricca et al., 2023; Chelli et al., 2024a; Ottaviani et al., 2019) and community weighted mean (Campetella et al., 2011; Chelli et al., 2019), finding contrasting relationships for different traits. The most studied ecological gradient is related to canopy closure, with consistent results showing that the environmental filter caused by the decrease of light transmittance leads to a decline in trait diversity (Campetella et al., 2011; Chelli et al., 2024a; Ottaviani et al., 2019). A similar decrease has been found with increasing basal area, a proxy of stand maturity (Ottaviani et al., 2019). A recent study exploring the influence of forest management on understorey functional diversity and redundancy in Europe has found that higher harvesting intensity silvicultural regimes—such as coppicing or clearcutting—are associated with a decrease in functional diversity that may hamper their ability to respond to the ongoing environmental changes, partly counterbalanced by an increase in functional redundancy, compared to unmanaged forests (Chianucci et al., 2024).

We therefore expect a reduction of functional diversity in mature stands with less intense or no management, potentially offset by higher heterogeneity, leading to an increase in beta diversity and functional clustering. Additionally, we expect redundancy to be higher (uniqueness to be lower) in stands with a less mature structure and a more open canopy. Provisionally, we have similar expectations to the γ scale for the understudied α scale, but our multiscale approach could reveal differing behaviours.

Our study complements the current knowledge in several ways:

1. While most studies have compared management strategies (Bricca et al., 2023; Chianucci et al., 2024) or considered chronosequences since last logging (Campetella et al., 2011; Scolastri et al., 2017), our study relates trait diversity to precise quantification of forest structure and canopy cover, whose trajectories can become unpredictable with stand age, as with canopy gaps and vertical stratification in old-growth forest (Messier et al., 2009). Penone et al. (2019) has shown the value of considering specific forest features and several aspects of biodiversity. Canopy cover was associated negatively with richness and abundance and positively with specialization for vascular plants and other taxa, while there was no evidence of a relationship with vertical or horizontal heterogeneity.
2. Usually, understorey diversity is evaluated at plot scale (Bricca et al., 2023; Chelli et al., 2024a; Ottaviani et al., 2019). We are also increasing the detail in our analysis of functional diversity, by considering, within the plot, nested ecological scales assessed at a range of spatial scales, as well as partitioning diversity into components of redundancy, spatial clustering, and taxonomic diversity.

Our aim is to identify forest structural features that are related with whole-stand biodiversity, ecosystem functioning, resilience to disturbances and global changes, and can represent clear goals and indicators for a management strategy focused on these aspects. The identification of components of functional diversity and spatial scales sensitive to structural features can also inform forest monitoring programs.

2. Methods

2.1. Study area

The study area is represented by the “Foreste Casentinesi, Monte Falterona e Campigna” National Park, in the Northern Apennines, Italy (Fig. 1). The park was established in 1993, and spans 36,000 ha, with temperate forests covering approximately 80% of its surface. The climate is temperate, with an average annual temperature of 9 °C and an annual precipitation of 1561 mm (Tsakalos et al., 2023). An altitudinal range of approximately 800 to 1500 m a.s.l. and slightly acidic soils over sandstone formations (Zhu et al., 2025) support the European syntaxa defined as acidophilous beech forest (Mucina et al., 2016). This area includes stands with a wide range of ages and management conditions, from active coppice to unmanaged old-growth forest, through high forest. In particular, the park includes the “Sasso Fratino” reserve, Italy's oldest strictly protected area, established in 1959 and now included in the UNESCO World Heritage multi-site of “Ancient and Primeval Beech Forests of the Carpathians and other regions of Europe”.

2.2. Sampling design and data collection

We sampled 28 beech forest 30 m × 30 m plots, including plots occurring in the “Sasso Fratino” and “La Pietra” strict reserves. Plots are considered representative of the forest stand they are in and were preferentially placed in collaboration with the land managers (National Park and Carabinieri Forest Service) by considering accessibility, park regulations, and the safety of surveyors. All plots lack soil disturbances and are all located well within the forested area, excluding the possibility for edge effects.

Through preliminary information provided by the forest service, we classified the plots into coppice (both active and abandoned), high forest, and old-growth forest. Collaborators evaluated and confirmed this classification during the botanical survey. An additional summary of the plots is available as Appendix A (Table A.1).

In each plot we sampled canopy features using digital cover photography (DCP) images, forest structure using terrestrial laser scanning (TLS), and understorey vegetation with a transect.

To quantify forest structure, we used the FARO FOCUS 3D instrument, which acquires data from fixed points through a 360° scan angle. The instrument uses a phase-shift-based technology with a maximum range of 120 m. It records and measures the x, y and z coordinates and the intensity of the laser returns with a scan ranging noise of ±1 mm (for details see Giannetti et al., 2018). In each plot, a minimum of 9 and a maximum of 12 scan positions were established during leaf-on conditions. White spherical targets were strategically positioned within the plot to aid the registration of scans. Once set up, the scanner took around 9 min to scan at each of the positions. Individual scans were stitched together to create a single three-dimensional point cloud of each plot, making use of the spherical targets. After registration, the obtained point cloud was imported into R and manipulated using the ‘lidR’ (Roussel et al., 2020) package. A normalization process was applied to eliminate slope effects from the point cloud.

