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Multi-faceted short-term dynamics of plant understory across forest regeneration stages*

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Abstract

Biodiversity is a multidimensional concept, and capturing its various facets simultaneously offers a more robust framework for predicting vegetation responses to anthropogenic disturbance. Yet, multifaceted studies exploring forest understory regeneration remain scarce. We investigate taxonomic (TD), functional (FD), and phylogenetic (PD) diversity in the understory plant communities of 38 hop-hornbeam forest stands in the Central Apennines (Italy), which differ in time since last coppice event, i.e., 20–25 years (younger stands) and 40–45 years (older stands). We tested differences in TD, and standardized effect sizes (SES) of FD and PD between younger and older stands using two-tailed t-tests. Further, we evaluated the presence of a random or non-random mechanism by checking the distribution of the SES-FD and SES-PD. Our results revealed no significant change in TD between the two forest age classes. However, SES-FD and SES-PD changed significantly. SES-FD shifted from convergence in younger forests to divergence in older ones, aligning with expectations that greater environmental heterogeneity in mature forests supports functionally distinct species. In contrast, SES-PD exhibited increasing convergence over time, suggesting that the forest understory becomes increasingly dominated by closely related species as regeneration progresses. This growing phylogenetic convergence may reflect long-term land-use impacts and a limited regional species pool, pointing to a gradual loss of evolutionary diversity. Overall, our findings emphasize that different facets of biodiversity shape the dynamics of forest regeneration, and that an integrated, multidimensional approach is essential to fully understand and predict these complex ecological processes.

Keywords

Chronosequences, coppicing, disturbances, functional diversity, phylogenetic diversity, plant traits

Introduction

Understanding how vegetation changes is a long-standing intriguing topic, yet the general principles governing plant community assembly remain debated (Götzenberger et al. 2012; Backhaus et al. 2021; Csecserits et al. 2021). In the face of accelerating human pressures on ecosystems, it is increasingly urgent to clarify how plant communities regenerate following disturbance, to predict better vegetation trajectories due to anthropogenic impact (Díaz et al. 2019; Pärtel et al. 2025).

Over the past decades, integrating multiple facets of biodiversity (i.e., taxonomic, functional, and phylogenetic; Bricca et al. 2025a) within permutation-based null models has significantly advanced our understanding of the processes shaping plant communities. By comparing observed diversity values to those expected by chance, it is possible to infer whether community assembly is governed by

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stochastic (random) or deterministic (non-random) processes (Götzenberger et al. 2016). When observed values do not differ from those expected by chance, stochastic processes such as dispersal events are likely at play (Götzenberger et al. 2012). However, interpreting non-random patterns is more complex, as different deterministic processes can yield similar outcomes. For instance, lower than expected functional or phylogenetic diversity (indicating convergence) may result from abiotic filtering or biotic processes like weak competition. Conversely, higher than expected diversity (indicating divergence) can stem from environmental heterogeneity or limiting similarity in species interactions (de Bello et al. 2013).

Chronosequence studies in post-industrial or glacier foreland environments often report predominantly stochastic patterns over time (Schleicher et al. 2011; Marteinsdottir et al. 2018). Yet in old fields, a transition from convergence due to filtering to divergence from competition or to random events has also been observed (Backhaus et al. 2021; Csecserits et al. 2021). Similar trends have been documented in beech forest understories, where divergence has been attributed more to increasing micro-environmental heterogeneity than to competition (Bricca et al. 2023). These mixed findings suggest that successional trajectories and the underlying mechanisms are context-dependent, reinforcing the need for multifaceted approaches that account for different dimensions of biodiversity.

In this study, we examine the regeneration of herbaceous understory communities in sub-Mediterranean secondary hop-hornbeam forests using a space-for-time substitution approach (Pickett 1989). This widely adopted method analyzes contemporary spatial patterns using static spatial data sets to infer temporal ecological processes, such as succession or the impacts of human activities (e.g., Garnier et al. 2004; Backhaus et al. 2021). It relies on the assumption that spatial variation among sites of different ages or successional stages reflects the trajectory of vegetation change over time, thereby allowing reconstruction of long-term dynamics from a single temporal snapshot. We focus on two groups of stands differing in time since the last disturbance: younger stands (logged 20–25 years ago) and older stands (last coppiced 40–45 years ago; Tardella et al. 2019). Our focus on the understory is driven by its ecological importance in temperate forests. Despite representing less than 1% of forest biomass, it harbours up to 90% of plant diversity and plays key roles in processes like litter decomposition and nutrient cycling (Gilliam 2014).

