RESEARCH ARTICLE

Silvicultural regime shapes understory functional structure in European forests

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Abstract

1. Managing forests to sustain their diversity and functioning is a major challenge in a changing world. Despite the key role of understory vegetation in driving forest biodiversity, regeneration and functioning, few studies address the functional dimensions of understory vegetation response to silvicultural management.

2. We assessed the influence of the silvicultural regimes on the functional diversity and redundancy of European forest understory. We gathered vascular plant abundance data from more than 2000 plots in European forests, each associated with one out of the five most widespread silvicultural regimes. We used generalized linear mixed models to assess the effect of different silvicultural regimes on understory functional diversity (Rao's quadratic entropy) and functional redundancy, while accounting for climate and soil conditions, and explored the reciprocal relationship between three diversity components (functional diversity, redundancy and dominance) across silvicultural regimes through a ternary diversity diagram.

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3. Intensive silvicultural regimes are associated with a decrease in functional diversity and an increase in functional redundancy, compared with unmanaged conditions. This means that although intensive management may buffer communities' functions against species or functional losses, it also limits the range of understory response to environmental changes.

4. *Policy implications*. Different silvicultural regimes influence different facets of understory functional features. While unmanaged forests can be used as a reference to design silvicultural practices in compliance with biodiversity conservation targets, different silvicultural options should be balanced at landscape scale to sustain the multiple forest functions that human societies are increasingly demanding.

KEYWORDS
ecosystem resilience, forest understory, functional diversity, functional redundancy, silvicultural regime, sustainable forest management, unmanaged forests

1 | INTRODUCTION

Understory represents the largest component of biodiversity in most forest ecosystems (Spicer et al., 2020) and thus plays a key role in forest ecosystems' processes and diversity (Gilliam, 2007). Despite its importance, the influence of overstory composition, structure and management on understory plant diversity is relatively poorly understood. This is a particularly relevant issue in European forests, whose overstorey composition and structure have been modified through various silvicultural systems for centuries or even millennia (Aszalós et al., 2022; Meyer & Ammer, 2022; Pretzsch et al., 2008; Puettmann et al., 2009). These modifications have often resulted in simplified stand structure (Puettmann et al., 2009), with negative consequences on biological communities, including the understory (Landuyt et al., 2024). Examples include traditional, timber-focused approaches like clearcutting and coppicing, which notoriously simplify structural and biological complexity (Fabbio, 2016; Puettmann et al., 2009), thus potentially reducing forest functioning and resilience (Fahey et al., 2018). Understanding the impact of forest management on understory vegetation would allow us to control and drive its response to disturbance and stresses (Hooper et al., 2005).

Managing forests to sustain both ecosystem functioning and biodiversity conservation has raised increasing concern in recent times, in light of the climatic changes and biodiversity losses observed worldwide (Fahey et al., 2018; Puettmann et al., 2009). Accordingly, new silvicultural strategies have emerged in the last few decades, to promote complexity in forest ecosystems. These include a greater consideration of uneven-aged or multi-layer silvicultural systems (Nolet et al., 2018), continuous cover forestry (Mason et al., 2022), irregular shelterwood (Raymond & Bédard, 2017), and variable retention forestry (Curzon et al., 2020; Fedrowitz et al., 2014), among other practices (for a review, see Trentanovi et al., 2023). As the portfolio of forest management options increases, so does the need of understanding the influence of these options on forest ecosystem processes and dynamics.

While it is expected that overstory-understory relationships are driven by overstory structure (Segar et al., 2022; Zellweger et al., 2020), yet the understory response to active management practices depends on a combination of associated environmental changes, pre-harvesting community composition and understorey functional traits (Ares et al., 2010; Bartemucci et al., 2006; Wilson et al., 2009). For instance, harvesting typically induces an increase in light transmittance, accompanied by an increase in water and mineral nutrients at the forest floor, which may lead to either an increase in understory species richness by reducing environmental filtering (Sabatini et al., 2014), or to a decrease in such richness due to higher competition (Grace et al., 2014) or selective selection (Mouillot et al., 2013), with cascading effects on forest succession and ecosystem processes (Gilliam, 2007; Spicer et al., 2020), also depending on the original community composition (Burton et al., 2013) and functional structure (De Lombaerde et al., 2021; Landuyt et al., 2019). Over the last few years, there has been increasing interest in evaluating the effect of forest management on functional diversity (Ford & Keeton, 2017; Monge-González et al., 2021; Stanturf et al., 2014), rather than on species diversity only. Forest management can lead to variations in plant communities' functional structure, affecting either their functional response to a disturbance, their functional effect on ecosystem processes, or both (Ares et al., 2010). Among the metrics of functional structure, the most often used to evaluate the community responses to natural or anthropogenic disturbance and alteration (Aquilué et al., 2020) are: *functional diversity*, which accounts for the range of functional traits, and *functional redundancy*, which accounts for the recurrence of functional traits. Functional diversity encompasses the diversity of ecological strategies present in a community, whereas functional redundancy reveals how these strategies are redundant, thus the potential impacts of species losses

on ecosystem functioning (Monge-González et al., 2021). The availability of many functionally distinct species, that is, high values of functional diversity, increases the probability that, in case of major perturbation, climatic instability or fluctuating disturbance regimes, some of them may exploit the new conditions, thus contributing to the ecosystem post-disturbance reorganization (Schmitt et al., 2020; Seidl & Turner, 2022). Accordingly, high functional diversity in understory species corresponds to a strong potential for forest tree regeneration, post-harvest productivity (Wei et al., 2021), and tree survival (Billing et al., 2022). The co-occurrence of species that perform similar functions, that is, high values of functional redundancy, ensures the maintenance of immediate ecosystem processes, such as productivity, carbon sequestration or nutrient cycling, and may support forest resilience after strong disturbance or perturbations (Pillar et al., 2013; Ricotta et al., 2016). Both functional diversity and redundancy have been recognized as proxies of ecological resilience (sensu Holling, 1973) through site-level studies performed in arid and mountain rangelands (Chillo et al., 2011; Sadeghinia et al., 2023) and in forests subjected to wildfires (Spasojevic et al., 2015) as well as through reviews and meta-analyses (Biggs et al., 2020; Standish et al., 2014).

