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Multiple drivers of functional diversity in temperate forest understories: Climate, soil, and forest structure effects

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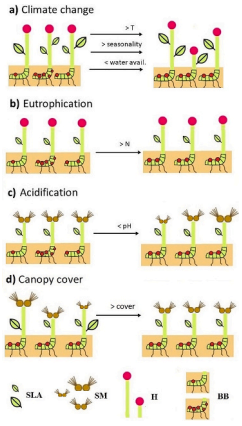
HIGHLIGHTS

- Functional diversity of forest understory plants is susceptible to global changes.
- Forest subcanopy temperature helps to unravel the effect of climate change.
- Climate change reduces the diversity of plant strategies in forest understory.
- Canopy closure affects the diversity of leaf-height-seed traits.
- Soil acidification and eutrophication impact the diversity of regeneration strategies.

GRAPHICAL ABSTRACT



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ABSTRACT

In macroecology, shifting from coarse- to local-scale explanatory factors is crucial for understanding how global change impacts functional diversity (FD). Plants possess diverse traits allowing them to differentially respond across a spectrum of environmental conditions. We aim to assess how macro- to microclimate, stand-scale

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measured soil properties, forest structure, and management type, influence forest understorey FD at the macroecological scale.

Our study covers Italian forests, using thirteen predictors categorized into climate, soil, forest structure, and management. We analyzed five traits (i.e., specific leaf area, plant size, seed mass, belowground bud bank size, and clonal lateral spread) capturing independent functional dimensions to calculate the standardized effect size of functional diversity (SES-FD) for all traits (multi-trait) and for single traits. Multiple regression models were applied to assess the effect of predictors on SES-FD.

We revealed that climate, soil, and forest structure significantly drive SES-FD of specific leaf area, plant size, seed mass, and bud bank. Forest management had a limited effect. However, differences emerged between herbaceous and woody growth forms of the understorey layer, with herbaceous species mainly responding to climate and soil features, while woody species were mainly affected by forest structure.

Future warmer and more seasonal climate could reduce the diversity of resource economics, plant size, and persistence strategies of the forest understorey. Soil eutrophication and acidification may impact the diversity of regeneration strategies; canopy closure affects the diversity of above- and belowground traits, with a larger effect on woody species. Multifunctional approaches are vital to disentangle the effect of global changes on functional diversity since independent functional specialization axes are modulated by different drivers.

1. Introduction

Temperate forests cover one fourth of Europe and play a crucial role in providing natural and cultural ecosystem services, supporting biodiversity, having recreational value, and sequestering carbon (Mucina et al., 2023). However, the longevity and integrity of these ecosystems face uncertainties due to growing pressure from climate change (Govaert et al., 2021a), pollution (e.g., nitrogen deposition; Dirnböck et al., 2014), and evolving land use (Happonen et al., 2021). Though trees, as primary biomass captors and major carbon sinks, are fundamental to forest ecosystems, our focus narrows to the understorey layer—a component hosting the majority of vascular plant diversity in temperate forests (Gilliam, 2007). The understorey layer plays a pivotal role in providing essential ecosystem services such as influencing litter quality, participating in nutrient cycling processes, and affecting tree regeneration (Landuyt et al., 2019).

The structure and diversity of the understorey layer are shaped by specific abiotic conditions (Förster et al., 2017). Understanding how these conditions affect the understorey remains a fundamental and open issue in ecology (Naqinezhad et al., 2022). Growing under the tree canopy exposes this layer to a unique microclimate (Zellweger et al., 2020; De Lombaerde et al., 2022). However, studies focusing on the climate—understorey relationships often rely on macroclimate data like WorldClim (Fick and Hijmans, 2017) or Chelsa (Karger et al., 2017), which overlook the ~2 degrees difference in temperature provided by canopy buffering (Haesen et al., 2021). Similarly, investigations into how changing soil properties, such as pH, nutrients, and water holding capacity affect understorey structure and diversity often rely on gridded soil data (Poggio et al., 2021) that might not represent the forest patch-scale heterogeneity (Simpson et al., 2016).

Human activities, such as specific management practices, directly alter forest structural characteristics (e.g., canopy cover), leading to changes in light and microclimate conditions (Campetella et al., 2011; De Pauw et al., 2022; Bricca et al., 2023). These alterations, in turn, impact the assemblages of understorey species (Decocq et al., 2004; Padullés Cubino et al., 2021; Happonen et al., 2021). However, the connection between management type and forest structure attributes—such as basal area, canopy cover, or deadwood volume—reveals varying degrees of correlation or, in some instances, no association at the macroecological scale (Ampoorter et al., 2016; Depauw et al., 2021). This nuanced relationship among direct human impacts (i.e., forest management) with changes in the structural attributes and subcanopy environmental conditions calls for a more in-depth exploration to unravel the dynamics shaping understorey species assemblages.