Previous studies suggest that younger stands may support high taxonomic and functional diversity, driven by greater light availability and lower competition (Bartha et al. 2008; Closset-Kopp et al. 2019; Chelli et al. 2023). In contrast, older stands often show reduced diversity due to stronger environmental filtering under closed canopies, as only species adapted to low-light conditions (e.g., those with taller stature, greater photosynthetic efficiency, or larger seeds) can persist (Decocq et al. 2004; Kermavnar et al. 2019; Vanneste et al. 2019; Blondeel et al. 2020). However, plant diversity may increase as succession progresses in older stands (Closset-Kopp et al. 2019). This shift is thought to result from a transition of the ecological processes from canopy-driven filtering toward micro-environmental heterogeneity. In this case, a patchy distribution of the resource creates diverse environmental microhabitats within the forest site, allowing for diverse species to establish. As such, older forests over time often develop more complex spatial structural features (e.g., taller trees, pronounced vertical stratification with tree and shrub layers, and greater amounts of lying deadwood) that can contribute to this late-successional rise in diversity (Hilmers et al. 2018; Bricca et al. 2023).

While trait-based approaches are valuable, they face limitations: identifying all ecologically relevant traits is impractical, and trait data are often incomplete. Phylogenetic diversity can address these gaps, providing complementary insights by capturing unmeasured trait variation and evolutionary history (de Bello et al. 2017). Prior research in these forest systems has shown shifts in dominant understory strategies across the regeneration gradient, from species with persistent green leaves and limited vegetative propagation in younger stands, to species with taproots, summer green leaves, and larger seeds in older ones (Tardella et al. 2019). However, a full picture of diversity patterns – incorporating taxonomic (TD), functional (FD), and phylogenetic (PD) dimensions, combined with a null model framework – has not yet been explored. To fill this gap, we applied a multifaceted diversity framework to assess community assembly processes in these hop-hornbeam forests. We also included traits representing key axes of plant functional variation – Westoby's LHS scheme (1998) and clonality traits (Klimešová et al. 2016) – which are particularly relevant to understory dynamics (Bricca et al. 2023).

Therefore, we hypothesized that: **H1**) taxonomic diversity increases in older stands; **H2**) the functional pattern shifts from convergence to divergence in older stands; and **H3**) the phylogenetic pattern shifts from convergence toward divergence in older stands; and that these patterns may result from processes related to environmental heterogeneity.

Materials and methods

Study area

We used published data of understory vegetation of the hop-hornbeam forest in the central Apennines (central Italy), in the hilly sectors of the Umbria-Marche Apennines (Marche Region) (Tardella et al. 2019). The bedrock is calcareous and climatically the area belongs to the transition zone between the Mediterranean and Temperate climate zones, defined as the sub-Mediterranean climate (Pesaresi et al. 2017). The mean annual rainfall ranges between 900 and 1,100 mm and the mean annual temperature is between 12 and 13 °C (Tardella et al. 2019).

The landscape is dominated by hop-hornbeam (*Ostrya carpinifolia*) forests coexisting mainly with *Fraxinus ornus* subps. *ornus*, *Acer opalus* subsp. *obtusatum*, and *Quercus cerris*. These forests are one of the most widespread forest types in the Central Apennines (Blasi 2010; Casavecchia et al. 2021) and they have been managed mainly as coppice-with-standards. This management practice consists of the logging of young shoots on short rotation favoring vegetative re-sprouting of new shoots from dormant buds on the cut stumps, while a variable number of trees is left uncut (hereafter "standards"), to ensure seed production and prevent soil erosion. However, after the rural exodus started at the end of World War II, this forest management was progressively abandoned (Ferrara et al. 2021). Thus, while the younger forest stands were still in their rotation period during the vegetation survey, the older forest stands are over their turn (>40 years for the regional law of the Marche Region).

Vegetation data

We extracted vegetation data on species distribution from Tardella et al. (2019). Specifically, the sampling design was based on a random stratified approach to select plots in similar environmental conditions in terms of bedrock composition (limestone), elevation (between 600–950 m a.s.l.), slope (20°–40°), and aspect (from north-west to north-east) (Table 1). In total, 38 vegetation plots (20 m × 20 m) were selected, partitioned into 19 plots in younger forest stands and 19 plots in older forest stands. Vegetation data consists of visually estimated percent cover values of forest-floor species inside each plot. The largest proportion of plots was located in private areas. More detailed information on sampling design and data collection is present in Tardella et al. (2019).