The possibility for a community to display both a high functional diversity and a high functional redundancy is limited by the overall species diversity of the community (Ricotta et al., 2023), which defines the potential number of species with recurrence traits for a wide range of functional traits' values. The joint analysis of the different components of diversity can be related to the ecological processes that contribute to shaping community organization to varying degrees under different environmental conditions (Ricotta et al., 2023). In forest ecosystems, a combined approach was indeed used to identify the pathways through which management shapes the functional structure of understorey (Bricca et al., 2020; Monge-González et al., 2021).

While the impact of management on understory functional diversity was the focus of some previous studies (Vanneste et al., 2019; Xie et al., 2023), few works have explored the influence of management on different components of understory functional structure (e.g. Aquilué et al., 2020; Monge-González et al., 2021). In addition, few studies have considered comparing the functional response to different available management alternatives (Cadotte, 2011), even though such understanding can be pivotal to evaluating current management approaches and shaping future forestry.

In this study, we tested whether the silvicultural regime influences the mutual relationship between the three diversity components (functional diversity, redundancy and species dominance) of understory in European forests. We hypothesized that different management regimes influence understory functional structure differently, with more intensive management regimes likely increasing redundancy, while limiting functional diversity of understory communities, due to the simplification of both stand structure and environmental conditions at the forest floor (Kusumoto et al., 2015; Laliberte et al., 2010). Conversely, silvicultural regimes pursuing structural heterogeneity are expected to host more functionally diverse understory communities (Kusumoto et al., 2015). We also expected to find that less intensive silvicultural regimes ensure high values of both functional diversity and redundancy, being more similar to 'unmanaged' conditions, where higher species diversity is expected (Paillet et al., 2010). By considering the most widespread management regimes in Europe, we provide nuance to the understanding of the ecological implications of forest management and inform sustainable forest management practices in Europe.

2 | MATERIALS AND METHODS

2.1 | Vegetation and silvicultural data

We used data from forest biodiversity studies conducted across Europe from 2000 to 2021, which were gathered in the framework of the COST Action BOTTOMS-UP (Burrascano et al., 2023). The data collection was conducted with the necessary authorizations from the competent authorities. We considered a subset of data having vascular plant abundance records, for a total of 2107 sampling units across 11 European countries (Figure 1). The sampling units consist of *plots* (i.e. delimited forest areas where sampling was performed) nested into 489 *stands* (i.e. management spatial units), which in turn are nested into 146 *sites* (i.e. environmentally homogeneous geographical areas). The distance between samples in a site ranges between 37 and 6180 meters, whereas the average distance is 330 ± 9 m.

Vascular plant data has been collected within fixed circular or square sampling units, mostly ranging from 75 to 1256 m^2 (for details, see Burrascano et al., 2021), considering understory vegetation, the individuals observed below 3–5 m of height. We purposely included woody species in the understory since they have a key role in determining the understory functional structure, especially in relation to its regeneration potential and to the ecological resilience of forest ecosystems. Species cover values were assigned in a percentage scale (0–100), which in some cases derived from cover-abundance scales (e.g. Braun-Blanquet, Van der Maarel, Raunkiær). Species nomenclature was checked using the *gnr_resolve()* function of the 'taxize' package (Chamberlain et al., 2020) in R version 4.1.1 (R Core Team, 2021). The function assigns a score, which is a measure of confidence or reliability associated with the taxonomic identification of a given species name. Species names obtaining scores greater than 0.90, that is, high confidence, were accepted. Further screening was performed through the 'WorldFlora' R package (Kindt, 2020).

Silvicultural regimes (Table 1) and forest categories (sensu Forest Europe, see also Barbati et al., 2014) (Table S1) were associated with each sampling unit (Burrascano et al., 2021; Figure S1). Silvicultural regimes were classified according to a gradient of harvesting intensity (Table 1) sensu Haeussler et al. (2002).

