



## Drivers and patterns of community completeness suggest that Tuscan *Fagus sylvatica* forests can naturally have a low plant diversity



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### ARTICLE INFO

#### Keywords:

Biodiversity  
Community ecology  
Dark diversity  
Forest structure  
Species absence  
Species pool

### ABSTRACT

European beech (*Fagus sylvatica* L.) forests can have a high variability in plant species richness and abundance, from monospecific stands to highly species-rich communities. To understand what causes the low plant diversity observed in some beech forests, we analyzed the drivers of plant community completeness in 155 vegetation plots. Data were collected in mature, closed-canopy beech forests in Tuscany, central Italy. Site-specific species pools were estimated based on species co-occurrences. We used Generalized Least Squares linear modeling to assess the effects of anthropogenic and environmental drivers on the community completeness of whole communities and on the set of specialist species of beech forests. We also tested the response of the total cover of the herb layer to the selected predictors and related both the predictive and response variables to species composition in a Non-metric Multidimensional Scaling ordination. The community completeness of whole communities and that of beech forest specialists were negatively affected by total beech cover and positively influenced by slope. Moreover, the community completeness of whole communities was negatively impacted by elevation and positively influenced by disturbance frequency. The cover of the herb layer decreased with increasing beech cover, elevation, and precipitation. High community completeness and high cover of the herb layer were associated with the presence of thermophilic species of mixed deciduous woods in low-elevation beech forests. Our results suggest that a low plant community completeness and a low cover of the herb layer are mainly due to the competition by beech itself when it forms pure forests in its ecological optimum. Such competition is better exerted at upper elevations and in sites with low slopes, where beech litter accumulation is a limiting factor for understory species. Such evidence suggests that species absence in mature beech forests is mainly due to natural drivers and should therefore not be considered an indicator of ecological degradation of the forest.

### 1. Introduction

Analyzing species richness alone may be insufficient to highlight conservation priority areas and to assess the conservation status of ecosystems (Pollock et al., 2017; Chauvier-Mendes et al., 2024). There are many examples of ecosystems being naturally species-poor due to strong environmental filters selecting few tolerant taxa, as it happens for vascular plants in dunes, forests, or wetlands (Acosta et al., 2009; Landucci et al., 2015; Leuschner and Ellenberg, 2017). Naturally

species-poor sites can have a disproportionate contribution to regional biodiversity, thanks to their uniqueness in species composition, so that their good conservation status and high conservation value might be overlooked with assessments only based on species richness (Harper et al., 2022). Dark diversity and community completeness are novel concepts that can help overcome such issues. Dark diversity refers to those taxa that are part of the species pool of a certain habitat in a region but are not observed in a sample due to dispersal barriers, disturbance, or ecological filters (Pärtel et al., 2011). Community completeness is the

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<https://doi.org/10.1016/j.fecs.2024.100276>

Received 12 June 2024; Received in revised form 16 October 2024; Accepted 14 November 2024

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ratio between the observed diversity and the dark diversity of a given site, expressing how “complete” a community is by relativising local diversity by the potential diversity. Community completeness proved useful to assess the conservation status of biotic communities regardless of their species richness (Pärtel et al., 2013) and can be considered as an effective tool for nature conservation (Lewis et al., 2017; Noreika et al., 2020).

European beech (*Fagus sylvatica* L.) is one of the most ecologically and economically important forest species in western, central, and southern Europe (von Wuehlisch, 2008). It usually grows in mesic sites on deep soils, either acid or base-rich, avoiding dry and regularly flooded areas. Given their importance for biodiversity and ecosystem services and their vulnerability to climate change, several types of beech forests are protected under the Annex I of the Habitats Directive (European Commission, 1992; Martínez del Castillo et al., 2022; Selvi et al., 2023). Despite some beech forests are species-rich, some others can be characterized by low plant diversity with respect to other forest types, like mixed broad-leaved forests (Vockenhuber et al., 2011; Hrivnák et al., 2014). This is because beech stands effectively intercept sunlight, water, and other resources, outcompeting understory plants and possibly leading to the so-called “*Fagetum nudum*”, a beech forest without or almost without an understory (Schmidt, 2005; Kučera et al., 2010).

The plant diversity of beech forests and its drivers have been intensively studied so far. Species richness is known to increase with increasing slope and soil pH, and to decrease with increasing potential solar radiation (Sabatini et al., 2014; Leuschner and Ellenberg, 2017). The effect of elevation is context-dependent, either increasing (Slezák and Hrivnák, 2019), decreasing (Ottaviani et al., 2019), causing U-shaped responses (Hrivnák et al., 2014; Ujházyová et al., 2016) or not affecting species richness (Willner et al., 2004). Forest cutting and the consequent canopy openness, habitat fragmentation, and the reduction of forested area increase species richness by favoring species from open habitats and disfavoring forest specialists (Bartha et al., 2008, 2020; Peña et al., 2011; Carranza et al., 2012). At the European scale, plant community completeness in beech forests is primarily influenced by their biogeographical history and environmental factors. Communities located closer to glacial refugia and in areas with higher soil pH and precipitation have a higher community completeness regarding both whole communities and the sub-pool of beech forest specialist species (Jiménez-Alfaro et al., 2018). Such patterns of plant diversity are also related to changes in species composition, especially in the herb layer. Temperature and soil pH are the main factors driving species turnover, followed by biogeography (Willner et al., 2017). Consistently, the two main beech forest types in Europe are distinguished in species composition after soil pH, which can be acid or non-acid (Chytrý et al., 2020). High management intensity (i.e., harvesting rates) generally causes a replacement of forest specialists with management-tolerant species (Asbeck et al., 2021). Thus, beech forest specialists increase in late-successional stages, especially after the conversion of coppices to high forests (Campetella et al., 2016). Species composition is also affected by forest structure, the latter directly reflecting management strategies (Burrascano et al., 2008, 2018).

In this work, we assessed the effects of a set of anthropogenic and environmental drivers on different diversity metrics in 155 probabilistically sampled beech forest vegetation plots in Tuscany, central Italy. By investigating the relative role of the environment and anthropogenic pressures in shaping observed plant diversity in relation to dark diversity and to the completeness of species pools, we aimed to verify if the low plant diversity that is recorded in some beech forests is due to natural causes or to human-induced habitat modifications, and if species absence is then an indicator of ecosystem degradation or not. We tested the influence of the selected drivers on the community completeness of whole plant communities, on the community completeness of the sub-pool of specialist species of beech forests, and on the total cover of the herb layer. Finally, we examined the variation in species composition of the studied communities across the gradients of both predictive and response variables, aiming to identify any consistent patterns.