The understorey layer of temperate forests is composed by both herbaceous and woody species. Despite coexisting within the same communities, these distinct growth forms represent key ecological strategies in relation to their environment and may differ in their proportional representation (Díaz et al., 2016; Taylor et al., 2023). However, many studies focusing on the understorey layer considered herbaceous species only (e.g., De Pauw et al., 2022; Govaert et al., 2024), thus ignoring potentially consistent or counteracting patterns of distinct growth forms in shaping the understorey—environment relationship.

Among the multiple facets of diversity, functional diversity (FD) has received considerable attention in ecology due to its ability to provide insights into assembly rules (Ricotta and Moretti, 2011). Environmental filtering influences FD by favoring certain species with specific functional trait values under different biotic and abiotic conditions (de Bello et al., 2012; Bricca et al., 2022). This process tends to reduce FD, leading to functional convergence and the increased prevalence of functionally similar species. Conversely, environmental factors can promote the presence of functionally diverse species assemblages (i.e., functional divergence) through environmental heterogeneity, such as a patchy distribution of nutrients at the understorey level that may be influenced by forest structure or disturbance (de Bello et al., 2013; Chelli et al., 2021).

While many functional traits exist, their intercorrelation imposes a manageable upper limit on plant functional diversity (Laughlin, 2014; Kattge et al., 2020). Research has aimed to reduce trait dimensionality while maximizing ecologically relevant functional responses (e.g., Díaz et al., 2016; Carmona et al., 2021). Westoby (1998)'s Leaf-Height-Seed (LHS) traits scheme, incorporating specific leaf area (resource economics), plant height (competition), and seed mass (dispersal ability), is widely used (e.g., Vanneste et al., 2019). However, traits related to plant persistence, vegetative sprouting, and space occupancy are comparatively less explored, especially in forests (i.e., clonal and bud bank traits; Klimešová et al., 2018; Yannelli et al., 2022; Molina-Venegas et al., 2022). Filling this gap can enhance our understanding of how a plant's capacity to perform diverse functions influences its resilience (persistence, survival) amid shifting environmental conditions and human-induced alterations.

Our paper aims to test the effect of climate, soil, forest structure, and management type on the functional diversity of forest understorey vascular plants across the temperate forests of Italy. To the scope, we used the ICP Forests (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests) Level I dataset, which provides understorey plant surveys with in-situ measurements of soil and forest structural parameters, as well as information on management type. These data were combined with modeled macro- and microclimate data (i.e., subcanopy; Haesen et al., 2021). Understanding how environmental changes along long spatial gradients shape communities, aids in predicting their responses to future conditions (Pickett, 1989; Chelli et al., 2023 and references therein). We asked the following three questions with related hypotheses:

Q1. How do climate, soil, forest structure, and management type affect the understorey FD in managed forests at the macroecological scale? We hypothesize a significant effect of all the predictors, with a central role played by climate and soil which are considered the main drivers of plant functioning at the macroecological scale (Simpson et al., 2016; Chelli et al., 2019a, 2019b).

Q2. Do different management types (i.e., coppice and high forest) determine a different response of the understorey FD to climate, soil, and forest structure? Due to the study area's long-lasting (i.e., centuries) management practices, we expect significant interactions between management type and the other predictors.

Q3. Is there a consistent response among the overall FD (i.e., all traits) and the FD of single traits mirroring different functions? Given that independent plant functions respond differently to environmental factors (Bruelheide et al., 2018), we hypothesize that plant functional traits are modulated by different predictors, leading to different responses of single and multiple trait FD.

Q4. Do the growth forms (i.e., herbaceous and woody species) of the understorey vegetation differ in their response? Considering that growth forms represent different overall plant strategies that respond differently to environmental factors (Taylor et al., 2023), we hypothesize that the responses of single and multiple trait FD differ between growth forms.

2. Materials and methods

2.1. Study area and sampling design

We chose Italy as our study area because of its diverse climate and evolutionary history, resulting in three biogeographical regions (i.e., Alpine, Continental, Mediterranean; Cervellini et al., 2020), which has led to the development of a flora with a high number of plant species (Cai et al., 2023). Italy has a relatively high forest cover (37 % of the country; INFC, 2015), mainly belonging to different forest types of the temperate biome (sensu Mucina, 2019; i.e., temperate deciduous broadleaf forests, temperate evergreen needleleaf forests, and warm-temperate evergreen broadleaf forests), with a pluri-centennial management history (Piussi, 2006). The data used for the present investigation were collected in the ICP Forests Level I framework (ICP Forests, 2016). It is based on a 16 km × 16 km grid overlaid on the entire country, with a sampling site located in a forest patch larger than 1 ha selected at each node of the grid (Chiarucci et al., 2019). This design reduces the spatial dependence of the sampling (Loiola et al., 2018) and enables a representative picture of Italian forests (Alessi et al., 2023).

We focused on those forests with designated management regimes from the original 201 surveyed sites in Italy for understorey vegetation. Specifically, we concentrated on two dominant management types, high forest, and coppice, constituting 42 % of the Italian forest cover (INFC, 2015). We also excluded non-natural forest stands, such as plantations, resulting in a selection of 155 sites (86 sites managed as high forests and 69 as coppice forests; Fig. S1).

