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Biodiversity Within and Beyond the Native Distribution of Tree Species: The Case of *Pinus nigra* Forests in Europe

Alessandro Bricca[1] | Borja Jiménez-Alfaro[2] | Milan Chytrý[3] | Kryštof Chytrý[3,4] | Josep Padullés Cubino[5,6] | Federico Fernández-González[7] | Dario Ciaramella[8] | Nicola Alessi[9] | Olivier Argagnon[10] | Bruno Cerabolini[11] | Alessandro Chiarucci[12] | Anh Tuan Dang-Le[13,14,15] | Michele Dalle Fratte[11] | Tetiana Dziuba[16] | Ali Kavgacı[17] | Ute Jandt[18,19] | Ülo Niinemets[20] | Mária Šibíková[21] | Kiril Vassilev[22] | Milan Valachovič[21] | Wolfgang Willner[4,23] | Gianmaria Bonari[8,24]

[1]Faculty of Agricultural, Environmental and Food Sciences, Free University of Bozen-Bolzano, Bolzano, Italy | [2]IMIB Biodiversity Research Institute (Univ. Oviedo-CSIC-Princ. Asturias), University of Oviedo, Oviedo, Spain | [3]Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic | [4]Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria | [5]Centre for Ecological Research and Forestry Applications (CREAF), Cerdanyola del Vallès, Spain | [6]Unit of Botany, Autonomous University of Barcelona, Cerdanyola del Vallès, Spain | [7]Department of Environmental Sciences, University of Castilla-La Mancha, Toledo, Spain | [8]Department of Life Sciences, University of Siena, Siena, Italy | [9]Institute for Environmental Protection and Research – ISPRA, Rome, Italy | [10]Conservatoire Botanique National Méditerranéen de Porquerolles, Antenne Languedoc-Roussillon, Montferrier-sur-Lez, France | [11]Department of Biotechnology and Life Science (DBSV), University of Insubria, Varese, Italy | [12]BIOME Lab, Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum University of Bologna, Bologna, Italy | [13]Department of Ecology – Evolutionary Biology, Faculty of Biology – Biotechnology, VNUHCM – University of Science, Ho Chi Minh City, Vietnam | [14]Vietnam National University, Ho Chi Minh City, Vietnam | [15]Center for Biodiversity Conservation and Endangered Species, Ho Chi Minh City, Vietnam | [16]M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine | [17]Forestry Faculty, Karabuk University, Karabuk, Turkey | [18]Department of Geobotany and Botanical Garden, Institute of Biology, Martin Luther University Halle-Wittenberg, Halle, Germany | [19]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany | [20]Chair of Crop Science and Plant Biology, Estonian University of Life Sciences, Tartu, Estonia | [21]Institute of Botany, Plant Science and Biodiversity Center, Slovak Academy of Sciences, Bratislava, Slovakia | [22]Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria | [23]Vienna Institute for Nature Conservation and Analyses (VINCA), Vienna, Austria | [24]National Biodiversity Future Center, NBFC, Palermo, Italy

Correspondence: Alessandro Bricca (alessandro.bricca@unibz.it)

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ABSTRACT

Aim: Forests dominated by non-native trees are becoming increasingly common. However, their impact on biodiversity remains uncertain, with a debate on whether they represent ‘green deserts’ or secondary habitats for biodiversity. We addressed this question by evaluating the patterns and ecological drivers of taxonomic and functional understory diversity between black pine (*Pinus nigra*) forests within and outside its native distribution range.

Location: Europe.

Methods: We collected a continental database of vegetation plots with full species composition and related functional traits. We compared α- and β-taxonomic (TD) and functional (FD) diversity between understories of *P. nigra* forests within and outside its native distribution range, and modelled the relative effects of climate, soil conditions, and canopy cover.

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Results: We found similar values of α- and β-TD and -FD in forests within and outside the native range. The response to local and large-scale drivers was also similar, with high canopy cover reducing α-TD and α-FD but enhancing β-TD and β-FD in both forest systems. Soil nutrients enhanced α-TD and α-FD and decreased β-FD only in forests within the native range, while drought reduced α- and β-diversities only in forests outside the native range.

Main Conclusions: The same dominant tree species under similar ecological conditions resulted in low diversity differentiation between forests both within and outside *P. nigra* native range. Nevertheless, understory diversity was sensitive to different ecological drivers, with stronger effects of soil fertility and moisture on forests within and outside native ranges, respectively. These results suggest that *P. nigra* forests established beyond the species' native range exhibit similar diversity metrics and ecosystem functions as those within its native range. Our findings may be linked to the fact that *P. nigra* forests outside the native range were placed in the same biogeographical region as the corresponding forest stands within the native range.

1 | Introduction

From 1990 to 2015 the area of planted forests increased from 0.17 to 0.28 billion hectares globally (Freer-Smith et al. 2019). In the coming years the area of planted forests is expected to expand significantly, driven by global tree-planting initiatives such as the One Trillion Tree Initiative (www.1t.org), an initiative of the World Economic Forum to support the United Nations Decade on Ecosystem Restoration, or the Bonn Challenge (www.bonnchallenge.org) supported by the IUCN and the European Union Biodiversity Strategy for 2030 (European Commission 2020). While safeguarding natural habitats remains the primary strategy to buffer biodiversity loss, planting forests has emerged as a potential complementary strategy in mitigating biodiversity decline. About 19% of the worldwide planted forests are composed of 'non-native trees' (NNT), that is, species occurring outside their native range (Payn et al. 2015; Zhu et al. 2020). Among the array of ecosystem services that plantations of NNT may provide (e.g., increasing carbon sequestration and soil stability improvement), their significant contribution often lies in rapid growth rates and higher timber production compared to native trees (Tapias et al. 2004; Payn et al. 2015; Ne'eman and Osem 2021). Additionally, the integration of NNT in managed forests can be a promising measure of forest adaptation to future climate change. For example, the increased temperatures and prolonged droughts may be detrimental for native trees, especially those in regions experiencing more stable climates. The introduction of NNT species from warmer regions in managed forests might be crucial for maintaining forest productivity and stability over time (Fuchs et al. 2022; Zsolnay et al. 2023). Nevertheless, despite long-time research on plantations of NNT trees (Booth 1896), the implications of their use on biodiversity are still controversial (Taylor et al. 2016; Wohlgemuth et al. 2022; Wang et al. 2022; Wildermuth et al. 2024).