## 2. Materials and methods

### 2.1. Study area

Our study was carried out in the beech forests of the Tuscany region, central Italy (Fig. 1). The study area is located between about 42.5° and 44.5° N, and 10.0° and 12.5° E (WGS 84). Beech forests are present in the mountain belt between approximately 700 and 1,900 m a.s.l. They are mostly distributed in the north along the Apennine chain, but isolated patches of beech forest are also present on the top of minor mountain complexes in the south (De Dominicis et al., 2010). In the regional distribution range of *Fagus sylvatica* the bioclimate is mainly temperate, which is distinguished from the Mediterranean type by the absence of summer drought (Pesaresi et al., 2017). Geological substrates are mainly acidic, represented by arenaceous and, subordinately, volcanic rocks. Basic rocks are less common and are represented by limestones and marbles (Tuscany Region, 2023).

### 2.2. Selection of sampling sites and field survey

We structured a probabilistic sampling design all over the extent of Tuscan beech forests, using QGIS version 3.12 (QGIS Development Team, 2020). The data were collected in the context of the Nat.Ne.T (Natural Network Tuscany) project, funded by the Tuscany Region for the monitoring of the animal species, plant species, and habitats present in the annexes of the 92/43 EEC Directive (Tuscany Region, 2022a). Prior to field sampling, a regional map of beech forests at a scale of 1:50,000 was drawn, based on all the available published and unpublished data about the regional distribution of beech forests. We then divided the surface occupied by beech forests in 1 km × 1 km cells. Of the 722 resulting cells, we randomly selected 200 cells. We planned to survey one sampling plot per each of the selected cells. The sampling plots were positioned haphazardly during field surveys in areas where closed-canopy beech forests - i.e., that were not cut for several decades - with *Fagus sylvatica* covering at least 50% of the plot surface was present. This approach ensured that data were collected exclusively from suitable forests, while providing flexibility to adapt to site inaccessibility or unexpected absence of beech stands, which could not be detected through remote sensing (Smith et al., 2017). Despite this, we could not find accessible sites or any suitable beech forest in 45 cells, so that we finally collected data from 155 vegetation plots. Plot distribution broadly covered the extension of beech forests in the study area, at elevations between 705 and 1,900 m a.s.l. (Fig. 1a). Moreover, all the beech forest types that occur in Tuscany were sampled, including acidophilous, neutrophilous, and basiphilous forests attributable to the EU Habitats 9110, 9130, 9150, 9210\*, 9220\*, and *Fagetum nudum* (Arrigoni et al., 1998; European Commission, 1992; Tuscany Region, 2022b).

Sampling plots had 200 m<sup>2</sup> size, as recommended for the sampling of European forest vegetation (Chytrý and Otýpková, 2003), and a circular shape. The subsequent collection of vegetation and structural data followed previous approaches to survey EU forest habitats in Tuscany (Angiolini et al., 2021). Within each sampling plot, we listed all the occurring vascular plant species. We measured the abundance of each species by visually estimating its percentage cover using the following values: 0.1%, 1%–10% at 1% intervals, and 10%–100% at 5% intervals. Different interval widths were used for lower and higher values, as smaller differences in plant cover can be estimated more accurately when a species' overall cover is low (Kent and Coker, 1992; Klimeš, 2003). We visually estimated the total percentage vegetation cover and the total percentage cover of the tree, shrub, and herb layers. In the same plot, we also measured the following structural attributes: i) diameter at breast height (DBH - measured at 130 cm from the ground, Köhl et al., 2006) of each tree of at least 5 cm diameter, grouped by width classes of 5 cm; ii) average tree height using a “Suunto” PM-5/1520 hypsometer (Suunto, Vantaa, Finland). Moreover, within a nested circular subplot of 50 m<sup>2</sup> located at the center of the main plot, we measured: i) the number of tree

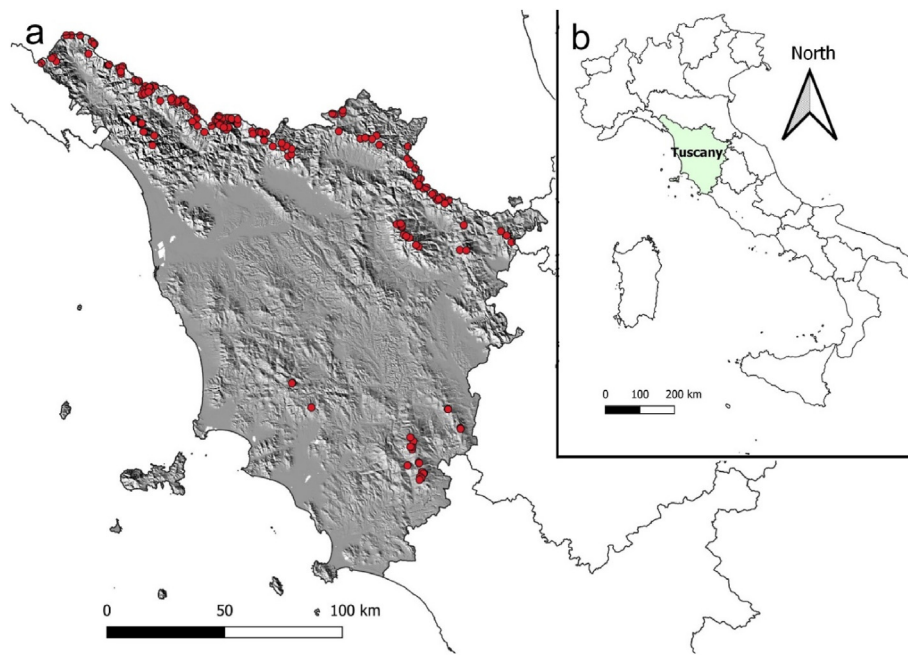


Fig. 1. a) Distribution of the surveyed vegetation plots (red dots) in the Tuscany region (shaded relief map, azimuth = 220°, elevation = 45°) and b) location of Tuscany in Italy.

seedlings per species; ii) the amount, length, and width of dead wood fragments. Using a smaller subplot to measure such attributes was due to their higher level of detail and aimed to ensure efficient and accurate data collection while reducing workload, as commonly done in similar studies (Juutilainen et al., 2011; Cowden et al., 2014). Finally, in the center of the plot, we recorded plot coordinates, slope, aspect, and elevation above sea level. Data were collected by the same team of botanists in the spring-summer months (April to August) of 2020 and 2021. Each plot was surveyed once. The main steps of the sampling procedure are summarized in Fig. 2.