The resulting data can be considered representative of the most widespread management conditions in European forests and of the different stand development phases, considering the time from the last intervention in the sampling units (Figure S2).
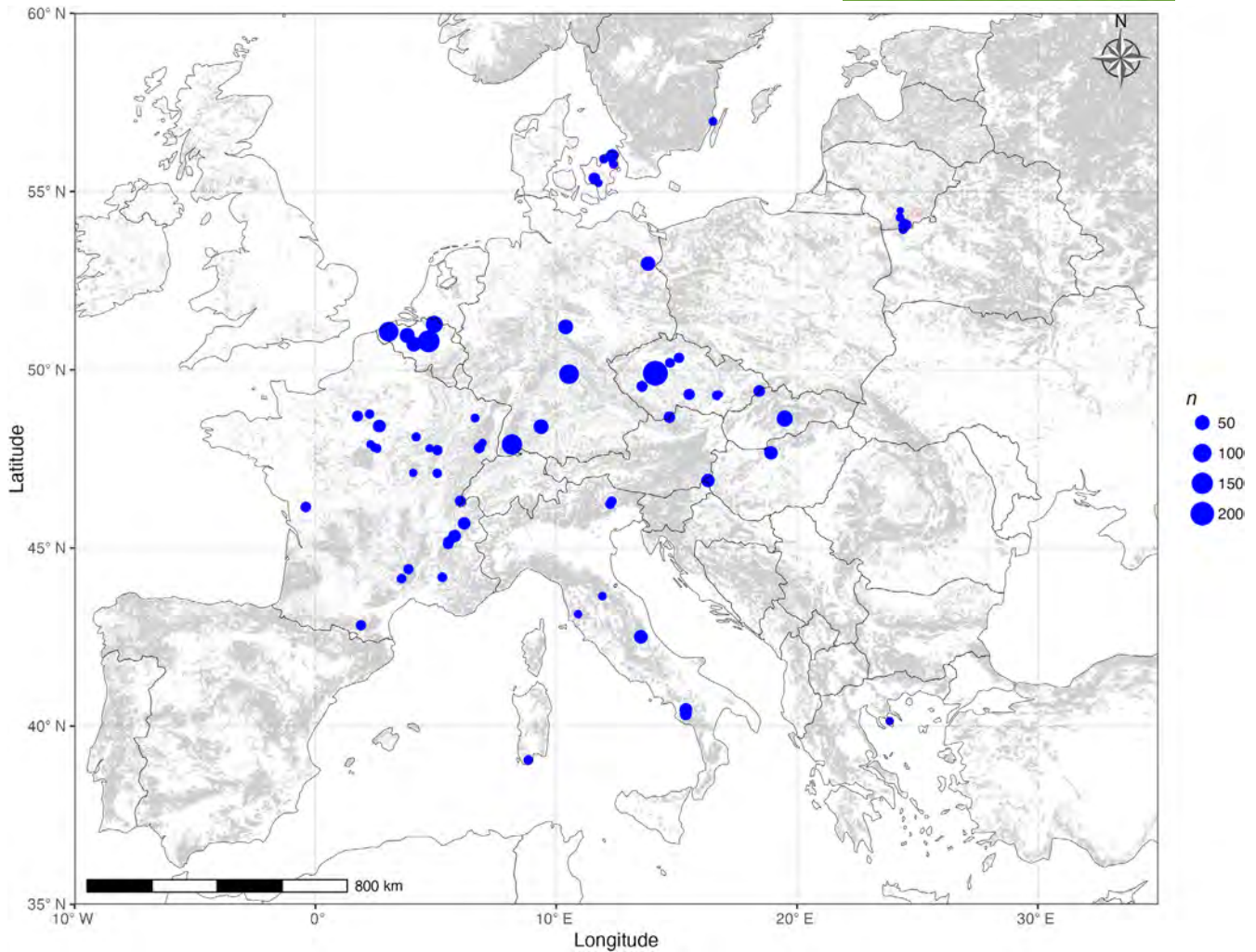
FIGURE 1 Spatial distribution of the study sites. The size of bullet points is proportional to the number of sampling units per site. Grey areas are covered by forests with a tree cover greater than 40% according to the map of Kempeneers et al. (2011).

2.2 | Assessing understory functional diversity and redundancy

We focused on three widely available traits that give insights into both the global spectrum of plant functions (Díaz et al., 2016; Vanneste et al., 2019) and the leaf-height-seed functional trait space (Westoby, 1998). Specific leaf area (SLA) reflects the trade-off between leaf longevity and photosynthetic rate (Wright et al., 2005), and thus controls the growth rate in response to varying levels of disturbance (Bernhardt-Römermann et al., 2011); plant height (H) determines species ability to compete for light and responds to various environmental stresses (Westoby, 1998); seed mass (SM) plays an important role in the colonization process by influencing dispersal distances, seed persistence, germination, establishment and survival (Burton et al., 2020; Moles et al., 2005). These attributes are linked to two major axes of the global spectrum: H and SM are related to size, while SLA is related to the leaf economic spectrum (Díaz et al., 2016).

Trait values were collected from available literature and database (Cerabolini et al., 2010; Chelli, Ottaviani, et al., 2021; Kattge et al., 2020; Kleyer et al., 2008). Depending on the trait, we

gathered trait values for 83%–94% of the species. Missing values were imputed using the 'mice' R package (Van Buuren & Groothuis-Oudshoorn, 2011). Most imputed values were relative to rare and/or less abundant species (Wasof et al., 2018), covering less than 10% of the sampling unit area in 97% of cases.

We calculated functional diversity for each sampling unit with the Rao quadratic entropy Q (Botta-Dukát, 2005):

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

where d_{ij} is the dissimilarity between species i and j ($i, j = 1, 2, \ldots, S$) with $0 \leq d_{ij} \leq 1$, $d_{ij} = d_{ji}$, and $d_{ii} = 0$, weighted for the corresponding species relative abundances $p_i \times p_j$. This index estimates the mean dissimilarity between two randomly selected individuals within the functional trait space. Therefore, by assessing the amount of multivariate trait dispersion between the species of a given assemblage (Gregorius & Kosman, 2017; Ricotta et al., 2021), the Rao quadratic diversity is directly related to the statistical notion of variance (Pavoine, 2012; Rao, 2010).

TABLE 1 Silvicultural regimes applied in the sampling units. For details, see the main text.

Silvicultural regimes	Treatment description	Silvicultural regime	Typical vertical structure	No. of sampling units (%)
Unmanaged	No silvicultural interventions applied in the recent past (50 years) or planned, and no clear visible indications of human disturbance	None	Uneven-aged stand	150 (7.2%)
Selection cutting	Felling and regeneration are not restricted to certain parts of the forest, but uniformly distributed. Both single-tree and group selection cutting are considered	Low	Uneven-aged stand	641 (30.4%)
Shelterwood	Overstorey trees in a forest stand are completely removed using a limited number of progressive cuts designed to promote regeneration making use of the shelter and seed source of remaining trees	Medium	Mostly even-aged stand	657 (31.2%)
Clearcutting with retention	The forest stand is clear-felled in a single harvesting operation except for solitary trees or tree groups (living or dead) that are deliberately spared	Medium	Mostly even-aged stand	384 (18.2%)
Clearcutting	The forest stand is entirely harvested in a single operation, resulting in a treeless open area	High	Mostly even-aged stand	180 (8.5%)
Coppice with standards	The two vertical tree layers of the forest stand are harvested by clearcutting and selection cutting, resulting in respectively an even-aged coppiced dominated layer, and trees of seed origin in the dominant layer	High	Two-storied stand	95 (4.5%)

Functional redundancy was then calculated according to Ricotta et al. (2023) as

$$R = S - Q, \qquad (2)$$

where S is the classical abundance-based Simpson diversity index: $S = 1 - \sum_{i=1}^{S} p_i^2$, defined as the probability that two randomly selected individuals from a given site belong to different species.