For canopy features, in each plot twelve upward-facing DCP images

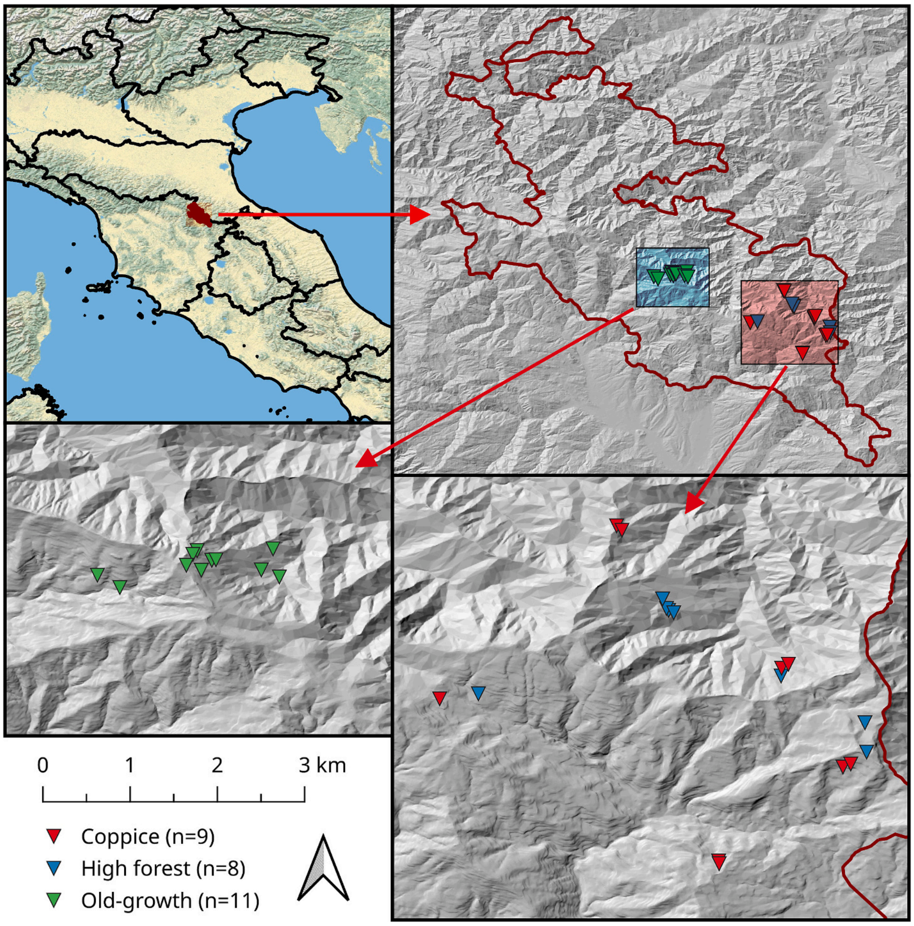

Fig. 1. Map of the study area and the surveyed plots, coloured by management category.

were collected in summer by dividing the plot in a 4 × 3 grid. Each image was acquired using a Nikon D90 digital lens reflex equipped with a Nikkor 50 mm lens, which yielded images with a 30° field of view (see Macfarlane et al., 2007). Images were collected in uniform sky conditions, at maximum resolution RAW, using a tripod, from a height of 1 m.

For the sampling of understorey plants, inside each plot we set a 100 m long transect, which is topologically a loop, composed of 1000 contiguous sample units sized 10 cm × 10 cm (Appendix B, Fig. B.1), where we recorded woody and herbaceous understorey (< 1.3 m, i.e., breast height) vascular plant species. This sampling design has the advantages of achieving a very large sample size and allowing spatial scaling (Podani, 1984). Compared to grid sampling, transect sampling can efficiently record spatial variability and heterogeneity (Bartha et al., 2020 and references therein).

For all the sampled species we assigned mean functional trait values from available databases. In detail, we selected six aboveground traits included in the “Global Spectrum of Plant Form and Function” (i.e., plant height, specific stem density, seed mass, individual leaf size, leaf mass per area, and leaf nitrogen content) reflecting the independent dimensions of plant size and resource economics (Díaz et al., 2016, 2022) from the provided dataset (Díaz, 2022), and four belowground traits included in the “Clonal trait space” (i.e., bud bank size, persistence of clonal connections, multiplication rate, and lateral spread), reflecting the independent dimensions of on-spot plant persistence and clonal multiplication (Chelli et al., 2024b) from CLO-PLA 3 (Klimešová et al., 2017). To match the recorded species with the database entries, we harmonized the taxonomic nomenclature using TNRS (Boyle et al., 2013), based on World Flora Online version 2023–06 (The World Flora Online Consortium et al., 2023). The results were manually checked for errors, and synonyms were used when they were present in the employed trait databases if the harmonized name was not present. Species with reported plant height ≥ 1.3 m in the database have been excluded, because those trait data refer only to adult individuals, while in our transect records they represent juveniles and seedlings of woody species, meaning there is an obvious discrepancy between the available traits and the observed individual.

For two species for which lateral spread data was missing, *Euphorbia amygdaloides* and *Viola reichenbachiana*, the averages, weighted by plot, of measurements from samples collected in the same plots were added to the trait data.

For the overall species by trait matrix, the per cent trait completeness was 90.8%, 88.8% for aboveground traits, 94% for clonal traits (after setting persistence, multiplication rate and lateral spread as 0 for species known as not clonal). Missing trait data was filled by imputation, using the function ‘impute’ in the package ‘funspace’ (Carmona et al., 2024). The phylogenetic eigenvectors used to aid with the imputation were derived from a phylogeny built with the package ‘V.PhyloMaker2’ (Jin and Qian, 2022).

2.3. *Rao's quadratic entropy*

Rao's Quadratic Entropy (Q) (Rao, 1982, 1984) is a very popular functional diversity index. In the usual multinomial form (Rao, 2010) it represents the expected distance between two randomly selected individuals:

$$Q = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} p_i p_j \tag{1}$$

Where S is the number of classes (species), p_i and p_j are the proportions of individuals in classes i and j, d_{ij} is the distance between classes i and j.

Often, the focus is on the species relative abundances p, which makes Q an extension of the Gini-Simpson index taking into account distances between classes. Instead, we view Q as a mean distance first and note that classes, or species, are not a necessary component of the index, which can even be re-expressed in terms of individuals (Appendix C). This is also true with the use of mean species trait values, as is the case here, but species are still implicitly used in the interpretation of indices that rely on the comparison with the case of maximally dissimilar species ($d_{ij} = 1$ for all $i \neq j$).

Unlike in related indices (Appendix C.2), in Rao's Q diversity does not increase by the addition of a species with a zero distance from an existing one (identical species principle); this is a desirable property if the goal is to explore ecosystem functioning or the rules of community assembly (Botta-Dukát, 2018), and summarize their local diversity and dissimilarity regardless of species identity (Ricotta et al., 2021). Indices with these properties, except in special cases (ultrametric distances for Q), are not maximized by including all categories (Pavoine, 2012) and have been defined as “weak diversity indices” to distinguish them from traditional measures, which are deeply rooted in counting categories. Weak indices complement traditional measures and are thought to describe ecological processes more convincingly (Ricotta et al., 2021).

The decomposition of Q according to the classical scheme into α, β and γ components (Lande, 1996; Whittaker, 1960, 1972) has been thoroughly investigated. Rao (1982, 1984) had already suggested an additive decomposition of the form $Q_\beta = Q_\gamma - Q_\alpha$, which was then fully characterized by Ricotta (2005).

The transformation of Q into an effective number of species (E) has then been proposed (Ricotta and Szeidl, 2009).

$$E = \frac{1}{1 - Q} \tag{2}$$

This transformation addresses the issues of using of Q to calculate β diversity (De Bello et al., 2010). It allows a meaningful multiplicative partitioning $E_\beta = E_\gamma / E_\alpha$ which satisfies the replication principle and makes β independent from α (Pavoine and Ricotta, 2024); this does not result in β approaching the minimum whenever species diversity is high, as with conventional additive and multiplicative partitioning (Jost, 2007). Additionally, it provides a more straightforward interpretation, with E_α and E_γ being the “equivalent number of maximally dissimilar and equally abundant species” and E_β the “equivalent number of equally diverse, equally large and maximally dissimilar assemblages” (Ricotta and Szeidl, 2009) or the “ratio of α to γ level similarity” (Pavoine and Ricotta, 2024). Since E is a monotonic transformation of Q, using either one or the other does not change the ranking of communities (Pavoine, 2012), therefore only the E forms will be presented here, with the Q forms available separately (Appendix D).