The current debate on the effect of plantations of NNT is dominated by two contrasting views (Pötzelsberger et al. 2020). One view considers plantations of NNT as 'green deserts' with deprived understory plant diversity and dynamics compared to forests of native trees. Another view considers that plantations of NNT might have positive effects on local environmental conditions and vascular understory vegetation, also preserving diversity at higher trophic levels (Pawson et al. 2008; Brockerhoff et al. 2008; Barbier et al. 2008; Horák et al. 2019; Wang et al. 2022; Zhu et al. 2020; Wohlgemuth et al. 2022; Wildermuth et al. 2024). These different views might stem from comparisons of understory plant diversity between forest systems, that is, broadleaved and conifer forests (Barbier et al. 2008; Horák et al. 2019; Wildermuth et al. 2024). Such comparisons assume that different forest systems in nearby locations and under similar abiotic conditions should host similar understory plant communities, with differences attributed solely to plantations of NNT. However, different leaf types (needle vs. broadleaved) have different impacts on the ecological condition of the understory. For example, needle leaves intercept more water compared to broadleaved leaves, selecting for a more drought-resistant understory plant diversity (Augusto et al. 2015). Thus, to gain a more insightful understanding of the effect of plantations of NNT, it is crucial to obtain reliable information on understory plant diversity between forests within and outside the native range of the same dominant tree species (Taylor et al. 2016; Landuyt et al. 2019). This will help to evaluate the benefits, if any, of NNT planting programs, considering ongoing global change and associated costs of ecosystem restoration.

Understory diversity patterns may be affected by different ecological drivers in different forest types (Večeřa et al. 2019; Padullés Cubino et al. 2021). Surprisingly, there is a scarcity of information regarding the role of these drivers in plantations of NNT, leaving a critical knowledge gap that prevents a more comprehensive understanding of the factors that influence their understory structure and functions. Community assembly theory predicts that the composition of local plant communities is the result of different spatial filters (Götzenberger et al. 2012). Climate represents a first large-scale filter with which species must cope whereas soil conditions and forest structure become prominent at finer scales (de Bello et al. 2013; Jiménez-Alfaro et al. 2018; Padullés Cubino et al. 2021). Consequently, soil and forest structure should be the principal drivers for local diversity (i.e., α-diversity) variation, while climate should predominantly shape within-region (i.e., β-diversity) variation (Mugnai et al. 2022). Traditionally, α- and β-diversity have been quantified with taxonomic metrics, playing a crucial role in assisting conservation and restoration planning (Socolar et al. 2016). However, using only a taxonomic approach prevents a full understanding of the mechanisms involved in community assembly, with repercussions for conservation efforts (Bricca et al. 2024). Taxonomic approaches consider all species similar, covering the diversity of their functional strategies. Species functional strategies can be quantified by functional traits, representing a useful tool to understand how species interact with environmental changes (Funk et al. 2017; Bricca, Bonari, et al. 2023). Studies that simultaneously consider different spatial components of plant diversity (α- and β- components) and different facets of diversity (taxonomic and functional) can greatly advance the understanding of the drivers underlying plant diversity.

This study aims to determine: (i) whether α- and β-taxonomic and functional plant diversity of understory differs between forests within and outside the native distribution range of a given tree dominant species, and (ii) what the relative effects of spatial filters (climate, soil conditions and canopy cover) on α- and β-taxonomic (TD), and functional (FD) diversity in forest understories within and outside the native range of the tree species. To evaluate α- and β-TD and FD, we combined forest vegetation plots from the European Vegetation Archive (EVA; Chytrý et al. 2016) with plant functional traits from The Plant Trait Database (TRY; Kattge et al. 2020) and environmental data. We focused on the relationships between understory plant diversity and climate, soil and canopy cover, and compared them between forests within and outside the native distribution range of *Pinus nigra* species.

2 | Material and Methods

2.1 | Study System

We studied forests dominated by the evergreen conifer tree *Pinus nigra* J.F.Arnold (European black pine) both within and outside the species native distribution range. *P. nigra* forests extend over more than 3.5 million hectares in the Mediterranean Basin, making it one of the most abundant and widespread pine species there. It has a predominantly mountain distribution which ranges from the Iberian Peninsula to easternmost Anatolia, having the northernmost spontaneous occurrence at the eastern margin of the Alps near Vienna, Austria (Caudullo et al. 2017). This circum-Mediterranean distribution depends strongly on its specific ecological features. *P. nigra* has a deep root system, a high seed production, fast growth rate, early maturity, long age, and a low nutrient requirement, making this species able to cope with different environmental conditions (Ne'eman and Osem 2021; Seda Keleş and Kavgacı 2025).

Within its native distribution range, *P. nigra* occurs in pure stands or in mixed stands with broadleaved or other conifer species, in particular with *Pinus sylvestris*. Mixed forests of *P. nigra* and *P. sylvestris* are classified as two habitats named 'Temperate and submediterranean montane *Pinus sylvestris*–*Pinus nigra* forest' and 'Mediterranean montane *Pinus sylvestris*–*Pinus nigra* forest' according to the European Nature Information System (EUNIS) habitat classification (Chytrý et al. 2020). They also belong to Natura 2000 priority habitat 9530* '(Sub)Mediterranean pine forests with endemic black pines' as defined by the EU Habitats Directive (92/43/EEC).

Historically, *P. nigra* has been planted across Europe within and outside its native distribution range, with the aim to ensure soil stability (i.e., protection forests) and to promote local economy mainly from the 19th century to the second half of 20th century (Ne'eman and Osem 2021), but these plantations often degraded valuable habitats, for example, grasslands of conservation importance. *P. nigra* forests within the species native range are mainly natural, but can also include plantations and self-sown stands (i.e., natural regeneration) deriving from plantations. In contrast, *P. nigra* stands outside the species native distribution range are plantations of NNT. This latter forest type can be referred to as 'old-established plantations' (Bonari et al. 2017). To a lesser extent, these forests can also include self-sown stands of NNT derived from plantations.