As such, functional redundancy (i.e. the amount of species diversity not expressed by functional diversity; Pillar et al., 2013) provides information on the mean functional *similarity* among the distinct species in a given plot. For details, see Ricotta et al. (2023).

From the above, it follows that Rao's quadratic diversity (Q), functional redundancy (R) and Simpson dominance (i.e. the complement of Simpson's diversity $D = 1 - S$, defined as the probability that two randomly selected individuals from a given site belong to the same species) sum up to one: $Q + R + D = 1$ Accordingly, using these three functional attributes, it is possible to describe the functional structure associated with each silvicultural regime using a ternary diagram (Ricotta et al., 2023).

Functional attributes were calculated for the three standardized traits using the 'adiv' R package (Pavoine, 2020) as follows. The Marczewski–Steinhaus coefficient used in the functions to calculate the dissimilarity d_{ij} is the complement of the Jaccard index

of similarity extended to include data on species abundances (see Ricotta et al., 2016 for details). To standardize traits, the function divides all values by the highest observed one. Community-weighted mean trait values (CWMs) were also calculated for each trait to characterize the mean understory functional composition, and its relationship with management, soil and environmental variables.

2.3 | Soil and climate data

Given the broad scale of the data, we accounted for the main environmental gradients by considering the soil and climatic features of each sampling unit in the analysis. Soil features were obtained from the European topsoil physical properties map based on Land Use and Cover Area frame Statistical survey (LUCAS) topsoil data (Ballabio et al., 2016). We considered

- available water capacity (expressed as a fraction of unit ground);
- bulk density derived from soil texture datasets (mg/m^3);
- soil textural classes derived from clay, silt and sand maps.

For each sampling unit, we calculated the mean soil properties over a 1000 m buffer from the centre of the sampling unit.

Climatic data were obtained from CHELSA v.2.1 (Karger et al., 2017), at 1000m resolution. Bioclimatic variables were derived as long-term means of maximum and mean temperature, and mean precipitation sums over the 1981–2010 period. We selected four variables as follows:

- mean annual temperature,
- annual range of air temperature (difference between the maximum of the warmest month and the minimum of the coldest month),
- annual precipitation and
- precipitation seasonality (standard deviation of the monthly precipitation).

The topographic influence on incident solar radiation was calculated as the heat load index (McCune & Keon, 2002) for each sampling unit based on latitude and on slope and aspect derived from Copernicus' European Digital Elevation Model (EU-DEM; https://www.eea.europa.eu/data-and-maps/data/copernicus-land-monitoring-service-eu-dem).

2.4 | Statistical analyses

We fitted generalized linear mixed models (GLMMs) using the 'lme4' R package (Bates et al., 2015) to assess the role of management in driving understory functional diversity and redundancy, with 'unmanaged' forests' sampling units as a reference. After evaluating the distribution of functional diversity and redundancy using the 'fitdistrplus' package (Delignette-Muller & Dutang, 2015), we opted for a Gaussian distribution. We included climate and soil variables in the fixed part of the model and standardized all the fixed continuous variables. We considered forest category (sensu Forest Europe; Barbati et al., 2014; EEA, 2006), site (i.e. environmentally homogeneous geographical areas, Burrascano et al., 2023), stand (i.e. uniformly managed spatial units) and sampling unit size as random intercept variables. Forest categories were meant to include broad-scale variability in species pools, which may affect functional diversity and redundancy. Site effect includes the variability across data sets, in terms of local conditions and sampling protocols. Considering the site/stand controls for nested data structure and explaining the spatial variability within the data, avoiding pseudo-replication issues due to the uneven distribution of the sampling units across Europe (Zuur et al., 2013). Finally, sampling unit size controls for the sampling effort. To deal with multicollinearity issues, we calculated the variance inflation factor (VIF) of each predictor using the 'car' R package (Fox & Wisberg, 2019), and we checked that VIF <4 (Zuur et al., 2013) which indicated no high correlation among predictors. We also verified the normality of residuals through visual inspection of Q–Q plots and computed conditional and marginal pseudo-R^2 (Nakagawa & Schielzeth, 2013) with the 'piecewiseSEM' R package (Lefcheck, 2016). The same analysis was also performed for each trait separately, using their CWM values.

A multiple comparison post hoc test was also performed using Tukey contrasts, with the aim of comparing functional diversity and redundancy across pairs of silvicultural regimes.

Finally, a ternary diagram (sensu Ricotta et al., 2023) was used to visualize the relationship between functional diversity, redundancy and (Simpson) dominance across silvicultural regimes. In the ternary diagram, the vertices of the triangle correspond to the three components of diversity, and each point corresponds to the median values of the three diversity attributes for each silvicultural regime.

3 | RESULTS

3.1 | Silviculture shapes understory functional diversity and redundancy

The GLMMs resulted in a similar total (conditional R^2) and fixed effects explanatory power (marginal R^2) for functional diversity (conditional $R^2 = 0.56$; marginal $R^2 = 0.06$) and functional redundancy (conditional $R^2 = 0.59$; marginal $R^2 = 0.08$). Functional diversity was diversely affected by different silvicultural regimes according to their harvesting intensity (Figure 2): high harvesting intensity regimes have mean lower functional diversity, where the difference is significant for simple clearcutting and coppice with standards, while selection (low harvesting intensity), and shelterwood (medium harvesting intensity) did not differ from unmanaged conditions. Soil parameters did not result in significant effects on functional diversity, while temperature factors positively affected it.

The model for functional redundancy gave opposite results, with a significant increase for high harvesting intensity silvicultural regimes (simple and retention clearcutting), negative relationships with mean temperature compared to unmanaged conditions (Figure 2).