Plant species were identified according to Pignatti et al. (2017–2019). Taxonomic nomenclature follows the Portal to the Flora of Italy v. 2023.1. The nomenclature of the mentioned syntaxa follows FloraVeg.EU (2023).

### 2.3. Calculation of community completeness and related metrics

We calculated species pools according to Carmona and Pärtel (2021). This method is used to estimate probabilistic dark diversity by calculating site-specific species pools based on pairwise species co-occurrence data. To improve the robustness of co-occurrence calculations, we built a database including phytosociological relevés from the literature carried out, from the year 1985–2012, in the beech forests (*Fagus sylvatica* covering at least 3 of the Braun-Blanquet scale – Braun-Blanquet, 1965) of Tuscany or of contiguous Apennine areas of Emilia-Romagna and Marche regions. Since plot size can influence species co-occurrence patterns (Bar-Massada et al., 2018), we selected from the literature only samples with a surface between 150 and 300 m<sup>2</sup>. For such samples, we preliminarily checked that there was no correlation between plot size and species richness by estimating Pearson’s correlation coefficient using the function *cor.test* in the package *stats* of R (R Core Team, 2023). Based on these criteria, we selected 794 samples from the literature, to which we added our 155 plots. We thus obtained a 447 species × 949 plots matrix. We calculated species probabilities of co-occurrence through the function *DarkDiv* in the package *DarkDiv* of R, using a hypergeometric distribution, which currently represents the most reliable method to derive the co-occurrence matrix (Carmona and Pärtel, 2021). For each species absent in a plot but present in the surrounding region, the

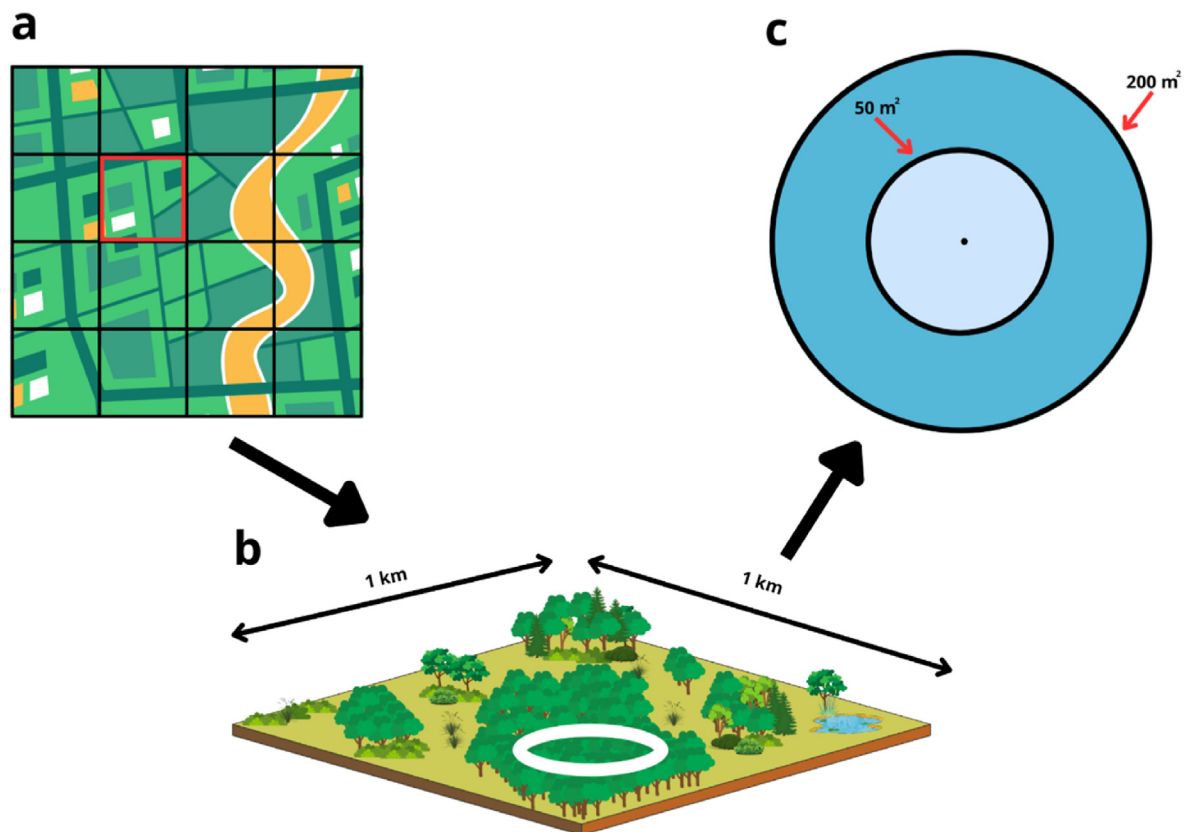
function gives a probability value which indicates how likely the species co-occur with a given species present in the study site expressed using standardized effect size. The absent species that co-occur more often than expected by the hypergeometric distribution define the dark diversity pool. The suitability of absent species for a given site was finally estimated by averaging the suitability indicator values from all the present species. We then calculated dark diversity and community completeness for each plot based on such probabilistic site-specific species pools. Dark diversity was calculated by summing the probabilities of occurrence of all the missing species in a given plot. Finally, we calculated the Community Completeness Index (CCI) for each plot, based on Eq. 1 (Pärtel et al., 2013):

$$CCI = \ln \left( \frac{\text{Observed diversity}}{\text{Dark diversity}} \right) \quad (1)$$

We repeated the calculation of all the metrics using only the “diagnostic” species of *Carpino-Fagetea sylvaticae*, as listed by FloraVeg.EU (2023). “Diagnostic” species of such communities were used as beech forest specialists. The plant communities classified in the *Carpino-Fagetea sylvaticae* represent the “mesic deciduous and mixed forests of temperate Europe, Anatolia, the Caucasus and Southern Siberia” (FloraVeg.EU, 2023). Starting from the original 447 species × 949 plots matrix, we built a new matrix only including beech forest specialists. This resulted in a 67 species × 949 plot matrix. Using this matrix, we recalculated species probabilities of co-occurrence, site-specific species pools, dark diversity, and community completeness of beech forest specialists.

