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Diversity, Distribution and Postglacial History of Native *Pinus sylvestris* Forests in the Iberian Peninsula

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ABSTRACT

Aim: *Pinus sylvestris* is the most widely distributed *Pinus* species in the world, highlighting its ecological, economic and socio-cultural importance. The Iberian Peninsula marks its south-western distribution limit, whose extent has been significantly reduced since the Mid-Holocene. In this study, we investigated the current diversity of native *Pinus sylvestris* forests in the Iberian Peninsula and their postglacial distribution and history.

Location: Iberian Peninsula, south-western Europe.

Taxon: *Pinus sylvestris* L.

Methods: We compiled 1299 vegetation plots from native *Pinus sylvestris* forests and performed a numerical classification, modified TWINSPAN, to identify major forest types. We characterized their floristic composition, diversity and environmental drivers. Ecosystem Distribution Models were fitted using climatic and edaphic variables to estimate their potential distributions during the Last Glacial Maximum (21 ka BP), Mid-Holocene (6 ka BP) and present. Model outputs were validated with palaeobotanical records.

Results: We identified four different forest types: acidophilous oromediterranean, acidophilous temperate, basophilous, and thermophilous mixed forests. These forests host unique assemblages of endemic, relict and broadly distributed plant species. Ecosystem Distribution Models revealed that, among the three studied periods, present climatic conditions are the most suitable for the development of *Pinus sylvestris* forests. Yet, their present-day distribution is considerably more restricted than predicted, a mismatch that agrees with palaeobotanical records.

Main Conclusions: Native *Pinus sylvestris* forests in the Iberian Peninsula display a wide ecological range. Their current distribution is more restricted than expected by suitable climatic conditions, suggesting the key role of anthropogenic historical pressures. Conservation strategies should not only consider future climate scenarios but also integrate historical land-use legacies.

1 | Introduction

Pinus sylvestris L. (Scots pine) is the most widely distributed *Pinus* species and the second most frequent conifer worldwide, occurring in multiple ecosystems across Eurasia. This tree species possesses a broad ecological range due to its ability to withstand frost and drought, and to grow under diverse edaphic conditions like siliceous, calcareous-dolomitic, gypsum, peat, sandstone and sedimentary sandy soils (Agundez et al. 1992; Sohn et al. 2016; Taeger et al. 2013). The ability to colonize new disturbed areas and poorly developed soils also makes *Pinus sylvestris* a pioneer species (Mátyás et al. 2004). When grazing and competition with shade-tolerant species are low, the species can thrive and dominate great extensions of mature forest, from lowlands in subarctic, boreal and temperate climates, to high mountains under Mediterranean climates (Houston Durrant et al. 2016). Thanks to this ecological plasticity, *Pinus sylvestris* has become one of the most important forestry species in Europe, with implications at ecological (e.g., carbon sequestration, rewilding), socio-cultural (e.g., natural heritage, recreation) and economic (e.g., highly productive, versatile timber) levels (Brichta et al. 2023; Krsnik et al. 2024; Torres et al. 2021).

The Iberian Peninsula represents the south-western limit of the global distribution of *Pinus sylvestris* (Cañellas et al. 2000; López-Sáez et al. 2018), persisting at the species' warmest and driest physiological limits (Cox and Moore 1993). These rear-edge populations have traditionally been addressed as marginal and prone to decline under climate change (Brown 1984; Safriel et al. 1994). Yet, rear-edge populations often show long-term persistence, high genetic uniqueness and heterogeneous responses to environmental changes, making them particularly informative for understanding vulnerability and resilience under current global warming (Vilà-Cabrera et al. 2019). Rear-edge populations also are a valuable system to assess regional biogeographical processes and to anticipate how core populations may respond to future climatic shifts (Allen et al. 2010). Despite human-made plantations are extensive across the Iberian Peninsula (Mason and Alía 2000), native forests dominated by *Pinus sylvestris* are still found, with some studies revealing the importance of these forests as genetic reservoirs for the species. Iberian lineages of *Pinus sylvestris* are genetically different from the rest of Europe (Cheddadi et al. 2006; Sinclair et al. 1999; Soranzo et al. 2000), pointing to an extended period of isolation that likely took place during the last glacial period, when the species found refugia in the southern European peninsulas (i.e., Iberian, Italian and Balkan) (Médail and Diadema 2009). This agrees with multiple charcoal, fossil and pollen records found in the Iberian Peninsula, with the oldest record dated from c. 45 ky BP (Carrión, Munuera, et al. 2022; Carrión, Ochando, et al. 2022; Franco Múgica et al. 2001; Peñalba 1994; Pons and Reille 1988).

After the Last Glacial Maximum (LGM, 21 ky BP), *Pinus sylvestris* spread northwards thanks to the milder climate of the Holocene, especially during the Mid-Holocene climatic optimum (6 ky BP). Under warmer and wetter conditions, the dominance of *Pinus sylvestris* forests alternated with forests dominated by broadleaved-deciduous trees (e.g., *Betula*, *Quercus*). During the climatic oscillations of the Holocene (Dansgaard et al. 1969; Schönwiese and Bayer 1995), *Pinus sylvestris* forests persisted in more continental, drier and oligotrophic situations (Gil García et al. 2002; Peñalba 1994), from which they spread again under favourable climatic conditions. However, this pattern was abruptly interrupted in the last two millennia (Morales-Molino et al. 2011, 2022), when the distribution of *Pinus sylvestris* forests significantly decreased throughout the Iberian Peninsula, an event that coincided with the spread and intensification of human activities (Carracedo et al. 2018; Carrión et al. 2003; Gil-Romera et al. 2010; Morales-Molino et al. 2013; Muñoz Sobrino et al. 2004). This process has been recently accelerated by climate change, which is already leading to reduced regeneration and higher mortality rates (Castro et al. 2004; Galiano et al. 2010; Martínez-Vilalta and Piñol 2002). Accordingly, climatic models predict shifts of the species to higher elevations and a gradual reduction of suitable climatic areas in the Iberian Peninsula (Benito Garzón et al. 2008; Reich and Oleksyn 2008). Thus, predicting the future distribution of the Iberian *Pinus sylvestris* forests will benefit from a better understanding of their late-Holocene demise, and whether it was caused by climatic shifts or human land use.

This study aims to investigate the diversity and postglacial distribution of native *Pinus sylvestris* forests in the Iberian Peninsula, as a tool to support the conservation efforts and forest management of this species. Our first objective is to identify the major habitat types dominated by *Pinus sylvestris* across large ecological gradients in the Iberian Peninsula. We expect the diversity of native *Pinus sylvestris* forests to be mainly driven by climatic and soil factors, reflecting the environmental heterogeneity of the Iberian Peninsula (Figure 1). Our second objective is to assess the historical distribution of the *Pinus sylvestris* forests during the Last Glacial Maximum (LGM, 21 ky BP), the Mid-Holocene climatic optimum (6 ky BP) and the present. Both LGM and Mid-Holocene represent extreme climatic situations since the most ancient record of *Pinus sylvestris* in the Iberian Peninsula (c. 45 ky BP), that is, cold and dry versus warm and humid conditions, respectively. If the downfall of *Pinus sylvestris* forests after the Mid-Holocene was mainly caused by climatic events, we expect distribution models to depict the Mid-Holocene as the optimal period for these forests, followed by a decrease towards the present (Figure 1). On the contrary, if human activities played a key role in their collapse, we expect the models to return similar potential distributions for both Mid-Holocene and the present.