To calculate γ, and therefore β, an issue with sample weighting needs to be made explicit: γ is calculated by pooling all the sampling units together, but there are two different approaches to calculate the proportions p. Calculating the proportions as average of the α proportions gives equal weight to each sampling unit; alternatively, sampling units could be weighted by their relative overall abundance, giving equal weight to each individual. The former approach, equally weighing samples regardless of local abundances, has been adopted here, because it is more widespread and preferable when β diversity is of interest (De Bello et al., 2010; Pavoine et al., 2016). This makes α diversity the average of the α values, and γ the diversity calculated from the average proportions across all subunits.

Q can be calculated using a distance function based on multiple traits, but β diversity partitioning requires the index to be concave, such that Q_β is not negative, or E_β not less than one. For indices based on Q, this is guaranteed when the distance matrix is squared Euclidean, i.e. the matrix of $\sqrt{d_{ij}}$ is Euclidean (Pavoine et al., 2005, 2016). Since all traits considered are quantitative, we chose the Mahalanobis generalized distance, which obeys the squared Euclidean property (Legendre and Legendre, 2012) and accounts for correlations between traits (Pavoine et al., 2009). The use of this distance is suitable because the distance matrix is kept fixed for all plots and scales (Botta-Dukát, 2005). The matrix has been scaled to the range [0,1] by dividing it by the maximum observed value, turning it into a dissimilarity matrix. This is a necessary step to make the index comparable with the Gini-Simpson index (when

$d_{ij} = 1$ for $i \neq j$) and because the denominator of E is a similarity (as 1 - dissimilarity). It is important for this step to be performed once globally to get comparable and meaningful results (Botta-Dukát, 2018; Pavoine et al., 2016).

Alternative transformations of the distance matrix into a dissimilarity matrix have been proposed (Leinster and Cobbold, 2012), also by introducing a threshold for maximum dissimilarity (Chao et al., 2019). The purpose is to achieve high β diversity for similarity matrices deviating from an identity matrix. This means forcing the functional diversity index to be similar to the case of the identity matrix, turning a purely functional diversity index into one which is sensitive to taxonomic distinctions, e.g. Fig.2c in Botta-Dukát (2018). Instead, we argue that prior transformation of the trait data distributions, often highly skewed, is fundamental to achieving a meaningful distance matrix: e.g. the difference between Fig.2a and 2b in Botta-Dukát (2018). Here, this was achieved by the Box-Cox transformation (Box and Cox, 1964), which generalizes the logarithmic and power transformations. The parameter λ has been chosen by maximum log-likelihood with the function 'boxcox' in the package 'MASS' (Venables and Ripley, 2002).

Partitioning schemes for Q_β and E_β into three multiplicative components each have been recently proposed (Pavoine and Ricotta, 2024). In particular, for Q_β:

$$Q_\beta = Q_{\beta tax} \times U_\gamma \times C \tag{3}$$

With $Q_{\beta tax}$ being Q_β calculated assuming maximally dissimilar species ($d_{ij} = 1$ for all $i, j; i \neq j$). U_γ is gamma uniqueness (Q_γ / $Q_{\gamma tax}$), a measure of how functionally distinct species are at the γ level; this index is also known as weighted mean pairwise dissimilarity (De Bello et al., 2016). C is relative clustering, a measure of strictly functional clustering taking into account the effect of species clustering:

$$C = \frac{Q_\beta}{Q_\gamma} \bigg/ \frac{Q_{\beta tax}}{Q_{\gamma tax}} \tag{4}$$

The decomposition for E_β is:

$$E_\beta = E_{\beta tax} \times U_\gamma^* \times R_\alpha^* \tag{5}$$

Where again $E_{\beta tax}$ is the taxonomic E_β, U_γ* is gamma uniqueness (E_γ / $E_{\gamma tax}$), but R_α* is a measure of functional redundancy at the α level ($E_{\alpha tax}$ / E_α), reflecting the local similarity of different species. In this study, in addition to the three E components, we are analysing U_γ*, C and R_α*, because they shed light on specific components of functional beta diversity.

The scripts attached to this article, based on those included in De Bello et al. (2010), Pavoine and Ricotta (2024), provide functions for calculating all the indices based on Rao's Q mentioned so far.

While we consider the sampling transect representative of the plot level (γ), a critical choice influencing the outcome of diversity measurements is which scale to choose for the subunit α level, which also influences the among-subunits β level: this scale determines which individuals are considered part of the same unit, and among which units β is assessed; there should be only slight fluctuations in γ, being calculated from averaged proportions, just with different grain sizes.

Realizing that there is no a priori correct choice of scale, our approach is to consider a series of subunit scales by combining adjacent units through computerized resampling (Podani, 1984, 1987; Tsakalos et al., 2022): each sample unit is aggregated with adjacent ones into rectangles of increasing length, allowing for overlap so that sample size is constant throughout the scaling process; keeping the sample size high for all steps, 1000 units, makes spatial autocorrelation between samples not an issue, even if it decreases the effective sample size. Indeed, for the analysis of vegetation structure, the overlap of plots produces no artifacts (Podani, 1987). This scaling process, which varies the grain size but not the extent, can be performed for all units, owing to the transect topology. Since some tests revealed that the indices used seemed to reach roughly asymptotic behaviour well within 25 m (a quarter of the transect length, while all units would become the same with a length of 100 m), 20 steps have been distributed according to a geometric progression from 0.1 m (i.e., the size of the original sampling unit) to 25 m, allowing for greater sensitivity at smaller scales, where the indices can change more abruptly.

2.4. *Structural and canopy indices*

The data from TLS and DCP were processed to provide plot-level structural and canopy variables. TLS data was analysed in two ways. A first set of four 3D features was obtained using the 'crossing3dforest' R package (Puletti et al., 2023). Following this approach, which relies on percolation theory, forest structure was characterized in terms of size, shape, and connectivity of the 3D empty space within the forest plot, particularly under the dominant forest canopy. Since indices based on the number of empty voxels increase trivially with volume, but the base area is fixed (900 m^2, the area of the plot), these have been normalized simply by division with the maximum return height to make them comparable across plots.

Another set of TLS features was more traditionally derived from the analysis of stand vertical profiles (Aalto et al., 2023): five structural metrics were assessed based on vertical plant profiles derived from TLS single scans. The point cloud was first transformed into voxels with a resolution of 25 cm and classified as vegetation voxel if the number of points was ≥45; then, the volume was subdivided into columns of 1 m^2 base area, and the vertical profile was calculated for each. Linear interpolation was used to extract height quantiles, averaged across the plot. A detailed description of each variable is shown in Table 1.