### 2.4. Selection of explanatory variables

We calculated a series of landscape metrics related to complexity, fragmentation, and disturbance in a 2,000 m circular buffer around each plot, in the package *landscapemetrics* of R (Hesselbarth et al., 2019). At this scale, such variables have the best explanatory power on the species richness of forest plant communities in the study area (Amici et al., 2015). For this purpose, we used the National Land Cover Map updated to 2021 (ISPRA, 2022). Since disturbance is almost exclusively anthropogenic in beech forests, we calculated the abundance-weighted mean of “disturbance frequency” indicator values at the plot level as an indirect



**Fig. 2.** Main steps of the field sampling procedure: **a)** random selection of a suitable  $1 \text{ km} \times 1 \text{ km}$  cell in the GIS environment; **b)** field placement of a plot (white circle) in a closed-canopy beech forest; **c)**  $200 \text{ m}^2$  plot for the sampling of vascular plants, diameter at breast height, and tree height and therein nested  $50 \text{ m}^2$  subplot for the sampling of dead wood and tree seedlings. Figure created using Canva.

measure of human impact (Midolo et al., 2022). The disturbance indicator values are a set of five expert-based indicators of disturbance severity, disturbance frequency, mowing frequency, grazing pressure, and soil disturbance developed for the European flora, expressed in continuous values. Of the five available indicators, we selected “disturbance frequency” as the most appropriate to express the main disturbance in beech forests, i.e., periodic cutting. We also calculated the Human Footprint Index (HFI) per plot (Venter et al., 2016). Per each plot, we retrieved the values of soil pH at 5-cm depth from the SoilGrids 2.0 database (Poggio et al., 2021). Mean annual temperature and mean annual precipitation (temporal range: 1970–2000) were retrieved from “WorldClim 2”, using the  $30 \text{ s}$  ( $\sim 1 \text{ km}$ ) grid size (Fick and Hijmans, 2017). Finally, structural and environmental variables measured in the field were added to the other explanatory variables. The variable dataset is available in Appendix A.

We carried out forward selection procedures of the retrieved variables against the community completeness of whole communities, the community completeness of beech forest specialists, and the total cover of the herb layer using the function *forward.sel* in the package *adespatial* of R (Dray et al., 2023). Overall, six variables were selected: two anthropogenic (DBH – as a proxy of time from the last cut – and disturbance frequency) and four environmental (elevation, beech cover, slope, mean annual precipitation). For the community completeness of whole communities, the selected variables were: i) elevation; ii) beech cover; iii) slope; iv) DBH; v) disturbance frequency. As regards the community completeness of beech forest specialists, the selected variables were: i) slope; ii) beech cover; iii) DBH. For the total cover of the herb layer, the selected variables were: i) beech cover; ii) elevation; iii) mean annual precipitation. Beech cover was intended as total beech cover, i.e., including all the forest strata together.

## 2.5. Statistical analyses

To explore the relationships between the diversity metrics, we assessed Spearman’s correlations between species richness, species pool size, dark diversity, community completeness of whole communities, community completeness of beech forest specialists, and total cover of the herb layer using the function *ggpairs* in the package *GGally* of R (Schloerke et al., 2024).

We used Generalized Least Squares (GLS) linear modeling to assess the effects of anthropogenic (DBH, disturbance frequency) and environmental (elevation, beech cover, slope, mean annual precipitation) drivers on the plant community completeness of whole communities, the community completeness of beech forest specialists, and the total cover of the herb layer. In the models, we added exponential correlations with plot latitude and longitude, to account for the effect of spatial autocorrelation. This approach ensures that the spatial dependencies between plots are incorporated, thus improving the model’s ability to distinguish true ecological patterns from spatially structured noise. Linear models were fitted using the function *gls* in the package *nlme* of R (Pinheiro et al., 2023). Effect plots were drawn using the function *effect* in the package *effects* of R (Fox and Weisberg, 2019).

To visualize the patterns of variation in species composition of the studied plant communities in relation to the selected predictors, to plant community completeness, and to the cover of the herb layer, we carried out an abundance-based (Hellinger standardization of species covers and Bray-Curtis dissimilarity matrix) non-metric multidimensional scaling (NMDS) ordination analysis using the function *metaMDS* in the package *vegan* of R (Oksanen et al., 2022). We then passively projected the predictive and response variables on the ordination plot, using the function *envfit* in *vegan*.

### 3. Results

#### 3.1. Patterns of plant diversity

The surveyed forests had a  $\gamma$ -diversity of 207 plant species, while the regional species pool included 447 species. Excluding *Fagus sylvatica*, the most frequent taxa in our 155 plots were all beech forest specialists such as *Luzula nivea* (58 plots), *Festuca heterophylla* (55 plots), and *Hieracium murorum* (54 plots). Table 1 summarizes descriptive statistics about species richness, species pool size, dark diversity, and community completeness for whole communities and beech forest specialists.

Most of the diversity metrics were positively correlated with one another. As an exception, the dark diversity of beech forest specialists and community completeness of beech forest specialists were negatively correlated (Fig. 3).

#### 3.2. Effects of predictive variables on community completeness and cover of the herb layer

Beech cover negatively influenced the community completeness of whole communities, the community completeness of beech forest specialists, and the total cover of the herb layer. The community completeness of whole communities and the total cover of the herb layer decreased with increasing elevation. The latter also decreased with increasing precipitation. Slope positively affected the community completeness of both whole communities and beech forest specialists. Increasing DBH had a marginally significant positive effect only on the community completeness of beech forest specialists. Finally, disturbance frequency positively affected the community completeness of whole communities (Fig. 4). The complete outputs of the models are reported in Appendix A.