2.2 | Plant Community Data Cleaning

All data manipulations and statistical analyses were done in R statistical programming language (R Core Team 2021). We collected European pine forest data that were not present in the European Vegetation Archive (EVA; Chytrý et al. 2016) and stored them in a thematic database (CircumMed Database; Bonari et al. 2019). Data on *P. nigra* forests included vegetation plots from within and outside the native distribution range in southern and central Europe. After making the CircumMed Database part of EVA, we requested georeferenced vegetation plots from EVA (Project no. 145; https://euroveg.org/eva-database/projects) for all plots containing *P. nigra*, excluding Macaronesia, Fennoscandia, and Russia. This dataset consisted of 10,907 plots. To have comparable biogeographical conditions between the understory of forests within and outside the native distribution range, we excluded all plots north of the Carpathians, which are the northernmost mountains within the native range of *P. nigra* (Caudullo et al. 2017).

Vegetation plots with a location uncertainty of more than 10 km were excluded. We standardised the nomenclature at the species level according to The Plant List using the R package 'Taxonstand'. To reduce potential inconsistencies across the dataset, we performed the following steps of data cleaning (Loiola et al. 2018; Bonari et al. 2021). First, we merged records of the same species in different layers into a single layer and we associated each species with its growth form (i.e., tree, shrub or herb) as indicated in the TRY database (Kattge et al. 2020). Second, we discarded all plots where *P. nigra* cover was lower than 15%, to exclude open vegetation with the presence of pines. Third, we discarded all plots where *P. nigra* cover was lower than the sum of the covers of the other tree species, thus focusing on *P. nigra*-dominated stands. Further, we removed: (i) non-identified species; (ii) bryophytes, lichens, and algae; (iii) species with less than five occurrences across the dataset. We also removed the plots with sizes of $<50\,\mathrm{m}^2$ and $>1000\,\mathrm{m}^2$, but plots without size information were retained assuming that most of them were within this size range. To reduce the effects of spatial autocorrelation, we assigned all plots to cells of a geographical grid of 1 km × 1 km, and we resampled the plots by randomly selecting one plot from each grid cell (Loiola et al. 2018). Lastly, we removed the plots with less than three species in the understory layer (i.e., herb and shrub species), since functional indices required at least three species to be computed. The final dataset comprised 1362 plots (68% with 1 km of accuracy, and 5% with 10 km of accuracy) and 918 understory vascular plant species. For each plot of the final dataset, we assigned a categorical status (i.e., within or outside native range) according to whether the plot fell within the *P. nigra* native range based on the most recent distribution map of *P. nigra* native distribution in Europe (Caudullo et al. 2017). Small areas identifying the native distribution of *P. nigra* in the map of Caudullo et al. (2017) falling outside the continuous range were added to the distribution range map as circles with a 20 km buffer. Then, we overlaid the selected plot located on the geographic grid of 1 km × 1 km with the distribution range of *P. nigra* to classify forest stands. Plots that overlapped with the distribution area were considered within the native range, while those that did not overlap were classified as outside the native range. We are aware this approach can misclassify those forest stands close to the native distribution range, but it ensures comparability across European regions. Identifying the degree of management of forest stands is impractical when working with a large database as detailed information on stand history is generally missing (Bonari et al. 2017, 2021; Chytrý et al. 2020). Our plots within the native species range are mainly represented by natural forests and plantations of a site-native tree that are impossible to disentangle at the continental scale using only species compositional data (Chytrý et al. 2020). Nonetheless, since in Europe primary forests are rare (< 1% of the European forest cover; Sabatini et al. 2018), we assume all forest stands within the native distribution range have been subjected to some degree of management. Forest stands falling outside the native distribution range of *P. nigra* are more homogeneous in terms of management, being mostly plantations of a NNT and potentially self-sown stands derived from NNT planted.

Forest stands within the native distribution range were represented by 839 plots with 754 vascular plant species, while forest stands outside the native distribution range were represented by 523 plots with 720 vascular plant species (Figure 1). Details on sources of the plots used for the analyses are reported in Appendix S1.

2.3 | Plant Trait Data

We considered four functional traits, namely plant height (H), seed mass (SM), leaf area (LA), and specific leaf area (SLA) that represent key strategies of forest understory species (Burton et al. 2020; Carmona et al. 2012). Specifically, H is a whole-plant trait related to competitive ability and dispersal ability. SM expresses competitive ability at the seedling stage and dispersal ability. SLA and LA are two leaf traits related respectively to the leaf economic spectrum and water balance strategies (Díaz et al. 2016). Moreover, we assigned each species to a growth form and selected only understory species, that is, all non-tree species. Trait data were obtained from the TRY database (Kattge et al. 2020) and their availability was 100% for H and SLA, 92% for SM, and 90% for LA.

2.4 | Environmental Data

Since we were interested in the relative effect of spatial filters on plant diversity (Jiménez-Alfaro et al. 2021), we considered three groups of environmental predictors related to different spatial scales: (i) climate, (ii) soil, and (iii) canopy cover.