2 | Methodology

2.1 | Vegetation Data

We initially retrieved 1415 vegetation plots (i.e., records of plant species co-occurring in one place at a given time) with *Pinus sylvestris* sampled in native forests. The identification of nativeness by the surveyors follows the current knowledge of the species in the Iberian Peninsula, in agreement with the official provenance areas used in forest management (Nicolás Peragón et al. 2024) (Figure 1). Our main data sources included the *Iberian and Macaronesian Vegetation Information System* (SIVIM, http://sivim.info/sivi; Font et al. 2010, 2012), the *CircumMed Database* (Bonari et al. 2019) and recent publications (López-Sáez et al. 2013, 2016). For the plots that were surveyed with the Braun-Blanquet methodology (Braun-Blanquet 1921), we transformed the species cover to mid-percentage values (e.g., Braun-Blanquet cover value of 3 equals a percentage cover value between 25% and 50%, thus transformed to 37.5%). To cover the gap observed in the Cantabrian Mountains (NW Spain), we additionally sampled 15 vegetation plots in relict native forests, recording the percentage of all vascular plants in 10 m × 10 m plots, as this was the most common area sampled in the other plots. As these forests occupy a very restricted area in the Cantabrian Mountains (three forests with a combined extent of approximately 370 ha) the number of plots included, although relatively small, was enough to capture their floristic diversity. The final dataset was filtered to remove plots with coordinates outside the Iberian Peninsula ($N = 10$) or duplicates ($N = 35$). Plots with cover values for *Pinus sylvestris*

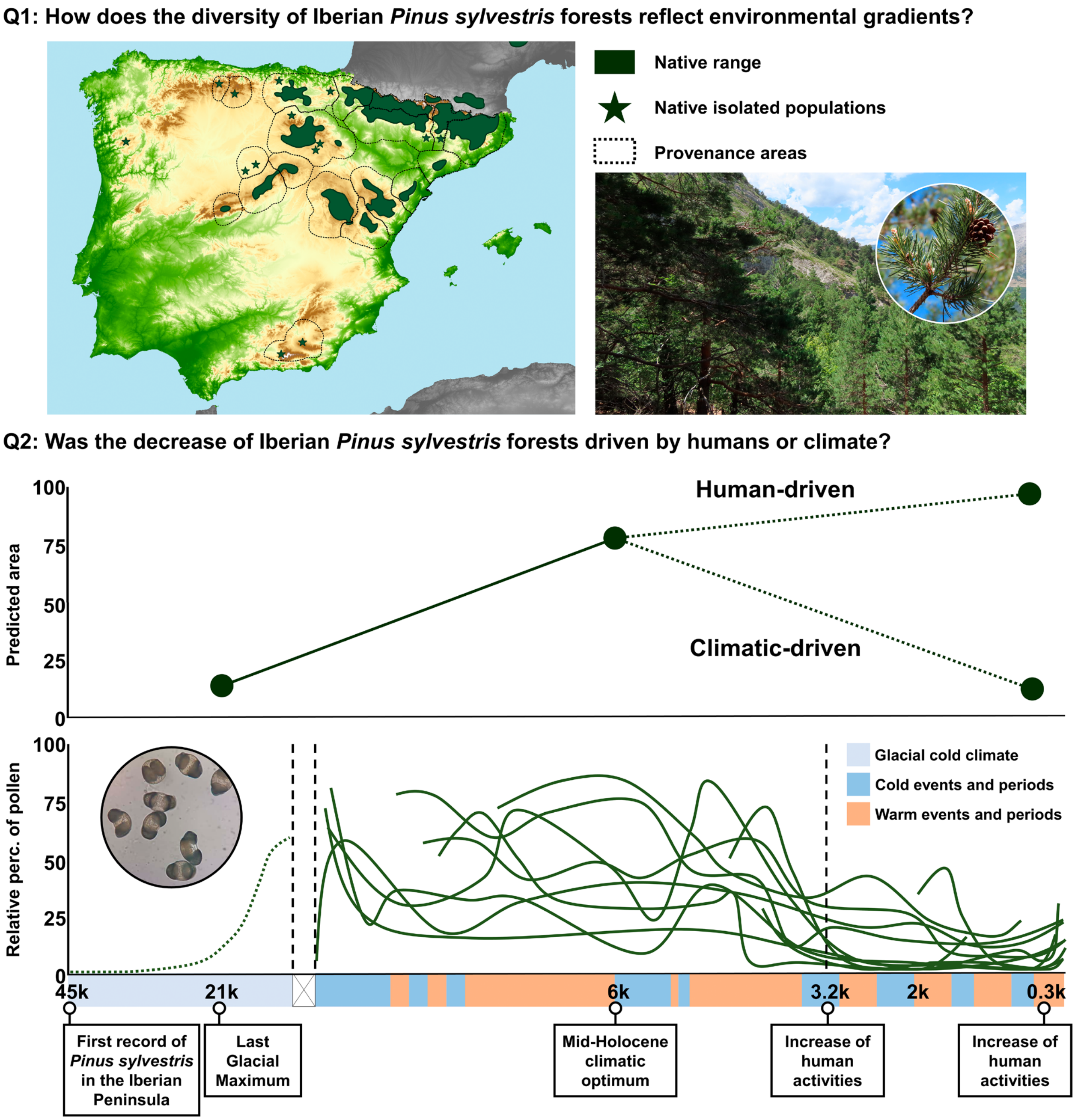

FIGURE 1 | Presentation of the two major questions addressed in this study. (Q1) Distribution map for the *Pinus sylvestris*, where large green areas and stars represent its native range in current Iberian Peninsula, extracted from Caudullo et al. (2017), and provenance areas considered in Spain (Nicolás Peragón et al. 2024). (Q2) Timeline since the last glaciation (light blue), postglacial cold events (blue) and warm events of the Holocene (orange), adapted from Dansgaard et al. (1969) and Schönwiese and Bayer (1995). On the upper panel, expected predicted area for each period, with a dichotomy in the present period depending on whether the current extent of Iberian *Pinus sylvestris* forests is driven by climate or human activities. On the lower panel, the relative percentage of *Pinus sylvestris* pollen registered in different Iberian locations, synthesized from Carrión, Ochando, et al. (2022), Franco Múgica et al. (1998), Morales-Molino et al. (2022), Muñoz Sobrino et al. (2004) and Ramil-Rego et al. (1998).

lower than 25%, or lower than any other tree species (i.e., when the species was not the dominant or co-dominant tree, $N=96$), were also discarded. Plots where *Pinus sylvestris* was present, but not dominant, were dominated by *Quercus* (e.g., *Quercus pubescens*, *Quercus faginea*) or other *Pinus* species (e.g., *Pinus nigra*, *Pinus pinaster*, *Pinus uncinata*). Although this threshold may exclude marginal populations under suboptimal environmental conditions, such populations would not represent well-developed forests and therefore fall outside the scope of this study. We made an exception in 10 plots from two areas (Ebro Basin and Serra do Gerês), for which all available plots had a cover value below the 25% threshold, but they were important to maintain geographic representativity (Loidi et al. 1994; Pavia et al. 2014). This decision did not influence the results of the numerical classification performed below, as shown in Appendix S1. The final database included 1299 plots and 978 different species, covering the entire natural distribution of *Pinus sylvestris* in the Iberian Peninsula (Houston Durrant et al. 2016; Nicolás Peragón et al. 2024).