When considering the three traits individually, the mean functional traits (quantified by the CWM values) responded differently to management, soil and climate conditions (Figure 3). Compared to unmanaged conditions, SLA was negatively impacted by all management conditions, except more high harvesting intensity silvicultural regimes (simple clearcutting and coppice with standards). SLA was also influenced by climate and partly by soil and climate since it was significantly correlated with temperature, heat load and available water content. Simple clearcutting has a negative effect on the CWM of plant vegetative height, while it has a non-significant effect for low to medium harvesting intensity silvicultural regimes. Plant vegetative height was also positively influenced by temperature, while SM was positively associated with bulk density and heat load, and negatively associated with temperature range. Marginal and conditional R^2 for the CWM models are, respectively, 0.22 and 0.83 for SLA, 0.04 and 0.76 for plant vegetative height and 0.03 and 0.70 for SM. The random effects included category, site, stand and sampling area.

Multi-comparison (Tukey's test) confirmed that functional diversity and redundancy significantly differed across silvicultural regimes, with intense regimes showing significant differences (lower
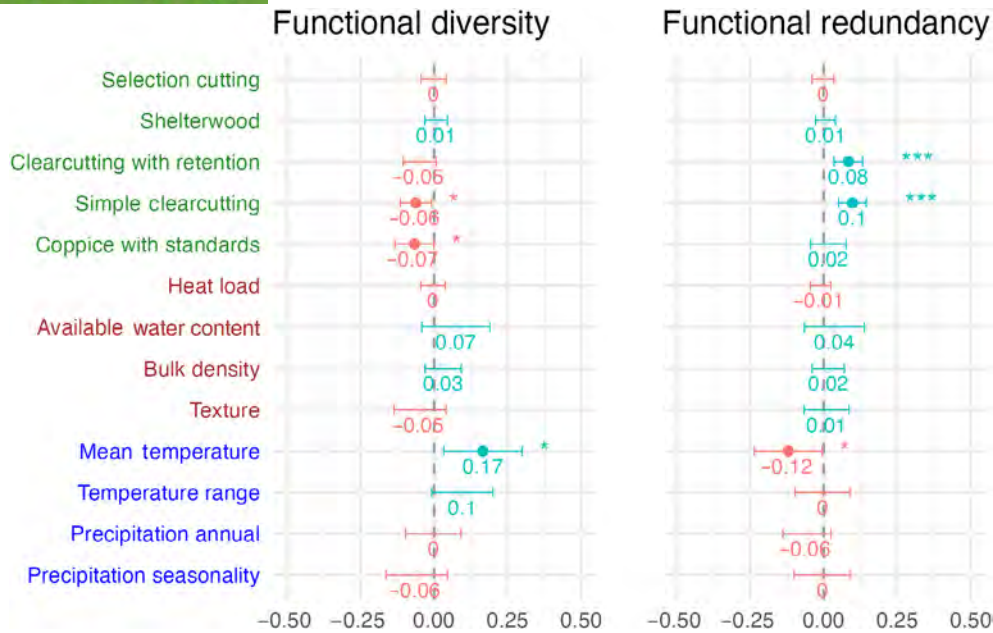
Functional diversity / Functional redundancy

FIGURE 2 Influence of silvicultural regimes (compared to unmanaged forests) and topographic, soil and climate variables on functional diversity and redundancy. Silvicultural regimes (Table 1) are listed according to a top-to-bottom gradient of increasing harvesting intensity. *$p \leq 0.05$, ***$p \leq 0.001$. The x-axis reports the model coefficients. The vertical dashed line indicates unmanaged forest conditions slope (reference). Dots indicate the slope coefficients for each predictor, and the horizontal lines their confidence interval. Positive coefficients are coloured in navy, whereas negative coefficients are coloured in red. Non-significant dots were plotted using transparency.
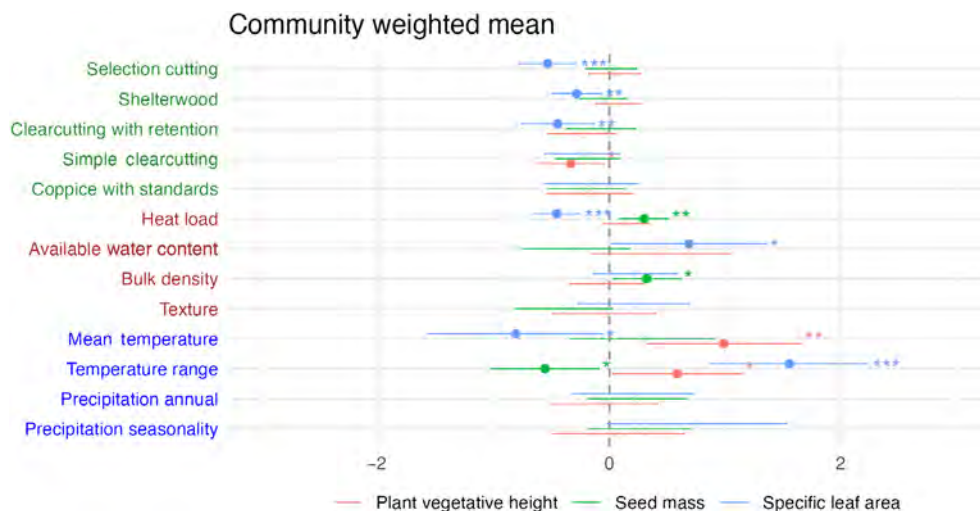
Community weighted mean

FIGURE 3 Effect of silvicultural regimes, soil and climate conditions on functional signature (CWM of individual traits). CWM values were rescaled between 0 and 1 to account for differences in units and range in the selected traits. *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$. The vertical dashed line indicates unmanaged forest conditions slope (reference). Dots indicate the slope coefficients for each predictor, and the horizontal lines their confidence interval. Positive coefficients are coloured in navy, whereas negative coefficients are coloured in red. Non-significant dots were plotted using transparency. When non-significant, the dots have been plotted using transparency (for definitions, see Section 2.3). CWM, community-weighted mean.

functional diversity, higher functional redundancy) compared to less intensive ones (Figure 4).