Table 1. Mean values and standard deviation of environmental variables in younger and older forest stands (20–25 and 40–45 years since the last logging, respectively).

Environmental variables	Younger forest stands	Older forest stands
Elevation (m a.s.l.)	772 ± 63	754 ± 48
Aspect (°)	45 ± 41	49 ± 26
Slope (°)	27 ± 5	30 ± 5
Tree layer cover (%)	94 ± 8.9	91 ± 2.9

Functional traits and phylogenetic data

We selected a set of plant traits capturing a wide spectrum of plant functional variation of forest understory species (Burton et al. 2020; Chelli et al. 2024b; Table 2), specifically, the specific leaf area (SLA) which captures the leaf economic spectrum, the plant height (H) for the plant size spectrum and the seed mass (SM) for sexual reproduction and dispersal ability. These traits made up the LHS scheme of Westoby (1998). In addition, we selected lateral spread (LS), the number of clonal offspring (CO), and the persistence of clonal growth organs (PCGO). These three clonal traits capture different functional dimensions that have received less attention, such as space occupancy, resource foraging and sharing, and ability to recover after physical damage, all factors that affect plant persistence (Klimešová et al. 2016).

We retrieved data on LHS from the LEDA database (Kleyer et al. 2008) and Campetella et al. (2020) publication, whereas clonal traits were retrieved only from the CLO-PLA3 database (Klimešová et al. 2017) (Table 2). We focused the analysis only on herbaceous understory and we removed shrubs, tree seedlings, and saplings since trait values of mature individuals obtained from databases and publications assigned to young shrubs or tree seedlings and saplings would overestimate their functional role. Therefore, in this study, the understory layer consisted only of herbaceous forest species. Values of plant traits were available for all those species whose relative cumulative cover reached at least 95% of the total cover of all species for at least one trait (Suppl. material 1: table S1) (Májeková et al. 2016). No significant relationships ($p < 0.05$) were detected between traits (Suppl. material 1: fig. S1).

We generated a phylogenetic tree using the most inclusive and updated phylogeny for vascular plants (Smith and Brown 2018). We adopted "Scenario 1" because it is the most cautious and avoids random solutions by adding genera or species as basal polytomies within families or genera (Jin and Qian 2019). Species nomenclature was standardized according to The Plant List (http://www.theplantlist.org/) before building the phylogenetic tree (Smith and Brown 2018). The phylogenetic tree was created with the *V.PhyloMaker* function in the V.PhyloMaker package (Jin and Qian 2019) in the R environment.

Table 2. List of plant traits considered in this study, their codes, and definitions. Aboveground traits and clonal traits have been retrieved in LEDA (Kleyer et al. 2008) and CLO-PLA3 (Klimešová et al. 2017), respectively.

Trait	Trait code	Trait definition
Vegetative height	H	Distance between the upper boundary of the main photosynthetic tissues of a plant and the ground level (m)
Specific leaf area	SLA	One-sided area of a fresh leaf (mm^2/mg) divided by its oven-dry mass
Seed Mass	SM	Dry weight of seed (mg)
Lateral spread	LS	Distance between parental and offspring shoots (cm/year)
Persistence of clonal growth organs	PCGO	The lifespan of the physical connection between mother and daughter shoots (year)
Clonal offspring	CO	Number of offspring shoots produced per parent shoot per year (n/year)

Phylogenetic signals

Phylogenetic and functional diversity are not necessarily independent from each other since a community characterized by similar functional species could be the consequence of phylogenetic clustering. In such cases, a strong association between traits and phylogeny due to underlying trait evolution (i.e., phylogenetic signals or trait conservatism), can lead to misleading interpretation since phylogenetically clustered species may still exhibit substantial functional diversity that is not captured by phylogenetic structure alone (de Bello et al. 2017). The phylogenetic signal was assessed by performing a Mantel correlation test between the phylogenetic dissimilarity matrix and the functional dissimilarity matrix calculated with multiple traits (Jucker et al. 2013). The phylogenetic dissimilarity matrix was obtained from the phylogenetic tree using the cophenetic distance. Values of cophenetic distance were then square-rooted and scaled in a range of 0–1, with 0 indicating the closest related species and 1 the furthest species in the phylogenetic tree (de Bello et al. 2017). The functional dissimilarity matrix was obtained using the Gower distance on species trait values. Gower distance standardizes the functional species distance values in a range of 0–1 (with 0 if two species have the same trait values, and 1 if two species have completely different trait values). Moreover, Gower distance handles missing values and therefore it is suitable for calculating a functional dissimilarity based on multiple traits (Pavoine et al. 2009). Since some species had missing values for certain plant traits, and Gower distance requires at least one shared trait without missing values between species, we excluded 9 out of 103 species that lacked information on plant height (the trait with the fewest missing values across species). Then, the significance of the Mantel correlation test was assessed by comparing observed values of the Mantel statistic to a random distribution generated through 999 permutations of the rows and columns of the functional dissimilarity matrix (Legendre and Legendre 2012). A more positive correlation than expected by chance indicates trait divergence, conversely a more negative correlation than expected by chance indicates trait conservatism (Jucker et al. 2013). Traits did not result phylogenetically conserved ($r = 0.01$; p-value = 0.35), therefore, we did not need to decouple trait information from phylogeny (de Bello et al. 2017).