To harmonize the taxonomy of vegetation plots, we followed Euro+Med PlantBase (Euro+Med 2024). We excluded non-vascular plants, fungi and algae, as vegetation plots are primarily focused on vascular plants and these other groups are rarely documented in most surveys. We also excluded plants only identified to the genus level or higher. All plants identified at the infraspecific level were merged at the species level, as in the specific case of *Pinus sylvestris*, whose varieties described for the Iberian Peninsula (i.e., var. *catalaunica*, var. *iberica*, var. *nevadensis*, var. *olivicola*, var. *pyrenaica*) were merged into *Pinus sylvestris*. For consistency, other taxa were also merged before data analysis, specifically those whose identification in the field is difficult due to morphological similarities, or those that experienced taxonomic changes (e.g., *Viola riviniana* and *V. reichenbachiana* were merged into *V. riviniana* aggregate).

2.2 | Numerical Classification

We classified the plots in the database into forest habitat types by performing a modified TWINSPAN algorithm (Roleček et al. 2009) using the software JUICE v. 7.1 (Tichý 2002). This algorithm is widely used in vegetation science (e.g., Ciaramella et al. 2024; Fernández-Pascual et al. 2025; González-García et al. 2024; Willner 2024), providing an ecologically interpretable divisive classification where sample units are usually correlated with environmental gradients (Wildi 2017). We used three pseudospecies cut levels (0%, 15% and 25%) of species percentage cover, a minimum group size of 10 plots and Sorensen's average dissimilarity. Additionally, we also computed a hierarchical clustering analysis in JUICE, using square-root transformed cover values of species, Sorensen's average dissimilarity and Ward's linkage method, to ensure the reliability of these groups when using a non-divisive algorithm. The synoptic table resulting from both approaches showed similar results, as shown in Appendix S2, so we kept modified TWINSPAN results as the baseline classification. To visualize the classified plots, we used the R package *vegan* (Oksanen et al. 2025) to fit a Non-Metric Multidimensional Scaling (NMDS) using the Bray–Curtis distance, calculated from the square-root transformed cover values of the dataset, and 999 iterations (stress value = 0.235). To facilitate the interpretation of the classification, we identified characteristic species (Chytrý et al. 2020) for each habitat type including: (i) dominant (species with more than 25% cover in at least 5% of the vegetation plots within the forest type), (ii) constant (species with a frequency higher than 50% within the forest type), and (iii) diagnostic (species associated with a specific forest type, calculated as the proportion of the average abundance of each species in the group relative to the total average abundance in all groups for each species). Diagnostic species were calculated with the R package *lbdsv* (Roberts 2005) using 999 iterations, keeping those whose IndVal had a p-value < 0.05.

To characterize the diversity of the resulting habitat types, we calculated alpha (α), beta (β) and gamma (γ) diversities. α-diversity was calculated as the mean richness of vascular plants per plot within each habitat type. Since the plot area was uneven, we only used those plots between 50 and 200 m^2. β-diversity was obtained from 100 plots randomly selected within each forest type to calculate Bray–Curtis dissimilarity; this was performed 20 times to ensure that every plot was selected at least once. γ-diversity was fitted with the R package *iNext* (Hsieh et al. 2015), using the species frequencies within forest types, 999 replicates and an endpoint equal to the highest number of plots for a single forest type ($N = 559$).

2.3 | Environmental Characterization

We extracted environmental data by using the geographic coordinates of vegetation plots. Original geographical coordinates of the plots had different levels of resolution, mainly ranging between 1 km × 1 km and 10 km × 10 km grid cell size. We kept the original coordinates for those vegetation plots with a resolution of ≤ 1 km, but to minimize potential scale mismatches, we applied a downscaling protocol for those plots with lower levels of spatial accuracy. We used the elevation recorded originally for each plot and a Digital Elevation Model (DEM) of the Iberian Peninsula at 1 km resolution: (i) to keep all 1 km DEM cells that matched with the original elevation (±50 m) within the corresponding 10 km × 10 km grid cell; (ii) to randomly select one of those cells; and (iii) to assign the centroid coordinates from that specific cell to the plot (González-García et al. 2024). These new coordinates were used to extract information of environmental variables, assuming similar climatic conditions in cells at similar elevations within the same 10 km × 10 km or 1 km × 1 km grid cells. We gathered bioclimatic variables from CHELSA v. 2.1 1 at c. 0.8 km × 0.8 km grid resolution (Karger et al. 2017), while soil pH was collected from Hájek et al. (2021) at the same grid resolution. From the 19 bioclimatic variables provided by CHELSA, we selected a subset that were not strongly correlated (correlation value > −0.7 and < 0.7; sensu Dormann et al. 2013) and accounted for a significant portion of the variance explained by the first two axes of a principal component analysis (PCA; see Appendix S3). For fitting distribution models of the forest types studied, we kept bio4 (temperature seasonality), bio6 (mean daily minimum air temperature of the coldest month), bio15 (precipitation seasonality) and bio17 (mean monthly precipitation amount of the driest quarter). To describe the environmental space of forest types, we used bio1 (mean annual temperature) and bio12 (annual precipitation amount), which usually drive the geographical distribution of forests (Bonan 2008; Cho et al. 2011), along with the four previously selected bioclimatic variables, elevation and soil pH. These same environmental variables were fitted onto the NMDS ordination to aid in the ecological interpretation of compositional patterns.

2.4 | Ecosystem Distribution Modelling

Ecosystem-based modelling relies on the occurrences of a specific ecosystem/habitat type for which we assume a primary role of environmental drivers (Franklin 2013; Horvath et al. 2019; Jiménez-Alfaro et al. 2018). We used the R package *biomod2* (Thuiller et al. 2025) to model the distribution of the different forest types across the Iberian Peninsula in the present and projected the models to the LGM (21 ky BP) and the Mid-Holocene climatic optimum (6 ky BP). To avoid niche averaging inherent to single-species models of generalist or widespread taxa, such as *Pinus sylvestris*, we adopted an ecosystem-based approach in which forest types were modelled separately, allowing the models to capture distinct environmental drivers defining each ecological unit. Predictor variables were retrieved from CHELSA bioclimatic data (Karger et al. 2023) and Hájek et al. (2021) soil pH. Variables related to human activities were not considered, as comparable spatial layers are unavailable for past climatic scenarios, and their inclusion would compromise temporal consistency among the studied periods. The preassigned coordinates for each plot were used as occurrences for model calibration. When several plots occurred in the same cell (at 0.8 km × 0.8 km grid resolution), we kept one plot per group and cell. Pseudoabsences were randomly sampled within the spatial extent of the Iberian Peninsula, matching the number of presences for each forest type. Pseudoabsences were constrained to avoid grid cells where the corresponding forest type occurred. As our dataset covers the complete distribution of *Pinus sylvestris* forests in the Iberian Peninsula, these pseudoabsences represent areas where the species is truly absent rather than unsampled presences, like a stratified modelling approach. To evaluate the potential effect of using different algorithms and pseudoabsence random selections, we performed an evaluation protocol (see Appendix S4) fitting four different types of models: Random Forest (RF), Generalized Additive Model (GAM), Generalized Linear Model (GLM) and Gradient Boosting Machines (GBM). We used 10 pseudoabsence datasets and a *k*-fold cross-validation test based on five replicates and on the even partition of the study area into 100 km side-hexagonal blocks: 80% of these blocks were used to fit the models, and the remaining 20% to validate them. RF had the best performance in two of the three statistics used to evaluate the models (TSS = 0.85, ROC = 0.95, KAPPA = 0.83) and thus was used to fit the final models, which were projected to estimate the potential area of occupancy for each forest type within the Iberian Peninsula in the LGM, the mid-Holocene and the present. To mask the more suitable areas on the projections, we used, for each forest type, a threshold based on the average cut-off value obtained during the evaluation protocol, using the true skill statistic (TSS) (see Appendix S5).