2.4.1 | Climatic Conditions

We used CHELSA data (Karger et al. 2021) to retrieve the following climatic features at 1-km resolution: mean annual temperature (bio1, °C), annual precipitation amount (bio12, kg m^{-2}), temperature seasonality (bio4, °C/100), precipitation seasonality (bio15, kg m^{-2}), growing season length (gsl, number of days), accumulated precipitation amount of growing season (gsp, kg m^{-2}), and snow cover days (scd, number of days $yr.^{-1}$). We also included potential net primary productivity (npp, g C $m^{-2} yr.^{-1}$) (Karger et al. 2021). We selected these variables as they profoundly influence vegetation (Jiménez-Alfaro et al. 2021; Padullés Cubino et al. 2021; Kambach et al. 2023). To summarise large-scale filters, we ran a principal component analysis (PCA) and extracted the scores of the first two PC axes (Appendix S2). The first PC axis (47% of explained variance) reflected a climatic gradient ranging from a cold continental climate with higher temperature seasonality (lower PC1 scores) to a warm oceanic climate with lower temperature seasonality (higher PC1 scores) (hereafter 'oceanicity gradient'). The second

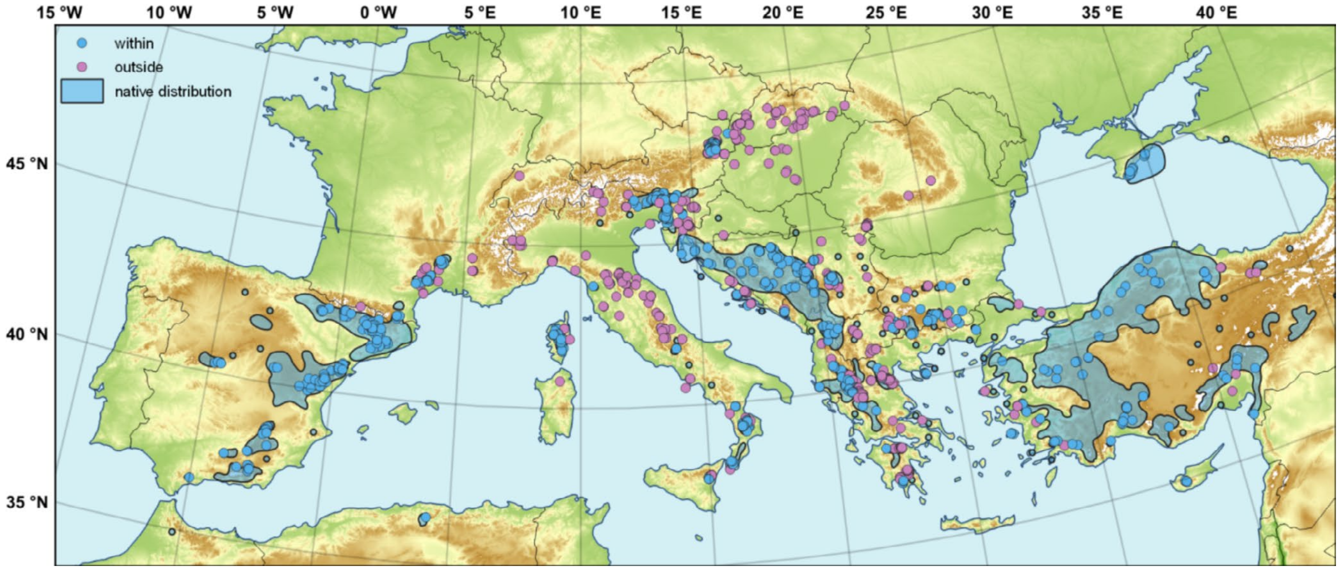

FIGURE 1 | Geographic distribution of the selected *Pinus nigra* forest vegetation plots across the Mediterranean Basin and adjacent areas. The plots within the native distribution range are in blue, while the plots outside the native distribution range are in violet (Caudullo et al. 2017). The native distribution range is shown in light blue. The size of the circles is for illustrative purposes only and does not reflect the actual size of forest stands.

PC axis (24% of explained variation) reflected a precipitation gradient ranging from lower precipitation (lower PC2 scores) to higher precipitation (higher PC2 scores) (Appendix S2).

2.4.2 | Soil Conditions

We retrieved the following soil variables (at 15 cm depth) from the SoilGrids database (Poggio et al. 2021) at a resolution of ~250 m, which we rescaled to 1-km resolution: cation exchange capacity (CEC, cmol(c) kg^{-1}), total nitrogen (N, g kg^{-1}), pH, soil organic carbon concentration (SOC, g kg^{-1}), soil content of clay, silt, and sand (%). To summarise small-scale filters, we ran a principal component analysis (PCA) and extracted the scores on the first two axes (Appendix S3). The first PCA axis (41% of explained variance) reflected a nutrient gradient ranging from nutrient-poorer soils to nutrient-richer soils (i.e., the higher nitrogen and soil organic carbon, the higher PC1 score). The second PCA axis (26% of explained variance) reflected a water-holding capacity gradient ranging from soil with lower water retention to soil with higher water retention (i.e., the higher sand content and lower clay and silt content, the higher PC2 score) (Appendix S3).

2.4.3 | Canopy Cover

We calculated the canopy cover for each plot using Jennings–Fischer's formula, which combines the covers of all tree species present in the plot into a single cover value that does not exceed 100% (Jennings et al. 2009; Fischer 2015).

2.5 | Statistical Analysis

We partitioned the understory plant diversity into α- and β- TD and -FD. We used species richness to estimate the α-TD and functional richness based on four traits (H, SM, SLA, and LA) to estimate the α-FD. Functional richness reflects how much functional space is occupied in a community, that is, the extent of community niche breadth (Cornwell et al. 2006). Species richness and functional richness are robust indices possessing significant explanatory power when investigating the relationship between ecosystem functions and biodiversity (Liu et al. 2024). We calculated α-FD using $\log_{10}$-transformed trait data to reduce the influence of (few) missing trait values (Májeková et al. 2016) in combination with Gower distance as a measure of species trait distance. Gower distance is the most appropriate distance measure for trait-based analysis as it handles missing trait values and standardises the functional distances into a range between 0 (two species have the same traits values) and 1 (two species have maximum different traits values) (Pavoine et al. 2009). To calculate functional richness, we used the *dbFD* function in the FD package (Laliberté et al. 2014).

For β-TD, we calculated the plot pairwise dissimilarity matrix with presence/absence species data and Jaccard distance as a dissimilarity measure, and using the *beta.pair* function in the betapart package (Baselga et al. 2023). The β-FD was calculated similarly to β-TD to have comparable facets, that is, with presence/absence species data and Jaccard distance, using the *beta.fd.multidim* function in the mFD package (Magneville et al. 2022).