To calculate cophenetic distance we used the *cophenetic* function in the picante package. We used the *rescale* function in the scales package to rescale cophenetic distance values in a range of 0–1. Gower distance was calculated with the *gowdis* function in the FD package. A Mantel correlation test was performed with the *mantel* function in the vegan package.

Data analysis

All the analyses were done in the R environment (R Foundation for Statistical Computing, Vienna, Austria; http://www.R-project.org).

Species composition characterization

We analyzed the species composition change over time by running a Non-metric Multidimensional Scaling (NMDS) for the two groups of stands (20–25 years and 40–45 years since the last coppices). Before running NMDS, we log(x+1) transformed cover data, and we calculated a distance matrix using the Bray-Curtis distance. Then, we square-rooted the Bray-Curtis distance matrix to have a distance with Euclidean properties and finally, we ran the NMDS (with 3 dimensions). With the same sqrt-Bray-Curtis dissimilarity matrix we tested whether the two groups of stands have i) different extents in beta diversity by performing multivariate homogeneity of groups dispersion (variances; Anderson et al. 2006); and ii) the amount of distinctiveness running analysis of similarity (ANOSIM). For ANOSIM, R-values close to 1 indicate highly dissimilar groups, while R-values close to 0 identify highly similar groups (Clarke 1993). Both analyses were run with 999 permutations to assess their significance. NMDS, multivariate homogeneity of groups dispersion, and ANOSIM were run with *NMDS*, *betadisper*, and *ANOSIM* functions in the vegan package.

Then, we investigated how the two understory plant communities differ in terms of social behavior type (SBT). Specifically, for each species we assigned an SBT from the European forest vascular plant species list (Heinken et al. 2022): i) species of forest interiors (SBT 1.1) – hereafter "forest specialist species"; ii) species of forest edges and forest openings (SBT 1.2) – hereafter "gap species"; iii) species that can be found in the forest as well as open vegetation (SBT 2.1) – hereafter "forest generalist species"; iv) species that can be found partly in the forest, but mainly in open vegetation (SBT 2.2) – hereafter "marginal species"; and v) species typical for non-forest vegetation (SBT 0) – hereafter "non-forest species". Since the list for Italy has not been published yet, we have used the list for the French mountains. This region is close to Italy in terms of biogeography. For species missing from the lists, we assigned the SBT by consulting the national flora (Pignatti et al. 2017–2019). Then, we quantified the relative frequencies (expressed as CWM) of each SBT class (Ricotta and Moretti 2011), and we compared them with time since the last coppicing event using a t-test.

Diversity's facets

We calculated taxonomic diversity (TD), functional diversity (FD), and phylogenetic diversity (PD) using Rao's Quadratic Entropy (Q). We selected Rao's Q because it provides a common methodological framework that efficiently synthetizes the different facets of diversity (de Bello et al. 2010). Rao's Quadratic Entropy expresses the expected dissimilarity between two individuals of a given assemblage randomly selected with replacement:

