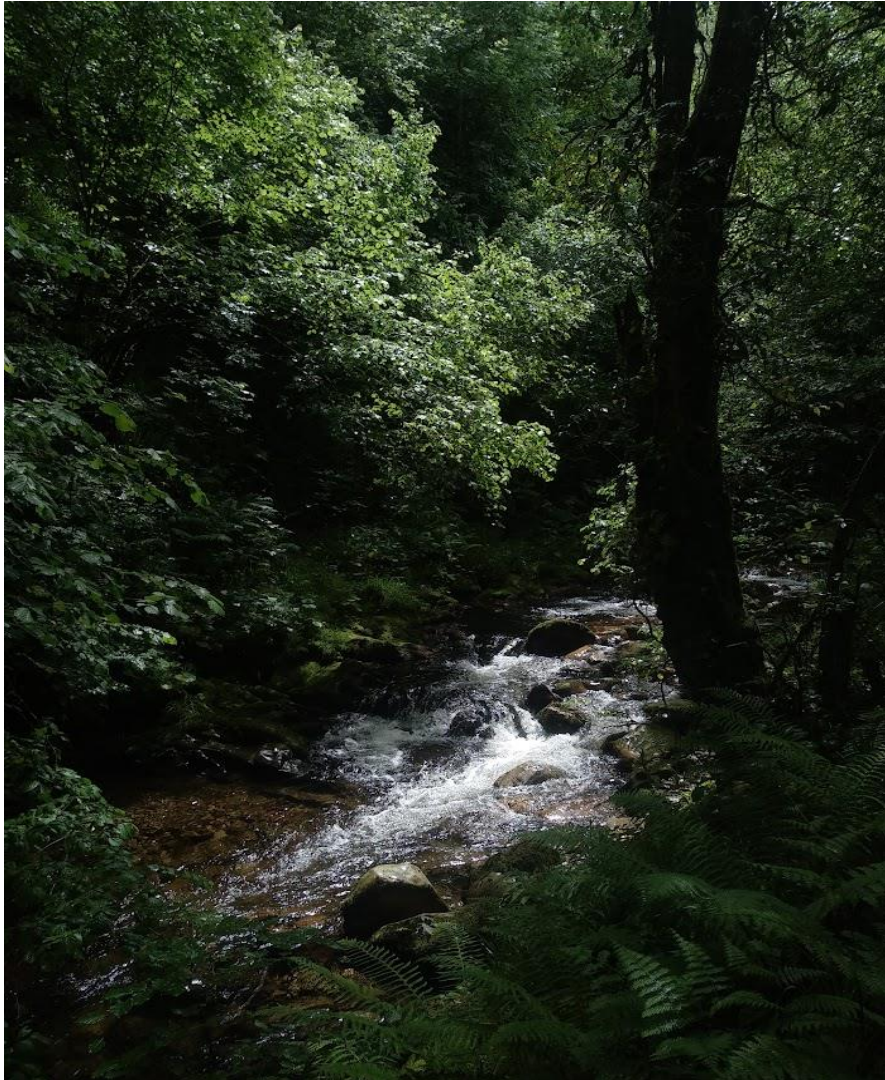


Máster en Biotecnología Aplicada a la Conservación y  
Gestión Sostenible de Recursos Vegetales

TRABAJO FIN DE MÁSTER

**BIOGEOGRAFÍA COMPARADA DE LOS TIPOS DE  
BOSQUE DEL NOROESTE DE LA PENÍNSULA IBÉRICA**



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COMPARATIVE BIOGEOGRAPHY OF THE FOREST TYPES IN THE  
NORTH-WESTERN IBERIAN PENINSULA

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## ABSTRACT

Broadleaved deciduous forests are the dominant functional ecosystem type in temperate Europe. However, under certain local conditions broadleaved or needle-leaved evergreen species can coexist or even become dominant. Climatic heterogeneity and refugium character, both enhanced by a complex topography, are the main drivers of such functional diversity of forests, especially in the southern peninsulas of Europe. The Cantabrian Mixed Forests, located in the North-Western Iberian Peninsula, is a clear example of co-existing functional forests in small areas. The aim of this study is (i) to determine how many types of forests are found in this ecoregion and (ii) to define their environmental space. Our analyses were based on the database of vegetation relevés from the Iberian and Macaronesian Vegetation Information System (SIVIM). Firstly, we used an expert system for European vegetation to separate forest plots. We then used a modified Two-Way Indicator Species Analysis (TWINSpan) and a semi-supervised k-means algorithm to classify them into EUNIS habitat types, obtaining 22 different types of forests. To determine their environmental space, we extracted bioclimatic and edaphic variables from CHELSA 2.1 and SoilGrids, respectively. Finally, we computed a Principal Component Analysis (PCA) and fitted Generalized Linear Models (GLMs) for each type of forest. Our results suggest that the distribution of forest types in the Cantabrian Mixed Forests Ecoregion is mainly triggered by oceanic influence and the amount and seasonality of precipitation. We also carried out a PERMANOVA to test the climatic differences among types of forests. Every forest displayed a climatic optimum, with certain overlap, especially in those that have been traditionally favoured by human activities. A complex climatic history and a wide human intervention in the ecoregion can be considered the main drivers of such forest diversity.

## RESUMEN

Los bosques caducifolios de hoja ancha son el principal ecosistema funcional de la Europa templada. Sin embargo, bajo ciertas condiciones, los bosques perennifolios de hoja ancha y de acículas pueden coexistir o incluso volverse dominantes. La heterogeneidad climática y el carácter de refugio, acentuados por una topografía compleja, son los principales impulsores de tal diversidad funcional de bosques, especialmente en las penínsulas del sur de Europa. La ecorregión de los bosques mixtos cantábricos, situada en el noroeste ibérico, es un claro ejemplo de la coexistencia de diferentes bosques funcionales en áreas pequeñas. El objetivo de este estudio es (i) determinar cuántos tipos de bosques se encuentran en esta ecorregión y (ii) definir su espacio ambiental. Nuestros análisis se basaron en la base del Sistema de Información de la vegetación Ibérica y Macaronésica (SIVIM). Inicialmente, usamos un *expert system* de vegetación europea para separar los inventarios de bosques. Seguidamente, usamos un TWINSpan (*Two-Way Indicator Species Analysis*) modificado y un algoritmo *k-means* semi-supervisado para llevarlos a la clasificación EUNIS de hábitats, consiguiendo 22 tipos diferentes de bosques. Para determinar su espacio ambiental utilizamos variables climáticas y edáficas de CHELSA 2.1 y SoilGrids, respectivamente. Finalmente, realizamos un PCA y GLMs para cada tipo de bosque. Nuestros resultados sugieren que la distribución de los tipos de bosques en la ecorregión de los Bosques Mixtos Cantábricos está principalmente dirigida por la influencia del océano y por la cantidad y estacionalidad de las lluvias. También llevamos a cabo un PERMANOVA para testar las diferencias climáticas entre los distintos tipos de bosques. Cada uno mostró un óptimo climático, con cierta superposición, especialmente en aquellos que han sido favorecidos tradicionalmente por la actividad humana. Una historia climática compleja y una amplia intervención humana en la ecorregión pueden ser considerados los principales causantes de tal diversidad de bosques.

## INTRODUCTION

The temperate broadleaf and mixed forest biome (*sensu* Olson *et al.* 2001) is characterised by tree-dominated ecosystems with a high seasonal variation in productivity and with less biological diversity than that found in tropical or subtropical biomes. Differences among soil fertility, fire regimes and gradients in temperature allow several different functional ecosystems to appear within this biome (Keith *et al.* 2020). Deciduous temperate forests could be considered the dominant functional ecosystem in temperate Europe, whose main type of forest is the broadleaved deciduous one. However, deciduous forests are not the only kind that we can find within this ecosystem, since other ones such as broadleaf evergreen or coniferous needle-leaved forests can also appear (Jahn 1991). These less frequent forest types can become locally dominant under certain suitable conditions, and thus ecoregions within the same biome can show different levels of functional forest diversity (Olson *et al.* 2001). Oceanic influence and elevation are among the main environmental drivers shaping functional forest diversity (Box & Fujiwara 2015). Additionally, a complex topography can also explain functional forest diversity by providing local refugia during less suitable climatic conditions, for example during the Last Glacial Maximum in Europe, whose effects can still be observed in the present diversity and distribution patterns of the European biota (Carrión *et al.* 2010, Jiménez-Alfaro *et al.* 2021a).

In the Quaternary, several species found refugia from the glacial-interglacial oscillations in central Europe (Willis & van Andel 2004), although these refugia were mainly located in the southern European peninsulas (Nieto Feliner 2011, Gentili *et al.* 2015, Comes & Kadereit 1998, Hewitt 2000). After the Last Glacial Maximum, the climate started to get warmer, triggering the reconfiguration of vegetation. Species that were confined to certain areas with microclimatic conditions (e.g. shores, steep slopes, deep canyons, intramontane valleys, etc.) became dominant thanks to this climate-shifting (Hewitt 1999, Pan *et al.* 2020). Broadleaved deciduous mesic tree species, such as *Quercus* or *Fagus*, found shelter in these zones from where they started their spread northward during the climatic optimum of the early Holocene (Brewer *et al.* 2002), becoming the dominant vegetation in current temperate Europe. This post-glacial reorganization of plant species and, thus, vegetation was determined by climatic and edaphic factors overall (Huntley 1990), which was enhanced in areas with greater climatic heterogeneity (Ramil-Rego *et al.* 1998). In the Iberian Peninsula, forests dominated by *Quercus* species colonized the territory from their refugia in the coast and other oceanic and thermic regions, forcing coniferous formations to refuge in the mountains or, at least, in more continental zones (Carrión *et al.* 2010). The natural history of broadleaved evergreen forests seems to be more complex and directly related to human activities, at least in North-Western Iberia (Zapata 2002). The current Iberian Peninsula landscape displays a great environmental heterogeneity, allowing the occurrence of a great richness of ecosystems and species, thanks to the convergence of climatic, edaphic, topographic, historical and biogeographic factors (Rey Benayas & Scheiner 2002).

The difficult topography of North-Western Iberia allows the occurrence of a great climatic heterogeneity, especially considering that Cantabrian Mountains have been widely reported as the boundary between the Mediterranean and temperate climates (Costa *et al.* 1998, Olson *et al.* 2001, Rivas-Martínez *et al.* 2002). The worldwide classification of terrestrial biomes by Olson *et al.* (2001) proposes the Cantabrian Mixed Forests

ecoregion as a distinct area defined by the Cantabrian Mountains and the temperate oceanic territories of North-Western Iberian Peninsula. In this ecoregion, the influence of the Atlantic Ocean and the climatic gradient towards the mountains creates suitable niches for functionally different species which are assembled into a high diversity of forest types. The combination of all these environmental factors and the refugium nature of certain areas results in a very complex landscape, where it is expected that climate plays a key role in the distribution of forests. In the Cantabrian Mixed Forests ecoregion there is a coexistence of deciduous and evergreen forests (Amigo *et al.* 2017) which does not occur northwards in the European temperate territories. We expect that these functional types of forests display a different environmental optimum with certain overlap in their climatic space and floristic composition, whose differences are more obvious when comparing ecological groups with distinct species composition. How climate shapes the diversity and distribution of forests at functional or ecological level has been barely described at the ecoregion level. This study aims to fill this gap and, specifically, (i) to determine how many different types of forests occur within the Cantabrian Mixed Forests ecoregion and (ii) to evaluate how the distribution of functional and compositional types is defined by environmental drivers such as climate and soil pH.

## **METHODS**

### **Study area**

Our study area is the WWF Cantabrian Mixed Forest ecoregion (Olson *et al.* 2001) within the deciduous temperate forest biome (Keith *et al.* 2020). The ecoregion is located at the transition between the Mediterranean and the temperate climatic zones in South-Western Europe. We corrected the geographic borders of the ecoregion at high spatial resolution using the most recent biogeographical map of the Iberian-Atlantic territories (Fernández Prieto *et al.* 2020), which includes all the area proposed by Olson *et al.* (2001) but adds small nearby territories from Northern Portugal and North-Western Spain and excludes most French territory (Fig. 1). The ecoregion encompasses all the Euro-Siberian territories (*sensu* Rivas-Martínez *et al.* 2017b) from the Iberian Peninsula, including a fraction of the Pyrénées-Atlantiques department in France, but excluding the Pyrenees. As defined here, the Cantabrian Mixed Forest Ecoregion occupies 79,891 km<sup>2</sup>. It is characterised by a temperate climate with average monthly temperatures from 6 to 20°C, and total annual precipitation between 1,100 and 2,600 mm, with some areas having warm-dry summers but without the distinctive drought of Mediterranean climates (Moreno *et al.* 1990, Costa *et al.* 1997, Rivas-Martínez *et al.* 2017a, 2017b).