RAW canopy images were converted to JPEG images using the 'bRaw' R package (Chianucci, 2022). The procedure allows for applying a linear contrast-stretch to the blue channel of a RAW image and saving it as a single-channel JPEG. The JPEG image is then processed using the coveR package (Chianucci et al., 2022). It allows the creation of a binary image of gaps (white) and canopy (black) pixels. Gap pixels are further classified as large, between-crown gaps, and small, within-crown gaps. From these attributes, crown cover (CC) is calculated as the complement of the large gap fraction, and crown porosity (CP) is calculated as the fraction of gaps within crown boundaries. Compared to hemispherical photography, the use of DCP with a narrow field-of-view features higher resolution and more uniform sky luminance, making it largely insensitive to sky conditions, camera exposure, and thresholding (Chianucci, 2022; Chianucci et al., 2022 and references therein).

The leaf area index (LAI), namely the leaf area adjusted for clumping, is calculated as:

$$LAI = \frac{CC \times \log(CP)}{k} \tag{6}$$

Where k is the extinction coefficient, which was set to 0.5. Then, the mean LAI and its coefficient of variation have been calculated across the 12 pictures within a plot.

2.5. *Variable selection*

Given the high number of variables available for modelling (Table 1), we followed a practical approach by detecting which of them can better discriminate among the three management categories assigned during sampling. We hypothesize then, that those variables are the ones that most dramatically change through stand ageing and management activities, and represent important conditions for understorey vegetation. This has been achieved by ranking the variables by importance, adjusted for correlations (Strobl et al., 2008), in a Random Forest model with the variables as predictors and the management categories as response, with the R package 'party' (Hothorn et al., 2006; Strobl et al., 2007). Additionally, this approach has been compared with Linear Discriminant Analysis (LDA), performed with forward and backward variable selection, using the management categories as classification (Appendix E).

Table 1
Summary of structural and canopy variables, and functional diversity indices.

Short name	Full name	Description	References
	Variables derived from TLS		
min_pc_norm[1,2]	Minimum percolation cluster section	Number of voxels of the smallest section of the percolating clusters in the *x* and *y* planes	(Puletti et al., 2023)
max_pc_norm[1,2]	Maximum percolation cluster section	Number of voxels of the largest section of the percolating clusters in the *x* and *y* planes	(Puletti et al., 2023)
sd_perc_clust[2]	Percolation cluster standard deviation	Standard deviation of the percolation cluster sections voxel size	(Puletti et al., 2023)
links_norm[1,2]	Number of linked voxels	Number of empty voxels with ≥4 links with other empty voxels, according to the Von Neumann kernel	(Puletti et al., 2023)
TopH	Maximum return height	Maximum height of the lidar returns	(Aalto et al., 2023)
VCI[2]	Vertical Complexity Index	A fixed normalization of the Pielou evenness of returns in height bins	(van Ewijk et al., 2011)
RH025	25% relative height	First quartile of the return height distribution excluding ground points	(Aalto et al., 2023)
RH050	50% relative height	Median of the return height distribution excluding ground points	(Aalto et al., 2023)
RH075	75% relative height	Third quartile of the return height distribution excluding ground points	(Aalto et al., 2023)
Variables derived from DCP			
LAI	Leaf Area Index	LAI, corrected for clumping effects	(Chianucci et al., 2022)
LAIsd	Standard deviation of LAI	Standard deviation of LAI within each plot	(Chianucci et al., 2022)
Functional diversity indices			
E_α	Effective α	Average effective number of species at the α level	(De Bello et al., 2010; Ricotta and Szeidl, 2009)
E_γ	Effective γ	Effective number of species at the γ level	(De Bello et al., 2010; Ricotta and Szeidl, 2009)
E_β	Multiplicative effective β	Effective number of sub-communities. $E_\beta = E_\gamma / E_\alpha$	(De Bello et al., 2010; Ricotta and Szeidl, 2009)
R_α*	α redundancy	Functional redundancy within sub-communities	(Pavoine and Ricotta, 2024)
U_γ*	γ uniqueness	Functional species uniqueness at the plot level	(Pavoine and Ricotta, 2024)
C	Clustering	Functional clustering among sub-communities, accounting for species clustering	(Pavoine and Ricotta, 2024)

Notes: [1] these indices have been normalized by TopH, [2] using a voxel side length/height bin width of 0.5 m.

The selected variables are used in the functional linear models (Ramsay and Silverman, 2005). Parallel to this, we clustered the plots according to these variables, to check their effectiveness in recognizing the categories. Categories, as for succession stages, can have hard to define thresholds, and our use of continuous variables in modelling, instead, acknowledges the continuous nature of these changes.

The clustering approach we used is fuzzy *k*-means clustering, $k = 3$, with the R package 'fclust' (Ferraro et al., 2019); this has then been evaluated against the classification using the fuzzy Rand index. Clusters, categories, and plots were then visualized on the principal component analysis space based on the selected variables. Variables have been standardized by subtracting the mean and dividing by the standard deviation for variable selection and clustering. Even if this is not necessary for the functional linear models, which would provide the same results, we used standardized variables there too, to make regression coefficients easier to compare and visualize.

2.6. Functional linear models

The diversity indices calculated above are not scalar values as in usual regression models, since they are a function of scale. Instead of compressing them into a single number, functional data analysis (Ramsay and Silverman, 2005) allows the consideration of models with functional predictors or responses. Here, they have been implemented using the R package 'GET', which allows fitting and testing functional linear models with a non-parametric approach based on global ranking of the curves (Mrkvička et al., 2021, 2022; Myllymäki and Mrkvička, 2024), avoiding the problems associated with multiple hypothesis testing. This global envelope test is a correct approach for a single null hypothesis over the whole functional domain (Xu and Reiss, 2020): we are interested in testing the association between the selected variables and functional diversity indices by explicitly considering that the relationship could be scale-dependent, but testing the overall effect, not at individual scales. Still, global envelope tests have an intrinsic graphical interpretation (Myllymäki and Mrkvička, 2024), allowing for the inspection of the functional domain responsible for rejecting the hypothesis.

For each of the functional indices considered, we fitted a model with the selected scalar variables as predictors. The model has been tested against 19,999 permutations with no nuisance factors (intercept-only model); in this special case, the test is exact (Mrkvička et al., 2022).

We considered separate models with indices based on all traits, only aboveground traits (Díaz et al., 2022), and only clonal traits (Klimešová et al., 2017), since they could respond differently (Chelli et al., 2024a). Although a unimodal relationship between tree layer variables and understorey functional diversity is a reasonable hypothesis, we have not found evidence of it when including quadratic terms in the model (Appendix F, Fig. F.1 – F.3), therefore we present here the simpler model with only linear terms. Functional γ diversity is continually assessed at the full transect scale; however, since the γ proportions have been calculated from the mean α proportions, which change with scale, it has been considered as a function of scale for consistency and to account for these fluctuations.