#### 3.3. Variation in species composition in relation to predictors and CC

The NMDS plot (Fig. 5) shows how increasing community completeness and herb cover coped with the presence of species of low-elevation mixed deciduous forests like *Crocus etruscus*, *Lathyrus venetus*, and *Ulmus minor*. Beech forest specialists, especially nemoral herbs like *Allium ursinum*, *Cardamine kitaibelii*, and *Galium odoratum*, and mesophilous trees like *Tilia cordata* and *Ulmus glabra*, were mostly related to high DBH. Other beech forest specialists like *Galium rotundifolium*, *Oxalis acetosella*, and *Prenanthes purpurea* were related to low community completeness and high elevation. Grass species from open habitats like *Brachypodium rupestre*, *Luzula multiflora*, and *Sesleria argentea* were associated with high slopes. Increasing beech cover was associated with several beech forest specialists (*Luzula* spp., *Poa nemoralis*, *Sorbus aria*), and negatively coped with the presence of other tree species (*Acer pseudoplatanus*, *Carpinus betulus*, *Ostrya carpinifolia*). Finally, communities with higher disturbance frequency were characterized by ruderal species like *Poa bulbosa*, *Silene latifolia*, and *Stellaria media*. Moreover, they were related to thermophilous species like *Acer campestre*, *Corylus avellana*, and *Quercus ilex*. Community completeness of beech forest specialists and

**Table 1**

Descriptive statistics about community completeness and related metrics for the sampled plots.

	Min	Max	Mean	SD
Species richness	1	38	12.3	7.6
Species richness (beech forest specialists)	1	22	7.7	4.4
Species pool size	187	295	247.1	28.4
Species pool size (beech forest specialists)	28	71	53.1	10.4
Dark diversity	181	274	234.7	24.3
Dark diversity (beech forest specialists)	24	64	43.4	8.9
Community completeness	-5.4	-1.9	-3.1	0.6
Community completeness (beech forest specialists)	-3.8	-0.7	-1.9	0.6

precipitation were not correlated with species composition.  $R^2$  values and  $p$ -values for the correlations between the variables and the NDMS axes are reported in Appendix A.

### 4. Discussion

Our analysis revealed novel evidence about the drivers of low plant diversity in beech forests. We highlighted how, in the studied plant communities, the competition exerted by beech in sites where the species is in its ecological optimum is the main factor determining a low-complete community and a low-covering understory. At the same time, topographic factors such as slope and elevation and anthropogenic factors, like disturbance frequency, significantly affected plant community completeness, herb-layer abundance, or both. These results point out that, in our case, species absence in mature beech forests was mainly due to natural drivers, and should therefore not be considered an indicator of degradation of the forest ecosystem. Species-poor beech forests also had a low community completeness. This is since most factors influencing species absence in the surveyed plots act on a local scale, so that locally absent species can still be present in the surrounding forest area under higher slope and low beech cover conditions, remaining part of local species pools.

#### 4.1. Patterns of diversity metrics

We found a high variability of all the calculated diversity metrics in our dataset (Table 1). Species richness ranged from only 1 species per plot, corresponding to monospecific *Fagus sylvatica* stands ("Fagetum nudum"), to 38 species per plot in low-elevation beech forests on calcareous substrates. The size of site-specific species pools was much larger than the observed diversity. This means that only a small fraction of potential plant diversity is locally realized in the studied beech forests, as highlighted by the negative values of community completeness and previously found in different forest ecosystems (de Oliveira Gonçalves-Araújo et al., 2024). In the case of smaller species pools, dark diversity can be lower than the observed diversity, so that community completeness has positive values (Pärtel et al., 2017).

As it can be expected from metrics being calculated in part from the same sources, positive correlations between species richness, dark diversity, and community completeness (Fig. 3) were already highlighted elsewhere in several habitats, including forests (Fløjgaard et al., 2020; de Oliveira Gonçalves-Araújo et al., 2024). In our case, the species pool size was positively correlated with such metrics. This suggests that, as the species pool size increases, plant species colonize the beech forests, increasing local species richness. This evidence is consistent with ecological theory, which highlighted that local species richness increases with the increasing size of the local species pool (Pärtel et al., 1996). Beech forest specialists' metrics showed similar patterns, except for dark diversity being negatively correlated with community completeness and having no correlation with species richness. This could be due to the higher specialization of beech forest specialists, with a lower possibility of turnover under changed ecological conditions (Devictor et al., 2008). The total cover of the herb layer was positively correlated with all the diversity metrics, except dark diversity of whole communities, dark diversity of beech forest specialists, and species pool size of beech forest specialists. Similar relationships were found between species richness and vegetation cover in several plant communities (Grytnes, 2000; Song et al., 2011). Regarding beech forests, herb layer species richness was previously found to be positively correlated with herb layer abundance, in terms of biomass (Mölder et al., 2008).

#### 4.2. Effects of the selected variables on community completeness and cover of the herb layer

Beech cover was the most important factor in explaining the variation of the community completeness of whole communities, the community