2.2. Data collection and collation

We prepared two data sets: the species matrix and the predictor matrix. The species matrix included the occurrence and cover of understorey species, following the ICP Forests sampling protocol for plant diversity (Canullo et al., 2011). Trained botanists conducted the assessments during the BioSoil biodiversity project (WGFB, 2011), compiling a species list and generating cover estimations of species within 400 m^2 plots. For our analyses, we exclusively considered vascular plant species from the understorey layer, including herbaceous and woody plants that were ≤ 5 m in height (Chelli et al., 2019a). Furthermore, tree seedlings and saplings were excluded from the analyses, since their functional traits available in literature refer to fully grown plants only (e.g., plant height).

Our predictor matrix was composed of four components: continuous climatic variables, continuous soil properties, categorical forest management, and continuous and categorical forest structural attributes (see Table 1). We collected mean annual precipitation (MAP), precipitation seasonality (PS), and mean monthly temperature from WorldClim V2's (Fick and Hijmans, 2017) averaged between 1970 and 2000. To download the WorldClim data, we used the *ce_download* function from 'climenv' package (Tsakalos et al., 2023). Then, we corrected the WorldClim temperature data by subtracting the temperature difference (canopy buffering) estimated by Haesen et al. (2021) across continental Europe. We used two variables derived from these climatic layers: subcanopy mean annual temperature (MAT) and subcanopy temperature seasonality (TS), which we calculated as the seasonal variance of subcanopy temperature (see Bede-Fazekas and Somodi, 2020). This data's spatial resolution is 30 arc *sec*, which translates to approximately 1 km grid at the equator. We chose these climate predictors because prior research has repeatedly shown their influence on various plant traits and functions (e.g., Ye et al., 2014; Chelli et al., 2019a, 2019b). We performed all calculations using the *diff* function from the 'terra' R package (Hijmans, 2023).

As part of our predictor matrix, the ICP Forests network collected soil samples at each study site to assess four soil properties (for details and methods, see Andreetta et al., 2013, 2016). Total N and nitrogen to carbon ratio (N/C) indicate soil nutrient status and nitrogen availability, which are crucial for plant growth (Rowe et al., 2011). Soil pH impacts the availability of essential nutrients in the soil required for plant growth. Effective soil volume provides insights into the amount of water available for plants (Andreetta et al., 2016).

Lastly, for each plot, we assessed the type of management and three stand structural variables for our predictor matrix. Management types consisted of high forest and coppice. As structural variables we used total deadwood, including standing and fallen dead trees, coarse woody debris, stumps, and snags (Puletti et al., 2017); basal area, related to stand productivity and age; canopy cover, assessed considering the shade casting ability of trees and their relative cover (see Verheyen et al., 2012).

2.3. Selection of plant functional traits and calculation of functional diversity

We selected a set of five traits from plant organs capturing different functions (Westoby, 1998; Díaz et al., 2016; Ottaviani et al., 2017; Klimešová et al., 2018): specific leaf area (SLA), a proxy for plant growth rate and resource economics, and a good surrogate for the ability to exploit light; plant height (H), pertinent to competitive ability and linked to the plant size spectrum; seed mass (SM), related to seedling establishment, the ability to persist in soil and seed dispersal; belowground bud bank size (BB), related to sprouting ability; clonal lateral spread (LS), related to space occupancy and resource exploration. These traits also represent independent axes of functional strategies adopted by forest understorey species (Burton et al., 2020; Padullés Cubino et al., 2021; see also Fig. S2). Trait values were collected from available literature and databases (Kleyer et al., 2008; Campetella et al., 2011; Klimešová et al., 2017; Chelli et al., 2019a, 2019b). Overall, our species × trait matrix was 75 % complete for SLA, 92 % for SM, 100 % for H, and 65 % for BB and LS.

To ensure normally distributed trait values, we $\log_{10}$ transformed H, SLA, and SM values, and square-root transformed BB and LS (Májeková et al., 2016). Additionally, we assessed the amount of trait information for each plot by merging the species matrix with the traits matrix and retained only those plots where the sum of the relative cover of species with trait values exceeded 70 % of the total species cover, aiming for

Table 1
Description of climatic, soil, forest structure, and management factors.