3. Results

3.1. Variable selection

Variable importance according to the Random Forest model trained on the classification reveals very low values for some variables, while three of them are clearly higher than the others (Fig. 2). There is agreement with the variable selection based on LDA for median tree height (RH050) and LAI (Appendix E); therefore, since RH075 (third quartile of tree height) probably provides very similar information to RH050, only RH050 and LAI will be used in a multiple function-on-scalar linear regression.

Fuzzy *k*-means clustering using the two variables shows good agreement with the classification (Fig. 3), with a Fuzzy Rand index of 0.66. Intuitively, coppices are characterized by low RH050 and intermediate LAI, high forest plots by high values of both variables, while old-growth plots by medium-high RH050 and low LAI. These two variables are capable of summarizing the qualitative differences between these categories, in particular the median height combines information about stand height and vertical stratification, as additional layers will shift the quantile lower; LAI is higher for the more closed canopy of high

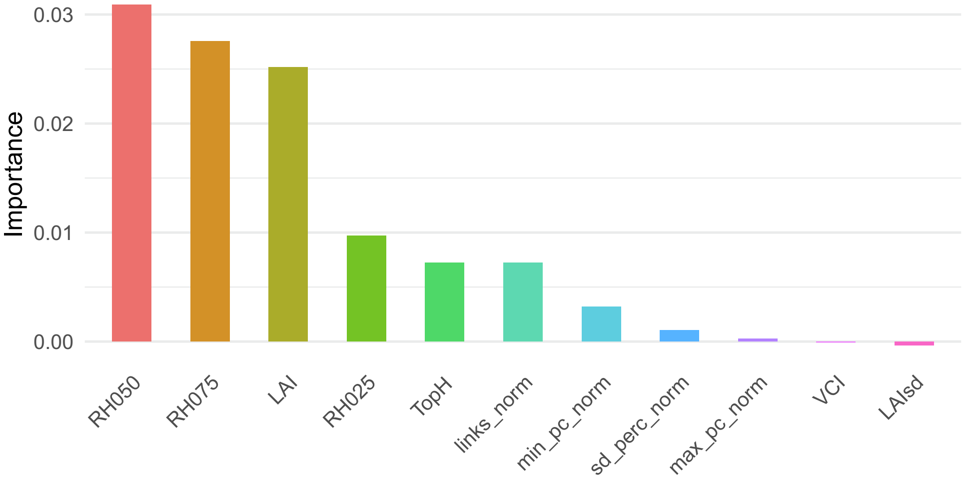

Fig. 2. Importance values of forest structure and canopy indices. The calculated indices have been sorted by their importance value, calculated based on a Random Forest model of three forest categories on those variables.

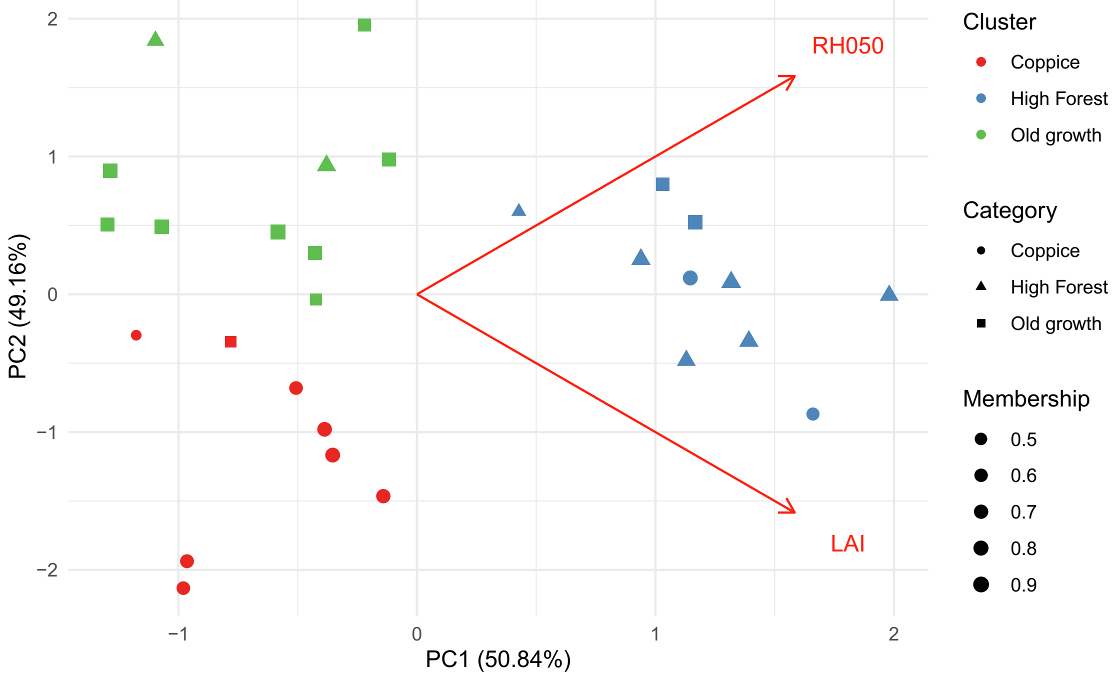

Fig. 3. Results of clustering based on the two selected variables (RH050 and LAI), and comparison with the categorization. Shapes represent the categorization made during survey, colours the assigned cluster, size the degree of membership. The results are shown on the first two components of a PCA, with variable loadings and variance percentage.

forest, while the gap dynamics of old-growth likely cause the low to intermediate values.

3.2. Functional linear models

The functional linear models of the functional diversity indices on RH050 and LAI show evidence of a positive relationship of E_α, clustering and α redundancy with RH050. The results for overall functional diversity (Fig. 4) were consistent with those for only aboveground (Fig. 5) or only clonal traits (Fig. 6), with the only difference being no evidence of clustering in the last. In particular, the scales of interest for E_α seem to be from the 0.1 m grain size up to 10–15 m; for clustering, there are two scales, ∼ 2.5 m (when considering all traits or aboveground traits) and ∼ 12 m (for aboveground traits only); for α redundancy, all scales seem to support the evidence, indicating weaker spatial structuring for this aspect, which only relates to the α level.

We refit these models using complete-case analysis instead of imputation, and they reached roughly the same results (Appendix G).