To validate our models, we retrieved geospatial information derived from pollen, charcoal and fossil data from the European Pollen Database (Giesecke et al. 2016) and also from the literature (Carrión, Munuera, et al. 2022; Carrión, Ochando, et al. 2022; del Cueto et al. 2023; Rubiales et al. 2008), keeping a buffer of ±3 ky around LGM (21 ± 3 ky BP) and Mid-Holocene (6 ± 3 ky BP) during the data gathering. We only kept those records identified as *Pinus sylvestris*, *Pinus sylvestris*-like, and *Pinus sylvestris*-type. Since the production of pollen is uneven across species, and it is well known that the genus *Pinus* produces massive amounts of it, these records were treated as presence and not as abundance data.

3 | Results

3.1 | Classification and Characterization of *Pinus sylvestris* Forests

The modified TWINSPAN classification showed four major groups whose differences could be attributed to macroclimatic and edaphic drivers, that is, ecological coherent units or habitat types. The first TWINSPAN division separated strictly Mediterranean forests from temperate ones, while the second division separated thermophilous forests with a more diverse canopy of tree species, and the third and fourth divisions separated acidophilous and basophilous forests, respectively (Figure 2). Further divisions (not shown) resulted in groups with subtle differences in floristic composition, but lower interpretability with climatic and edaphic drivers, so they were discharged. Based on the floristic and environmental information linked to each cluster, the four habitat types are described as follows:

1. Acidophilous oromediterranean *Pinus sylvestris* forests. Forests dominated by *Pinus sylvestris*, occurring at high elevations (990–2100 m a.s.l.), on acid soils, in areas with strong seasonality of both temperature and precipitation and dry summers (mean summer precipitation = 94.9 mm).

2. Acidophilous temperate *Pinus sylvestris* forests. Forests dominated by *Pinus sylvestris*, developed at mid elevation (760–1990 m a.s.l.), in acid soils with relatively high summer precipitation (mean summer precipitation = 168.6 mm) and cold winters (mean temperature of winter = −5.01°C).

3. Basophilous *Pinus sylvestris* forests. Forests dominated by *Pinus sylvestris* in a wide altitudinal range (650–2150 m a.s.l), established on alkaline soils, where the rainfall is mostly continuous but scarce throughout the year, and with a marked seasonality of temperatures.

4. Thermophilous mixed forests with *Pinus sylvestris*. Forests dominated by *Pinus sylvestris* but with a rich canopy shared with broadleaved deciduous (e.g., *Fagus sylvatica*, *Quercus pubescens*) and/or evergreen (e.g., *Quercus ilex*) trees, growing at lower elevations (520–1700 m a.s.l.), on basic soils, in sites with milder winters (mean temperature of winter = −1.77°C) and low precipitation seasonality.

These forest types represent unique assemblages of plant species in which more widely distributed plants (e.g., *Clinopodium alpinum*, *Juniperus communis*, *Juniperus sabina*) co-occur with endemic and relict species. These include Ibero-Maghrebian (e.g., *Berberis hispanica*, *Lonicera arborea*, *Polygala boissieri*) and Iberian (e.g., *Carduus carpetanus*, *Festuca merinoi*, *Leucanthemopsis pallida*, *Luzula lactea*) endemisms, but also species with more restricted distributions, specific to some mountain ranges within the Iberian Peninsula, as in the Baetic System in Southern Spain (e.g., *Lonicera splendida*, *Prunus ramburii*, *Vella spinosa*), the Central System (e.g., *Armeria caespitosa*, *Echinospartum barnadesii*) or Gredos (e.g., *Festuca gredensis*) in Central Spain.

The four habitat types were floristically described in the first two axes of the NMDS (Figure 3). The first axis represented a gradient of soil pH (acidophilous plots to the left) and precipitation (wetter summers to the right), while the second axis represented a gradient of elevation (higher plots to the top) and temperature (greater seasonality to the bottom). See Appendix S6 for a more detailed description of the fit of the environmental drivers onto the NMDS ordination.

The environmental characterization of each habitat type was used as a basis for ecological interpretation (Appendix S7). Acidophilous oromediterranean forests had the highest precipitation seasonality and the lowest summer precipitation, as well as the most acid soils and highest elevations, indicating a clear preference for continental and Mediterranean sites. In contrast, thermophilous mixed forests had the lowest elevations and the warmest temperatures throughout the year,