Group	Variable	Unit	Range	Notes
Climate	Subcanopy mean annual temperature (MAT)	°C	−0.3–17.15	Source: Fick and Hijmans (2017), WorldClim V2 and Haesen et al. (2021)
	Subcanopy temperature seasonality (TS)	SD*100	485–680	Source: Fick and Hijmans (2017), WorldClim V2 and Haesen et al. (2021)
	Annual precipitation (MAP)	mm	300–2013	Source: Fick and Hijmans (2017), WorldClim V2
	Precipitation Seasonality (PS)	CV (%)	0.14–0.64	Source: Fick and Hijmans (2017), WorldClim V2
Soil	Total N	g/kg	1.2–16.1	Source: Andreetta et al. (2013)
	N/C	Adimensional	0.04–0.17	Source: Andreetta et al. (2016)
	Soil pH	–log(H+)	4.0–8.6	Source: Andreetta et al. (2016)
	Soil effective volume	cm^3	4.5–170	Proxy of water holding capacity. Source: Andreetta et al. (2016)
Forest structure	Total deadwood	$m^3/400\ m^2$	0–14.6	Standing and fallen dead trees + coarse woody debris + stumps + snags (Puletti et al., 2017)
	Basal area	m^2/ha	2.8–66.1	Related to total biomass and proxy of stand age
	Canopy cover	Adimensional	1–5	Shade casting ability of trees and thus, light availability at the understorey layer (Verheyen et al., 2012)
Forest management	Management type	Classes	HF or C	High forest; coppice

unbiased functional indices (Májeková et al., 2016). This filtering based on information content within the plots further reduced their number from 155 to 145 (82 managed as high forest and 63 as coppice forest), resulting in approximately 74,000 observations for 1024 species.

We selected Rao's Quadratic Entropy to measure functional diversity (FD; de Bello et al., 2010). Rao's Quadratic Entropy expresses the expected functional dissimilarity between two individuals of a given assemblage selected at random with replacement:

$$FD = \sum_{i,j}^{S} d_{ij} p_i p_j \quad (1)$$

where S is the number of species, d_{ij} is the functional distance between the i-th and j-th species, p_i and p_j are the relative cover of i-th or j-th species. We expressed the functional distance between species (d_{ij}) with the Gower distance because it handles missing trait values and multiple traits together. Gower distance standardized the trait values from 0 when two species share the same trait (or combination of traits) values and 1 when two species have opposite trait (or combination of traits) values (Pavoine et al., 2009). We calculated i) multiple traits functional diversity, namely, FD_{Multi}, which included all the traits, and ii) single trait functional diversity (FD_H, FD_{SLA}, FD_{SM}, FD_{BB}, FD_{LS}). We computed all the functional diversity indexes using the R function *Rao* (de Bello et al., 2010). Then, to remove the influence of species composition from the indexes and to detect patterns of functional convergence/divergence, we calculated the standardized effect size (SES; Botta-Dukát and Czúcz, 2016) for each index as follows:

$$SES - FD = \frac{(ObservedFD - MeanExpectedFD)}{StandardDeviationExpectedFD} \quad (2)$$

where SES-FD values <0 indicate observed FD being lower than FD expected by chance (convergence) and vice versa for SES values >0 (divergence), while values close to zero mean random process operating. Expected FD values were created by shuffling 999 times trait values across all species occurring in the database ("between-plots randomization", Botta-Dukát and Czúcz, 2016). We applied the above-mentioned approach for the overall understorey layer as well as for the two growth forms separately, i.e., herbaceous and woody species.

2.4. Data analysis

Preliminarily, quantitative predictors were log-transformed to improve their normal distribution when needed. Then, we assessed the degree of correlation among the selected quantitative predictors using the Pearson coefficient. Since they showed no strong correlation pattern ($-0.5 < r < 0.5$; Fig. S3), they were all included in the following model.

We investigated the effect of the predictors on the SES-FD (Q1, Q3) by fitting six separate multiple regression models, one for each SES-FD (FD_{Multi}, FD_H, FD_{SLA}, FD_{SM}, FD_{BB}, FD_{LS}). We built a full model for each index, including the abovementioned predictors (Table 1). Moreover, to determine whether the predictors differently affected FD under different forest management regimes (i.e., high forest and coppice), we introduced forest management as an interaction term (Q2). We decided to account for forest management in the models to accommodate that SES-FD can differ because of management practices or other unmeasured variables (Bricca et al., 2023). Thus, we did not use mixed models with management type as a random effect because we were interested in examining the direct effect of management type (Harrison et al., 2018).

Then, we selected the simplified model using the Akaike information criterion (AIC) based model selection procedure. For each simplified model, we checked the presence of multicollinearity among the selected predictors by calculating each predictor's variance inflation factor (VIF). In the case of multicollinearity, i.e., VIF values >3, we removed the predictor showing the higher VIF value, and we re-run the simplified model until all the predictors were independent (VIF values <3) (Zuur et al., 2010). Lastly, we assessed the predictors' significance for each final model and checked model assumptions (normality and homoscedasticity) by visually inspecting the residual pattern (Zuur et al., 2010; Harrison et al., 2018). We determined that our models were free from spatial autocorrelation using mantel tests of the residual distance matrix and geographic coordinates' distance matrix (Table S1). We built multiple regression models using the *lm* function in the 'stat' package and performed model selection using the *dredge* function in the 'MuMIn' package (Bartoń, 2023). We assessed multicollinearity using the *vif* function in the 'car' package (Fox and Weisberg, 2019) and conducted the Mantel test with the *mantel* function in the 'vegan' package (Oksanen et al., 2022). We run all the analyses in R environment (R Core Team, 2023) for the overall understorey layer as well as for the two growth forms separately, i.e., herbaceous and woody species.