Before exploring if the α-TD and α-FD of understory plant communities were different between forests within and outside the native distribution range of the dominant tree species, we checked if both α-diversity facets followed a normal distribution with the Shapiro test. Since they did not follow a normal distribution, we applied an unpaired two-tailed Mann–Whitney *U* test (*wilcox.test* function in the stats package). To compare the values of environmental variables (oceanicity, precipitation, soil nutrients, soil water-holding capacity, and canopy cover) between forests within and outside the native distribution range of the dominant tree species, we used an unpaired two-tailed *t*-test (*t*.test function in the stats package) since all the environmental variables showed normal distribution except for canopy cover, which showed non-normal distribution. In this case, an unpaired two-tailed Mann–Whitney *U* test was applied.

We then tested whether β-TD and β-FD were different between forests within and outside the native distribution range of the dominant tree species, running multivariate homogeneity of variances using the *betadisper* function in the vegan package (Oksanen et al. 2022). To visualise the patterns in the multivariate space, we ran principal coordinate analysis (PCoA). Further, we tested the degree of distinctiveness (R-value) of β-TD and β-FD by performing the analysis of similarity with the *anosim* function in the vegan package between forests within and outside the native distribution range. R-values close to 1 indicate highly dissimilar (or distinctiveness) groups, while R-values close to 0 indicate scarcely dissimilar (or distinctiveness) groups (Clarke 1993).

We used multiple linear regression to investigate the relative effect of climate, soil, and canopy cover on patterns of α-TD and α-FD. Because we used plots of different sizes, and larger plots can host more species or more functionally dissimilar species, we incorporated plot size as a covariate in the models. The predictors were centered to the mean and scaled by one standard deviation (*decostand* function in the vegan package). Model assumptions, namely normality and homoscedasticity of residuals, were evaluated visually, while the multicollinearity of predictors was evaluated using variance inflation factors (VIF). We adopted a stringent threshold and considered predictors with values higher than 4 multicollinear (Zuur et al. 2010). The presence of spatial autocorrelation in the models was tested using the Mantel test (*mantel* function in the vegan package) between the distance matrix of model residuals and the distance matrix of geographic coordinates. We did not find any significant autocorrelation in the models' residuals (Appendix S4). Since no assumptions of the multiple linear regression model were violated, we did not need to transform explanatory variables or adopt more sophisticated statistics (St-Pierre et al. 2018). Finally, we examined the relative contribution of single and joint effects of climatic and soil variables and canopy cover on α-TD and α-FD using variation partitioning (*varpart* function in the vegan package).

To investigate the effect of climate, soil, and canopy cover on β-TD and β-FD, we performed multiple regression on distance matrices (*MRM* function in the ecodist package; Goslee and Urban 2007). We controlled for the effect of geographic distance by including a matrix of distance between coordinates as a predictor in the models. We ran 999 permutations to determine statistical significance for each regression (Legendre et al. 1994) and obtained the standardised regression coefficient for each predictor in the models to compare the effects on a common scale. In addition, to examine the amount of relative variance explained by the single and joint effects of climate, soil, and canopy cover on β-taxonomic and functional diversity, we used generalised dissimilarity modelling (*gdm.partition.deviance* function in the gdm package; Fitzpatrick et al. 2020).

3 | Results

3.1 | Forest Diversity Within Versus Outside the Native Range of the Dominant Tree Species

Forests within and outside the native distribution range did not differ significantly in α-TD (z-score $= -0.85$, $p = 0.4$), both having on average 18 species. The lack of significant difference was also found for α-FD (z-score $= -0.08$, $p = 0.9$), with native and planted forests having α-FD values of 0.7 (Figure 2; Appendix S5).

Forests within and outside the native distribution range did not differ significantly in the degree of oceanicity, soil nutrient content, and canopy cover, although forests within the native range were characterised by slightly more precipitation and lower water-holding capacity (Appendix S6).

Regarding β-TD, the analysis of variance detected a significant difference ($p < 0.01$) between the understories of forests within and outside the native distribution range. However, the average distance from centroids was very similar for both forest types (0.67 and 0.66 for forests within and outside the native range, respectively), leading to a very small variance explained ($R^2 < 1\%$). Accordingly, both systems showed a highly similar extent (Figure 3a) and a strong overlap (i.e., similar species composition; Figure 3a) in the multidimensional space (R-value $= 0.02$; $p < 0.01$). For β-FD, we found a similar small variance explained by forest systems as for β-TD ($R^2 < 1\%$), but we did not find a significant difference in the average distance between the centroids of the two forest systems (0.62 and 0.62 for forests within and outside the native distribution range, respectively; Figure 3b). Also, the understory of forests within and outside the native distribution range showed similar composition in trait values (R-values < 0.01; $p > 0.3$).

3.2 | Drivers of Alpha Diversity

Understory diversity of forests within and outside the native distribution range responded significantly to the three sets of predictors: climate, soil, and canopy cover. Canopy cover affected α-diversities negatively in both forest systems (Figure 4a,b). Oceanicity also exerted a negative effect on α-TD in both forest systems (Figure 4a,b), but negatively influenced α-FD only in forests within the native range (Figure 4a). All the other predictors affected only one of the two forest systems. Specifically, soil nutrients affected positively solely the α-TD and α-FD in forests within the native range, soil water-holding capacity affected solely species richness in forests outside the native range (Figure 4b) and precipitation affected species and functional richness in forests outside the native range (Figure 4b). Model results are reported in Appendix S7.