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

where S is the number of species, d_{ij} is the distance or dissimilarity between the i-th and j-th species, and p_i and p_j are the relative covers of i-th or j-th species in the sampling unit. For FD and PD, we used the functional and phylogenetic dissimilarity matrices used for the Mantel test (see above). For TD, the species distance can assume only two values: 1 for all $i \neq j$ and 0 for all $i = j$. In this context, TD consists of the well-known Simpson index of dominance ($D = \sum_{i=1}^{S} p_i^2$) and it represents the upper limit that FD and PD may achieve. However, to remove the influence of species composition on FD and PD indices, and to shed light on assembly rules, we used the null-model approach in which observed functional and phylogenetic diversity values were compared with a random distribution of expected values (Götzenberger et al. 2016; de Bello et al. 2017). Expected values were generated by shuffling all species traits together for FD and by shuffling species' distance in the phylogenetic distance matrix. We calculated the standardized effect size (SES) for both FD and PD as follows:

$$\text{SES} = (I_{\text{obs}} - I_{\text{sim}})/\sigma_{\text{sim}} \quad (2)$$

where I_{obs} is the observed value of the index, I_{sim} is the mean of the expected index, and σ_{sim} is the standard deviation of the expected index. Then, we assessed whether the distribution of SES values for both FD and PD was significantly different from zero using a two-tailed t-test. Significant distribution of positive SES values (>0) indicates higher observed values than expected (i.e., "trait or phylogenetic divergence"), while significant distribution of negative values (<0) indicates lower observed values than expected (i.e., "trait or phylogenetic convergence"). Values close to zero indicate a random assembly pattern (de Bello et al. 2017). Thus, variation of TD, SES-FD, and SES-PD about time since the last coppicing event was quantified using a t-test. Time since the last coppicing event was treated in the model as a categorical variable with two levels: younger and older forest stands. We are aware that pooling together all traits in a multi-FD index can mask finer functional patterns, thus, we also calculated the SES-FD for each single trait, i.e., plant height (SES-FD_H), specific leaf area (SES-FD_{SLA}), seed mass (SES-FD_{SM}), clonal offspring (SES-FD_{CO}), lateral spread (SES-FD_{LS}) and persistence of clonal growth organs (SES-FD_{PCGO}) and we tested if their values changed across the two forest systems. To calculate them, we shuffled species traits independently.

Taxonomic diversity (TD), functional diversity (FD), and phylogenetic diversity (PD) at the plot level were calculated with the *RaoRel* function in the cati package. A two-tailed t-test was performed using the *t-test* function in the stat base package. A list of references for each package is reported in Suppl. material 1: table S2.

Results

The non-metric multidimensional scaling analysis (NMDS, stress = 0.12; Fig. 1) revealed that the two groups of stands of hop-hornbeam understory vegetation have dissimilar compositions, as confirmed by ANOSIM analysis (R-value = 0.39; p-value = 0.001). Moreover, older hop-hornbeam understory vegetation showed significantly higher beta diversity (average distance from centroid: 0.55), compared to younger hop-hornbeam understory vegetation (average distance from centroid: 0.51), according to the multivariate homogeneity of groups dispersion (p-value <0.05). Regarding the analysis of social behavior type, we found that younger stands compared to older ones were characterized by lower proportions of gap species (12% vs 27%; t = -3.2, p-value <0.01) but higher proportions of forest generalist species (42% vs 22%; t = 3.1, p-value <0.01) (Fig. 2). The other social behavior type did not show significant differences.

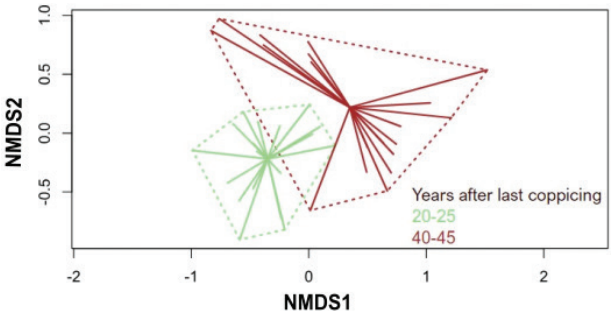

Figure 1. Non-metric Multidimensional Scaling (NMDS; stress = 0.12) ordination of species composition in forest stands coppiced 20–25 and 40–45 years ago. Dotted contours represent convex hulls enclosing plots from each age class. Continuous lines indicate the distance of each plot from its group centroid.

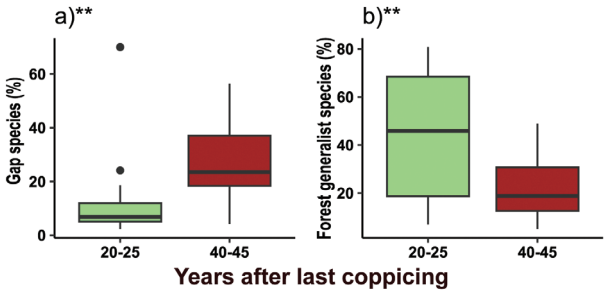

Figure 2. Significant variation of the relative frequencies for a) gap species and b) forest generalist species between stands coppiced 20–25 years and 40–45 years before. Asterisks in the title of each figure refer to significant differences according to the t-test (p-value < 0.01**).