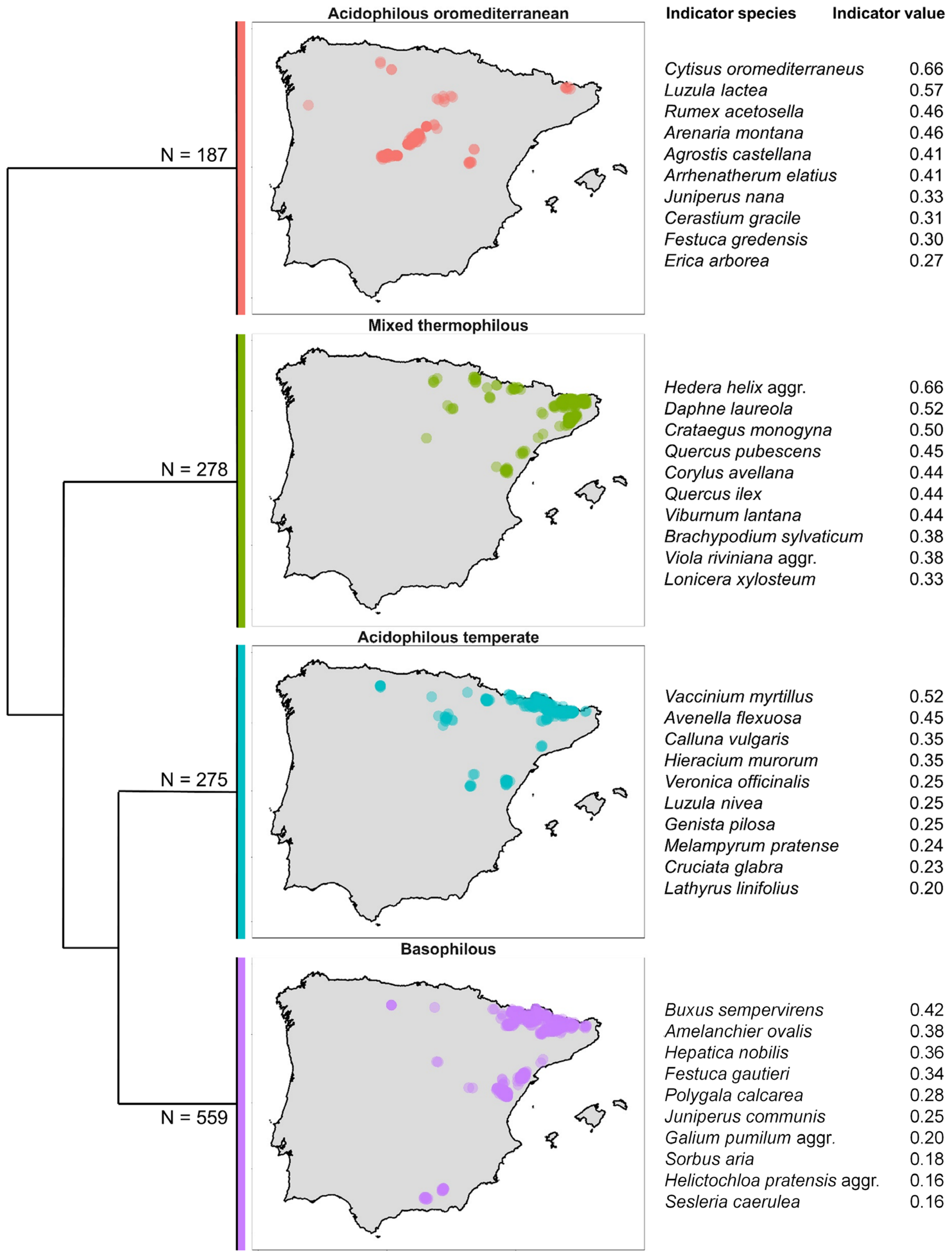

FIGURE 2 | Classification of native Iberian forests dominated by *Pinus sylvestris* based on the floristic composition of 1299 vegetation plots and the modified TWINSPAN algorithm. The number of plots for each forest type is specified in its corresponding cluster. For each forest type, both the distribution of the plots and their 10 most characteristic (indicator) species are shown.

but especially during winter. Acidophilous temperate forests could be considered the temperate counterpart of acidophilous oromediterranean forests, as soil pH was not different among these groups, but the former developed preferably in wetter and colder sites. While the classification differentiated between Mediterranean and temperate acidophilous forests, basophilous forests remained independent of their macroclimate, with intermediate values of precipitation, temperature and elevation. The species composition of each group was characterized by a set of diagnostic, constant and dominant species that support the ecological descriptions reflected by environmental data (Appendix S8).

Plant diversity within each habitat type was found to be uneven (Figure 4). Acidophilous oromediterranean forests were identified as the least diverse at both local (α-diversity) and regional (γ-diversity) levels. However, it was also the second most heterogeneous, as the species turnover (β-diversity) was only exceeded by the thermophilous mixed forests, which were detected as the most diverse at local level and with a regional diversity similar to acidophilous temperate forests. Basophilous forests stood out for being the most diverse group at the regional level, but with the highest homogeneity among plots, since their species turnover was the lowest one.

3.2 | Distribution Models

For each habitat type, Ecosystem Distribution Models predicted the potential area of occupancy and the relative importance of the environmental variables (see Appendix S9). The models showed that the current climate is the most suitable for the dominance of *Pinus sylvestris*, as the maximum potential distribution for these forests was found for this period (> 76k km^2, Figure 5); but only slightly greater than the potential area calculated for the Mid-Holocene (c. 75k km^2).

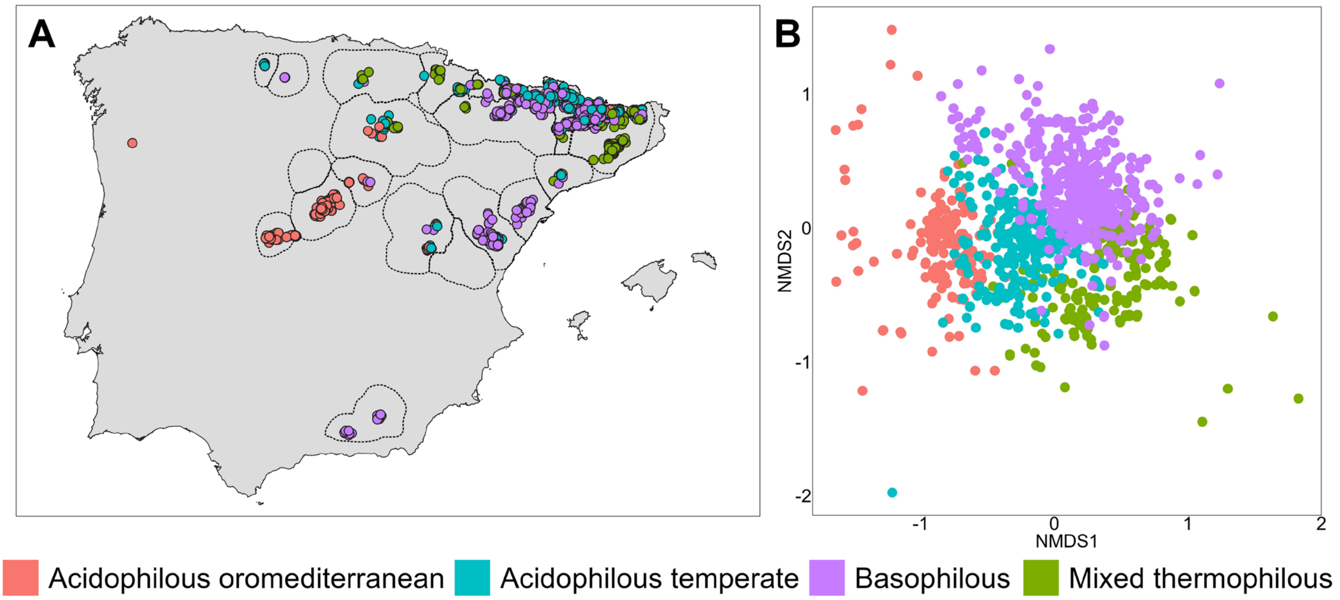

FIGURE 3 | Distribution and floristic composition of Iberian *Pinus sylvestris* forests. (A) Location of *Pinus sylvestris* native forests in the Iberian Peninsula. Dashed lines refer to the ‘provenance areas’ used to delimit the different genetic lineages of *Pinus sylvestris* in Spain. (B) NMDS showing the relationships among plots based on their floristic composition (stress value = 0.235). In both cases, vegetation plots have been classified into four compositional types.

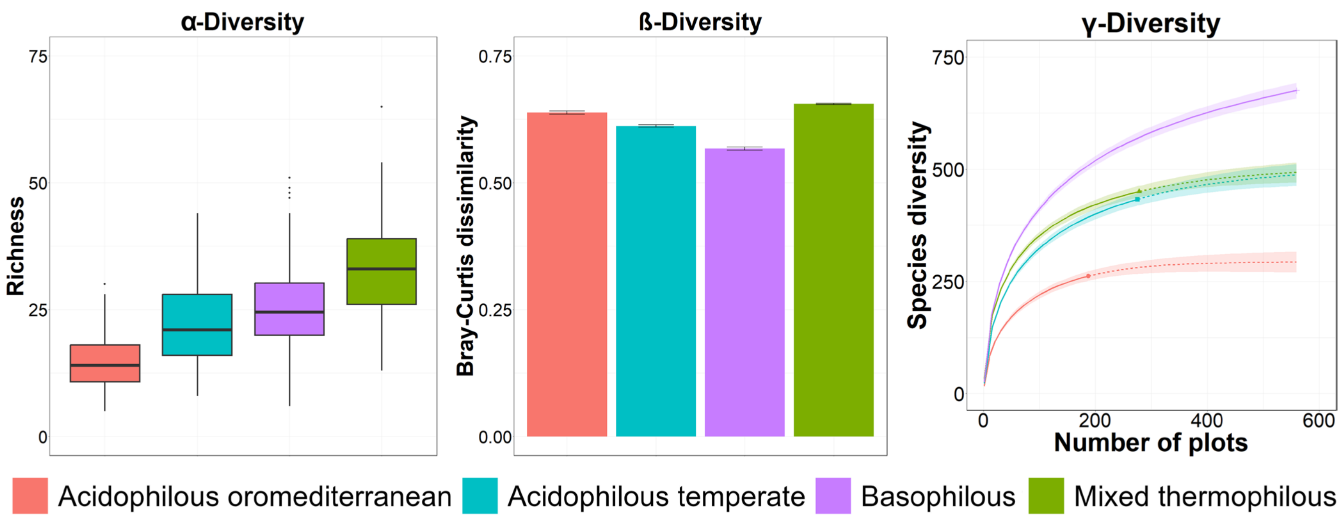

FIGURE 4 | Metrics of local species richness (α-diversity), species turnover (β-diversity) and regional pool size (γ-diversity) in four major forest types dominated by *Pinus sylvestris* in the Iberian Peninsula, obtained from vegetation plot data sampled in native forest stands.