3.2 | Relationship between diversity components

The pattern of diversity decomposition into functional diversity, redundancy and species dominance differed across silvicultural regimes

(Figure 5). In terms of functional diversity, the highest values were found for unmanaged forests and low to intermediate harvesting intensity silvicultural regimes, namely selection cutting, shelterwood and clearcutting with retention. Among these regimes, unmanaged forests were those displaying the best combination of high functional diversity and low dominance. Compared to these regimes, simple clearcutting is characterized by the highest values of redundancy but low values of functional diversity, while coppice with standards
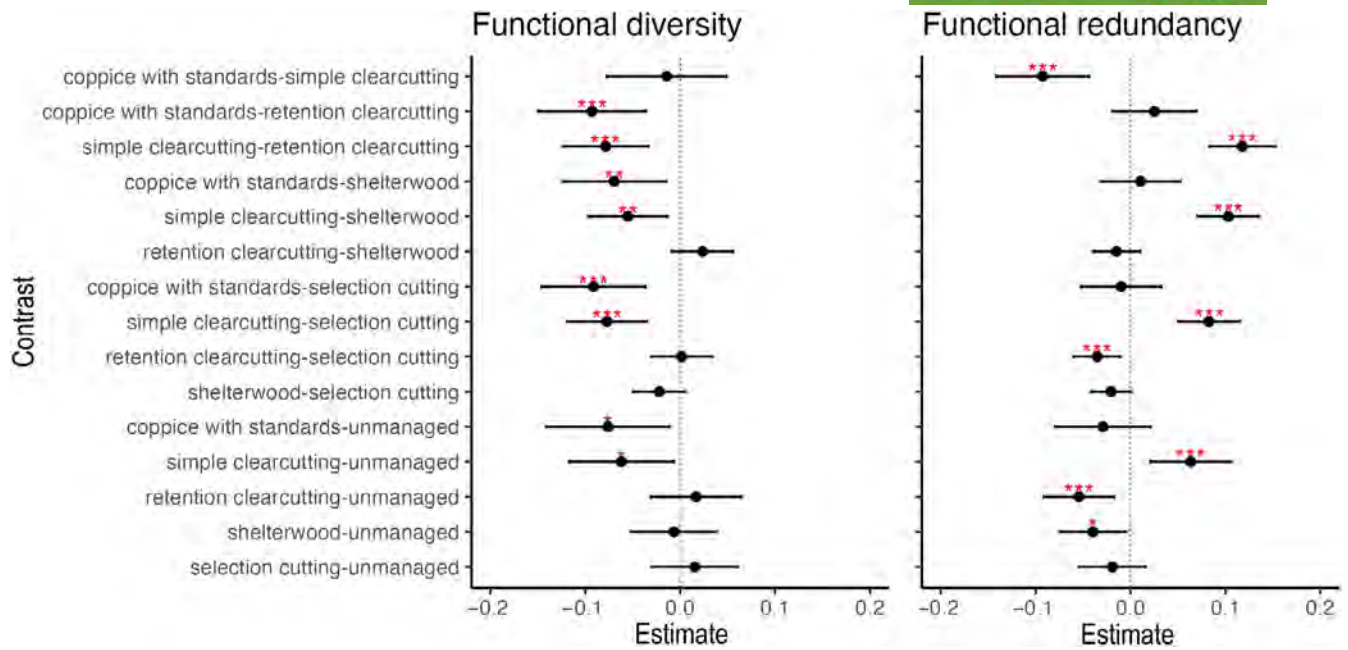
FIGURE 4 Multi-comparison (Tukey's test) of functional diversity and redundancy according to silvicultural regimes. Asterisks indicated significant differences among treatments. *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$. Values on the left of the vertical dotted line indicate that the left-hand term of the contrast has a lower mean value than the right-hand term and vice versa for the values on the right of the vertical dotted line. For example, simple clearcutting has significantly lower mean functional diversity, and significantly higher mean functional redundancy, compared to selection cutting ($p < 0.001$).

have low values of functional diversity and the highest degree of dominance.

4 | DISCUSSION

4.1 | Silviculture shapes understory functional diversity and redundancy

We demonstrated that silviculture has a relevant impact on the functional structure of understory vegetation in European forests. High 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. Low harvesting intensity silvicultural regimes, that is, shelterwood and selection cutting, maintained understory functional diversity and redundancy at levels comparable to unmanaged forests. On the one hand, the periodic thinning performed for the shelterwood regime causes a temporary opening of the canopy cover, thus enabling seed regeneration (Cutini et al., 2015) while promoting understory plant diversity through the gradual changes in light intensity, conversely to what happens in more intensive silvicultural regimes (Dormann et al., 2020; Helbach et al., 2022). On the other hand, selection cutting sustains heterogeneous light conditions in the understory (Helbach et al., 2022), which maintains a functionally diverse understory community (Burton et al., 2014; Donoso et al., 2020; Monge-González et al., 2021) with

a high recurrence of traits (high redundancy) resulting in highly resilient understory communities (Messier et al., 2019).

Soil conditions did not affect functional diversity and redundancy, thus we confirmed that forest plant diversity is mainly driven by stand complexity and, in turn, by light heterogeneity rather than by soil attributes (Helbach et al., 2022). However, it should be noted that to cope with the broad geographical scope of our study, we considered broad-scale soil attributes, which may be less relevant than fine-scale soil conditions in explaining plant diversity at the plot level (Chelli et al., 2024; Gautam et al., 2016). It is likely that part of the variability due to different soil conditions was included in the regional variable 'site' that we used as a random effect, as suggested by the low marginal R^2. Climate influenced understorey vegetation functional diversity and redundancy likely by modifying understory microclimate (e.g., soil temperature and humidity) (Weigel et al., 2019). Especially, temperature has a positive influence on functional diversity, likely due to greater seasonal differences that occur in the areas with higher annual temperature and promote the co-occurrence of functionally different species (Gallagher et al., 2013; Vanneste et al., 2019).