### **Vegetation and environmental data**

We obtained 28,775 vegetation relevés (i.e. records of plant species coexisting in a given sampling plot at a given date) from the Iberian and Macaronesian Vegetation Information System (SIVIM, <http://sivim.info/sivi>; Font *et al.* 2010, 2012) representing all vegetation types in our study area (i.e. forest and non-forest). Since these plots were sampled by different authors throughout the decades, there was no taxonomical consistency among them, so we homogenised all taxon names and unified the nomenclature for all plots. We followed the methodology of Jiménez-Alfaro *et al.* (2021b) for the Cantabrian

Mountains, which includes c. 80% of the flora in the study area, to create a new checklist of the ecoregion based on the Euro+Med Plantbase (Euro+Med 2022). Other vascular plants that were not included in Euro+Med (e.g. several *Quercus* or *Salix* hybrids, non-native species, etc.), as well as the bryophytes, were classified according to Plants of the World Online (POWO 2022). Fungi and algae were removed. We merged taxa into aggregates (i) when there were sets of very close species with a difficult identification in the field (e.g. *Viola riviniana*, *V. reichenbachiana* and *V. sylvestris* were merged into *Viola reichenbachiana* aggr.), (ii) when the taxon was recently separated in different taxa (e.g. *Hedera helix*, *Hedera hibernica* and *Hedera canariensis* were merged into *Hedera helix* aggr.) and (iii) when it was assumed that not all authors were able to identify or recognize infraspecific taxa (e.g. all *Narcissus pseudonarcissus* subspecies and varieties were merged into *Narcissus pseudonarcissus* aggr.). A complete list of merged taxa is provided in Supplementary 1.

The geographical location of vegetation relevés in SIVIM was recorded as 10 km x 10 km (52.2%) and 1 km x 1 km (47.8%) grid cells. We assigned more precise geographic coordinates to these plots using the elevation recorded originally by the authors and a Digital Elevation Model (DEM) of the Iberian Peninsula at 200 m grid resolution. In the original 10 km x 10 km or 1 km x 1 km grid cell of each relevé, we (i) kept only those 200 m cells that agreed with the relevé's elevation ( $\pm 50$  m); (ii) randomly selected one of these 200 m cells; and (iii) assigned to the relevé the coordinate of the 200 m cell's centroid, in decimal degrees. By doing this, the plots were downscaled at higher resolution within the 10 km x 10 km cells, assuming that 200 m cells at similar elevations within the same grid cell also have similar climatic conditions. The coordinates were used to extract climatic data from CHELSA v2.1 at c. 0.8 km x 0.8 km grid resolution (Karger *et al.* 2017). The selected variables included the 19 bioclimatic metrics (bio1 to bio19), cmi\_m (mean monthly climate moisture index), gdd5 (growing degree days heat sum above 5°C), hurs\_m (mean monthly near-surface relative humidity) and scd (snow cover days). Soil pH was obtained from SoilGrids (Hengl *et al.* 2017). Although we also tried other data sources (e.g. Batjes 1995; Hájek *et al.* 2021), we found that the SoilGrids variable provided the best performance to distinguish acidophilous and basiphilous forests in a preliminary test.

### **Classification of forest types**

We classified forest plots according to the EUNIS pan-European habitat classification (ICES 2000). EUNIS is a hierarchical classification for all European habitat types, partly based on plant species composition. Our goal was to assign our plots to the EUNIS level-4 classification, i.e. regionalized habitat types.

As a first step, we used the expert system created to classify vegetation plots into EUNIS European habitat types (Chytrý *et al.* 2020). The expert system uses the floristic composition of plots to assign them to habitat types depending on the presence and abundance of diagnostic species. In the first round, we used the expert system to identify plots belonging to forests, resulting in 4,346 plots. Of these, we excluded 35 plots that belonged to non-native forests (e.g. *Eucalyptus* plantations). Thus, we kept 4,311 native forest plots for further analysis, of which 2,897 (67%) were classified as a specific EUNIS forest type while the rest, 1,414 (33%), were classified just as forests.

Later, we divided our forest plots into three major functional groups: (i) T1 deciduous broadleaved forests; (ii) T2 evergreen broadleaved forests; and (iii) T3 evergreen coniferous forests. Only the plots classified as some specific type of forest by the expert system were used in this step. All plots within T2 and T3 were merged into one single group, respectively. In the case of T1, we created different ecological subgroups due to the large amount of data by using their assigned EUNIS codes. Thus, we merged all riparian forests in one single subgroup, as well as for acid-soiled *Quercus* forests and the beech forests. All hybrid taxa were removed in this step, except *Crocsmia x crocosmiiflora*, an invasive non-native taxon whose parental species are not found in our territory (González Costales 2007) and *Populus x canadensis*, another non-native taxon with just one of its parental occurring in our study area (González Costales 2007). Within each of the three functional groups, we used a modified Two-Way Indicator Species Analysis (TWINSPAN, Roleček *et al.* 2009) to classify plots into specific EUNIS forest types. We used 3 pseudospecies cut levels (0, 15, 25) with a minimum group size of 10 plots, a maximum of 10 final clusters and Sørensen average dissimilarity. In addition, we used the “NbClust” R Package (Charrad *et al.* 2014) as guidance for determining the optimum number of clusters within each functional group, according to the Silhouette, Dunn, Duda, Cindex and Hartigan validity indices. After this analysis, two clusters were removed from our dataset: *temperate mountain Abies forests* with only 6 plots occurring in the easternmost boundaries of the ecoregion; and *temperate continental Pinus sylvestris forests* with 15 plots, all of them belonging to human-made plantations despite the fact that natural *Pinus sylvestris* forests do exist as relicts in our study area (Ramil-Rego & Aira Rodríguez 1993, García *et al.* 1997, García-Gil *et al.* 2003). At the end of this step, we had 2,876 plots, each of them assigned to one EUNIS forest type.

The next step was to apply a semi-supervised classification to assign the so far unclassified plots to one of the resulting EUNIS types. Semi-supervised classification uses previously defined existing groups of data to assign the unclassified plots to them (as in supervised classification) but also creates new groups to place the data points that do not match the already existing groups (as in unsupervised classification), allowing to detect new groups and to update the previous classification, if any (De Cáceres *et al.* 2010, Tichý *et al.* 2014). We used the plots that we had already classified into EUNIS forest types as a priori groups for the semi-supervised classification. At this point, we removed from this step the plots belonging to the *southern European mountain Betula and Populus tremula forest on mineral soils* since there were only 3 plots, an insufficient quantity to create a reliable centroid for the k-mean semi-supervised classification method. The remaining forest groups (N = 19) were used as a priori information for the semi-supervised algorithm, which defined the centroid of each group by selecting 5 random plots of each group and assigned plots to groups by their proximity to the centroids. We performed the analysis with non-fixed centroids, which limits the effect of outliers and creates more coherent clusters (Tichý *et al.* 2014). We allowed the analysis to create 6 new more groups in addition to the 19 predefined ones. The final 25 groups provided by this analysis were analysed by TWINSPAN again to check their consistency. At last, we established a final number of 21 groups by matching the clusters with the EUNIS classification and the definition of ecologically consistent groups according to the regional literature of the study area. We used EUNIS names down to level three in our classification, and assigned new regionalized names to the fourth level. In some cases we needed to create new EUNIS codes, and to do this we added a lowercase letter to

the third level EUNIS code. To visualise the relationship among the three major functional groups and the final forest types, we calculated a Non-Metric Multidimensional Scaling (NMDS) based on floristic composition, using the Bray-Curtis distance. We used JUICE v7.1 (Tichý 2002) to do the expert system, TWINSpan and semi-supervised k-means classification.

### **Environmental drivers of the forest types**

We plotted the forest plots on a Whittaker biome diagram defined by mean annual temperature and annual rainfall (Whittaker 1970) using the R package 'plotbiomes' (Stefan & Levin 2022). Then, we did a Principal Component Analysis (PCA) of the CHELSA bioclimatic variables to reduce the climatic variation to the first three axes, which explained 83.6% of the variation (Supplementary 2). We interpreted PCA axis 1 (33.8% of variation) as a gradient of continentality, being related negatively to winter temperature and positively to the diurnal and annual range of temperatures; axis 2 (29.2%) as total precipitation, being negatively related to annual precipitation; and axis 3 (20.6%) as precipitation seasonality, being negatively related to precipitation seasonality and the amount of precipitation during the wettest season. The values of the forest plots along the three PCA axes were then compared in a box-plot to evaluate their climatic preferences along the major gradients. We further tested the differences among forest types using the CHELSA bioclimatic variables in a PERMANOVA (Permutational Multivariate Analysis of Variance, Anderson 2001) using the 'Adonis' function in R with 999 permutations and Euclidean distance. In addition, a pairwise PERMANOVA was carried out to assess the differences between each pair of forest types.

Finally, we fitted Generalized Linear Models (GLM) to understand the main drivers of the forest types as a function of bioclimatic and soil pH variables. To select the best predictors as independent variables, we calculated a correlation matrix based on Pearson's correlation coefficient. From pairs of variables with correlations > 0.6, we kept those with the highest contribution to the PCA axes. The variables finally selected were: bio6 (mean daily minimum air temperature of the coldest month), bio7 (annual range of air temperature), bio12 (annual precipitation) and bio15 (precipitation seasonality). In addition, soil pH was included in the model as well. The dependent variable of the GLMs was binary and reflected the presence (1) or absence (0) of the forest type. To have an equal proportion of presences/absences, a random selection was carried out among the full forest dataset to match the number of presences and absences. The random selection was repeated several times, obtaining constant results each time we performed the analysis. All the analyses were computed separately for the three major functional forest types and for the 21 compositional forest types.

## **RESULTS**

### **Classification of the Cantabrian Mixed Forests**

We recognized 22 different types of natural and semi-natural forests and woodlands in our study area: 12 *deciduous broadleaved forests*, 6 *evergreen broadleaved forests* and 4 *coniferous forests* (Table 1). NMDS showed a clear differentiation between broadleaved deciduous and evergreen forests (Fig. 2). However, certain overlap was



observed, as for example the centroid of the *thermophilous Quercus forests* is within the evergreen zone, and the centroid of the *Ilex woodlands* appears in the deciduous zone. Coniferous forests showed a scattered pattern across the compositional space, with *Taxus woodlands* centroid within the deciduous zone, *Juniperus woodlands* one within the evergreen zone and the *Pinus pinaster forests* one just in between.

Geographically, broadleaved deciduous forests are distributed throughout the study area, while evergreen forest are limited either to the coast (e.g. *Quercus ilex forests*) or to specific valleys (e.g. *Quercus suber* or *Quercus rotundifolia forests*) (Fig. 1). Most coniferous forests are found in the western Galician coast as *Pinus pinaster forests*, many of them probably favoured by plantations within their original native range. Other coniferous forests were semi-natural *Taxus woodlands* and relict *Juniperus woodlands*. The main characteristics of the forest types are described below.

### *T1 Broadleaved deciduous forests*

T111 Cantabrian *Salix - Populus* riparian forests. Riverine forests dominated by different willows (*Salix* spp.) and black poplar (*Populus nigra*), with species with a preference for Mediterranean climates such as *Fraxinus angustifolia*, *Salix alba* or *Vitis vinifera*.

T121 Cantabrian *Alnus* riparian forests. Riverine forests dominated by alder (*Alnus glutinosa*, including *Alnus lusitanica*). With species that are dependent on high soil moisture such as *Carex pendula*, *Carex reuteriana* or *Osmunda regalis*.

T172 Cantabrian *Fagus* forests on non-acid soils. Eutrophic to neutral mesic forests dominated by beech (*Fagus sylvatica*), mainly at medium to high elevations, with base-loving understory plants like *Helleborus viridis* or *Hepatica nobilis*.

T182 Cantabrian *Fagus* forests on acid soils. Mesic forests dominated by beech (*Fagus sylvatica*), mainly at higher elevations, with acid-loving species such as *Blechnum spicant* or *Avenella flexuosa*.

T197 Cantabrian thermophilous *Quercus* forests. Mainly base- and warmth-loving forests, restricted to the southern margin of the Cantabrian mountains and the upper Ebro basin, with pubescent oak (*Quercus pubescens*) and/or Portuguese oak (*Quercus faginea*) as the dominant trees.

T19A Cantabrian *Quercus pyrenaica* forests. Forests dominated by Pyrenean oak (*Quercus pyrenaica*), occurring in relatively dry and continental areas, mainly but not exclusively on acid soils, with understory species like *Arenaria montana* or *Festuca elegans*.