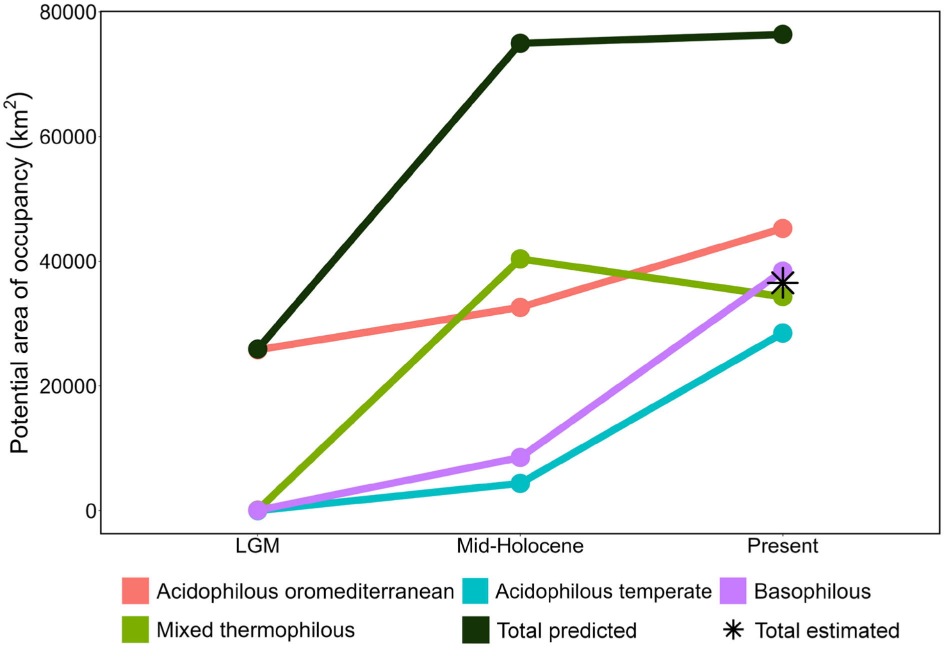

FIGURE 5 | Potential area of occupancy of *Pinus sylvestris* forests in the Iberian Peninsula, obtained from Ecosystem Distribution Models computed from vegetation plots sampled in native stands, for the last glacial maximum (LGM), the Mid-Holocene and the present climatic conditions. Total predicted area was obtained by merging the potential area of the four forest types in each period. The total estimated area of current native forests in the Iberian Peninsula was obtained from Caudullo et al. (2017).

Predictions of potential distributions were strongly reduced during the LGM (c. 26k km^2), when only the acidophilous oromediterranean *Pinus sylvestris* forests showed a considerable amount of suitable environmental areas (Figure 6), while the rest were confined to a few locations. This pattern is consistent with the spatially restricted palaeobotanical evidence available for this period, which is largely concentrated on the northern Iberian Peninsula (see small dots in maps of Figure 6). During the Mid-Holocene, the occupancy area of these four forest types dominated by *Pinus sylvestris* was predicted to be more widely distributed compared to the previous period, a trend also reflected in the palaeobotanical data, which was found across all the Iberian Peninsula.

4 | Discussion

4.1 | Diversity of Iberian *Pinus sylvestris* Forests

Our results show that native *Pinus sylvestris* forests from the Iberian Peninsula occur in a wide range of climatic and edaphic conditions, from temperate to Mediterranean climates and from acidic to alkaline soils, supporting the wide ecological niche of the species (Castro et al. 2004, 2005). We also distinguished four floristically and ecologically different forest types, which is a relatively small number when compared to traditional existing phytosociological classifications performed in Iberian *Pinus sylvestris* forests at association level. From a syntaxonomical point of view, Rivas-Martínez et al. (2001) pointed out more than 10 different associations for Iberian forests dominated by this species, a number that has increased in later years (Benito Alonso 2010; Carreras et al. 2015; López-Sáez et al. 2013, 2016). Similar classifications from other authors (Blanco Castro et al. 1998; Martínez García and Montero 2000) have largely separated these forests based on their geographic distribution rather than on major ecological gradients. Our classification is therefore intended to synthesize major ecological groups with broad geographical ranges, which are also more likely to be projected into distribution models under past climate conditions. Our approach is in line with synthetic classifications, such as the EUNIS classification of European habitats (Chytrý et al. 2020) or the European classification of Forest Types (Barbati et al. 2006), which are mostly based on environmental drivers (e.g., climate, soil) as a proxy for higher levels of classification, using higher hierarchical levels only for local units differentiated by local species composition.

Our findings also suggest that Iberian *Pinus sylvestris* forests are richer in plant species than their European counterparts. For example, a study carried out in Germany with a similar number of plots found only 563 plant species, including both vascular plants and bryophytes (Zerbe et al. 2007), in contrast with the 978 species we recorded for vascular plants. A similar climatic-driven trend was already pointed out by Ellenberg (1988), which differentiated *Pinus sylvestris* forests from Central Europe between 'southern' or 'species-diverse' forests and 'northern' or 'species-poor' forests. This pattern was also observed comparing Iberian *Pinus sylvestris* forests with other European *Pinus*-dominated forests. Iberian forests showed higher species richness (approximately 25 species on average, with values of 21, 25 and 33 in acidophilous temperate, basophilous and thermophilous mixed forests, respectively) than European *Pinus nigra* forests in both their native and non-native range (18 species on average) (Bricca et al. 2025). Only oromediterranean acidophilous forests displayed a lower richness (15 species). Although some ecologically informative taxonomic groups could not be incorporated into our analyses due to constraints inherent to the original dataset (e.g., bryophytes, fungi), our results highlight these Iberian forests as biodiversity-rich systems. This