For α-TD, we found canopy cover alone explained a higher variation for both forests within and outside the native distribution with similar contributions (35% and 34%, respectively). We detected an overall higher contribution of climatic conditions and local factors in forests outside than within their distribution range (i.e., soil and its interaction with canopy cover). In the case of α-FD, we found a contrasting pattern, with canopy cover (32% and 19% for forests within and outside the native distribution range, respectively) and the joint

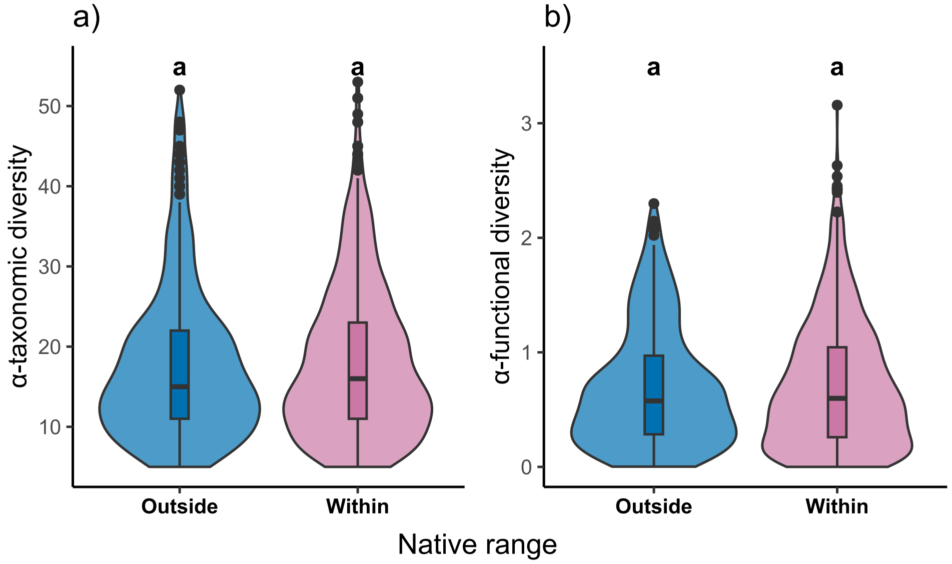

FIGURE 2 | Comparison of α-diversity between European forests dominated by *Pinus nigra* within and outside the native distribution range of the dominant tree species; (a) taxonomic diversity (expressed as species richness), (b) functional diversity (expressed as functional richness). Same letter equals lack of statistical difference according to unpaired two-tailed *t*-test.

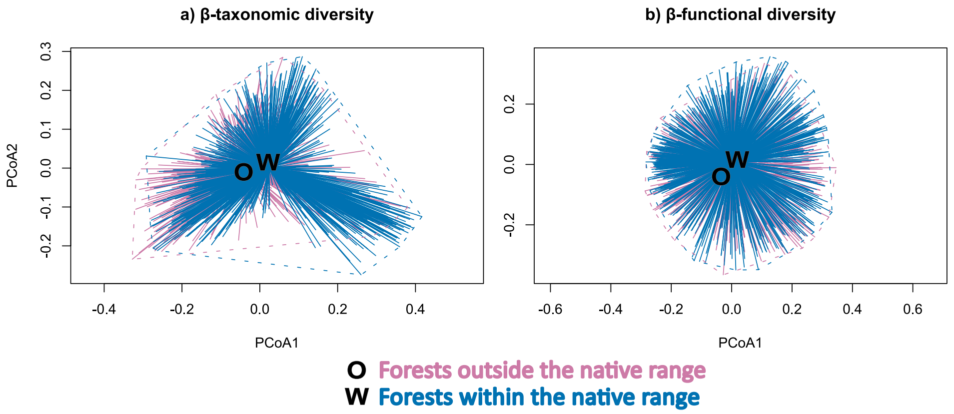

FIGURE 3 | β-diversity comparison of *Pinus nigra* forests within and outside the native distribution range of the dominant tree species: (a) β-taxonomic diversity, (b) β-functional diversity. The centroids are labelled with 'W' for forests within the native distribution range of *P. nigra* (blue) and 'O' for forests outside its native distribution range (violet).