T1Bx Cantabrian mixed forests on acid soils. Acid-loving, mesic, mainly lowland forests with a mixed dominance of pedunculate oak (*Quercus robur*), Pyrenean oak (*Quercus pyrenaica*) and chestnut (*Castanea sativa*).

T1By Cantabrian mountain *Quercus* forests on acid soils. Mesic forests of the Cantabrian Mountains dominated by sessile oak (*Quercus petraea*) or, in the timberline, orocantabrian oak (*Quercus orocantabrica*), with acidophilous understory species like *Avenella flexuosa* or *Vaccinium myrtillus*.

T1D1 Cantabrian lowland *Betula* forests. Mainly acid-loving forests dominated by Carpetan birch (*Betula celtiberica*), with the occasional presence of silver birch (*Betula pendula*) at lower elevations, with an understory made of acid-loving (e.g. *Holcus mollis*) or water-loving (e.g. *Carex reuteriana*, *Viola palustris*) plants.

T1D7 Cantabrian mountain *Betula* forests. Mainly acid-loving forests dominated by Carpetan birch (*Betula celtiberica*) at higher elevations, with frequent occurrence of acid-loving species such as *Erica arborea* or *Vaccinium myrtillus*.

T1E1 Cantabrian mixed forests on non-acid soils. Eutrophic and mesic forests with non-dominant tree composition, commonly with European ash (*Fraxinus excelsior*). Includes forests of the lowlands and the Cantabrian Mountains.

T1Fx Cantabrian *Acer* - *Fraxinus* forests on acid-rich soils. Forests found locally on well-drained and fertile soils within an acid soil matrix, allowing a greater diversity of species.

## T2 Broadleaved evergreen forests

T211 Cantabrian *Quercus suber* forests. Warmth-loving and relatively dry forests on acid soils, dominated by cork oak (*Quercus suber*) with presence of warmth- and dry-loving species such as *Cistus salviifolius*, *Lavandula pedunculata* or *Phillyrea angustifolia*.

T21x Cantabrian *Quercus ilex* forests. Mainly coastal and lowland forests on limestone dominated by holly oak (*Quercus ilex*), frequently accompanied by *Phillyrea latifolia*, *Smilax aspera* or bay laurel (*Laurus nobilis*).

T21y Cantabrian *Quercus rotundifolia* forests on non-acid soils. Forests dominated by holm oak (*Quercus rotundifolia*) in relatively drier soils on limestone bedrocks, allowing the presence of warmth- and dry-loving species such as kermes oak (*Quercus coccifera*) or *Lavandula latifolia*.

T21z Cantabrian *Quercus rotundifolia* forests on acid soils. Warmth-loving and relatively dry forests dominated by holm oak (*Quercus rotundifolia*) in areas with Mediterranean microclimates, with the occurrence of warmth- and dry-loving species such as *Genista hystrix* or *Lavandula pedunculata*.

T221 Cantabrian laurophyllous forests. Forests of warm-temperate and humid conditions, including coastal and inland forests dominated by bay laurel (*Laurus nobilis*), coastal low forests with common olive (*Olea europaea*) and inland forests with high presence of Portugal laurel (*Prunus lusitanica*).

T27x Cantabrian *Ilex* woodlands. Mountain semi-natural and open woodlands dominated by European holly (*Ilex aquifolium*), which have been favoured by human activities, mainly traditional husbandry.

## T3 Coniferous evergreen forests

T35x Cantabrian *Pinus sylvestris* forests. Forests dominated by Scots pine (*Pinus sylvestris*), represented by only a few relict remnants in southern continental valleys of

the Cantabrian Mountains, sustaining relict populations of cold-loving species such as *Eriophorum vaginatum* and *Equisetum sylvaticum*.

T3A1 Cantabrian *Pinus pinaster* forests. Acid-loving maritime pine (*Pinus pinaster*) forests of lowlands, mostly in old-established plantations on eroded soils, with heathland species such as *Calluna vulgaris*, *Erica cinerea* or *Ulex europaeus*.

T3C1 Cantabrian *Taxus* woodlands. Semi-natural and open mountain woodlands, mainly on acid soils, dominated by common yew (*Taxus baccata*) and with high frequency of Carpetan birch (*Betula celtiberica*), European holly (*Ilex aquifolium*) or European mountain ash (*Sorbus aucuparia*).

T3D6 Cantabrian *Juniperus* woodlands. Continental relict open woodlands on limestones, dominated by Spanish Juniper (*Juniperus thurifera*) and savin juniper (*Juniperus sabina*), with the occasional occurrence of Portuguese oak (*Quercus faginea*) or alpine juniper (*Juniperus communis* subsp. *nana*) and with a high presence of warmth-loving (e.g. *Rhaponticum coniferum*) and base-loving (e.g. *Helianthemum apenninum*) plants.

### Environmental drivers

According to the Whittaker biome plot (Fig. 1), the forest types analyzed occupy a wide gradient from temperate grasslands to temperate rainforest zones. This gradient is more variable in terms of precipitation than temperature. Cantabrian deciduous forests stretch across all this climatic gradient, but evergreen forests are mainly located in the warmest and driest areas. Coniferous forests stretch across the precipitation gradient, but show a bimodal pattern in the temperature gradient, being more common at the coldest and warmest sites, and more scarce in the intermediate zone.

The distribution of EUNIS forest types across the PCA axis indicated the preference of each forest type along major climatic gradients (Fig. 3, Supplementary 3). The continentality PCA1 axis separates mountain and inland forests (e.g. *Fagus* forests on acid and non-acid soils, thermophilous *Quercus* forests, *Quercus pyrenaica* forests, mountain *Betula* forests, mountain *Quercus* forests on acid soils, *Taxus* woodlands, *Juniperus* woodlands) from forests that appear closer to the coast (e.g. *Quercus ilex* forests, laurophyllous forests, *Pinus pinaster* forests). The annual precipitation PCA2 axis separates forests that grow in high-rainfall zones (e.g. *Fagus* forests on acid and non-acid soils, lowland and mountain *Betula* forests, *Ilex* woodlands) from low-rainfall forests (e.g. thermophilous *Quercus* forests, *Quercus pyrenaica* forests, *Quercus suber* forests, *Juniperus* woodlands). Finally, the precipitation seasonality PCA3 axis separates mainly deciduous from mediterranean-influenced forests (e.g. *Quercus suber* forests, *Quercus rotundifolia* forests on acid soils), since deciduous ones are associated with low precipitation seasonality (i.e. a regular distribution of rainfall throughout the year, without a marked dry season), although some evergreen forests follow this same trend (e.g. *Quercus ilex* forests, *Quercus rotundifolia* forests on non-acid soils, laurophyllous forests). It seems that evergreen *Quercus* forests on siliceous soils are restricted to inland areas and are the ones which present a higher precipitation seasonality (e.g. *Quercus suber* forests, *Quercus rotundifolia* forests on acid soils), while those developed on limestone show the opposite pattern, either occurring in the coast (e.g. *Quercus ilex*

forests) or inland (e.g. *Quercus rotundifolia* forests on non-acid soils). Among coniferous forests, we can distinguish *Juniperus woodlands*, with a low seasonality of precipitation, due in part to the lack of rainfall throughout the year; and *Pinus pinaster* forests, with a high seasonality due to the Mediterranean influence, and *Taxus woodlands*, with intermediate values.

Adonis analysis showed significant but slight differences between functional forest types ( $R^2 = 0.08$ ,  $p = 0.001$ ,  $N = 3$ ). In contrast, the dissimilarities were stronger for the EUNIS level-4 types ( $R^2 = 0.480$ ,  $p = 0.001$ ,  $N = 21$ ). This was consistent with the pairwise analysis results (Supplementary 4). Although some forest pairs showed low  $R^2$  values, we found that many of them were significantly different from each other, with few exceptions. On the one hand, the more bioclimatically distinct forests were the *Mountain Betula* forests, the *laurophyllous* forests and the *Pinus pinaster* forests, since they obtained the highest  $R^2$  values when compared to the rest of the forests (Fig. 4). On the other hand, the more similar forests (i.e. lowest  $R^2$  values) were the *Ilex woodlands* and *Taxus woodlands* when compared to each other or to other mountain forests such as *Fagus forests on non-acid soils*, *mountain Quercus forests on acid soils* or *mountain Betula forests*.

The results from the GLMs showed that different environmental variables determine the occurrence of different functional types and EUNIS level-4 forests (Table 3). In general, higher precipitation seasonality was associated with a higher probability of broadleaved evergreen forests and a lower probability of broadleaf deciduous and coniferous forests. Within the deciduous forest group, some forest types were positively related to precipitation seasonality (e.g. *Quercus pyrenaica* forests), while others did not respond to this variable (e.g. *Fagus forests on non-acid soils*). The most important variable determining the presence of broadleaved evergreen forests was winter minimum temperature, with a higher probability of appearing in sites with warmer winters. Some dry-loving forests were positively related to soil pH (e.g. *Quercus ilex* forests, *Quercus rotundifolia* forests on non-acid soils, *Juniperus woodlands*), since most of them develop on limestone, which promotes edaphic drought during the summer months. We found some unusual results since some of the acid-loving forests appeared to be positively related to soil pH (e.g. *Quercus pyrenaica* forests) while some base-loving forests negatively responded to this variable (e.g. *T172 Fagus forests on non-acid soils*).

## DISCUSSION

Our results indicate a wide climatic variation in the Cantabrian Mixed Forests ecoregion, occupying several biomes as defined by Whittaker's terrestrial biome classification (Whittaker 1970). This climatic heterogeneity is accompanied by a high diversity of forest types. Traditionally, an ecoregion containing functional ecosystem types that diverge from their assigned biome has been seen as a characteristic of tropical ecoregions, and not of temperate ones (Olson *et al.* 2001). To our knowledge, the drivers behind such functional ecosystem diversity have been poorly studied in either tropical or temperate climatic world regions. The occurrence of both broadleaved evergreen and deciduous forests in transitional climatic zones has been reported in temperate climates (Box & Fujiwara 2015), while coniferous forests are more often referred to mediterranean or boreal climates. In our study area, broadleaved deciduous forests are the most

widespread forest type, as expected by their general climatic conditions. However, broadleaved evergreen vegetation is locally dominant in climatic zones with mild winter temperatures, mainly in coastal areas, where we find a vegetation dominated by sclerophyllous species such as *Arbutus unedo*, *Laurus nobilis*, *Olea europaea*, *Phillyrea latifolia*, *Quercus ilex* or *Rhamnus alaternus*. The Cantabrian coast, therefore, is a current climatic refugium, and probably was a similar refugium for warmth-loving species during the Last Glacial Period (Figueiral 1995) and Early Holocene (Carrion *et al.* 2010). In the current climate warming scenario, the coast could serve as a source for re-colonisation of warm-temperate evergreen forests inland. Indeed, Benito Garzón *et al.* (2008) appointed an increase of the distribution of thermophilous species, while temperate and submediterranean species, as well as mountain coniferous trees, would suffer a reduction of their current distribution, especially the latter ones.

The classification of forests has shown a clear differentiation among functional types, not only in their dominant trees but also in their understory species, especially between evergreen and deciduous forests. Respecting the EUNIS 4-level classification, our results show a lower number of types of forests than phytosociological classifications (Rivas-Martínez *et al.* 2001, 2002, Rodríguez-Gutián *et al.* 2012, Mucina *et al.* 2016). This same pattern has been seen during the last years with the appearance of new methodologies for classification of vegetation (Rodríguez-Rojo *et al.* 2017, Bonari *et al.* 2019, Noriyuki *et al.* 2021). However, despite the reduction of vegetation types, all of them have ecological consistency, as it reflects their environmental space, discussed down below, and their diagnostic species (Table 2). Each forest displays a unique set of diagnostic species with just a few of them shared, mostly because of their similar environmental conditions (e.g. *Salix cinerea* and *Carex reuteriana*, are shared between the *riparian Alnus forests* and the *lowland Betula forests*, both of them linked to water currents to a greater or lesser extent). The greatest overlap we found is the *Quercus suber forests* with both *Quercus rotundifolia on acid soils forests* and *Pinus pinaster forests*, which could be explained as the combination of being developed on acid soils with a clear mediterranean influence, while the dominance of one or another species could be due to human activities, favouring the presence *Pinus pinaster* for logging and indirectly the presence of *Quercus suber* because of wildfires (Francos *et al.* 2016, Rodríguez-Gutián *et al.* 2020). However, our results found enough differentiation to classify them as separated forests, highlighting human activities as another driver for vegetation diversity, along with climatic and edaphic factors.