4.2 | Silvicultural regime influences mean community traits

The effects of different silvicultural regimes on CWM traits related to resource acquisition are mainly determined by light and water availability. The general trend of reducing SLA in actively managed
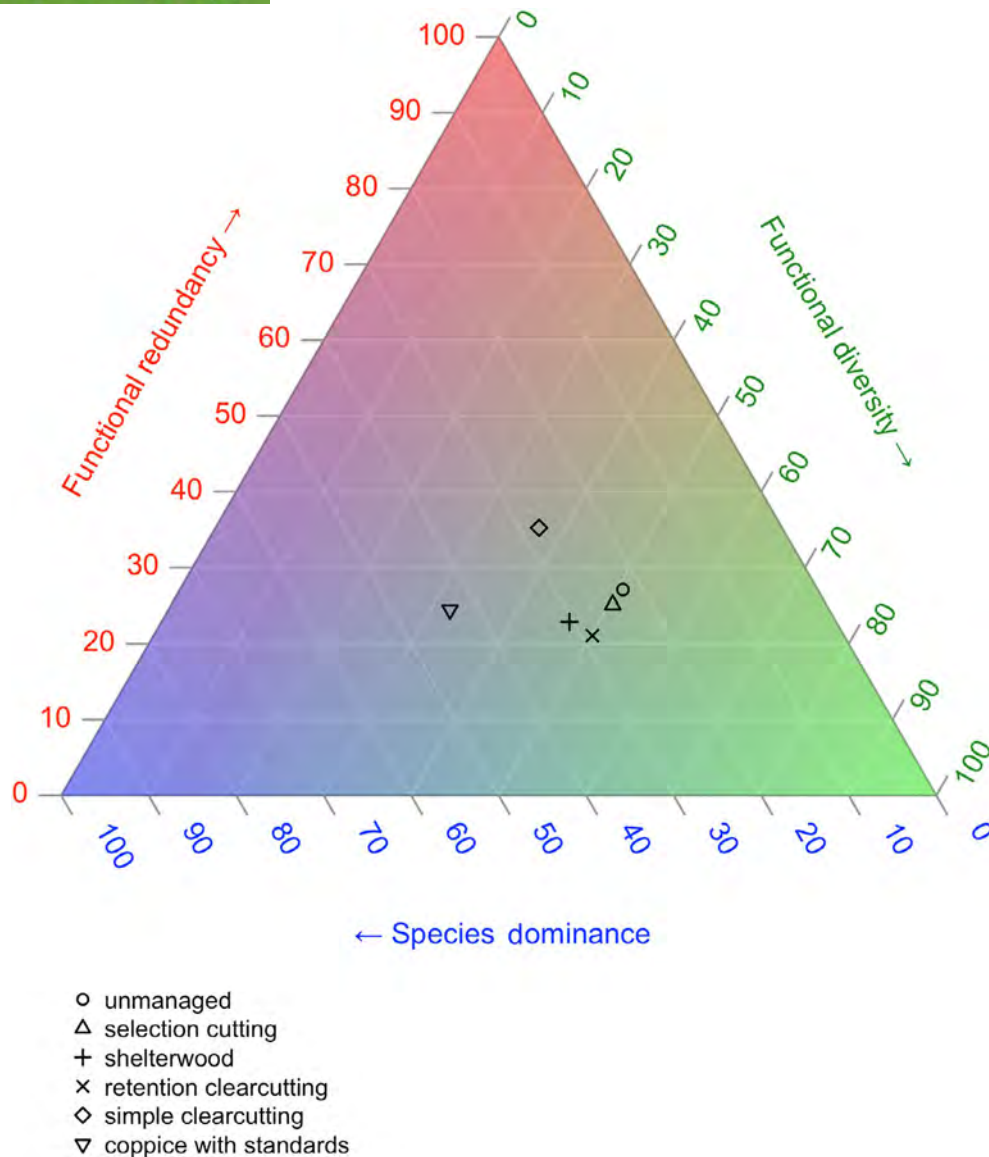
FIGURE 5 Ternary diagram of functional diversity (Q; Equation 1), functional redundancy (Equation 2) and species dominance across different silvicultural regimes. The point corresponds to the median value of the diversity attributes, calculated for each silvicultural regime.

forests was attributed to canopy opening, which may alter soil moisture conditions (Horváth et al., 2023), and—through reduced water availability—may likely influence the plant strategies to cope with water stress. Lower SLA is often associated with plants adapted to drier conditions, as they tend to have thicker, more durable leaves that reduce water loss through transpiration. The outcome is supported by the observed positive association between higher SLA and climate heterogeneity (temperature range and precipitation seasonality). Conversely, coppicing leads to non-significant changes in SLA compared with unmanaged forests, which can be the result of increasing light availability, which may modify resource acquisition strategies (Freschet et al., 2013) supporting several fast-growing pioneer species with high SLA (Kermavnar et al., 2019).

Environmental conditions drive the exchange in the soil–plant-atmosphere continuum and plant functional traits are known to follow relatively predictable patterns across large environmental and species ranges (Alonso-Forn et al., 2020). In this view, it is not surprising that SLA is influenced by soil and climate conditions, since it is related to root growth suitability and soil permeability (Keller et al., 2021), supporting more diversified strategies (Schellenberger Costa et al., 2017). Temperature range increased SLA suggesting that high variability in this factor widens the range of acquisition strategies to cope with stressors (Kramp et al., 2022). Height increases with available water content since it can be related to high diversity in the root system, which in turn facilitates the uptake of water from different soil depths (Fusaro et al., 2015). SM responded to environmental variables differently from resource acquisition traits. Temperature range was negatively related to SM since drought reduces the niche complementarity, which is also affected by soil structure (O'Keefe et al., 2019).