3. Results

Considering the overall understorey layer, four out of six models were significant (i.e., plant height, specific leaf area, seed mass, belowground bud bank size). Plant height ($SES\text{-}FD_H$; Fig. 1a, b, c) was negatively affected by canopy cover and effective soil volume and positively affected by subcanopy mean annual temperature with a variance explained by the model of 17 % ($P < 0.01$; Table 2). Moreover, we also found a significant effect of management types, with high forest having higher plant height diversity compared to coppice management (Fig. 1d). Specific leaf area ($SES\text{-}FD_{SLA}$; Fig. 1a, e, f) was affected by

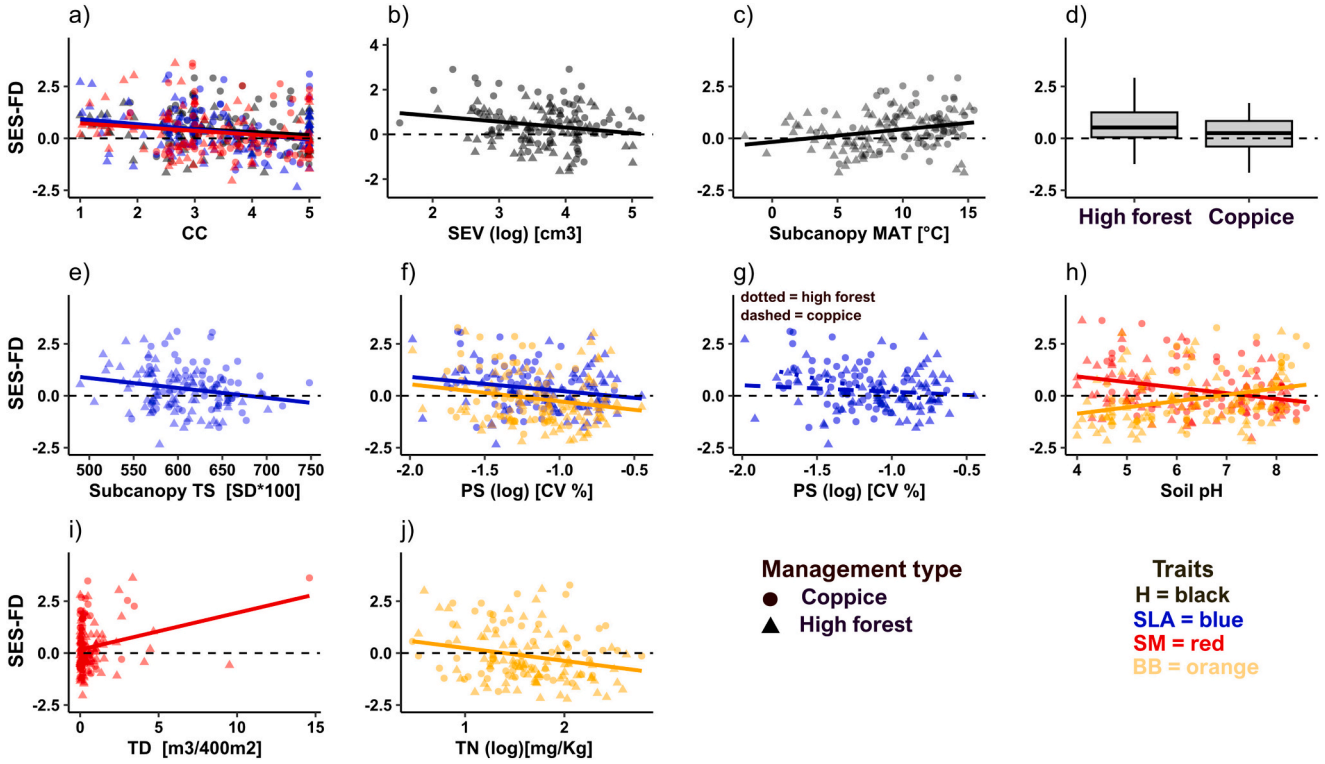

Fig. 1. Relationship between predictors and the standardized effect size of functional diversity (SES-FD) of the overall understorey layer for the selected traits (H, plant height; SLA, specific leaf area; SM, seed mass; BB, belowground bud bank size) with **a)** canopy cover (CC); **b)** soil effective volume (SEV); **c)** subcanopy mean annual temperature (MAT); **d)** management type (high forest vs. coppice) **e)** subcanopy temperature seasonality (TS); **f)** precipitation seasonality (PS); **g)** precipitation seasonality interacting with management type; **h)** soil pH; **i)** total deadwood (TD); **j)** total nitrogen (TN).

climate, soil, and forest structure, with variance explained by the simplified model of 24 % ($P < 0.001$; Table 2). In this case, our model detected a negative effect of subcanopy temperature seasonality, precipitation seasonality, and canopy cover. Also, we found a significant interaction of precipitation seasonality with management types (Fig. 1g). Soil features and forest structure modulated seed mass (SES-FD_{SM}; Fig. 1a, h, i), and the final model, which explained 18 % of the total variance, was statistically significant ($P < 0.001$; Table 2). Specifically, SES-FD_{SM} decreased with higher soil pH and denser canopy cover, while total deadwood had a positive effect. Belowground bud bank size (SES-FD_{BB}; Fig. 1h, j) was affected by soil features and climate, with a total explained variance of 17 % ($P < 0.001$; Table 2). Here, we detected a positive effect of soil pH and a negative effect of total nitrogen and precipitation seasonality. The models for multiple traits and for lateral spread were not significant (Table 2).