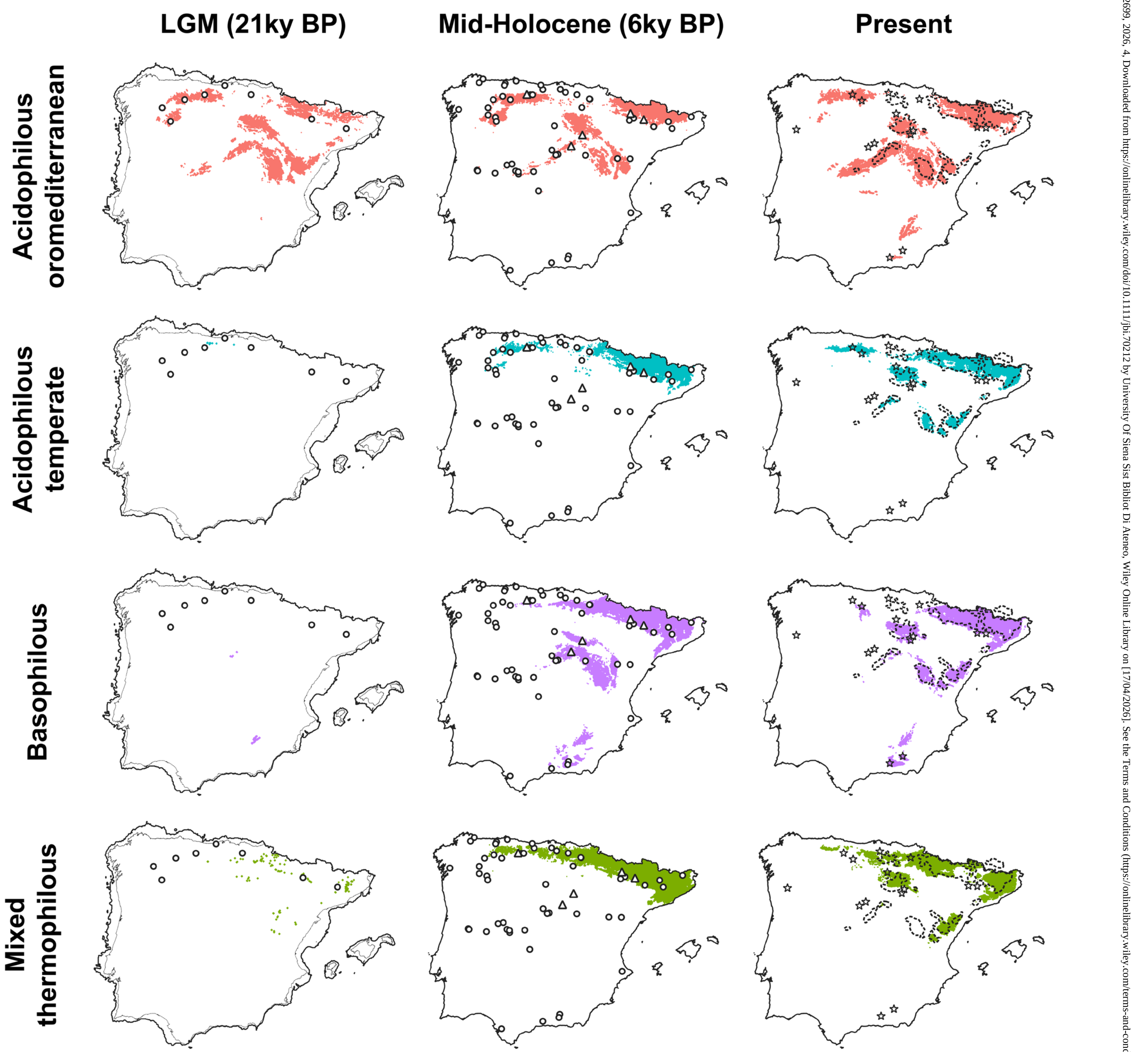

FIGURE 6 | Projection of the potential distribution for *Pinus sylvestris*-dominated forest types in the Iberian Peninsula, using a threshold value of 0.49 for the acidophilous oromediterranean forests, 0.59 for the acidophilous temperate, 0.51 for the basophilous forests and 0.49 for the mixed thermophilous. For the LGM projections, the patches have been oversized for visualization, except for the acidophilous Mediterranean forests. Dashed lines in LGM maps represent the current profile of the Iberian Peninsula. Pollen records from the LGM and the Mid-Holocene are represented by dots (○), while fossil and charcoal are represented by triangles (△). Dashed lines and stars (☆) show the current natural distribution of *Pinus sylvestris* in the Iberian Peninsula.

is particularly relevant given that their species pool includes a noticeable proportion of endemic or narrow-ranged species, as mentioned earlier. Accordingly, our findings suggest that *Pinus sylvestris* forests from the southern European peninsulas contain relatively higher species richness, contributing to their biogeographical relevance within Europe. However, to our knowledge, few studies have compared biodiversity patterns of *Pinus sylvestris* forests across their natural range or their diversity between native and non-native ranges. Such studies are still necessary to understand the biogeographical patterns of European conifer forests and the potential correlations across taxonomical groups.

Previous studies underlined the effect of soil pH as the main driver of plant species richness and composition in *Pinus sylvestris* forests, with base-rich soils hosting higher diversity in both herbaceous and woody plants than those found on acid soils (Pausas 1994; Zerbe et al. 2007). This pattern agrees with our results: basophilous *Pinus sylvestris* forests were the second most diverse forests, following the mixed thermophilous forests, which were also found on basic soils. However, other studies have emphasized the importance of temperature and multi-species canopy in explaining species richness (Estevan et al. 2007; Zerbe et al. 2007). It is unclear whether a diverse canopy directly relates to a diverse understory, or if this is a consequence of occurring at lower elevations, where milder temperatures allow a higher number of species to thrive (Pausas 1994). Moisture seems to be another important driver behind the floristic diversity of *Pinus sylvestris* forests. Other factors, such as naturalness or slope (Roche et al. 2009), may also contribute, but were not tested in this study.

4.2 | Historical Distribution of Iberian *Pinus sylvestris* Forests

Our models predicted climatically and edaphically suitable regions for *Pinus sylvestris* forests under the present climatic conditions where native *Pinus sylvestris* forests already occur, but also regions where other coniferous or mixed forests are dominated by the ecologically similar *Pinus nigra*, by a combination of broadleaved and conifer trees (e.g., *Quercus rotundifolia* and *Pinus pinaster*), or where no present native *Pinus*-dominated vegetation exists. Because our models estimate potential distributions based exclusively on climatic and edaphic variables, they do not reproduce the effects of historical human activities. The mismatch between modelled suitability and the current distribution of *Pinus sylvestris* forests supports our initial hypothesis of highly relevant human-driven effects, especially when compared to palaeobotanical evidence and historical records. Under this integrative framework, anthropogenic pressures could be considered as the most plausible non-climatic drivers behind *Pinus sylvestris* late-Holocene decline in the study area. Accordingly, the potential area for these forests was found to be much larger than their current known distribution, with new regions where these forests do not exist, but where the climate is potentially suitable. Additionally, our results demonstrate that a stratified, ecosystem-based approach is a reliable tool to reconstruct the heterogeneous postglacial dynamics of these forests by predicting the potential distribution of ecologically defined ecosystems.

Our findings also showed a notorious increase in the potential distribution area of *Pinus sylvestris* forests from LGM to Mid-Holocene and a subtle but steady increase towards the present era. This trend contrasts with the current distribution and palaeobotanical evidence available for the Iberian Peninsula (Rubiales et al. 2007, 2008, 2010), showing a much-restricted current distribution than in past ages. According to our second major question, it is reasonable to think that other drivers, rather than climate, particularly the human factor, played a key role in the downfall of these forests. Additionally, our models match the distribution projected in other studies focused on *Pinus sylvestris* itself (Benito Garzón et al. 2006, 2007, 2008; López-Tirado and Hidalgo 2014), rather than the forests dominated by this species.