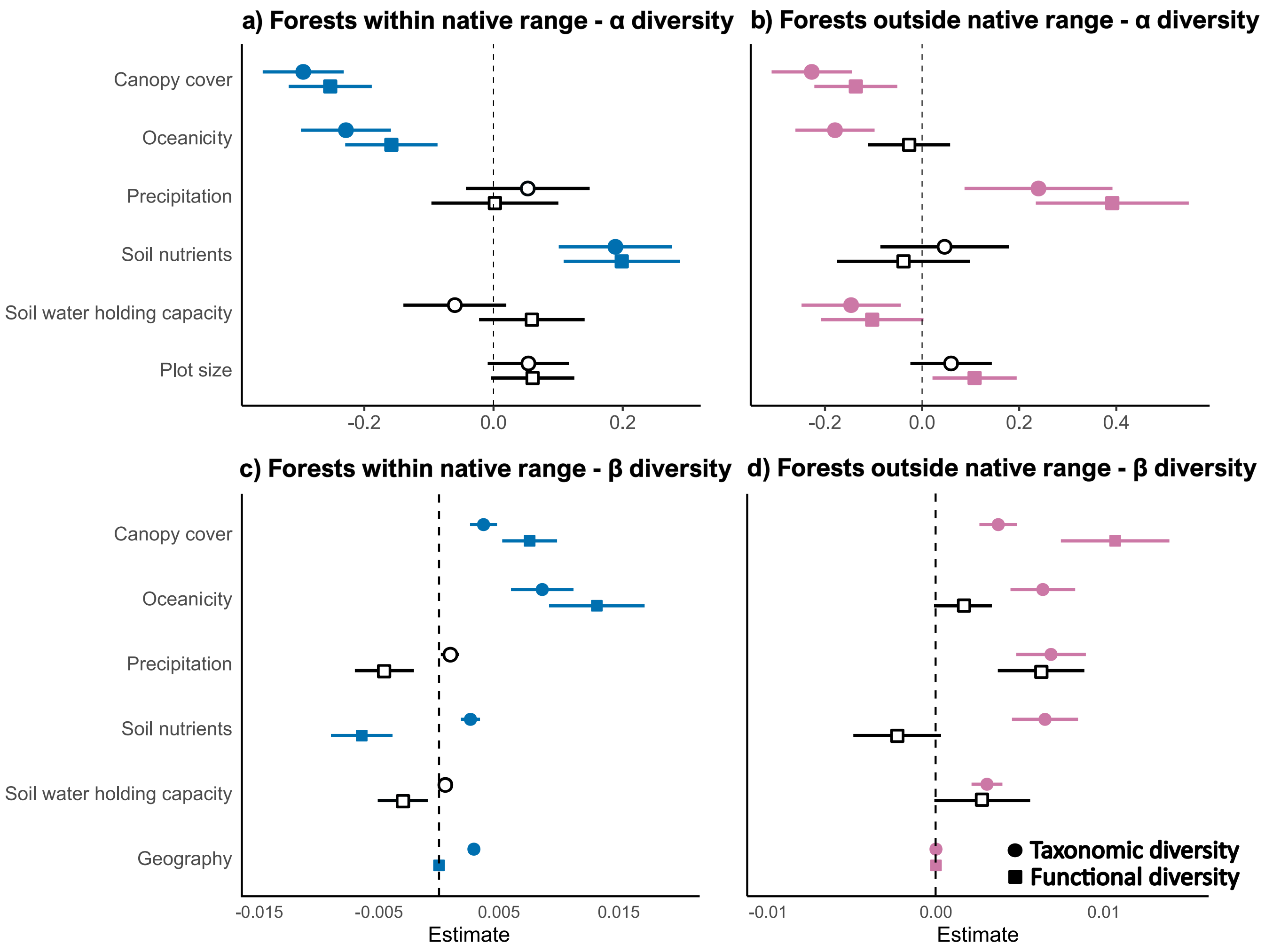

FIGURE 4 | Estimated coefficients (±95% confidence intervals) for all standardised predictors included in the models; (a and b) for α-taxonomic diversity (expressed as species richness) and α-functional diversity (expressed as functional richness); (c and d) for β-taxonomic and functional diversity. Soil water-holding capacity ranges from soil with low capacity (high values of the predictor) to soil with high capacity (low values of the predictor). For details about predictors see Appendices S3 and S4. Empty black symbols indicate non-significant effects. Significant effects are highlighted by filled blue and violet symbols for within and outside the native distribution range of *Pinus nigra*, respectively. Both α-diversities are scaled to the mean and centered around zero to facilitate graph visualisation.

effect of climate and soil having higher relative importance in forests within the native distribution range compared to the forests outside the native distribution range (27% and 13%, respectively). In forests outside the native range, we found higher importance of climatic conditions (47%) than in forests within the native distribution range (12%). Detailed results are reported in Appendix S8.

3.3 | Drivers of Beta Diversity

Overall, we found that climate, soil conditions, and canopy cover influenced β-TD and β-FD of understory plant communities (Appendix S9). Considering β-TD, we found consistent and positive effects of oceanicity, soil nutrients, and canopy cover for both forests within and outside the native distribution range, while precipitation and soil water-holding capacity affected positively only β-TD of forests outside the native range (Figure 4c,d). Similarly to β-FD, we found some predictors having a consistent influence for both systems and others affecting only one of them. Specifically, canopy cover was the only predictor influencing both systems in a positive manner, while oceanicity and soil nutrients affected positively and negatively only the functional β-diversity of forests within the native distribution range of the dominant tree species (Figure 4c,d).

Regarding the relative contribution of climate, soil, and canopy cover to β-diversity (see details in Appendix S10), we found that for β-TD climate conditions alone explained a higher variation for both forests within and outside the native distribution range than other predictors. Nonetheless, we detected greater importance of climate for forests within than outside the native range (50% and 31%, respectively). We also found that canopy cover alone explained a higher variation for forests within the native range (30%), whereas soil conditions alone explained a higher relative variation for forests outside the native range (28%). Further, we found a joint effect of climate with soil in explaining the higher relative contribution for forests within the native range (12%), and canopy cover alone for forests outside the native range (20%). Regarding β-FD, we found canopy cover alone explained a higher variation than other predictors for forests within and outside the native distribution range (52% and 57%, respectively). Climate only explained a higher variation than other predictors for forests within and outside the native distribution range (49% and 29%, respectively).

4 | Discussion

In this study we compared forest plant diversity within and beyond the native range of the same dominant tree species at the macroecological scale. Such an approach allowed us to test the effect of plantations of non-native trees by excluding the effect of leaf shape of different forest systems (needle-leaves vs. broadleaved-leaves; Augusto et al. 2015) on understory plant diversity. This approach provided new insights to the existing literature on the effects of plantations of NNT on biodiversity (Barbier et al. 2008; Brockerhoff et al. 2008; Horák et al. 2019; Taylor et al. 2016; Wang et al. 2022; Wohlgemuth et al. 2022).

We found that plantations of non-native *Pinus nigra* in Europe show, in general, similar understory biodiversity patterns as corresponding forests within the species native range. This finding can be explained by different factors, which jointly contribute to a low differentiation between the two systems: (i) the filtering effect exerted by dominant tree species; (ii) the similar ecological conditions; and (iii) the biogeography of the planted non-native tree (NNT). NNT can operate as environmental filters that affect species in the understory (Šibíková et al. 2019; Wohlgemuth et al. 2022), but the result of that filtering had not yet been documented between forests within and outside the native distribution range dominated by the same tree species. Our results suggest that, at least for European plantations of *P. nigra* outside the species' native range, the filtering effect of the tree layer on understory plant diversity is comparable to that of forests within the native range. While some studies found that different canopy trees can select different sets of understory species (e.g., Slabejová et al. 2019), others have found differences in ecological conditions to be more important than dominant tree species (Piwczyński et al. 2016; Padullés Cubino et al. 2021). In our study system, all forest plots not only share the same dominant tree species, but also a similar range of ecological conditions, which can jointly contribute to the lack of compositional and functional differentiation between forests within and outside the native range. Among the ecological conditions, canopy cover, a proxy of light availability in the understory, has been recognised as one of the most important factors influencing understory diversities not only in natural forests within native distribution ranges but also for plantations of NNT (Wang et al. 2022). The lack of compositional and functional differentiation can also be attributed to the biogeographic origin of the non-native planted tree. Recent studies highlighted how the major impacts on plant diversity in plantations derive from the use of NNT belonging to biogeographical regions different from native species (Wohlgemuth et al. 2022). Plantations of NNT belonging to the same biogeographic area are generally more similar in habitat structure to native forests than plantations of NNT coming from other biogeographic areas, making the understory more suitable for hosting natural vegetation (Wang et al. 2022). Accordingly, *P. nigra* had a larger range in the Pleistocene than today (Scotti-Saintagne et al. 2019) and many of its forests outside the current native range are in the areas where the species was native before the onset of the Holocene. In contrast, plantations of NNT species in Europe from different biogeographical regions, such as *Eucalyptus globulus* from Tasmania, or *Robinia pseudoacacia* from North America, strongly alter the understory of plant communities (Šibíková et al. 2019; Slabejová et al. 2019; Ho et al. 2023). Despite all these considerations, we are aware that we lack precise information about the exact age of the plantations and their related management, preventing us from drawing more specific conclusions. However, their impact on model performance might be inconsistent, since forest understory demonstrates a high level of variation primarily during the initial years after plantation establishment, especially for understory richness data (ca. 25–30 years; Wang et al. 2022; Chelli, Tsakalos, et al. 2024), while management practices tend to be less important factors with increasing spatial scale (Chelli, Bricca, et al. 2024).