4. Discussion

We found evidence of a positive linear relationship of median tree height (i.e, RH050), but not of canopy cover (i.e., LAI), with some of the understorey multiscale functional indices considered. These results are

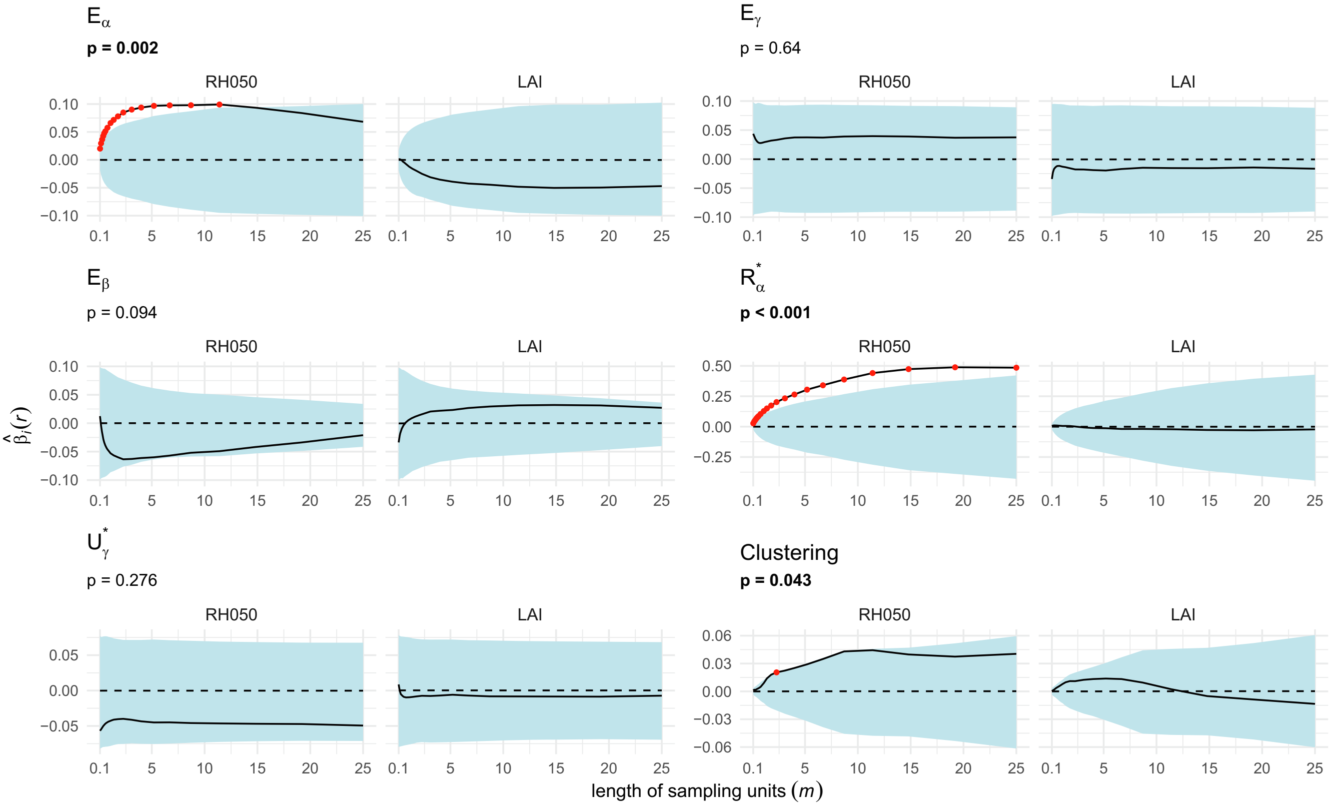

Fig. 4. Functional linear models based on all traits. For each diversity index, the scale-varying regression coefficients are shown for median tree height (RH050) and leaf area index (LAI). The permutation envelope is shown, with the coefficients exiting it, marked in red, if and only if $p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

confirmed when considering either the above- or the belowground plant compartments instead of the whole set of traits, despite them mirroring different and independent functions (Chelli et al., 2024b; Díaz et al., 2016). High median tree height characterizes mostly high forest plots, while it is intermediate for old-growth forests and low for coppices.

In particular, RH050 is positively associated with small-scale functional diversity and redundancy, and functional clustering. We hypothesize that the scales at which positive clustering was detected (around 2.5 × 0.1 m and 12 × 0.1 m) reflect habitat heterogeneity in these structurally more complex and mature plots; clustering is a measure of functional β normalized both by the plot-scale diversity and by species clustering, so it better reflects aggregation of functionally similar species, regardless of the plot's overall functional diversity, as a possible result of environmental patchiness. These patterns would likely be missed using conventional vegetation sampling approaches, which typically operate at coarser spatial resolutions (e.g., 10 × 10 m or 20 × 20 m plots).

An alternative interpretation is that lower median height, as in coppices, results in a decrease in clustering, that is, functional overdispersion of different species at small scales, together with higher uniqueness (but not at the plot scale), and lower functional diversity. It is interesting to note that we found no evidence of an association between the two modelled variables and E_γ, as we did for E_α. Since $E_\beta = E_\gamma / E_\alpha$ this implies a decrease in E_β, for which there is some evidence, albeit weak; there is stronger evidence of a reduction for Q_β (Appendix D, Fig. D.1 and D.3), but this could be caused by Q_β being more influenced by Q_α and species richness than the alternative form, or the fact that Q_β is only influenced by γ redundancy, and not by α redundancy (Pavoine and Ricotta, 2024).

Redundancy increased with RH050 at small scales but not at the plot scale (i.e. $1 / U_\gamma^*$). Redundancy has been associated with environmental filtering, resulting in the coexistence of a large set of locally adapted species with similar features, leading to an increase in taxonomic but not functional diversity (Pavoine and Ricotta, 2024). In general, redundancy has been associated with ecological stability and resilience (Biggs et al., 2020). Still, it is worth noting that our results pertain to small-scale redundancy, not plot-scale redundancy, so it is possible that there is a comparable increase in functional diversity at the latter scale, or a decrease of taxonomic diversity, although we did not find strong evidence of either. R_α^* means that co-occurring species in the same sampling unit are functionally similar, being a ratio of taxonomic over functional diversity. Clustering, which is also increasing, is similar to redundancy, but is instead relative to the similarity with species in other sub-communities within the same plot (Pavoine and Ricotta, 2024), so that, regardless of species, functionally similar individuals segregate to different parts of the transect.

Scale usually is not accounted for in the study of redundancy, even if α redundancy can differ from γ redundancy (Lamothe et al., 2018); a terminology has been suggested to distinguish local redundancy (within a scale, redundancy in the strict sense) from cross-scale reinforcement (species and processes at a different scale can maintain that function) (Angeler and Allen, 2016).