In general, the occurrence of most forest types does not seem to be related to annual precipitation, possibly due to the generally high precipitation regime in the ecoregion. Some exceptions would be the *Quercus rotundifolia forests on non-acid soils* and the *Juniperus woodlands*, both of them dominated by dry-loving species. In these two types of formations, soil pH seems to be a relevant co-driver of their occurrence, since the combination of low rainfall and limestone would increase the summer drought conditions in which these species have their optimum (Rivas-Martínez 2017a, Jiménez *et al.* 2003). The presence of calcareous substrate also plays a key role in the dominance of *Cantabrian Quercus ilex forests* in the coast of the ecoregion, explaining their absence in more acidic territories such as Eastern Asturias and Galicia. Winter temperature seems to be a decisive driver in the differentiation between coastal/lowland vs. mountain forests, but also between broadleaved evergreen forests and the other functional types,

being the dominance of the former favoured by milder temperatures (Box & Fujiwara 2015).

Despite the relatively small area of the Cantabrian Mixed Forests ecoregion and the high diversity of forest types we have found, our results indicate that most of these forests have a well-defined environmental optimum. On the one hand, this environmental space is shared and partially overlapped with other forests with similar climatic requirements; on the other hand, local edaphic and topographic variations allow the occurrence of microclimatic conditions that enhance the diversity of forests within the same area. Forests that could be expected to differ only in soil pH were found as significantly different, such as both *Fagus* forests (although with a very low dissimilarity value). The *Cantabrian mountain Betula* forests and the *Cantabrian laurophyllous* forests showed the most climatic differences when compared with the rest of our study area. *Betula* and other boreal deciduous forests, such as *Alnus* or *Salix* ones were dominant during the late glacial period, but they began to decline at the beginning of the Holocene in favour of deciduous *Quercus* forests, which had been restricted to intramontane valleys until then (Carrión *et al.* 2010). Thus, *Cantabrian mountain Betula* forest could be considered as relict boreal forests in the very limit of their distribution. This is consistent with the results of del Río *et al.* (2021), who modelled the impacts of climate change on habitat suitability for Iberian deciduous species and found that *Betula celtiberica* would suffer the largest losses of habitat due to rising temperatures. Our results suggest a similar pattern, since the more important environmental variables for the occurrence of this forest are low annual and winter temperatures. In the opposite situation, *laurophyllous* forests would be survivors from warmer periods of the Neogene (Barrón *et al.* 2010) that were able to cope with glacial periods in the Cantabrian coastline.

Some forests showed a clear overlap in their climatic space. The *Cantabrian Acer - Fraxinus* forests on acid-rich soils, which include ravine forest (Chytrý *et al.* 2020), would not be climatically different from the *Cantabrian Fagus* forests on acid soils. Differences in species composition could be due to the well-drained and fertile soil of the former, allowing other species such as *Acer pseudoplatanus*, *Corylus avellana*, *Fraxinus excelsior* or *Tilia platyphyllos* to compete with *Fagus sylvatica* (Mucina *et al.* 1993, Košir *et al.* 2008), highlighting the importance of microtopographic drivers in forest composition. Additionally, human activities have changed vegetation structure and distribution (Beltrán *et al.* 2014, Song *et al.* 2018), favouring the presence of some tree species and explaining other cases of climatic overlapping, like the *Ilex* woodlands and the *Taxus* woodlands. *Taxus baccata* and *Ilex aquifolium* are shade-tolerant trees which appear naturally as isolated individuals or small groups of trees (Benham *et al.* 2016; Guerrero Hue *et al.* 2016). Their tolerance of low light availability makes them one of the few woody plants able to live under a *Fagus sylvatica* canopy and become relatively abundant in beech forests (Scarnati *et al.* 2009, Zitti *et al.* 2014), especially on acid soils. Thus, it is not surprising that the compositional and climatic space of these two types of woodlands overlaps with *Fagus* forests and with *mountain Betula* forests, which have been widely reported as the replacement of *Fagus* formations in more degraded or recently perturbed areas (Costa *et al.* 1997). However, although both woodlands share diagnostic species with each other (*Galium rotundifolium* and *Sanicula europaea*), they do not share any with the *Fagus* or *Betula* forests. Nevertheless, the abandonment of their traditional management makes these *Ilex aquifolium* and *Taxus baccata* formations scarce today. On the other hand, the *Cantabrian Pinus pinaster* forests, another human-

favoured forest, were found to be climatically distinct from other forests despite the fact that they share several diagnostic species with *Quercus suber* forests and most of them are old-established plantations (Bonari *et al.* 2019), being virtually impossible to distinguish natural and artificial formations. This likely indicates that these plantations occur in zones where this species would have occurred naturally (Figueiral 1995, De-Lucas *et al.* 2009), even when its status as native species is sometimes called into question. But just as the presence of some native species has been favoured by humans, such as *Castanea sativa* (Roces-Díaz *et al.* 2018), *Pinus pinaster*, *Taxus baccata* or *Ilex aquifolium*, other trees have seen their distribution range reduced or even removed from this ecoregion: *Pinus sylvestris* forests are naturally restricted to only two locations in our ecoregion (García *et al.* 1997) and there are no remnant *Abies* forests, despite the fact that this would be a suitable habitat for them and Quaternary palynological records do exist within the ecoregion (Alba-Sánchez *et al.* 2010).

In conclusion, the Cantabrian Mixed Forests ecoregion can be considered as a hotspot of functional and ecological forest types within the temperate deciduous forest biome. This forest diversity is explained by meso- and microhabitat variability that determines a high heterogeneity of climatic niches available for different tree species. A complex climatic history and a long legacy of human intervention have maintained this forest diversity, which now offers a multitude of potential trajectories for species shifts in face of global climate change.

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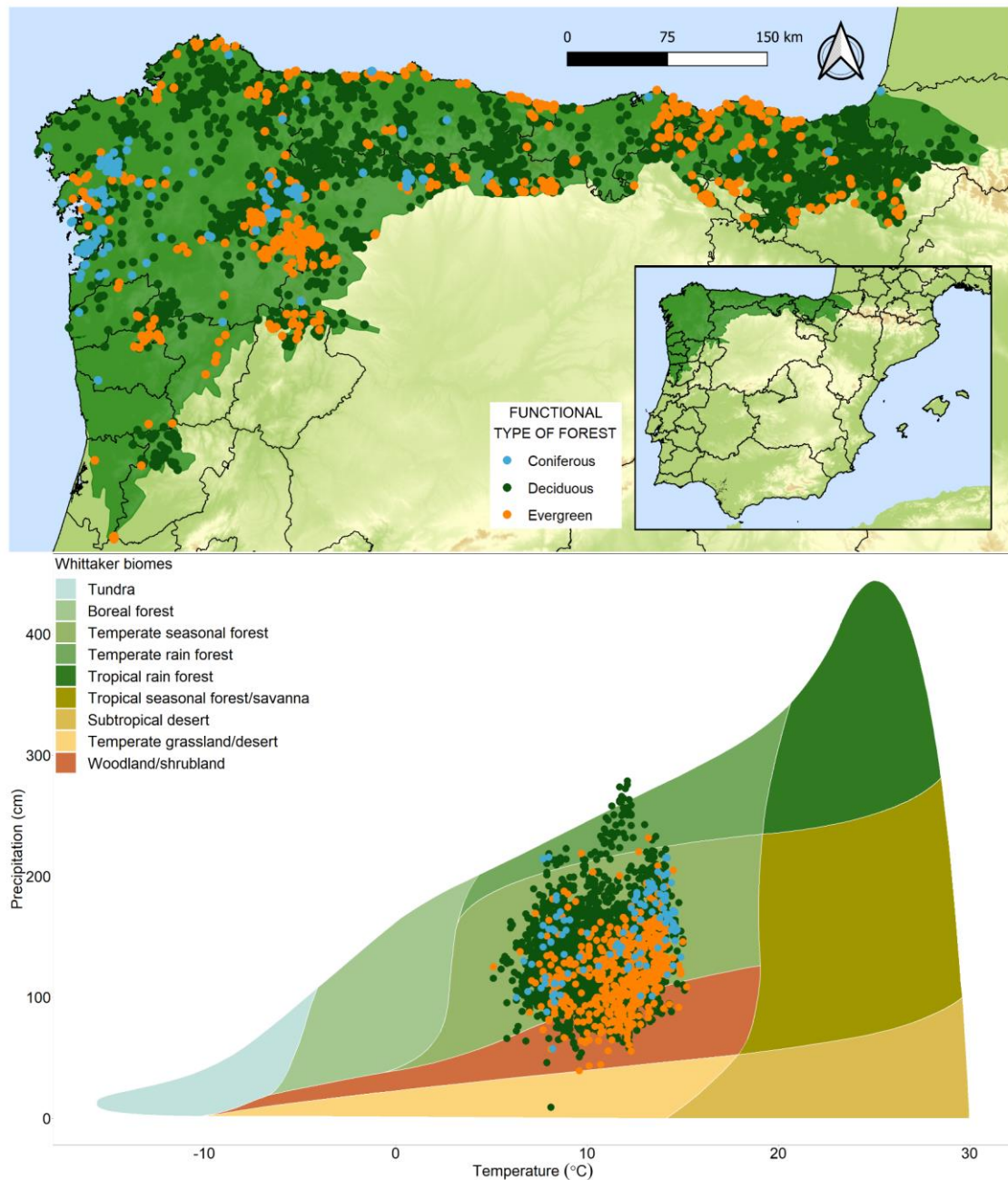
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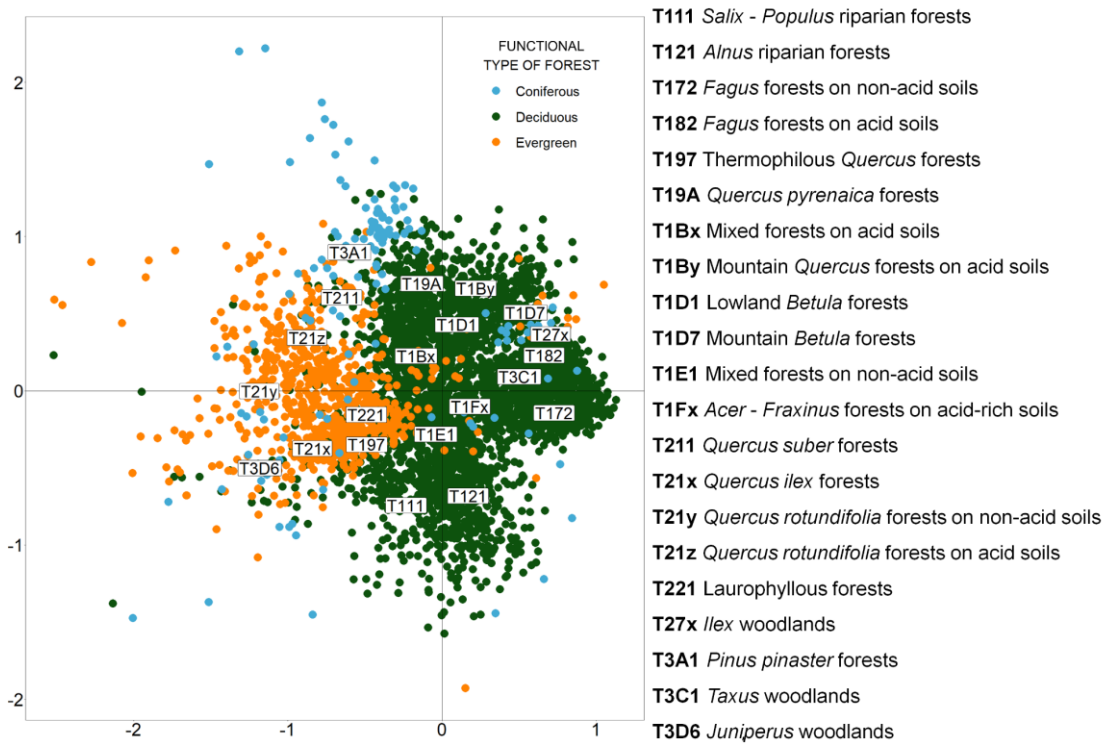
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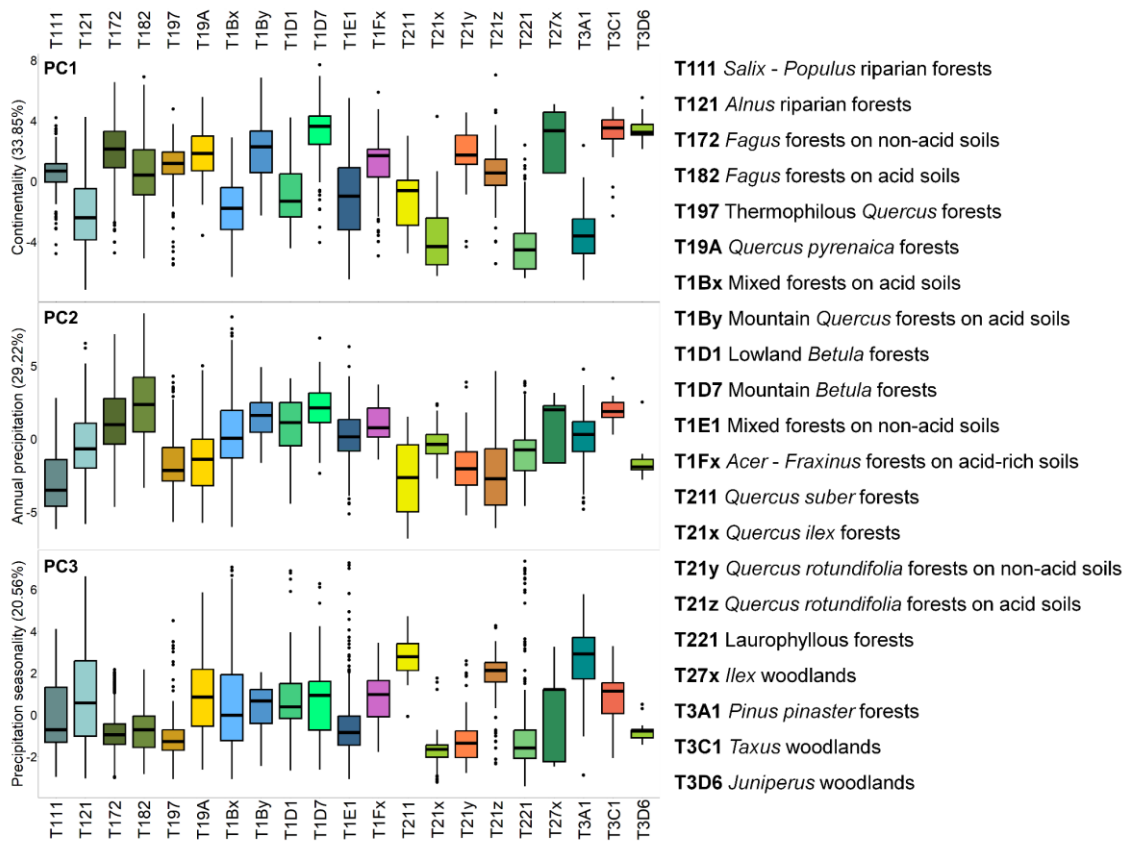
## FIGURES