Considering single growth forms (i.e., herbaceous and woody species), there was a reduction of the explained variance (7–10 % for herbaceous species, Table S2, Fig. S4; 6–21 % for woody species, Table S3, Fig. S5). In detail, when focusing on herbaceous species, forest structural variables (i.e., canopy cover and deadwood) were not relevant, while soil pH, as well as climatic variables related to temperature and precipitation mean and variability, maintained their importance (Table S2; Fig. S4). Regarding woody species, forest structure (mostly canopy cover) and soil features (soil pH and nutrient availability) were more relevant than climatic variables (Table S3; Fig. S5).

4. Discussion

We examined how climate, soil, forest structure, and type of management impact the functional diversity of the understorey layer of Italian forests. Our macroecological findings indicate that climate, soil, and forest structure significantly affect the functional diversity of four traits used: specific leaf area, plant height, seed mass, and belowground bud bank (Q1). While specific leaf area, plant height, and seed mass are associated with the recognized global spectrum of plant form and function, representing the leaf economics and plant size axes (Díaz et al., 2016), belowground bud bank is part of an additional and overlooked independent functional specialization axis that reflects a species' capacity to tolerate and resprout after disturbance (Chelli et al., 2024). Our findings suggest that changes in climatic conditions, soil features, and forest structure (canopy cover and deadwood) not only impact mean trait values of the understorey (as found by Govaert et al., 2024), but also the way in which species assemble into a community, by acting on independent plant functions. The management type directly affected the functional diversity of plant height, while it interacted with precipitation seasonality in shaping patterns of specific leaf area (Q2). Additionally, we observed that the functional diversity of multiple traits did not respond to the studied predictors, probably because the functional diversity of individual traits exhibited distinct – and often contrasting – responses (Q3). However, differences emerged when focusing on single growth forms of the understorey (i.e., herbaceous and woody species), suggesting that the understorey layer's functional response to environmental and anthropogenic factors may arise from distinct behaviors of different plant growth forms (Q4).

4.1. Climate change affects the diversity of leaf economics, plant size, and persistence strategies

Climate significantly influences the functional diversity of three traits – specific leaf area, plant height, and belowground bud bank – among the five traits studied. This insight is crucial for predicting how these traits might respond to future climate challenges (space-for-time substitution; Wieczynski et al., 2019). Giorgi and Lionello (2008) project that Southern Europe will undergo increased temperatures and more precipitation variability. Surprisingly, subcanopy microclimate, while historically stable, is showing a mean temperature increase of 0.40 °C

Table 2
Detailed information on predictors of the simplified linear model between standardized effect size of functional diversity (SES-FD) for multiple-traits (Multiple, all traits) and for single traits (H, vegetative height; SLA, specific leaf area; SM, seed mass; BB, belowground bud bank size; LS, lateral spread) with the management type, forest structure (total deadwood, basal area, canopy cover), soil (soil effective volume, total nitrogen, soil pH, N/C ratio, and pH), and climate (sub MAT, subcanopy mean annual temperatures; sub TS, subcanopy temperature seasonality; MAP, mean annual precipitation; PS, precipitation seasonality) for the overall understorey layer (i.e., herbaceous and woody species). Interactions of climate, forest structure, and soil with management type are shown. We report the coefficient values of the predictors and the Adjusted R^2 values (%) of each final model. Significant predictors and models ($p < 0.05$) are reported in bold.

		Forest structure & management				Soil				Climate				Interactions			
FD	Intercept	Type of manag. (High forest)	Basal area	Deadwood	Canopy cover	Soil effective volume	Total N	N/C	Soil pH	Sub MAT	Sub TS	MAP	PS	Sub MAT: type of manag.	PS: type of manag.	Adj R^2
Multiple	5.11		0.007	0.06	**−0.25**	−0.26		−0.68	−0.14	**0.06**	−0.003	−0.51	**−0.87**	−0.03		8 %
H	2.32	**−0.39**	0.009		**−0.17**	**−0.39**				**0.06**	−0.002		−0.42			**17 %**
SLA	7.72			0.08	**−0.29**			−0.34			**−0.009**	−0.43	**−1.18**		**0.40**	**24 %**
SM	1.18			**0.13**	**−0.21**	−0.22		−0.68	**−0.29**	0.039			−0.37	−0.03		**18 %**
BB	−0.18				−0.11		**−0.66**	−0.78	**0.26**	0.04		−0.51	**−0.76**	0.007		**17 %**
LS	1.31		0.007		−0.06				−0.15				0.11		−0.14	2 %