We found a significant effect of the time since the last coppicing event on two out of three diversity facets. Specifically, TD did not show significant variation between the two groups of stands (Fig. 3a). On the contrary, we found higher mean SES-FD for older forest stands compared to younger forest stands (Fig. 3b). The distribution of the standardized effect size of FD of two groups of stands was significantly different from zero, pointing out a pattern of functional convergence (mean = -0.45;

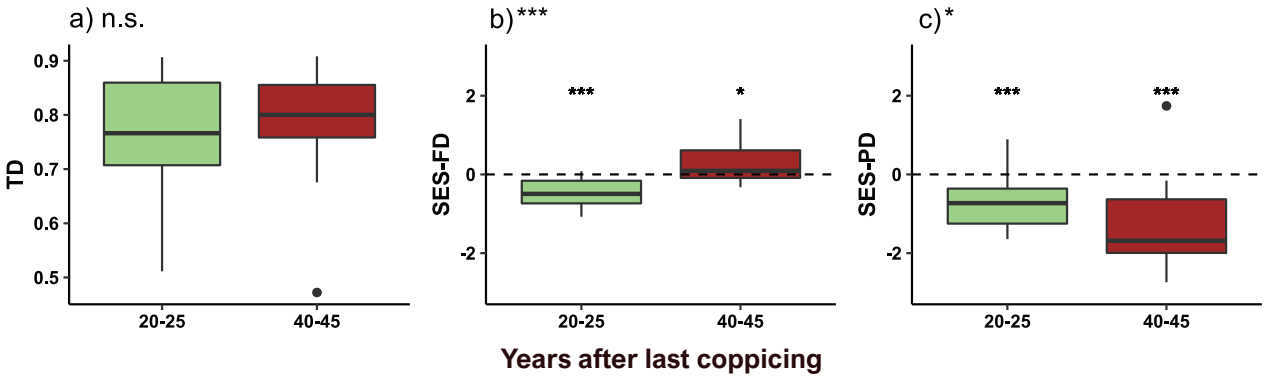

Figure 3. Comparison between younger and older forest stands in terms of taxonomic diversity (TD), standardized effect size of functional diversity (SES-FD), and standardized effect size of phylogenetic diversity (SES-PD) according to t-test. The level of significance of the t-test is reported as n.s., non-significant; $p < 0.05$*; $p < 0.001$*** in the title of each figure. Asterisks over box plots refer to significant differences according to the t-test of SES-FD and SES-PD distribution from zero for each group of forest stands ($p < 0.05$*; $p < 0.001$***).

$p < 0.001$) for younger forest and a pattern of functional divergence (mean = 0.28; $p = 0.02$) for older forest.

We found a significant variation of SES-PD between the two groups of stands, contrary to the functional pattern (Fig. 3c). Indeed, younger forest stands were characterized by higher SES-PD while older forest stands showed lower SES-PD values. The comparison between observed and expected phylogenetic values pointed out an increase of convergence moving from younger forest stands (mean = -0.67; $p < 0.001$) to older forest stands (mean = -1.48; $p < 0.001$).

The results of the variation of each single trait between forest systems are reported in Suppl. material 1: figs S2, S3.

Discussion

In this study, we investigated the patterns and processes of plant understory since the last coppice event, considering the taxonomic, functional, and phylogenetic diversity. Contrary to our first hypothesis (**H1**), which predicted higher taxonomic diversity in older stands, we detected no change in taxonomic diversity. However, the pattern of functional diversity changed from convergence to divergence, confirming our second hypothesis (**H2**). Finally, we found a variation of phylogenetic diversity, but in the opposite way compared to our expectation and compared to functional diversity, specifically, with a strengthening of the convergence pattern (**H3**).

Taxonomic diversity

Theoretically, under closed forest stands TD should be greater because of the presence of different micro-habitats preventing the establishment of few dominant species (Chelli et al. 2023). However, we did not find any significant variation. This can be attributed to the different trajectory of TD since the last disturbance event (Scolastri et al. 2017), or to the length of our regeneration gradient that might not be broad enough to capture it. According to the literature, TD should grow after logging, but during the succession (especially in the first 25–30 years after logging), it should decline due to the progressive tree canopy closure (Roberts and Gilliam 1995; Howard and Lee 2003; Catorci et al. 2011; Chelli et al. 2024a). Eventually, TD rebounds when the forest reaches an old-growth stage, following a U-shaped trajectory (Hilmers et al. 2018). In our study, the older forest stands cannot yet be classified as old-growth, as they are only a few decades old. Consequently, our sampling likely captured two points along the plateau of the U-shaped curve, explaining the absence of significant differences in TD between the two forest stands.