4.3 | Silvicultural regime influences forest diversity composition

In unmanaged forests, the median value of functional diversity occurred at relatively high values of functional redundancy, with relatively similar results for selection forests, while for similar functional diversity values, both shelterwood and retention clearcutting regimes showed a lower functional redundancy and a higher species dominance. Unmanaged forests are often defined by their high degree of structural heterogeneity, that is, denser, more stratified canopy structure, with higher quantities of standing and lying deadwood (Paillet et al., 2015; Wirth et al., 2009). This structural complexity creates heterogeneous living conditions for plants, for instance in terms of light intensity in temperate forests, which were demonstrated to allow for the coexistence of a high number of redundant species across highly different ecological strategies (Bartels & Chen, 2010; Helbach et al., 2022), that is, the niche differentiation diversifies resource-use or requirements and decreases competitive exclusion (Blonder, 2018; Kraft & Ackerly, 2014). Communities with high functional diversity supported by redundant species are likely to be resilient to a wide spectrum of stressors and disturbances (Messier et al., 2019). By contrast, in actively managed forests, even when functional diversity values are comparable to those of unmanaged forests, we found lower values of functional redundancy and higher values of species dominance than in unmanaged forests, meaning that management may maintain a relatively high functional diversity but not in combination with a high functional redundancy and species evenness (Figure 4). Silvicultural regimes with higher harvesting intensity, as simple clearcutting, showed lower levels of functional diversity balanced by higher functional redundancy. Coppice with standards showed a high degree of dominance at the expense of the two functional components.

4.4 | Policy implications

Our results give useful indications on how to maintain the functional structure of understory communities in the face of environmental changes and potential disturbances (Mina et al., 2022). High harvesting intensity silvicultural regimes decrease functional diversity and increase functional redundancy, thereby influencing the relationship between these two facets of understory functional structure and jeopardizing forest's ability to retain ecosystem functioning. Given the complexity of such interactions, our results do not point to a 'universally best' silvicultural regime. Intensive management options have a positive influence on functional redundancy at the expense of functional diversity; therefore, the former may be considered for socio-economic targets limitedly to areas where dramatic environmental changes are not expected. Low harvesting intensity regimes maintained functional diversity and redundancy values comparable to unmanaged conditions, simultaneously allowing to exploit wood resources. Our results also supported the importance of maintaining, promoting and monitoring

unmanaged forests to assess their ecological properties and to compare and strengthen active silvicultural practices. Taken together, these considerations support the need to effectively plan the spatial and temporal patterns of the silvicultural regimes at the landscape level to achieve the multiple needs and goods that are demanded by forest, as hypothesized in the triad paradigm (Betts et al., 2021; Himes et al., 2022).

4.5 | Limitations and opportunities

We used a simple, yet effective classification of silvicultural regimes, to cope with a large-scale, European-wide comparison. However, within each silvicultural regime, thinning type, harvesting intensity, rotation, and period may vary widely among regions (Trentanovi et al., 2023). For instance, the thinning period is crucial for supporting vegetation recovery under gradually decreasing canopy density depending on the stand features (Aszalós et al., 2022). The same consideration holds for unmanaged forests, as their ecological features depend on their management history, which is usually extremely complex in European forests (Paillet et al., 2010).

In this study, we were unable to consider the influence of historical disturbance regimes on 'unmanaged' forests, even though some unmanaged forests considered in this study may have not reached the full diversity potential (in terms of stand structure, light heterogeneity and microclimate) as in old-growth forests (Schall et al., 2021) but give results similar to forests managed at low harvesting intensity.

Combining silvicultural regimes with quantitative data on recent and historical management (e.g. cutting frequency, biomass harvested, gaps dimension, time from the last intervention) and including forests in the old-growth phase would contribute to refining the analysis and evaluating the mechanistic links between biodiversity and the temporal lag from the last disturbance or residual canopy structure.

AUTHOR CONTRIBUTIONS
Francesco Chianucci, Sabina Burrascano and Francesca Napoleone conceived the ideas and designed methodology; Kris Vandekerkhove, Pallieter De Smedt, Luc Lens, Lionel Hertzog, Kris Verheyen, Jenyk Hofmeister, Jan Hošek, Radim Matula, Inken Doerfler, Jorg Müller, Wolfgang W. Weisser, Jan Helbach, Peter Schall, Markus Fischer, Jacob Heilmann-Clausen, Rasmus Riis-Hansen, Irina Goldberg, Erik Aude, Sebastian Kepfer-Rojas, Inger Kappel Schmidt, Torben Riis Nielsen, Anders Mårell, Yann Dumas, Philippe Janssen, Yoan Paillet, Frederic Archaux, Fotios Xystrakis, Flóra Tinya, Péter Ódor, Réka Aszalós; János Bölöni, Andrea Cutini, Simonetta Bagella, Tommaso Sitzia, Gediminas Brazaitis, Vitas Marozas, Mariana Ujházyová, Karol Ujházy, František Máliš, Björn Nordén and Sabina Burrascano collected the data; Francesco Chianucci and Carlotta Ferrara analysed the data; Francesco Chianucci, Sabina Burrascano, Francesca Napoleone, Carlo Ricotta, Carlotta Ferrara, Lina Fusaro, Lorenzo Balducci, Giovanni Trentanovi, Owen Bradley, Bence Kovács, Marco Mina and Bruno E. L. Cerabolini led the writing of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could influence the study.

DATA AVAILABILITY STATEMENT

Data and associated code are available from Zenodo: https://doi.org/10.5281/zenodo.11454277 (Chianucci et al., 2024).

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SUPPORTING INFORMATION

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

Figure S1. Heatmap of numerosity of sampling units according to forest category.

Figure S2. Distribution of sampling units in each management category according to the time from the last intervention (number of years).

Table S1. Forest category description (Barbati et al., 2014).