per decade, and this change is 45 % more variable than macroclimate (Zellweger et al., 2020). Our findings reveal that (a) higher subcanopy temperatures enhance plant height diversity, while (b) greater climatic seasonality, including precipitation- and subcanopy temperature-seasonality, reduce specific leaf area and belowground bud bank diversity. Additionally, precipitation seasonality's impact on specific leaf area diversity varies with forest management, with coppice stands exhibiting more pronounced reductions than high forest management. Probably, the relatively more frequent and intense disturbance which characterize coppice management, as well as the lower temperature buffering capacity, make the plant communities more susceptible to changes in climate seasonality (Scolastri et al., 2017; De Frenne et al., 2021).

Fig. 2. Conceptual figure synthetising the potential functional diversity response (H, plant height; SLA, specific leaf area; SM, seed mass; BB, belowground bud bank size) of forest understorey (including the herbaceous and woody components). **a)** A warmer and more seasonal climate with reduced water availability (water avail.) is expected to generate convergence in SLA and BB, and divergence in H; **b)** eutrophication is expected to generate convergence in BB; **c)** soil acidification is expected to induce convergence in BB and divergence in SM; **d)** higher canopy cover is expected to induce convergence in H, SLA, and SM. Modified from Klimešová et al. (2019) and Ottaviani et al. (2020).

Overall, our findings suggest that the increasing warmth and variability of subcanopy microclimates may drive a gradual convergence in leaf economics and persistence strategies among plants, alongside the emergence of diverse plant size strategies (Fig. 2a). These effects arise from intricate responses of the herbaceous and woody growth forms. However, both natural factors like tree dieback, pests, and extreme weather events, and anthropogenic disturbances affecting canopy cover such as harvesting, could shape the extent of this scenario (Zellweger et al., 2020; De Frenne et al., 2021). In-situ daily measurements of subcanopy microclimatic conditions might help to better understand plant thermal niches, as well as the seasonal effect of canopy cover under different natural and anthropogenic disturbances (Zellweger et al., 2020; Santi et al., 2023).

4.2. Soil governs the diversity of plant size and regeneration strategies through seeds and buds

We observed a negative impact on the functional diversity of understorey plant height due to soil effective volume, a proxy of water holding capacity (Andreetta et al., 2016). This effect, where higher water availability promotes convergent patterns in plant size (Fig. 2a), can be attributed to the process of "weaker competitive exclusion" (de Bello et al., 2013). Essentially, in conditions of abundant resources, strong competitors tend to outcompete functionally distinct, weaker species (de Bello et al., 2013). However, this effect disappears when considering single growth forms, suggesting that this result depends on biotic interactions among growth forms. This interpretation is supported by the presence and high cover of woody species in plots with greater soil volume, for example *Rubus ulmifolius*, which potentially negatively impact herbaceous species.

Total nitrogen and soil pH actively influenced the functional diversity of plant regeneration via seeds and buds. These findings gain importance in light of global changes tied to fossil fuel emissions, fertilizers, and intensive animal farming, leading to increased nitrogen deposition (Fowler et al., 2013; Galloway et al., 2014). Despite emission control measures, many European forest sites exceed critical nitrogen deposition thresholds (Waldner et al., 2014; Cecchini et al., 2021), which has disrupted nitrogen biogeochemical cycles (Steffen et al., 2015). Our study underscores that increased nitrogen deposition may impact the diversity of regeneration strategies, potentially affecting understorey plant sprouting after disturbance (Fig. 2b). This is partially in line with findings of a long-term experiment in which nitrogen addition, in combination with other factors, generated biotic homogenization of the understorey (Govaert et al., 2021b).

Soil pH had contrasting effects on the functional diversity of seed mass and belowground bud bank. The positive relationship between higher soil pH and belowground bud bank diversity aligns with previous research in temperate forest understories (Kermavnar et al., 2021) and other habitats (Vojtkó et al., 2017). The negative link between pH and seed mass diversity, despite being confirmed for the overall understorey layer as well as the herbaceous and woody species, remains less conclusive, yielding inconsistent findings in the literature (e.g., Kermavnar et al., 2021; De Pauw et al., 2021). Human activities have accelerated forest soil acidification due to prolonged exposure to nitrogen and sulfur. While sulfur emissions have declined with control measures (Lajtha and Jones, 2013), European soils have not yet recovered (Johnson et al., 2018), suggesting a delayed response to emission reductions. Our results indicate that prolonged soil pH improvements may foster trade-offs, potentially enhancing diversity in vegetative sprouting via bud banks while species with similar seed dispersal and establishment strategies. Conversely, increased soil acidification could lead to opposite patterns (Fig. 2c).