Interestingly, despite the stability in TD, we observed significant species turnover, with younger and older stands exhibiting distinct species compositions. This variation is primarily driven by the greater proportion of gap species (such as *Melittis melissophyllum* and *Viola alba*) in older forest stands. The presence of gap species highlights the existence of microenvironmental gradients within these forests, such as variations in light availability, soil moisture, and nutrient distribution created by canopy gaps. These microhabitats provide niches that support a broader range of species, thereby contributing to higher beta diversity in older stands compared to younger ones.

Functional diversity

Functional patterns shifted from convergence in early regeneration stages to divergence patterns in later ones (Backhaus et al. 2021; Csecserits et al. 2021). In the younger forest stands, the progressive canopy cover closure after logging selects a shaded flora mainly composed of earlier-regeneration species (Bartha et al. 2008; Catorci et al. 2011, 2012). After canopy closure, the increase of micro-environmental conditions allows different functional species to colonize different niches (Closset-Kopp et al. 2019; Vanneste et al. 2019; Bricca et al. 2023). As such older stands have a certain degree of opening in the tree canopy as pointed out also by the higher presence of

gap species (Tardella et al. 2019). Overall, older stands are characterized by species displaying a taller size, higher photosynthetic ability, and larger seeds, all functional adaptations that resemble those of species occurring in more mature stands (Vanneste et al. 2019; Blondeel et al. 2020). On the contrary, the higher number of clone offspring having short-lived connections to the maternal individual is unexpected (Bricca et al. 2023). Probably, different forest types (e.g., hop-hornbeam vs. beech forest) filter species exhibiting specific clonal functional strategies.

When considering single traits, we did not find consistency with the trend depicted by SES-FD_{Multi}. Specifically, we found either a weakening of functional convergence (i.e., SM, PCGO) or a shift from convergence to a random pattern (i.e., H, SLA, LS). Only for CO, we found a shift from a random pattern to functional divergence. Thus, variation of the SES-FD_{Multi} is probably mainly driven by the CO pattern. Since the pattern of SES-FD_{Multi} may mask the functional pattern of different single traits, this reinforces the consideration that plant traits should be evaluated singly (Backhaus et al. 2021; Csecserits et al. 2021). Specifically, forest investigation should not be restricted to the selection of a few aboveground traits (LHS scheme) but should also include clonal traits, as they represent fundamental strategies of species coexistence in such an environment (Bricca et al. 2023).

Phylogenetic diversity

In general, phylogenetically clustered plant communities are typical of early regeneration stages, i.e., more disturbed environments, whereas higher phylogenetic divergence tends to characterize later successional stages with reduced disturbance (Letcher et al. 2012). This pattern is based on the assumption that disturbance filters species according to their functional traits (Zhang et al. 2014). However, this assumes a significant phylogenetic signal in key traits, an assumption not supported by our data.

Moreover, most phylogenetic studies have focused on tropical forests (e.g., Vamosi et al. 2009; Letcher et al. 2012), whereas investigations in old-growth temperate forests have revealed more variable patterns (Ottaviani et al. 2019; Closset-Kopp et al. 2019; Roy et al. 2021). These inconsistencies may stem from differences in study design, e.g., the inclusion of gymnosperms and cryptogams, the use of stand age or basal area as successional indicators, or the choice of phylogenetic metrics.

In our case, we observed a clear pattern of increasing phylogenetic convergence. This suggests a consistent filtering effect exerted by mature forest conditions. However, this pattern may also reflect the influence of anthropogenic disturbance in fostering phylogenetic diversity, particularly in earlier successional stages. In younger forests, the most abundant species belong to six families (*Cyperaceae*, *Juncaceae*, *Lamiaceae*, *Poaceae*, *Primulaceae*, and *Ranunculaceae*), some of which are also associated with grassland habitats. The lower phylogenetic diversity observed in older forests may indicate the absence of a "ghost of competition past" effect (Connell 1980), which would typically promote phylogenetic divergence through biotic interactions such as competitive exclusion (Violle et al. 2011). Instead, our results suggest that abiotic filtering plays a stronger role in shaping community composition. Alternatively, the relatively recent origin of Central Italy's mountain forests (Magri et al. 2006) may have constrained long-term evolutionary diversification. As a result, only a limited number of closely related lineages may have successfully adapted to more mature forests, unlike tropical forests that have experienced long-term stability and species diversification (Lepš 2012). These hypotheses are not mutually exclusive, and together they may help explain the trend toward increasing phylogenetic convergence in our temperate understory communities. Nonetheless, the limited number of phylogenetic diversity studies in temperate understories continues to constrain our ability to generalize these findings.