Our multiscale approach allowed us to disentangle the effects of structure and canopy cover—two features that are only moderately correlated in early forest development stages (Kane et al., 2010). Surprisingly, canopy features did not show a strong relationship with understorey functional diversity, which contrasts with previous studies emphasizing canopy openness (De Pauw et al., 2022; Landuyt et al., 2024). However, we should acknowledge that the range of LAI values considered here is typical of mature beech forests (Chianucci et al., 2016; Leuschner et al., 2006), between 4 and 7.5, and does not include the lower values of recently felled stands (Holst et al., 2004), so we

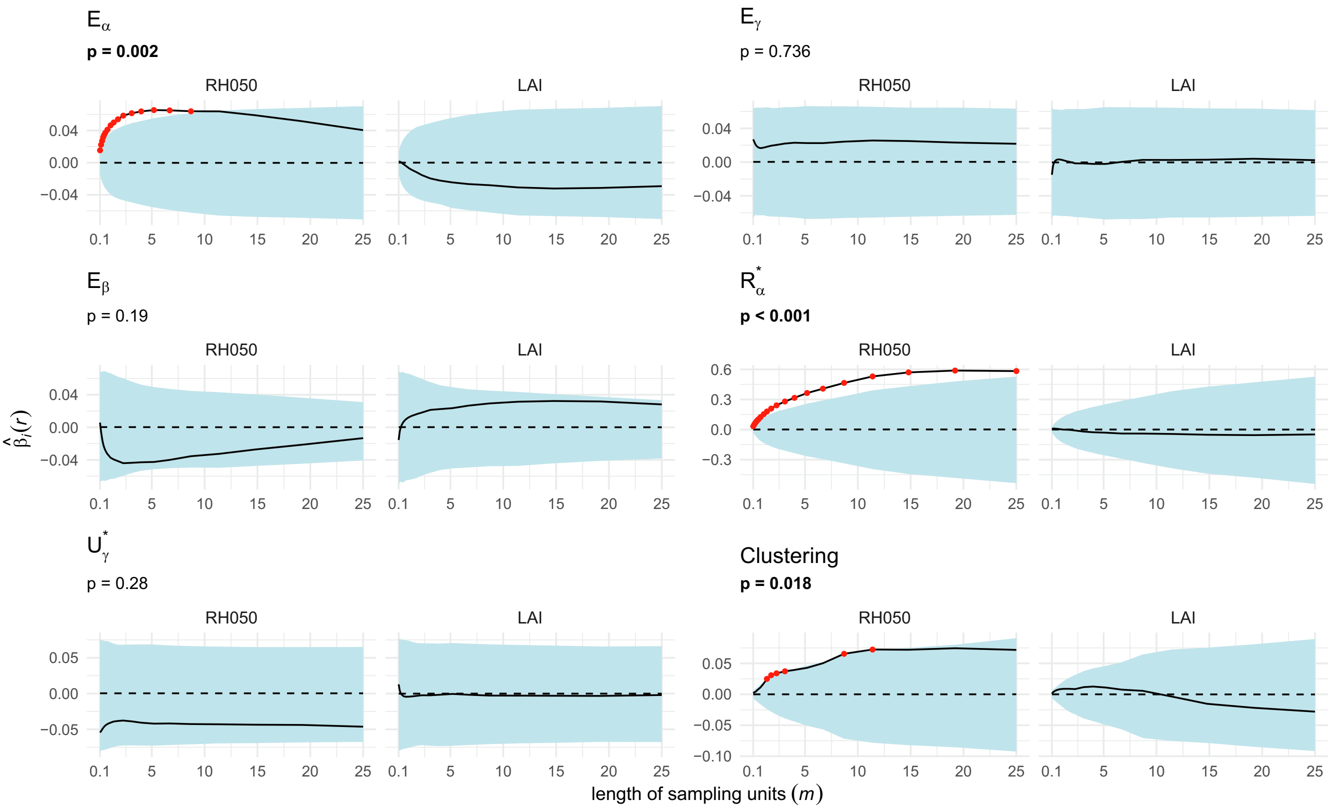

Fig. 5. Functional linear models based on aboveground traits. For each diversity index, the scale-varying regression coefficients are shown for median tree height (RH050) and leaf area index (LAI). The permutation envelope is shown, with the coefficients exiting it, marked in red, if and only if $p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

cannot exclude a saturation effect and different results for more open canopies. What previous research has usually analysed is plot-scale functional diversity, i.e. E_γ: we attribute the different results found here to the explicit treatment of scale, which helps to separate different processes and consider spatial heterogeneity, and to the consideration of individual overstory features. However, when focusing on independent trait dimensions of aboveground and clonal traits, LAI showed evidence of a negative relationship with the aboveground dimension mainly reflecting plant resource economics (Appendix H, Fig. H.3). This is consistent with previous studies observing a decrease of functional diversity with canopy closure (Chelli et al., 2024a), and in particular the overall decrease of both E_γ and E_α at all scales implies spatial homogeneity, with E_β staying constant, except at very small scales.

To check if functional diversity showed associations with LAI without conditioning on RH050, we fitted single-predictor models on each variable. These confirmed our main findings (Appendix F, Fig. F4 – F9), excluding a confounded relationship between LAI and functional diversity, or one mediated by structure. Those simpler models show evidence of a decrease in E_β with RH050 for overall and clonal trait diversity: this is accompanied by an increase in E_α and no apparent change in E_γ, which means higher RH050 is related to the local coexistence of more diverse clonal strategies out of the plot-level set, implying lower spatial heterogeneity.

Within the adopted framework (Pavoine and Ricotta, 2024), the mathematical relationships between the indices imply corresponding relationships for taxonomic diversity, which can be verified separately. In detail, the weak decrease in E_β, combined with the increase in R_α* implies a decrease in $E_{\beta tax}$ that counteracts it (Eq. 5); the combined increase in R_α* and E_α means $E_{\alpha tax}$ must be increasing as well, and more than its functional counterpart; the weak decrease of U_γ* together with the weak increase of E_γ implies an increase in $E_{\gamma tax}$. Models based on those indices have the expected coefficient signs and magnitudes, although there is strong evidence only in support of the increase of $E_{\alpha tax}$ with RH050 (Appendix D, Fig. D.1 – D.3).

The plots in this study were well distinguished along two axes, one of which reflects the vertical structural component (RH050, RH075), and one the horizontal canopy filling (LAI); both features were identified as drivers of the microclimate temperature buffering effect of forest canopies (Gril et al., 2023; Steinparzer et al., 2025). Canopy cover and RH050 were shown to be the two strongest predictors of logging disturbance (Ghizoni Santos et al., 2022). In addition to canopy height, RH050, which we found to be associated with different components of understorey functional diversity, can indicate higher or lower understorey production and canopy packing efficiency (Aalto et al., 2023). Since our plots included uneven-aged forest stands with several canopy layers, we think that the median height is more sensitive to this vertical stratification compared to the traditional “total tree canopy height” (TopH), which remains roughly constant, except in the youngest stands. Vertical structural complexity can discriminate between managed and primary beech forests, reaching a minimum in abandoned optimum phase stands (Stiers et al., 2018). However, in our case, neither VCI nor any of the percolation-based indices was found to be effective in distinguishing between categories, suggesting either the lack of a clear discrimination, or just small variation among the studied plots.

Regarding the associations we analysed of LAI and RH050 with understorey functional diversity, while a clear causal relationship can be established for the former variable through light interception and availability (Chelli et al., 2024a; Landuyt et al., 2018), we can still say that RH050 reflects the management history and age of the stand (Aalto et al., 2023).