**FIGURE 1.** Representation of all forest plots grouped by the three functional types of forests: deciduous broadleaved forests (dark green), evergreen broadleaved forests (orange) and coniferous forests (blue). **ABOVE.** Spatial distribution of the plots in the Cantabrian Mixed Forests ecoregion, NW Iberian Peninsula. **BELOW.** Climatic distribution of the plots according to Whittaker's terrestrial biome classification based on the mean annual temperature (°C) and the annual precipitation amount (cm).

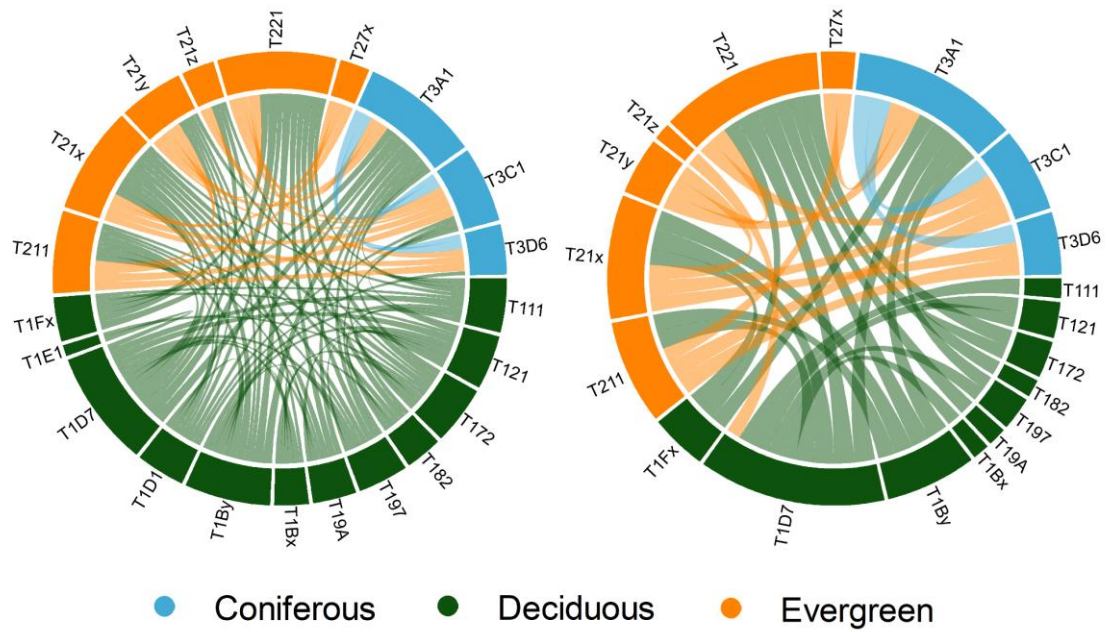


**FIGURE 2.** Axes 1 and 2 of a Non-metric Multidimensional Scaling (NMDS) ordination based on the floristic composition of the 21 different forest types in the Cantabrian Mixed Forest ecoregion (the centroid of each group is represented by a label using the EUNIS level-4 classification), using the Bray-Curtis' distance. The forest plots are coloured by functional types.



**FIGURE 3.** Boxplot of the three first axes from the Principal Component Analysis (PCA) for each type of forest.





**T111** *Salix* - *Populus* riparian forests

**T182** *Fagus* forests on acid soils

**T1Bx** Mixed forests on acid soils

**T1D7** Mountain *Betula* forests

**T211** *Quercus suber* forests

**T21z** *Quercus rotundifolia* forests on acid soils

**T3A1** *Pinus pinaster* forests

**T121** *Alnus* riparian forests

**T197** Thermophilous *Quercus* forests

**T1By** Mountain *Quercus* forests on acid soils

**T1E1** Mixed forests on non-acid soils

**T21x** *Quercus ilex* forests

**T221** Laurophyllous forests

**T3C1** *Taxus* woodlands

**T172** *Fagus* forests on non-acid soils

**T19A** *Quercus pyrenaica* forests

**T1D1** Lowland *Betula* forests

**T1Fx** *Acer* - *Fraxinus* forests on acid-rich soils

**T21y** *Quercus rotundifolia* forests on non-acid soils

**T27x** *Ilex* woodlands

**T3D6** *Juniperus* woodlands

**FIGURE 4.** Chord diagram representing bioclimatic dissimilarities ( $R^2$  from Pairwise ANOVA analysis) among the different types of EUNIS level-4 forests. More and wider links indicate higher dissimilarity. **Left.** Links with  $R^2 > 0.25$ . **Right.** Links with  $R^2 > 0.5$ .

## TABLES

**TABLE 1.** Classification of forests found in our study area with the proposed EUNIS Code and Name (both regionalized), the Number of plots, the Average number of vascular plant species, the Average number of tree species and the Number of diagnostic Species ( $\Phi \geq 0.3$ ).

EUNIS Code	EUNIS Name	No. of plots	Average No. of species	Average No. of trees	No. of diagnostic species
<b>T1 Deciduous broadleaved forests</b>					
T111	Cantabrian <i>Salix</i> - <i>Populus</i> riparian forests	231	32.7±12.9	6.9±2.5	25
T121	Cantabrian <i>Alnus</i> riparian forests	387	23.9±10.5	4.7±2.0	10
T172	Cantabrian <i>Fagus</i> forests on non-acid soils	703	22.4±8.7	2.9±2.1	6
T182	Cantabrian <i>Fagus</i> forests on acid soils	380	18.2±6.5	3.3±2.0	3
T197	Cantabrian thermophilous <i>Quercus</i> forests	170	24.7±9.1	4.1±2.0	5
T19A	Cantabrian <i>Quercus pyrenaica</i> forests	295	27.8±9.7	2.8±1.8	8
T1Bx	Cantabrian mixed forests on acid soils	437	22.9±8.0	4.7±2.0	2
T1By	Cantabrian mountain <i>Quercus</i> forests on acid soils	104	21.5±6.4	4.1±1.9	6
T1D1	Cantabrian lowland <i>Betula</i> forests	113	23.8±10.9	4.8±2.0	8
T1D7	Cantabrian mountain <i>Betula</i> forests	153	22.2±7.0	4.2±1.6	4
T1E1	Cantabrian mixed forests on non-acid soils	379	34.1±10.3	6.7±2.1	1
T1Fx	Cantabrian <i>Acer</i> - <i>Fraxinus</i> forests on acid-rich soils	77	31.6±9.6	7.4±2.1	7
<b>T2 Evergreen broadleaved forests</b>					
T211	Cantabrian <i>Quercus suber</i> forests	49	23.2±9.6	2.9±1.7	20
T21x	Cantabrian <i>Quercus ilex</i> forests	146	18.2±7.1	3.0±2.0	6
T21y	Cantabrian <i>Quercus rotundifolia</i> forests on non-acid soils	143	21.5±9.0	2.4±1.4	12
T21z	Cantabrian <i>Quercus rotundifolia</i> forests on acid soils	165	21.3±7.0	2.1±1.0	6
T221	Cantabrian laurophyllous forests	211	18.2±7.9	2.6±1.9	6
T27x	Cantabrian <i>Ilex</i> woodlands	13	17.5±7.2	3.8±1.5	9
<b>T3 Coniferous forests</b>					
T35x	Cantabrian <i>Pinus sylvestris</i> forests	0	NA	NA	NA
T3A1	Cantabrian <i>Pinus pinaster</i> forests	86	16.7±5.5	1.9±0.9	15
T3C1	Cantabrian <i>Taxus</i> woodlands	26	27.6±10.8	6.0±2.4	11
T3D6	Cantabrian <i>Juniperus</i> woodlands	22	27.6±12.1	2.1±1.1	44

**TABLE 2.** Reduced Synoptic table of the fidelity of the diagnostic species of forests obtained by the Expert System, TWINSpan and Semi-supervised combined analysis. Species are sorted by decreasing values of the phi coefficient ( $\Phi$ ) for each type of forest, only species with  $\Phi \geq 0.3$  are grey shaded.