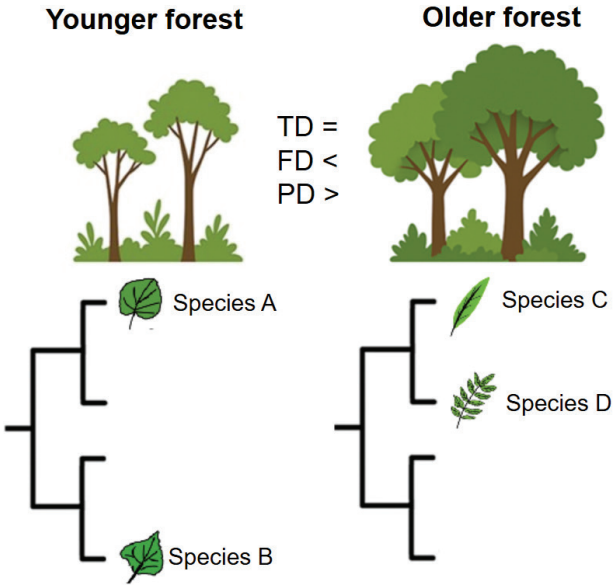

Figure 4. Conceptual illustration of the results showing the different kinds of relationships between the diversity facets of the temporal gradient. Our results indicate that each facet of diversity, namely taxonomic diversity (TD), functional diversity (FD), and phylogenetic diversity (PD), changes independently over time for the forest understory. TD showed an absence of variation over time (indicated by the same number of leaves), FD shifted from convergence in younger forest stands to divergence in older forest stands (indicated by the shape of the leaves), and PD showed convergence over time (indicated by the position of the leaves at the end of the phylogenetic branches).

Conclusion

Our results provide evidence that multiple assembly processes act simultaneously on understory plant communities affecting differently each of the three diversity facets (Fig. 4). While taxonomic diversity did not change over time (despite strong species turnover), we observed a variation in the functional and phylogenetic patterns. We showed that in younger forest stands, there

is a convergence pattern of functional and phylogenetic diversity, probably due to the environmental filtering effect exerted by the restoration of shaded conditions. On the contrary, older forest stands are characterized by functional divergence but stronger phylogenetic convergence, suggesting that a different community assembly seems operating. This pattern ensures that while the restored ecosystem supports closely related species, it also encourages a broad range of ecological functions, promoting a resilient and dynamic understory. Accordingly, as the three diversity facets change independently, the results suggest that they may reach a peak at different times. These results support the importance of vegetation monitoring programs, which should go beyond the mere taxonomic aspect. As diversity facets showed distinct trends, conservation planning and priorities may be defined according to which diversity facet has major relevance, which is often context- or case-dependent. In this regard, by selecting different rotation periods, forest managers can actively promote one facet of diversity over another. For example, phylogenetic diversity may benefit from shorter rotations, whereas functional diversity may be enhanced by allowing longer successional development. However, we are aware of the limits of this research that used a limited temporal gradient and the space-for-time substitution approach. Further investigation should be carried out into a larger temporal gradient with continuous samplings of post-disturbance forest communities. Finally, although the information on social behaviour type was related to French mountain areas, the patterns detected were in line with previous studies performed in the same areas.

Authorship contribution

Alessandro Bricca: Conceptualization, Formal analysis, Writing – original draft. Federico Maria Tardella: Methodology, Writing – review & editing. Andrea Catorci: Data curation, Supervision, Writing – review & editing.

Competing interest

The authors declare that they have no conflict of interest. Alessandro Bricca is a Guest Editor for topical collection in Vegetation Ecology and Diversity, but took no part in the peer review or decision-making process for this manuscript.

Data accessibility

Species composition data are available in Tardella et al. (2019), while plant traits data are available in Kleyer et al. (2008). Data used to run the analysis are stored in the Zenodo repository at the following link: https://doi.org/10.5281/zenodo.16083650 (Bricca et al. 2025b).

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Supplementary material 1

Supplementary figures and tables

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