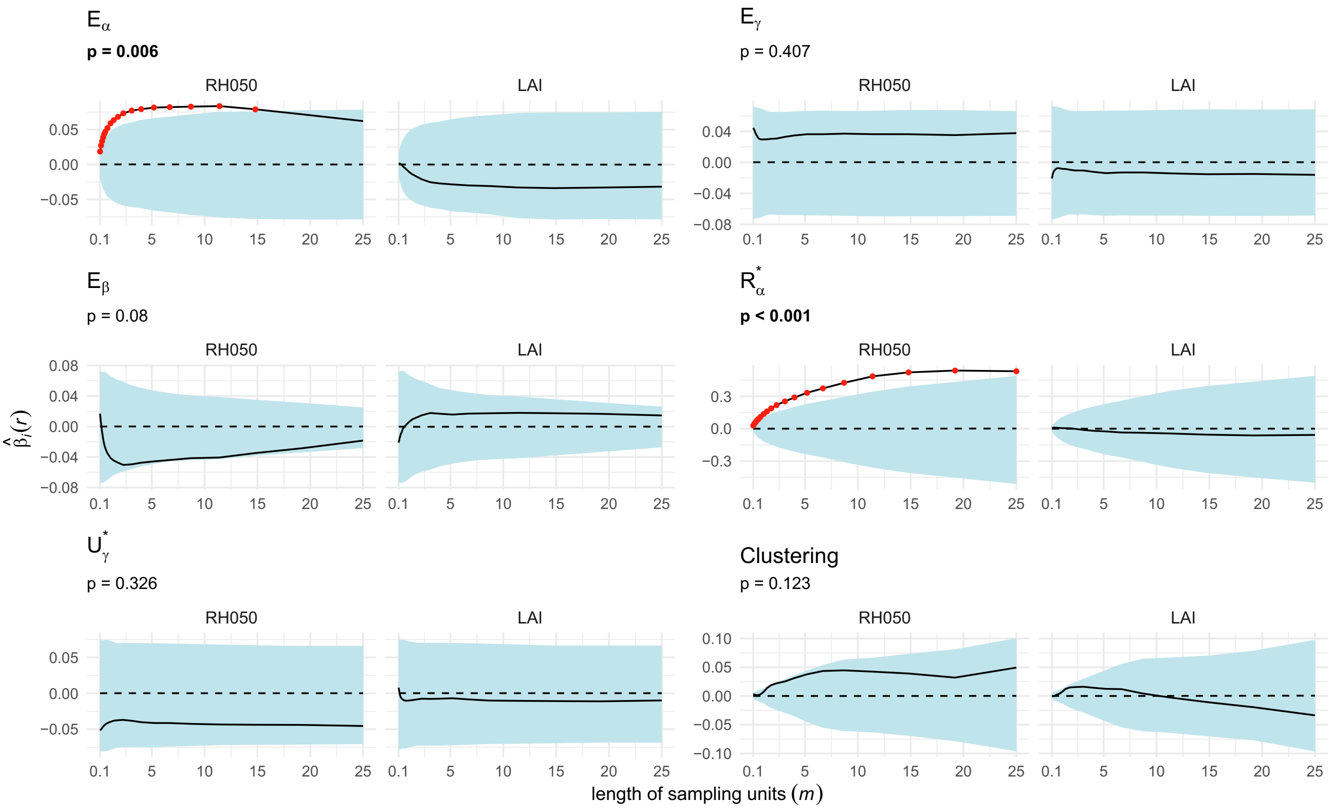

Fig. 6. Functional linear models based on clonal traits. For each diversity index, the scale-varying regression coefficients are shown for median tree height (RH050) and leaf area index (LAI). The permutation envelope is shown, with the coefficients exiting it, marked in red, if and only if $p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Conclusions

Our results have implications for forest monitoring and management. The pan-European set of criteria and indicators for sustainable forest management is one of the most successful and supported policy instruments of its kind, guiding many international and national strategies (Linser and Wolfslehner, 2022). Still, its current revision adopts a narrow view on biodiversity, with no explicit consideration of understorey biodiversity or functional diversity. The present study exemplifies how biodiversity can be leveraged beyond its intrinsic value to inform understanding of communities and ecosystems, while also incorporating relationships with indicators of sustainable forest management that are typically considered separately (i.e., forest structure in Criterion 1 and biodiversity in Criterion 4; Forest Europe, 2021).

In particular, while plant ecologists and forest practitioners are usually focused on changes in canopy features as the main drivers of understorey taxonomic and functional shifts, we suggest a relevant role of median tree height (RH050); monitoring protocols making use of TLS should consider this as a simple indicator of stand-level ecosystem function, especially if the spatial organization of the understory is of interest. We do not exclude different relationships with other structural and canopy variables, but we followed a motivated approach in selecting variables.

This study considers a wide variety of management practices but focuses on acidophilous beech forests. We encourage future research to extend this approach to other systems. The transect grain size used here should be suitable for other forest types, but a different trade-off between resolution and sampling efficiency could be considered (Bartha et al., 2020).

While we acknowledge that the sampling design is laborious (approximately one hour with four people, in this case), it, along with the following analysis enabled the detection of relationships at specific spatial and ecological scales that might not have emerged with a single plot-level scale. Indeed, we were able to find an increase in functional redundancy at specific scales, accompanied by an increase in functional diversity (and hence a larger increase in taxonomic diversity) at small (α) scales but not at the plot (γ) scale. We conclude that high RH050, as in high forests, correlates with patches of functionally and taxonomic diverse plants, without a corresponding change in the overall diversity. While this implies a decrease in spatial heterogeneity (β), there is weak evidence supporting it. Instead, when quantifying this heterogeneity relative to the plot-level diversity and to species clustering, we found evidence of higher functional clustering in those forests.

Functional data analysis promises to be a valuable tool in ecology, for the explicit evaluation of variables as a function of, for example, time or space. We effectively applied this approach to simultaneously consider biodiversity indices as they vary with scale, showing the importance of this often-overlooked aspect and incorporating it in our modelling and testing.

Finally, while we could not consider intraspecific trait variability in our study, it can be incorporated in the methods used with overlap distance measures (Botta-Dukát, 2018; Carmona et al., 2016) and making the similarity of a species with itself lower than 1 (Botta-Dukát, 2018; Chiu and Chao, 2014).

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2026.114687.

CRediT authorship contribution statement

Luciano Ludovico Maria De Benedictis: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Stefano Chelli: Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Zhengxue Zhu:** Validation, Software, Investigation. **Marco Cervellini:** Writing – review & editing, Investigation. **Roberto Canullo:** Investigation. **Francesco Chianucci:** Writing – review & editing, Methodology, Investigation. **Nicola Puletti:** Writing – review & editing, Methodology, Investigation. **James Lee Tsakalos:** Writing – review & editing, Investigation. **Sándor Bartha:** Writing – review & editing, Methodology. **Giandiego Campetella:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data and code necessary to reproduce all the analyses are openly available at https://doi.org/10.5281/zenodo.15088594 and https://doi.org/10.5281/zenodo.15088549 respectively.

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