EUNIS Code	T111	T121	T172	T182	T197	T19A	T18x	T1By	T1D1	T1D7	T1E1	T1Fx	T211	T21x	T21y	T21z	T221	T27x	T3A1	T3C1	T3D6
No. of plots	231	387	703	380	170	295	437	104	113	153	379	77	49	146	143	165	211	13	86	26	22
<b>Cantabrian Salix - Populus riparian forests</b>																					
<i>Fraxinus angustifolia</i>	61.9	17.6														3					
<i>Rubus caesius</i>	53.9										2										
<i>Populus nigra</i>	53.8	6								1.6	1.5										
<i>Ulmus minor</i>	52.3	1.2								5.6											
<i>Salix euxina</i>	50.3	1.8																			
<i>Salix purpurea</i>	49.4																				
<i>Alliaria petiolata</i>	49.3	0.5								4.5										5.6	
<b>Cantabrian Alnus riparian forests</b>																					
<i>Lycopus europaeus</i>	7.2	39.6																			
<i>Osmunda regalis</i>		39.1							17.2		1.7	3.6					1.8		0.2		
<i>Angelica sylvestris</i>	19.9	33.7									11	3.2									
<i>Oenanthe crocata</i>	7.9	33.6							26												
<i>Carex pendula</i>	26.3	32								8.5	2.9										
<i>Solanum dulcamara</i>	24.8	31.4																			
<i>Lythrum salicaria</i>	22	31.2																			
<b>Cantabrian Fagus forests on non-acid soils</b>																					
<i>Helleborus viridis</i>			38.5	3.3	3.6	0.1					19.3										1.6
<i>Isopyrum thalictroides</i>			33.6																		
<i>Hepatica nobilis</i>			30.2		15.7						8.2			1.8	6.2						
<i>Carex sylvatica</i>	4.9	1.9	30.1	1.7						20.2	0.1								2.6		
<b>Cantabrian Fagus forests on acid soils</b>																					
<i>Blechnum spicant</i>		4.1		32.4			17		23.4	12.9		12.4							2		4.2
<b>Cantabrian thermophilous Quercus forests</b>																					
<i>Quercus pubescens</i>					40.7						1.5				2.2						
<i>Viburnum lantana</i>	19.3				40.4										8.4						9
<i>Prunus spinosa</i>	11.6				36.6					10.9					11	5.6	1.3	1.2			
<i>Juniperus communis</i>					31.2									0.6	27.3					2.1	16.7
<b>Cantabrian Quercus pyrenaica forests</b>																					
<i>Quercus pyrenaica</i>					0.4	60.9	8.4						6			1.1					1.3
<i>Crucjata glabra</i>					3	46.7	0.5			0.3	3.1										
<i>Clinopodium vulgare</i>					0.3	37.3							7.2		6	26.4					10.6
<i>Physospermum cornubiense</i>						37.2	7.3	20.6													
<i>Arenaria montana</i>						36.6	11	12.1												9.3	2.7
<i>Festuca elegans</i>						33.1				0.6						25.5					
<i>Prunella grandiflora</i>					0.9	31.1	2		3.1		1.2										
<b>Cantabrian mixed forests on acid soils</b>																					
<i>Quercus robur</i>			2.1				37.6		30		17.3			1			0.3			13.1	
<i>Castanea sativa</i>			2.2			0.5	33.2		14.7		18.3	8.7									
<b>Cantabrian mountain Quercus forests on acid soils</b>																					
<i>Quercus orocantabrica</i>								35.9													
<i>Eragrostis atrovirens</i>								30.3													
<b>Cantabrian lowland Betula forests</b>																					
<i>Deschampsia cespitosa aggr.</i>	13.1	3.9								42.5		3.3									
<i>Senecio nemorensis aggr.</i>		17								37.4		5.8									
<i>Holcus mollis</i>				7.2		24.6	8.2	15.5		36.9		9.6									4.9
<i>Viola palustris</i>		13.7								32.8	0.8	7						0.8			
<i>Crocus serotinus</i>			6				0.1			30.2		0.5									
<b>Cantabrian mountain Betula forests</b>																					
<i>Erica arborea</i>						9.2	1.9	25.9	16.9	31.8			15.7			7.5					
<b>Cantabrian mixed forests on non-acid soils</b>																					
<i>Fraxinus excelsior</i>	10.8	19.5									35.8	24.3									
<b>Cantabrian Acer - Fraxinus forests on acid-rich soils</b>																					
<i>Acer pseudoplatanus</i>	0.7	2.5						1.1	2.7		10.4	43.7							12.1		12.1
<i>Valeriana pyrenaica</i>		11.8							0.4		9.2	35.1									0.7
<i>Corylus avellana</i>	5.2				0.6			8.6		1.7	25.3	33.8							11.4		24.4
<i>Luzula sylvatica</i>		0.9		16.5				13	1.1	27.5		33.2									19.5
<i>Saxifraga clusii</i>		2.5								7.8		33.1									
<i>Chrysosplenium oppositifolium</i>												32.7									
<b>Cantabrian Quercus suber forests</b>																					
<i>Quercus suber</i>													77.6		4.4	0.7					
<i>Anarrhinum durimium</i>													42								
<i>Vulpia myuros</i>													40.6							5	
<i>Cistus salvifolius</i>													40.1	9.2	12.2	20.4					
<i>Genista tridentata</i>								1.7					37.4			3.9				6.5	
<i>Arbutus unedo</i>							1.9						36.2	26.4	14.7	17.5	0.9				
<i>Sesamoides purpurascens</i>													35.5								1.1
<b>Cantabrian Quercus ilex forests</b>																					
<i>Quercus ilex</i>										3					89.3						
<i>Phillyrea latifolia</i>				1.4											62.1	10.4					
<i>Rhamnus alaternus</i>				9.9											46.4	23.6					
<i>Rubia peregrina</i>				20.4						0.7			7.3		37.3	25	20.4	25.8			
<i>Rosa arvensis</i>		0.6		24.7							17.6				35.7						
<b>Cantabrian Quercus rotundifolia forests on non-acid soils</b>																					
<i>Spiraea hypericifolia</i>					11.4											48.9					
<i>Carex halleriana</i>					1.5											48.4					
<i>Amelanchier ovalis</i>					15.4											46.7					
<i>Quercus coccifera</i>					9											40					
<i>Juniperus phoenicea</i>					2.1											38					
<i>Dorycnium pentaphyllum</i>					5.5								0.2	6.9	37.8						
<i>Lavandula latifolia</i>					2.5										35.3						
<b>Cantabrian Quercus rotundifolia forests on acid soils</b>																					
<i>Pistacia terebinthus</i>													8.4	11.5	3.7	34.6					
<i>Genista hystrix</i>													10			33.3					
<b>Cantabrian laurophyllous forests</b>																					
<i>Parietaria judaica</i>														3.5					56.1		
<i>Laurus nobilis</i>		6.1					3.5			2.5		5.3							18		52.4
<i>Olea europaea</i>														5.5							37.2
<i>Digitaria sanguinalis</i>																					33.7
<i>Crithmum maritimum</i>													12.6								30.8
<b>Cantabrian Ilex woodlands</b>																					
<i>Stellaria nemorosa</i>																				65.7	6
<i>Veronica montana</i>	2.9	0.9	7.6								4.1	0.6									44.2
<i>Thelypteris limbosperma</i>				9.9			0.8	4.4	5.7		1.2										38.8
<i>Dryopteris dilatata</i>				14.3			4	2.9	13.8		21.2										38.7
<i>Paris quadrifolia</i>			4.6						1.7		3.8										37.6
<i>Scrophularia scorodonia</i>																					



**TABLE 3.** Results of the Generalized Linear Models (GLMs) for three functional types and 21 EUNIS level-4 forest types in the cantabrian Mixed Forests ecoregion . It is shown the z value for all variables of every model and their significance (\*\*\*)  $\leq 0$ , \*\*  $\leq 0.001$ , \*  $\leq 0.05$ , .  $< 0.1$ ), as well as the explained deviance (%).

	Bio6 Winter temperature	Bio7 Annual range of air temperature	Bio12 Annual precipitation amount	Bio15 Precipitation seasonality	Soil pH	Explained deviance (%)
<b>All deciduous</b>	-6.4 ***	3.2 **	6.1 ***	-9.0 ***	-6.7 ***	17.2
T111	6.5 ***	7.7 ***	-3.1 **	-4.6 ***	n.s.	41.1
T121	8.7 ***	4.4 ***	n.s.	1.6	-1.8 .	19.5
T172	-17.2 ***	n.s.	n.s.	-10.9 ***	-3.9 ***	31.8
T182	-9.0 ***	-4.9 ***	n.s.	-8.5 ***	-7.1 ***	29.7
T197	3.5 ***	4.7 ***	-1.7 .	-5.2 ***	3.0 **	29.2
T19A	n.s.	5.1 ***	-1.8 .	2.6 *	1.8 .	24.4
T1Bx	9.2 ***	6.8 ***	2.6 **	-2.8 **	-7.3 ***	21.0
T1By	-5.6 ***	n.s.	2.1 *	1.5	n.s.	24.2
T1D1	n.s.	-3.8 ***	n.s.	4.5 ***	-3.3 ***	25.8
T1D7	-8.3 ***	-4.8 ***	n.s.	4.8 ***	-2.3 *	43.7
T1E1	3.9 ***	3.1 **	2.7 **	-6.7 ***	n.s.	6.7
T1Fx	-4.0 ***	-2.3 *	n.s.	3.4 ***	-2.3 *	24.7
<b>All evergreen</b>	14.5 ***	n.s.	-6.3 ***	7.2 ***	5.7 ***	17.7
T211	3.1 **	2.7 **	n.s.	2.9 **	n.s.	60.6
T21x	7.5 ***	n.s.	n.s.	-5.0 ***	2.0 *	46.9
T21y	-4.6 ***	n.s.	-4.2 ***	-2.2 *	3.3 **	38.9
T21z	4.6 ***	6.5 ***	n.s.	5.2 ***	n.s.	39.6
T221	3.4 ***	-1.9 .	n.s.	3.9 ***	n.s.	49.2
T27x	-2.4 *	n.s.	n.s.	2.0 *	n.s.	41.2
<b>All coniferous</b>	-2.7 **	-4.4 ***	n.s.	6.7 ***	2.6 **	24.2
T3A1	5.4 ***	n.s.	n.s.	5.0 ***	-1.4	47.8
T3C1	-2.8 **	n.s.	n.s.	1.9 .	n.s.	31.2
T3D6	-2.1 *	n.s.	-2.2 *	1.9 .	1.9 *	83.1

**SUPPLEMENTARY 1.** List of all aggregated taxa in our forest plots. Aggregates considered necessary by us are shown grey shaded, while the ones created by the Expert System are not. Taxa in bold are the different species contained within each aggregate, while the rest are the subspecies and synonyms found in our raw data from SIVIM. Aggregates with just one species or one species and one subspecies were created by Expert System and maintained as aggregates to perform the analysis. Aggregates with another aggregate within were created following the Euro+Med nomenclature system.

AGGREGATES SPECIES, SUBSPECIES AND SYNONIMS	FAMILY
<i>Acer opalus</i> aggr. <b><i>Acer opalus</i> Mill.</b> <i>Acer opalus</i> Mill. subsp. <i>opalus</i>	Sapindaceae
<i>Achillea millefolium</i> aggr. <b><i>Achillea millefolium</i> L.</b> <i>Achillea millefolium</i> L. subsp. <i>millefolium</i>	Asteraceae
<i>Aconitum napellus</i> aggr. <b><i>Aconitum napellus</i> L.</b> <i>Aconitum napellus</i> subsp. <i>lusitanicum</i> Rouy <i>Aconitum napellus</i> subsp. <i>vulgare</i> Rouy & Foucaud	Ranunculaceae
<i>Allium senescens</i> aggr. <b><i>Allium lusitanicum</i> Lam.</b>	Amaryllidaceae
<i>Anacamptis palustris</i> aggr. <b><i>Anacamptis laxiflora</i> (Jacq.) R. M. Bateman, Pridgeon &amp; M. W. Chase</b> <i>Orchis laxiflora</i> Lam. <b><i>Anacamptis palustris</i> (Jacq.) R. M. Bateman, Pridgeon &amp; M. W. Chase</b> <i>Orchis palustris</i> Jacq.	Orchidaceae
<i>Anthoxanthum odoratum</i> aggr. <b><i>Anthoxanthum odoratum</i> L.</b>	Poaceae
<i>Arabis hirsuta</i> aggr. <b><i>Arabis hirsuta</i> (L.) Scop.</b> <i>Arabis glabra</i> Boiss. & Heldr. <i>Arabis hirsuta</i> subsp. <i>sagittata</i> (Bertol.) Čelak. <i>Arabis hirsuta</i> subsp. <i>sagittata</i> (Bertol.) Nyman <i>Arabis hirsuta</i> subsp. <i>sagittata</i> (Bert.) Rchb. <i>Arabis hirsuta</i> var. <i>glabra</i> L. <i>Arabis hirsuta</i> var. <i>sagittata</i> (Bertol.) DC. <i>Arabis sagittata</i> (Bertol.) DC.	Brassicaceae
<b><i>Arenaria aggregata</i> aggr.</b> <b><i>Arenaria aggregata</i> (L.) Loisel.</b> <i>Arenaria aggregata</i> (L.) Loisel. subsp. <i>aggregata</i> <i>Arenaria aggregata</i> subsp. <i>racemosa</i> (Willk.) Font Quer <i>Arenaria racemosa</i> Willk.	Caryophyllaceae
<i>Bromopsis ramosa</i> aggr. <b><i>Bromopsis benekenii</i> (Lange) Holub</b> <b><i>Bromopsis ramosa</i> (Huds.) Holub</b> <i>Bromus ramosus</i> Huds.	Poaceae
<i>Bupleurum baldense</i> aggr. <b><i>Bupleurum baldense</i> Turra</b>	Apiaceae
<i>Campanula patula</i> aggr. <b><i>Campanula patula</i> L.</b>	Campanulaceae