The vegetation of the Iberian Peninsula during the LGM remains relatively unknown, being mainly supported by paleopalynological records (Carrión 2001; Carrión, Ochando, et al. 2022) and modelling-based studies (Benito Garzón et al. 2007; Casas-Gallego et al. 2025; Rodríguez-Sánchez et al. 2010). In this context, both the modelling-derived results and the palaeobotanical evidence should be interpreted as supporting the persistence of small, spatially isolated refugial populations rather than widespread *Pinus sylvestris* forests during the LGM. Yet, both approaches agree on the key role of pines during this period (Badal et al. 1994; Carrión 2002; Gómez-Orellana et al. 2007). Although we adopted a conservative approach, considering only records clearly identified as *Pinus sylvestris*, less specific records (i.e., identified as *Pinus sylvestris*/*Pinus nigra*-type) could support some regions predicted by our models in both Spain (Fernández et al. 2021; Franco Múgica et al. 1998; Pons and Reille 1988) and Portugal (Figueiral and Carcaillet 2005). During the dawn of the Holocene, a general tendency towards a warmer and wetter climate (Bell and Walker 1992; Willis et al. 1998) allowed the expansion of species once confined to refugia during the colder and drier glacial period (Clark et al. 1998; Feurdean et al. 2013; Petit et al. 2002; Svenning and Skov 2007), causing vegetation shifts from coniferous to broadleaved forests that favoured the increase of transitional vegetation (Huntley 1990). This agrees with our findings, showing that thermophilous mixed forests could have been the most abundant during the Mid-Holocene. The wide climatic range of *Pinus sylvestris* would allow the species to outcompete broadleaved trees (Rehfeldt et al. 2002) and even to proliferate, at least locally (Muñoz Sobrino et al. 2001; Sanz Montero et al. 2003), especially in southern Europe, c. 6 ky BP (Greig and Turner 1974; Jahns 1993).

Our results, along with both paleopalynological records (Carrión, Munuera, et al. 2022; Franco Múgica et al. 2001; Pérez-Obiol et al. 2011) and modelling studies (Benito Garzón et al. 2006, 2007, 2008) also suggest a phase of dominance, or at least co-dominance, of *Pinus sylvestris* during the Mid-Holocene. Yet, the Iberian vegetation, like most of Europe, experienced a profound transformation due to human activities associated with logging, deforestation, fires or grazing at least during the last 10 millennia (Anderson et al. 2011; Carrión et al. 2007; Colombaroli et al. 2008; Morales-Molino et al. 2011; Rubiales et al. 2008) with some forests disappearing abruptly in a span of 100–200 years (Bridge et al. 1990). The deforestation of the Iberian Peninsula was coupled with the increase of grasslands, shrublands and heathlands, a tendency that took place especially between 3.2 and 1.5 ky BP (Morales-Molino et al. 2011) and continues up to the present (Carracedo et al. 2018; Rubiales et al. 2011). Although human activities decreased considerably around 1.3–1.25 ky BP, enabling the regeneration of forests (Morales-Molino et al. 2011), the remaining *Pinus sylvestris* stands had already undergone a substantial reduction or had even completely disappeared due to continuous fires, grazing, and land degradation. Along with the emergence of new competitors that took advantage not only of the new climatic conditions but also of newly available, human-mediated habitats, these drivers prevented *Pinus sylvestris* from reclaiming its former dominance (Morales-Molino et al. 2011, 2022). In the temperate region, this competition process was mainly starred by *Fagus sylvatica*, which occupies a potential niche similar to that of *Pinus sylvestris* and whose natural range expanded c. 4–3 ky BP, spreading from scattered glacial refugia and further reinforced by postglacial migration from continental Europe (López-Merino et al. 2008; Sobrino et al. 2009); while more thermophilous, fire-adapted conifers expanded in the Mediterranean region, such as *Pinus halepensis* or *Pinus pinaster* (Finlayson et al. 2009; Gil-Romera et al. 2010).

The ecological and historical differentiation among Iberian *Pinus sylvestris* forest types may also reflect underlying genetic structure. Phylogeographic studies indicate that Iberian populations, although not involved in the postglacial recolonization of Europe, harbour the highest genetic diversity at the continental scale and include multiple lineages associated with glacial refugia (Cheddadi et al. 2006; Robledo-Arnuncio et al. 2005). The contrasting postglacial trends identified in our models agree with a limited connectivity among glacial and interglacial refugia, particularly in northwestern Iberia, where forests appear as the oldest ones in our reconstructions and align with genetically distinct relict populations (Prus-Głowacki et al. 2012). Integrating ecosystem-level classifications with population genetic data in future studies would help to confirm if these forest types correspond to distinct genetic lineages or refugial histories. From a broader perspective, these heterogeneous historical trajectories (Benito Garzón et al. 2008; Rubiales et al. 2008), their genetic singularity (Prus-Glowacki et al. 2003) and current vulnerability (Castro et al. 2004) support the role of Iberian *Pinus sylvestris* forests as rear-edge populations, providing an early-warning system to forecast how core populations in Central and Northern Europe may respond to climate change.

5 | Conclusions

This study provides the first synthesis of the diversity and distribution of native forests dominated by *Pinus sylvestris* in the Iberian Peninsula, which represents the south-westernmost limit of its native range. The identification of four compositional and ecological different forest types, mainly driven by climatic and edaphic variables, highlights the wide ecological range where *Pinus sylvestris* can thrive and become dominant. The persistence of these forests under different climatic periods and anthropic-driven disturbance regimes emphasizes their ecological resilience. From a biogeographical point of view, Iberian *Pinus sylvestris* forests encompass unique assemblages of plant species, including endemic and relict species that co-occur with more widely distributed Central European and Mediterranean plants. Despite the present climate being the most suitable for Iberian *Pinus sylvestris* forests, their current distribution is significantly restricted when compared to the mid and late Holocene, likely due to anthropogenic pressures. This suggests the necessity to incorporate historical land legacies, and not only future climate scenarios, when developing effective conservation strategies. Based on our findings, such strategies should prioritize areas where the distribution and extent of these forests have decreased significantly (e.g., the Cantabrian Mountains, Serra do Gerês), as well as regions where sensitivity to climate change is particularly high (e.g., the Baetic System). In addition, such strategies should consider restoring forests in areas where they no longer occur, but where environmental conditions are regionally and locally suitable, as these ecosystems could enhance biodiversity at the regional scale and act as refugia for associated taxa.

Author Contributions

Víctor González-García: conceptualization, methodology, formal analysis, investigation, data curation, writing – original draft, visualization. **Gianmaria Bonari:** resources, data curation, writing – review and editing. **Eduardo Fernández-Pascual:** investigation, writing – review and editing, supervision. **Adrián Lázaro-Lobo:** investigation, writing – review and editing. **Jose V. Roces-Díaz:** investigation, writing – review and editing. **Borja Jiménez-Alfaro:** conceptualization, methodology, investigation, writing – review and editing, supervision, funding acquisition.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The vegetation data that support the findings of this study are available at Iberian and Macaronesian Vegetation Information System (SIVIM, http://sivim.info/sivi; Font et al. 2010, 2012), CircumMed Database (Bonari et al. 2019), and literature (López-Sáez et al. 2013, 2016).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Classification results after excluding plots with low *Pinus sylvestris* cover. **Appendix S2:** Comparison of modified TWISNPAN and hierarchical clustering. **Appendix S3:** Selection of environmental variables for Ecosystem Distribution Modelling. **Appendix S4:** Ecosystem Distribution Modelling evaluation. **Appendix S5:** Ecosystem Distribution Modelling occupancy area. **Appendix S6:** NMDS environmental fit. **Appendix S7:** Environmental characterization of *Pinus sylvestris* forest types in the Iberian Peninsula. **Appendix S8:** Factsheets for native *Pinus sylvestris* forests in the Iberian Peninsula. **Appendix S9:** Ecosystem Distribution Modelling relative importance of variables.