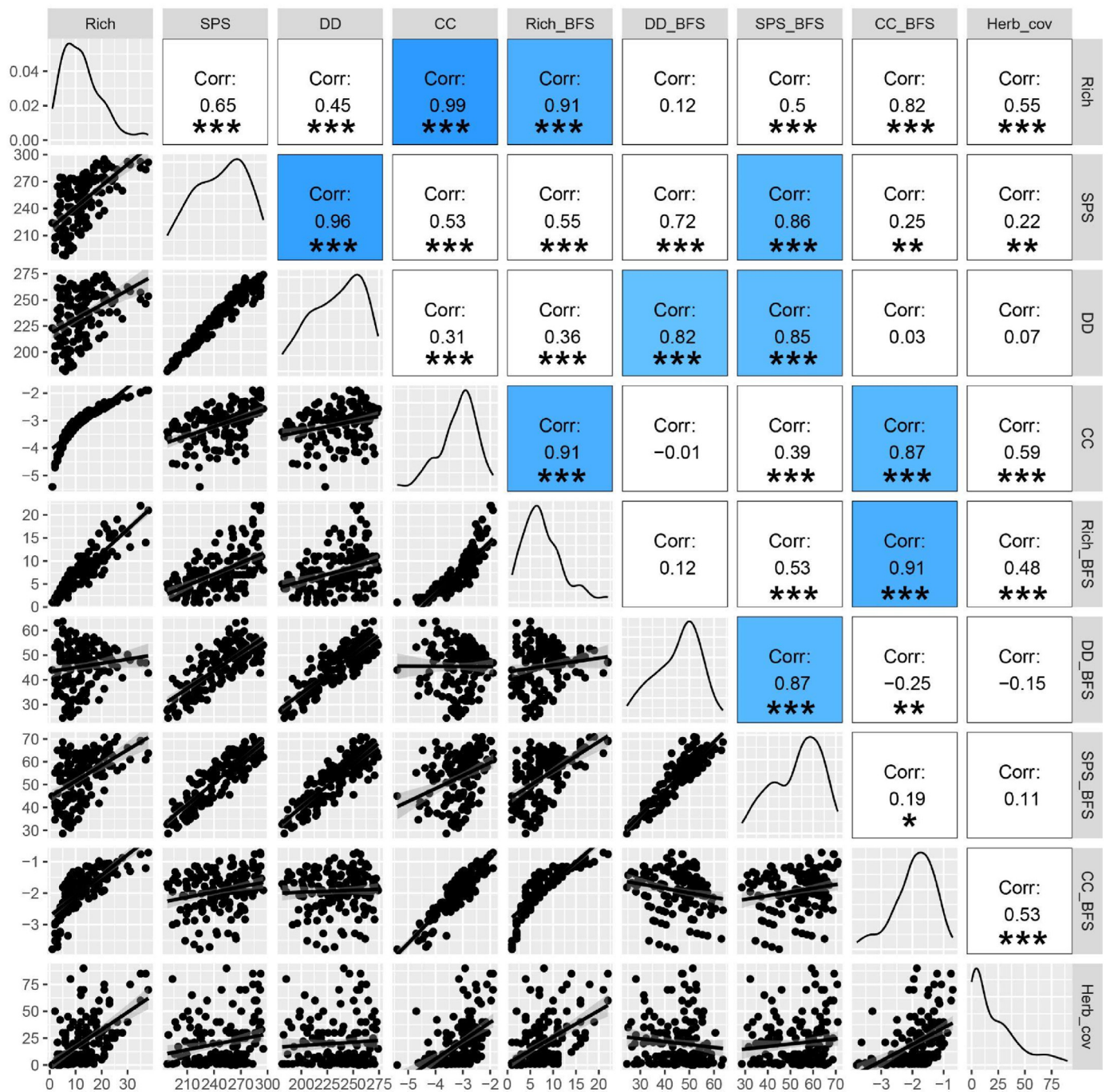
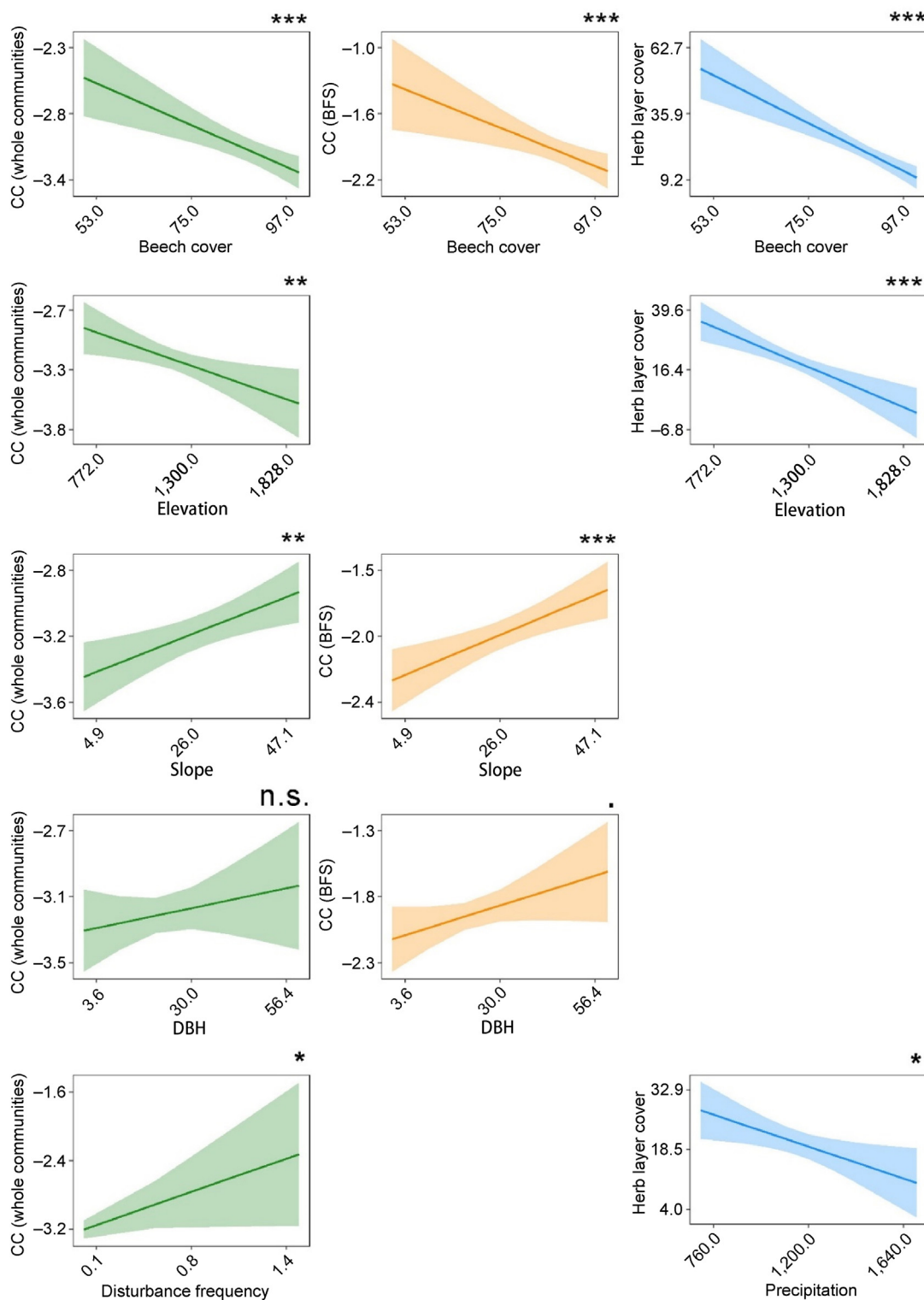


Fig. 3. Spearman's correlations between the calculated diversity metrics. \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ . Rich = species richness; SPS = species pool size; DD = dark diversity; CC = community completeness; BFS = beech forest specialists. Boxes in blue tones highlight correlations higher than |0.8|.

completeness of beech forest specialists, and the total cover of the herb layer, having a negative relationship with all of them (Fig. 4). This is consistent with the high competition exerted by beech towards other species, both in the overstory and in the understory, especially in terms of shading, water uptake, beech litter thickness, and soil acidification (Schmidt, 2005; Mölder et al., 2008; Ligot et al., 2013; Ujházyová et al., 2024). Moreover, beech seedlings have much more shade tolerance than those of other tree species and are more competitive in forest understoreys, which contributes to form pure beech stands that outcompete other plant species within beech's ecological optimum (Ligot et al., 2013). Such effects can be local and unevenly distributed across the forest, so that community completeness can increase in adjacent forest areas with lower beech abundance or steeper slopes. From this

perspective, the structural heterogeneity typical of unmanaged beech forests is important to maintain high levels of plant diversity in the understorey (Mölder et al., 2014).