**SUPPLEMENTARY 1.** (Continued).

<i>Campanula rotundifolia</i> aggr.	Campanulaceae
<p><b><i>Campanula rotundifolia</i> L.</b>  <i>Campanula rotundifolia</i> subsp. <i>legionensis</i> (Pau) M. Lainz  <i>Campanula rotundifolia</i> subsp. <i>hispanica</i> (Willk.) O. Bolòs &amp; Vigo  <i>Campanula rotundifolia</i> L. subsp. <i>rotundifolia</i></p>	
<i>Cardamine impatiens</i> aggr.	Brassicaceae
<p><b><i>Cardamine impatiens</i> L.</b>  <i>Cardamine impatiens</i> L. subsp. <i>impatiens</i></p>	
<i>Carduus defloratus</i> aggr.	Asteraceae
<p><b><i>Carduus defloratus</i> L.</b></p>	
<i>Carlina corymbosa</i> aggr.	Asteraceae
<p><b><i>Carlina corymbosa</i> L.</b>  <i>Carlina corymbosa</i> L. subsp. <i>corymbosa</i>  <b><i>Carlina hispanica</i> Lam.</b>  <i>Carlina corymbosa</i> subsp. <i>hispanica</i> (Lam.) O. Bolòs &amp; Vigo  <i>Carlina corymbosa</i> subsp. <i>major</i> (Lange) J. López &amp; Devesa</p>	
<i>Carlina vulgaris</i> aggr.	Asteraceae
<p><b><i>Carlina biebersteinii</i> Hornem.</b>  <b><i>Carlina vulgaris</i> L.</b>  <i>Carlina vulgaris</i> L. subsp. <i>vulgaris</i></p>	
<i>Cyanus triumfettii</i> aggr.	Asteraceae
<p><b><i>Cyanus triumfettii</i> (All.) Á. Löve &amp; D. Löve</b>  <i>Centaurea graminifolia</i> (Lam.) Muñoz Rodr. &amp; Devesa  <i>Centaurea triumfettii</i> subsp. <i>lingulata</i> (Lag.) Dostál  <i>Centaurea seusana</i> Chaix  <i>Cyanus triumfettii</i> (All.) Á. Löve &amp; D. Löve  <i>Cyanus triumfettii</i> subsp. <i>axillaris</i> (Čelak.) Štěpánek</p>	
<i>Dactylorhiza maculata</i> aggr.	Orchidaceae
<p><b><i>Dactylorhiza maculata</i> (L.) Soó</b>  <i>Dactylorhiza maculata</i> subsp. <i>caramulensis</i> Verm.  <i>Dactylorhiza maculata</i> subsp. <i>elodes</i> (Griseb.) Soó  <i>Dactylorhiza maculata</i> subsp. <i>ericetorum</i> (E. F. Linton) P. F. Hunt &amp; Summerh  <i>Orchis elodes</i> Griseb.  <i>Orchis maculata</i> L.  <i>Orchis maculata</i> subsp. <i>elodes</i> (Griseb.) K. Richt.</p>	
<i>Deschampsia cespitosa</i> aggr.	Poaceae
<p><b><i>Deschampsia cespitosa</i> (L.) P. Beauv.</b>  <i>Deschampsia cespitosa</i> (L.) P. Beauv. subsp. <i>cespitosa</i>  <i>Deschampsia cespitosa</i> subsp. <i>subtriflora</i> (Lag.) Ehr. Bayer &amp; G. López  <i>Deschampsia media</i> (Gouan) Roem. &amp; Schult.</p>	
<i>Dryopteris affinis</i> aggr.	Dryopteridaceae
<p><b><i>Dryopteris affinis</i> (Lowe) Fraser-Jenk.</b>  <i>Dryopteris affinis</i> (Lowe) Fraser-Jenk. subsp. <i>affinis</i>  <b><i>Dryopteris borrieri</i> (Newman) Oberh. &amp; Tavel</b>  <i>Dryopteris affinis</i> subsp. <i>borrieri</i> (Newman) Fraser-Jenk.  <i>Dryopteris tavelii</i> Rothm.</p>	
<i>Elytrigia repens</i> aggr.	Poaceae
<p><b><i>Elytrigia repens</i> (L.) Nevski</b>  <i>Elymus repens</i> (L.) Gould  <i>Elymus repens</i> (L.) Gould subsp. <i>repens</i>  <i>Elytrigia repens</i> (L.) Nevski subsp. <i>repens</i></p>	

## SUPPLEMENTARY 1. (Continued).

<i>Erysimum duriaei</i> aggr. <b><i>Erysimum duriaei</i> Boiss.</b> <i>Erysimum mayorii</i> Álv.Mart., Nava & Fern.Casado <b><i>Erysimum gorbeanum</i> Polatschek</b>	Brassicaceae
<i>Festuca rubra</i> aggr. <b><i>Festuca arenaria</i> Osbeck</b> <i>Festuca rubra</i> subsp. <i>arenaria</i> (Osbeck) Syme <b><i>Festuca heteromalla</i> Pourr.</b> <i>Festuca rubra</i> subsp. <i>fallax</i> (Thuill.) Nyman <b><i>Festuca rubra</i> L.</b> <i>Festuca rubra</i> subsp. <i>eu-rubra</i> <i>Festuca rubra</i> subsp. <i>litoralis</i> (G. Mey.) Auquier <i>Festuca rubra</i> subsp. <i>pruinosa</i> (Hack.) Piper <i>Festuca rubra</i> L. subsp. <i>rubra</i> <b><i>Festuca trichophylla</i> (Gaudin) K. Richt.</b> <i>Festuca rubra</i> var. <i>trichophylla</i> Gaudin	Poaceae
<i>Galeopsis tetrahit</i> aggr. <b><i>Galeopsis tetrahit</i> L.</b> <i>Galeopsis tetrahit</i> var. <i>arvensis</i> Schldtl.	Lamiaceae
<i>Galium mollugo</i> aggr. <b><i>Galium album</i> Mill.</b> <i>Galium album</i> Mill. subsp. <i>album</i> <i>Galium mollugo</i> subsp. <i>erectum</i> Syme <b><i>Galium mollugo</i> L.</b> <i>Galium mollugo</i> L. subsp. <i>mollugo</i>	Rubiaceae
<i>Galium palustre</i> aggr. L. <b><i>Galium palustre</i> L.</b> <i>Galium palustre</i> L. subsp. <i>palustre</i>	Rubiaceae
<i>Geranium sylvaticum</i> aggr. <b><i>Geranium sylvaticum</i> L.</b>	Geraniaceae
<i>Globularia nudicaulis</i> aggr. <b><i>Globularia nudicaulis</i> L.</b> <i>Globularia nudicaulis</i> L. subsp. <i>nudicaulis</i> <i>Globularia nudicaulis</i> subsp. <i>occidentalis</i> <b><i>Globularia fuxeensis</i> Giraudias</b>	Plantaginaceae
<i>Hedera helix</i> aggr. <b><i>Hedera canariensis</i> Willd.</b> <b><i>Hedera helix</i> L.</b> <i>Hedera helix</i> Lowe subsp. <i>helix</i> <b><i>Hedera hibernica</i> (G. Kirchn.) Carrière</b>	Hederaceae
<i>Juniperus oxycedrus</i> aggr. <b><i>Juniperus oxycedrus</i> L.</b> <i>Juniperus oxycedrus</i> subsp. <i>badia</i> (H. Gay) Debeaux <i>Juniperus oxycedrus</i> L. subsp. <i>oxycedrus</i> <i>Juniperus oxycedrus</i> subsp. <i>transtagana</i> Franco <i>Juniperus navicularis</i> Gand.	Cupressaceae
<i>Jasione crispa</i> aggr. <b><i>Jasione cavanillesii</i> C. Vicioso</b> <b><i>Jasione crispa</i> (Pourr.) Samp.</b> <i>Jasione crispa</i> (Pourr.) Samp. subsp. <i>crispa</i> <i>Jasione humilis</i> (Pers.) Loisel. <b><i>Jasione maritima</i> (Duby) Merino</b>	Campanulaceae



**SUPPLEMENTARY 1.** (Continued).

*Jasione maritima* subsp. *gallaecica* (Rivas Mart.) Fern.Prieto, Nava & Bueno Sánchez  
*Jasione maritima* var. *sabularia* (Cout.) Sales & Hedge  
*Jasione sessiliflora* Boiss. & Reut.

<i>Leontodon crispus</i> aggr.	Asteraceae
<p><b><i>Leontodon crispus</i> Vill aggr.</b>  <i>Leontodon crispus</i> Vill</p>	
Leucanthemum vulgare Vill	Asteraceae
<p><b><i>Leucanthemum vulgare</i> Lam. aggr.</b>  <i>Chrysanthemum leucanthemum</i> L.  <i>Leucanthemum vulgare</i> Lam  <i>Leucanthemum vulgare</i> subsp. <i>eliasii</i> (Sennen &amp; Pau) Sennen &amp; Pau  <i>Leucanthemum vulgare</i> subsp. <i>praecox</i> Horvatić</p>	
<p><i>Linum strictum</i> aggr.</p> <p><b><i>Linum strictum</i> L.</b>  <i>Linum strictum</i> L. subsp. <i>strictum</i></p>	Linaceae
<p><i>Linum suffruticosum</i> aggr.</p> <p><b><i>Linum appressum</i> Caball.</b>  <i>Linum milletii</i> subsp. <i>appressum</i> (Caball.) Rivas Mart.  <i>Linum suffruticosum</i> subsp. <i>appressum</i> (Caball.) Rivas Mart.  <b><i>Linum suffruticosum</i> L.</b>  <i>Linum suffruticosum</i> L. subsp. <i>suffruticosum</i></p>	Linaceae
<p><i>Luzula campestris</i> aggr.</p> <p><b><i>Luzula campestris</i> (L.) DC.</b>  <i>Luzula campestris</i> (L.) DC. subsp. <i>campestris</i>  <b><i>Luzula multiflora</i> (Ehrh.) Lej.</b>  <i>Luzula multiflora</i> (Ehrh.) Lej. subsp. <i>multiflora</i>  <i>Luzula campestris</i> subsp. <i>carpetana</i> Rivas Mart.  <b><i>Luzula congesta</i> (Thuill.) Lej.</b>  <i>Luzula campestris</i> subsp. <i>congesta</i> (Thuill.) K. Richt.  <i>Luzula multiflora</i> subsp. <i>congesta</i> (Thuill.) Arcang.</p>	Juncaceae
<p><i>Melica ciliata</i> aggr.</p> <p><b><i>Melica ciliata</i> L.</b>  <i>Melica ciliata</i> subsp. <i>glauca</i> (F. W. Schultz) K. Richt.  <i>Melica ciliata</i> subsp. <i>magnolii</i> (Gren. &amp; Godr.) K. Richt.</p>	Poaceae
<p><i>Molinia caerulea</i> aggr.</p> <p><b><i>Molinia arundinacea</i> Schrank</b>  <i>Molinia caerulea</i> subsp. <i>arundinacea</i> (Schrank) H. K. G. Paul  <b><i>Molinia caerulea</i> (L.) Moench</b>  <i>Molinia caerulea</i> (L.) Moench subsp. <i>caerulea</i></p>	Poaceae
<p><i>Myosotis scorpioides</i> aggr.</p> <p><b><i>Myosotis laxa</i> Lehm.</b>  <i>Myosotis laxa</i> subsp. <i>caespitosa</i> (Schultz) Nordh.  <b><i>Myosotis scorpioides</i> L.</b></p>	Boraginaceae
<p><i>Narcissus bulbocodium</i> aggr.</p> <p><b><i>Narcissus bulbocodium</i> L.</b>  <i>Narcissus bulbocodium</i> L. subsp. <i>bulbocodium</i>  <i>Narcissus bulbocodium</i> subsp. <i>quintanilhae</i> A. Fern.  <i>Narcissus bulbocodium</i> var. <i>conspicuus</i> (Haw.) Baker  <b><i>Narcissus nivalis</i> Graells</b>  <i>Narcissus bulbocodium</i> subsp. <i>nivalis</i> (Graells) K. Richt.  <i>Narcissus bulbocodium</i> var. <i>nivalis</i> (Graells) Baker</p>	Amaryllidaceae