4.3. Higher canopy cover reduces the diversity of leaf economics, plant size, and seed regeneration strategies

Among the different forest structure predictors, only canopy cover and the deadwood amount influenced the diversity of plant height, specific leaf area, and seed mass. However, this effect is exerted on the woody component of the understorey layer and not on the herbaceous one, suggesting a larger sensitivity of woody species to changes in forest structure.

Research has indicated that the impact of forest structure is scale-dependent, being more pronounced in relatively uniform environments (Chelli et al., 2021), and is less relevant at the macroecological scale (Ampoorter et al., 2016; Chelli et al., 2019a, 2019b; De Pauw et al., 2021). However, we highlight that changes in canopy cover, even on a macroecological scale, can profoundly affect the functional diversity of the forest understorey (Fig. 2d), mostly acting on the woody component. Variations in light availability, influenced by tree canopy density, can contribute to this pattern. Denser canopies reduce light availability, filtering out light-demanding woody species (e.g., *Lonicera xylosteum* and *Juniperus* sp.) of the understorey (Decocq et al., 2004) and forming plant communities with similar traits adapted to low-light environments (i.e., shade-tolerant woody species; Campetella et al., 2011). Natural and anthropogenic disturbances making forest canopies more open could generate opposite functional patterns and might amplify the effect of climate change and nitrogen deposition (Gilliam, 2019; De Frenne, 2023).

Notably, the filtering effect of tree canopy influences not only traits within the LHS scheme (specific leaf area, plant height, seed mass; Westoby, 1998), which pertain to aboveground plant characteristics, but also BB and multiple traits (see woody species; Table S3, Fig. S5), highlighting the association of canopy cover with both aboveground (i.e., light) and belowground resource constraints (i.e., nutrients).

The effect of deadwood amount on seed regeneration strategies at our study scale is mostly exerted on woody species and confirms the importance of deadwood as a fundamental component of forest ecosystems, capable of regulating diversity (Forest Europe, 2020). The positive shift in the functional diversity of SM aligns with the concept that greater deadwood abundance enhances water and nutrient availability, increasing heterogeneity and thereby fostering the coexistence of species with more diverse strategies related to seed regeneration than expected by chance (Chelli et al., 2021; Fravolini et al., 2018). However, it is essential to exercise caution because our dataset includes only a limited number of forest stands characterized by high deadwood quantities.

4.4. The limited role of forest management at the macroecological scale

At the macroecological scale of our study, we observed that forest management directly impacted plant size only. Similar findings of minimal forest management effects were reported by resurvey studies in boreal and central European forests (Bernhardt-Römermann et al., 2015; Happonen et al., 2021). We speculate that even in regions with centuries-old forest management traditions, such as Italy, potential shifts in management practices driven by socio-economic factors or national and international policies (e.g., transitioning from coppice to high forest) may produce relatively modest effects on understorey functioning at the biogeographical scale. In contrast, research focused on local study cases highlighted the relevance of management practices on forest understorey (e.g., Müllerová et al., 2015; Bricca et al., 2023). However, more detailed data on a wider range of management practices, as well as the age since the last logging, are needed to confirm our speculation (Bernhardt-Römermann et al., 2015).

5. Conclusions

This study holds major implications for the field of global change science. The functional diversity of forest understorey plants is highly susceptible to the impacts of climate change, soil eutrophication, acidification, and alterations in forest structure, but not to management type. However, differences emerge between growth forms (i.e., herbaceous and woody components of the understorey layer). Moreover, it underscores the necessity of adopting a multifaceted approach to unravel the influence of environmental factors on functional diversity at the macroecological scale. Relying solely on a comprehensive functional diversity index may obscure the distinct patterns of individual plant traits, each representing an independent functional specialization axis. Furthermore, different traits and functions are shaped by concurrent processes, highlighting the importance of cautious interpretation of functional diversity results when using a single trait. Extending generalizations to overall plant strategies can be misleading, highlighting the importance of making precise connections between inferences and the specific functions reflected by each trait. Finally, we recommend i) studies that assess temporal changes in functional diversity through resurveys across broad spatial scales, and ii) the use of additional diversity faces (e.g., phylogenetic and taxonomic diversity) to comprehensively understand the intricate effect of global changes on understorey plants.

CRediT authorship contribution statement

Stefano Chelli: Writing – review & editing, Writing – original draft, Conceptualization. **Alessandro Bricca:** Writing – review & editing, Formal analysis, Data curation, Conceptualization. **James L. Tsakalos:** Writing – review & editing, Writing – original draft, Formal analysis, Conceptualization. **Anna Andreetta:** Writing – review & editing, Investigation. **Gianmaria Bonari:** Writing – review & editing, Methodology. **Giandiego Campetella:** Writing – review & editing, Methodology, Investigation. **Stefano Carnicelli:** Writing – review & editing, Methodology, Investigation. **Marco Cervellini:** Writing – review & editing. **Nicola Puletti:** Writing – review & editing, Methodology, Investigation. **Camilla Wellstein:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Roberto Canullo:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

We have no conflicts of interest to disclose.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.170258.

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