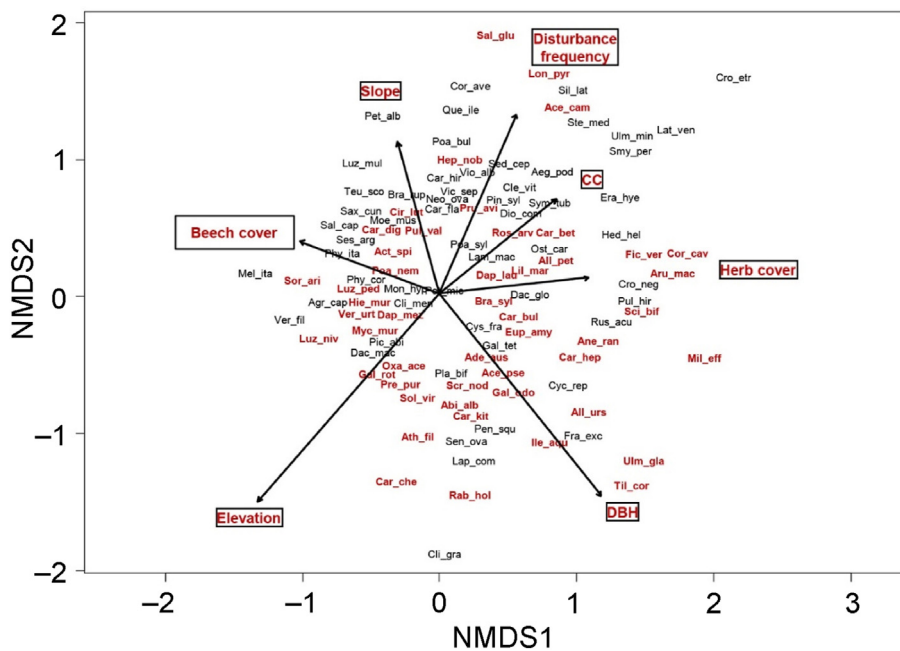
The reduction of community completeness of whole communities with increasing elevation is relatable to a natural loss of species along such gradient, with a decrease of both species pool sizes and species richness. This is consistent with the trends usually observed at middle latitudes, where harsher climatic conditions cause a decrease of species richness at higher elevations (McCain and Grytnes, 2010). However, the community completeness of beech forest specialists was not affected by elevation in our study since such species are related to mountain ecosystems in the Mediterranean (Pignatti, 1998; Willner et al., 2009). Conversely, species from mixed deciduous and conifer woods can



**Fig. 4.** Results of the GLS linear models showing the effects of the selected drivers on the community completeness of whole communities, on the community completeness of beech forest specialists, and on the total cover of the herb layer. CC = Community completeness; BFS = beech forest specialists; DBH = Diameter at Breast Height. n.s. = not significant; . =  $p < 0.1$ ; \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ . Units of measurement: Elevation = m a.s.l.; Beech and herb layer cover = %; Slope = °; DBH = cm; Precipitation = mm.

increase species richness in beech forests located at lower and upper elevations, respectively (Hrivnák et al., 2014). Such species contribute to the species pool size of beech forests located close to the limits of beech ecological optimum, positively affecting community completeness. However, we only observed increased community completeness at lower

elevations, especially due to the presence of species from mixed deciduous woods since in the study area there is no upper conifer forest belt, but shrublands, heaths, and/or mountain grasslands (De Dominicis et al., 2010). Species from such open habitats have high light requirements (FloraVeg, 2023) and do not colonize forests. Moreover, most mountain



**Fig. 5.** Non-metric Multidimensional Scaling ordination plot of the studied plant communities with predictor and response variables passively transposed. All the variables were significantly correlated with the species composition, except for community completeness of beech forest specialists and precipitation, which were omitted from the plot. Beech forest specialists are highlighted in bold red. Species abbreviations are explained in Appendix A. Stress = 0.17. CC = community completeness; BFS = Beech forest specialists; DBH = Diameter at Breast Height.

areas of the study region are not high enough to reach the treeline (approximately 1,800–1,900 m a.s.l.), so that beech forests are often the upper vegetation belt. This may reduce species pool size, species richness, and community completeness in high-elevation beech forests. Increased dominance and competition by *Fagus sylvatica* with increasing elevation may also play a role, due to higher shading, water uptake, and deposition of slowly decomposing litter in pure beech forests with respect to mixed stands of lower elevations (Hrivnák et al., 2014). The notable decrease of the total cover of the herb layer with increasing elevation could be due to multiple reasons, such as increased beech dominance, loss of tree diversity, and the disappearance of thermophilous species (Vockenhuber et al., 2011; Hrivnák et al., 2014).

Increasing precipitation did not affect community completeness, but significantly reduced the total cover of the herb layer. This suggests increased competition by beech in areas with more humid climates. *Fagus sylvatica* is highly sensitive to drought, so that its biomass productivity increases under wetter conditions (Leuschner, 2020). Higher precipitation leads to a higher deposition of organic matter on the beech forest floor (Meier and Leuschner, 2014), which could decrease the herb layer's abundance.

The positive effect of slope on community completeness may be linked to decreased litter accumulation. Beech litter is rich in lignin, acidifies the soil, and decomposes very slowly (Mölder et al., 2008). Such factors suppress understory species, locally decreasing community completeness of both whole communities and beech forest specialists in flat sites. The accumulation of large amounts of leaf litter in flat sites can result in the so-called “*Fagetum nudum*”, i.e., a beech forest without or almost without a herb layer (Sydes and Grime, 1981; Leuschner and Ellenberg, 2017). From this perspective, litter amount acts as a local environmental filter that reduces community completeness in low slope conditions, disfavoring any understory species including beech forest specialists. Conversely, steeper slopes can lead to a better expression of the local species pool (Hrivnák et al., 2014; Ujházyová et al., 2024), with a consequent increase in community completeness. However, a study from Spanish beech forests found no influence of litter cover and depth on understory species richness, despite the positive effect of slope (Sabatini et al., 2014).