Despite the lack of difference in α- and β-TD and -FD, we found contrasting contributions of spatial filters on the two forest systems. The total explained variance was relatively high, considering that we did not include other factors reflecting landscape, forest management, or historical effects (Bruelheide et al. 2018; Jiménez-Alfaro et al. 2018). In line with the community assembly theory, local filters (canopy cover and soil conditions) exerted a stronger influence than regional ones on α-TD and α-FD of forests within the native range (Zhang et al. 2014; Mugnai et al. 2022). Nonetheless, comparing the relative contribution of the local filters, we found that light condition represents the main ecological driver in affecting local diversity (Padullés Cubino et al. 2021). In contrast, for plantations of NNT, we found the strongest contribution of regional filters (climate) and local filters (soil conditions), respectively, on α- and β-diversity. Such an opposite pattern can be related to the fact that plantations of NNT are man-made ecosystems whose origin is related to specific purposes such as preventing soil erosion (i.e., protection forests) or timber production.

We found that canopy cover was the only environmental variable that affects understory diversity of both forest systems. The effect of canopy cover on reducing both TD and FD is well-documented in the literature, indicating that low light availability under denser canopy acts as an ecological filter that species must overcome (DeClerck et al. 2005; Chelli, Bricca, et al. 2024). This pattern was consistent both within and outside the native range of *Pinus contorta* (Taylor et al. 2016). The filtering effect exerted by canopy cover acts not only within plots but also between plots, influencing species and functional turnover. These results reinforce the concept that only certain species with specific trait syndromes can persist under shady conditions of dense forest canopies. We also found water availability and precipitation showing different effects in plantations of NNT and forests within the native distribution range. Our results are in line with previous evidence showing that aridity can reduce the species richness without altering the functional composition of the community (de Bello et al. 2006). This filtering effect also occurs at a large scale since increased drought conditions act as a driver promoting different plant communities (β-TD). Whilst wetter and drier conditions are responsible for a considerable β-TD (Carmona et al. 2021), oceanicity and soil nutrients strongly affected the understory of forests within the native range of the dominant tree species. In our case, higher oceanicity implies a lower temporal intra-annual variability, which in turn may support less diverse functional strategies (Lancaster et al. 2017). Such filtering occurs not only at the local scale (forest sites under lower oceanicity host higher α-TD and α-FD) but also at a broader scale by positively influencing β-TD and β-FD, as different conditions of oceanicity are associated with different species and functional strategies.

Soil nutrients represent another key driver influencing the diversity of forest understory (Zhang et al. 2014). Our results align with previous investigations finding a parallel decrease of α-TD in relation to productivity not only for overstory but also for understory (Liang et al. 2016; Zhang et al. 2017), though exceptions to this relationship exist (e.g., Oberle et al. 2009). Nutrient-poor soils filter for lower species, some of them strongly adapted to low mineralisation (e.g., undemanding species; Grime and Pierce 2012; Mouchet et al. 2010; Mugnai et al. 2022; Bricca, Sperandii, et al. 2023). However, different soil nutrient conditions are responsible for consistent variation in β-TD and β-FD with different trends. Accordingly, forest sites with different soil conditions host different species with similar functional strategies.

5 | Conclusion

Our findings suggest that forests dominated by a native tree and plantations of the same tree species outside its native range, but in the same biogeographical region, show similar vascular plant species and functional richness. These biodiversity metrics were driven by similar environmental factors, except for soil fertility and moisture. In our study system, *Pinus nigra* is commonly planted in climatic conditions similar to its native habitats. This resemblance between *P. nigra* forests within their native distribution range and plantations outside its native range may serve as an example for Southern Europe of maintaining understory plant diversity patterns with a native species from the same biogeographical region. We found that the understory diversity in plantations of NNT is shaped by a combination of unique ecological drivers (such as water availability) and more general ecological factors (such as canopy cover) that affect both forest systems. However, the latter have less pronounced effects compared to their impacts in forests within their native distribution ranges. Plantations of non-native trees may, over time, come to resemble the diversity of forests within the native distribution range and perform similar ecosystem functions, but it is essential to avoid oversimplified perceptions of their role. Although our results highlight that in certain cases plantations of non-native trees may recover certain ecosystem services, a 'do-not-harm' conservation principle should be followed. When a first choice based on native species is not possible, a careful selection of tree species belonging to the same biogeographical area, planted in similar environmental conditions of the native range, might result in similar biodiversity services.

Author Contributions

A.B., B.J.-A., and G.B. conceived the idea. G.B., with the contribution of D.C., and F.F.-G., prepared the gap-filling dataset. A.B. with the contribution from K.C., B.J.-A., and J.P.C., did the analyses. K.C. prepared the map. A.B. wrote the manuscript with contributions from B.J.-A., M.C., K.C., J.P.C., and G.B. All the other authors provided data and commented on the manuscript. All the authors approved the final version.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and R codes that support the findings of this study are available on *Zenodo* repository: https://doi.org/10.5281/zenodo.14917259.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.