Increasing DBH had no effects on the community completeness of whole communities, but it had a marginally significant positive effect on the community completeness of beech forest specialists. DBH is known to

increase with greater temporal distance from forest cutting, serving as a reliable indicator of forest maturity and successional stage (Meyer et al., 2021). Consistently, previous evidence showed that the number of species decreases in time after beech forest cutting, due to the gradual disappearance of species from open habitats (Bartha et al., 2008, 2020). Meanwhile, beech forest specialists are expected to increase in number in older forests with higher DBH (Campetella et al., 2016). Since we surveyed mature forests, such an increase in community completeness of beech forest specialists with increasing forest age was limited in our results.

Disturbance frequency had a positive relationship with the community completeness of whole communities. Consistently, species richness is known to increase after disturbance in forest ecosystems (Boch et al., 2013). This is due to the colonization by species from open habitats, which are only temporarily part of the species pool of beech forests at the moment in which they are severely altered by human interventions. Higher community completeness in disturbed forest ecosystems was also highlighted in tropical dry forests, though limited to tree species (de Oliveira Gonçalves-Araújo et al., 2024). In contrast with our results, recent studies in different forest types showed a lower community completeness in disturbed temperate forests, with respect to more natural ones (Wani et al., 2023).

#### 4.3. Relationships between species composition, predictor variables, community completeness, and herb layer cover

Increasing community completeness was related to species from lower elevations and warmer sites (Fig. 5), having their optimum in mixed deciduous woods more than in beech forests (Sabatini et al., 2011). Such species from neighboring communities are known to increase species richness in beech forests at low elevations (Hrivnák et al., 2014). In this context, high community completeness coped with the presence of other tree species besides beech, for instance, *Carpinus betulus*, *Ostrya carpinifolia*, and *Ulmus minor*. Such species are less competitive than *Fagus sylvatica* towards understory species, so that tree species diversity positively affects herb species richness in beech forests (Godefroid et al., 2005; Hrivnák et al., 2014). On the other side, low community completeness was still associated with species of undisturbed beech forests at upper elevations (*Galium odoratum*, *Oxalis acetosella*), suggesting a good conservation status of these communities despite the



low community completeness. There was also a tendency for beech forest specialists to occur more frequently at higher elevations and in mature forests, reflecting their known ecological preferences for moist and cool sites (Jiménez-Alfaro et al., 2018). Higher beech cover was negatively associated with thermophilous and basophilous species, such as *Arum maculatum*, *Corydalis cava*, and *Scilla bifolia*, whose presence coped with higher covers of the herb layer. In the study area, such species are linked to low-elevation beech forests and mixed deciduous woods (De Dominicis et al., 2010). Grass species of open habitats were associated with high slopes. In such conditions, temporary droughts are known to promote the presence of grasses instead of herbs in beech forests (Leuschner and Ellenberg, 2017). Higher DBH values were associated with tree species such as *Acer pseudoplatanus*, *Tilia cordata*, and *Ulmus glabra*. These species are typically found in undisturbed forests located in sites with low accessibility, like gorges and ravines (*Tilio-Acerion* vegetation) (Angiolini et al., 2012). Disturbance frequency was related to just a few ruderal species entering the studied beech forests, and only at low elevations. In fact, ruderal plants are known to decrease in number and abundance with increasing elevation and decreasing temperature (Halbritter et al., 2013). Upper elevations may also host fewer donor habitats for ruderal plants, due to the higher naturalness of the landscape (Ravnjak et al., 2022). The presence of thermophilous trees and shrubs in forests with higher disturbance and lower DBH can also be relatable to management, which favors other tree species in spite of beech (Petritan et al., 2012).

## 5. Conclusions and implications for ecosystem status assessments

Using a novel approach that examines the patterns of species richness in relation to the size of local species pools, we demonstrated that low observed plant diversity in *Fagus sylvatica* forests does not necessarily indicate ecosystem degradation. In our study, natural drivers - particularly the competition exerted by beech itself - were the main drivers of low plant diversity. This finding aligns with the presence of beech forest specialists that thrive in communities with naturally low completeness, suggesting that species-poor beech forests can still represent well-preserved ecosystems, supporting species adapted to minimal disturbance. Conversely, anthropogenic factors such as disturbance frequency tended to enhance community completeness. Since species absence in beech forests was primarily driven by local-scale factors, expanding the scale of observation to capture the spatial variability of plant diversity across forests could provide a deeper understanding of the features and ecological status of these ecosystems.

## CRedit authorship contribution statement

**Emanuele Fanfarillo:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Leopoldo de Simone:** Writing – review & editing, Data curation. **Tiberio Fiaschi:** Writing – review & editing, Methodology, Investigation, Data curation. **Bruno Foggi:** Writing – review & editing, Investigation, Data curation. **Antonio Gabellini:** Writing – review & editing, Investigation, Data curation. **Matilde Gennai:** Writing – review & editing, Investigation, Data curation. **Simona Maccherini:** Writing – review & editing, Validation, Methodology, Formal analysis, Data curation. **Emilia Pafumi:** Writing – review & editing, Formal analysis, Data curation. **Enrico Tordoni:** Writing – review & editing, Validation, Formal analysis, Data curation. **Daniele Viciani:** Writing – review & editing, Investigation, Data curation. **Giulio Zangari:** Investigation, Data curation. **Claudia Angiolini:** Writing – review & editing, Validation, Methodology, Investigation, Data curation, Conceptualization.

## Data availability

Upon request to corresponding author.

## Funding

This study was funded by the Tuscany region (project Nat-NET). Project funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 - Call for tender No. 3138 of 16 December 2021, rectified by Decree n.3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union – NextGenerationEU. Project code CN\_00000033, Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP B63C22000650007, Project title “National Biodiversity Future Center - NBFC”.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Claudia Angiolini reports financial support was provided by Tuscany Region. Emanuele Fanfarillo reports financial support was provided by European Union. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2024.100276>.

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