**SUPPLEMENTARY 1.** (Continued).

<i>Narcissus pseudonarcissus</i> aggr. <b><i>Narcissus pseudonarcissus</i> L.</b> <i>Narcissus nobilis</i> var. <i>leonensis</i> (Pugsley) A. Fern. <i>Narcissus pseudonarcissus</i> subsp. <i>leonensis</i> (Pugsley) Fern. Casas & Laínz <i>Narcissus pseudonarcissus</i> subsp. <i>nobilis</i> (Haw.) A. Fern. <i>Narcissus pseudonarcissus</i> subsp. <i>pallidiflorus</i> (Pugsley) A. Fern. <i>Narcissus pseudonarcissus</i> L. subsp. <i>pseudonarcissus</i> <i>Narcissus pseudonarcissus</i> var. <i>humilis</i> Pugsley	Amaryllidaceae
<i>Narcissus triandrus</i> aggr. <b><i>Narcissus cernuus</i> Salisb.</b> <i>Narcissus triandrus</i> subsp. <i>pallidulus</i> (Graells) Rivas Goday <b><i>Narcissus triandrus</i> L.</b> <i>Narcissus calathinus</i> Delarbre <i>Narcissus triandrus</i> L. subsp. <i>triandrus</i>	Amaryllidaceae
<i>Odontites vulgaris</i> aggr. <b><i>Odontites vulgaris</i> Moench</b> <i>Odontites serotinus</i> Dumort. <b><i>Odontites vernus</i> Dumort.</b>	Orobanchaceae
<i>Papaver dubium</i> aggr. <b><i>Papaver dubium</i> L.</b>	Papaveraceae
<i>Plantago coronopus</i> aggr. <b><i>Plantago coronopus</i> L.</b>	Plantaginaceae
<i>Poa pratensis</i> aggr. <b><i>Poa angustifolia</i> L.</b> <b><i>Poa pratensis</i> L.</b> <i>Poa pratensis</i> subsp. <i>irrigata</i> (Lindm.) H. Lindb. <i>Poa pratensis</i> L. subsp. <i>pratensis</i>	Poaceae
<i>Ranunculus acris</i> aggr. <b><i>Ranunculus acris</i> L.</b> <i>Ranunculus acris</i> subsp. <i>friesianus</i> (Jord.) Syme <i>Ranunculus acris</i> subsp. <i>despectus</i> M. Laínz	Ranunculaceae
<b><i>Rosa canina</i> aggr.</b> <b><i>Rosa canina</i> L.</b> <i>Rosa andegavensis</i> Bastard <i>Rosa blondeana</i> Ripart <i>Rosa squarrosa</i> (A. Rau) Boreau	<b>Rosaceae</b>
<i>Rosa rubiginosa</i> aggr. <b><i>Rosa micrantha</i> Sm.</b> <b><i>Rosa agrestis</i> Savi</b>	Rosaceae
<i>Rubus fruticosus</i> aggr. <b><i>Rubus castellarnau</i> Pau</b> <b><i>Rubus castroviejo</i> Mon.-Huelin</b> <b><i>Rubus genevieri</i> Boreau</b> <b><i>Rubus grabowskii</i> Weihe</b> <i>Rubus thyrsoides</i> Wimm. <b><i>Rubus henriquesii</i> Samp.</b> <b><i>Rubus lainzii</i> H. E. Weber</b>	Rosaceae
<b><i>Rubus hirtus</i> aggr.</b> <b><i>Rubus hirtus</i> Waldst. et Kit. aggr.</b> <i>Rubus hirtus</i> Waldst. et Kit.	<b>Rosaceae</b>

**SUPPLEMENTARY 1.** (Continued).

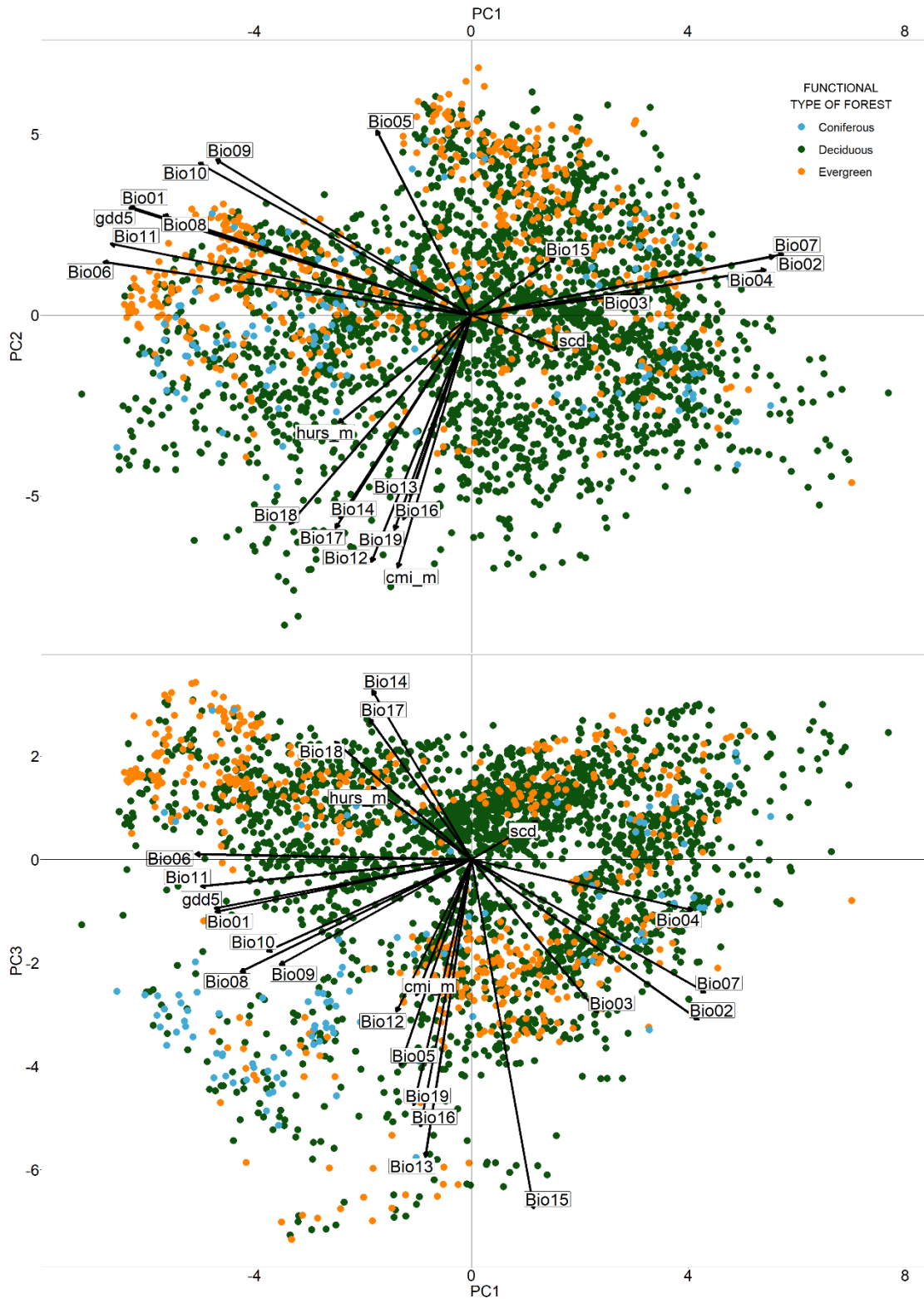
<i>Sanguisorba minor</i> aggr. <b><i>Sanguisorba minor</i> Scop.</b> <i>Poterium dictyocarpum</i> Spach <i>Sanguisorba minor</i> subsp. <i>balearica</i> (Nyman) Muñoz Garm. & C. Navarro <i>Sanguisorba minor</i> Scop. subsp. <i>minor</i>	
<b><i>Santolina chamaecyparissus</i> aggr.</b> <b><i>Santolina chamaecyparissus</i> L. aggr.</b>	<b>Asteraceae</b>
<i>Santolina rosmarinifolia</i> aggr. <b><i>Santolina rosmarinifolia</i> L.</b> <b><i>Santolina semidentata</i> Hoffmanns. &amp; Link</b>	Asteraceae
<i>Scabiosa columbaria</i> aggr. <b><i>Scabiosa columbaria</i> L.</b> <i>Scabiosa columbaria</i> subsp. <i>affinis</i> (Gren. & Godr.) Nyman <i>Scabiosa columbaria</i> L. subsp. <i>columbaria</i> <i>Scabiosa columbaria</i> subsp. <i>tineensis</i> M.Laínz <b><i>Scabiosa pyrenaica</i> All.</b> <i>Scabiosa columbaria</i> subsp. <i>pyrenaica</i> (All.) P. Fourn.	Dipsacaceae
<i>Senecio doria</i> aggr. <b><i>Senecio doria</i> L.</b> <i>Senecio doria</i> subsp. <i>laderoi</i> (Pérez Morales & al.) Blanca <b><i>Senecio legionensis</i> Lange</b> <i>Senecio doria</i> subsp. <i>legionensis</i> (Lange) Chater	Asteraceae
<i>Senecio nemorensis</i> aggr. <b><i>Senecio bayonnensis</i> Boiss.</b> <i>Senecio nemorensis</i> subsp. <i>bayonnensis</i> (Boiss.) Nyman <b><i>Senecio nemorensis</i> L.</b> <i>Senecio jacquinianus</i> Rchb. <i>Senecio nemorensis</i> subsp. <i>jacquinianus</i> (Rchb.) Čelak. <i>Senecio nemorensis</i> L. subsp. <i>nemorensis</i> <b><i>Senecio ovatus</i> (G. Gaertn. &amp; al.) Hoppe</b> <i>Senecio fuchii</i> C. C. Gmel. <i>Senecio nemorensis</i> subsp. <i>fuchii</i> (C. C. Gmel.) Ces.	Asteraceae
<i>Sideritis hyssopifolia</i> aggr. <b><i>Sideritis fruticulosa</i> Pourr.</b> <b><i>Sideritis hyssopifolia</i> L.</b> <i>Sideritis hyssopifolia</i> L. subsp. <i>hyssopifolia</i>	Lamiaceae
<i>Silene italica</i> aggr. <b><i>Silene coutinhoi</i> Rothm. &amp; P. Silva</b> <b><i>Silene italica</i> (L.) Pers.</b> <i>Silene italica</i> (L.) Pers. subsp. <i>italica</i> <i>Silene nemoralis</i> Waldst. & Kit.	Caryophyllaceae
<i>Silene nocturna</i> aggr. <b><i>Silene nocturna</i> L.</b>	Caryophyllaceae
<i>Sorbus aria</i> aggr. <b><i>Sorbus aria</i> (L.) Crantz</b> <i>Sorbus aria</i> (L.) Crantz subsp. <i>aria</i>	Rosaceae
<i>Sparganium erectum</i> aggr. <b><i>Sparganium erectum</i> L.</b> <i>Sparganium erectum</i> L. subsp. <i>erectum</i> <b><i>Sparganium neglectum</i> Beeby</b> <i>Sparganium erectum</i> subsp. <i>neglectum</i> (Beeby) Schinz & Thell.	Typhaceae

**SUPPLEMENTARY 1.** (Continued).

<i>Symphytum tuberosum</i> aggr. <b><i>Symphytum tuberosum</i> L.</b> <i>Symphytum tuberosum</i> L. subsp. <i>tuberosum</i>	Boraginaceae
<i>Valeriana officinalis</i> aggr. <b><i>Valeriana excelsa</i> Poir.</b> <i>Valeriana officinalis</i> subsp. <i>repens</i> (Host) O. Bolós & Vigo <b><i>Valeriana officinalis</i> L.</b> <i>Valeriana officinalis</i> L. subsp. <i>officinalis</i>	Valerianaceae
<i>Veronica chamaedrys</i> aggr. <b><i>Veronica chamaedrys</i> L.</b> <i>Veronica chamaedrys</i> L. subsp. <i>chamaedrys</i>	Plantaginaceae
<i>Viola reichenbachiana</i> aggr. <b><i>Viola reichenbachiana</i> Boreau</b> <i>Viola sylvestris</i> Lam. <i>Viola sylvestris</i> Lam. subsp. <i>sylvestris</i> <b><i>Viola riviniana</i> Rchb.</b> <i>Viola sylvestris</i> subsp. <i>riviniana</i> (Rchb.) Tourlet	Violaceae

**SUPPLEMENTARY 2.** Contribution of every bioclimatic variable to the three first axes of the Principal Component Analysis (PCA). The three most contributing variables for each axis are grey shaded.

<b>CHELSA 2.1 Bioclimatic variables</b>		<b>PC1 (33.85%)</b>	<b>PC2 (29.22%)</b>	<b>PC3 (20.6%)</b>
Bio01	Mean annual air temperature	-0.31	0.15	-0.07
Bio02	Mean diurnal air temperature range	0.26	0.08	-0.21
Bio03	Isothermality	0.16	0.03	-0.20
Bio04	Temperature seasonality	0.27	0.0	-0.07
Bio05	Mean daily maximum air temperature of the warmest month	-0.09	0.26	-0.26
<b>Bio06</b>	<b>Mean daily minimum air temperature of the coldest month</b>	<b>-0.34</b>	0.07	0.01
Bio07	Annual range of air temperature	0.29	0.08	-0.17
Bio08	Mean daily mean air temperatures of the wettest quarter	-0.28	0.13	-0.14
Bio09	Mean daily mean air temperatures of the driest quarter	-0.24	0.21	-0.14
Bio10	Mean daily mean air temperatures of the warmest quarter	-0.25	0.21	-0.12
<b>Bio11</b>	<b>Mean daily mean air temperatures of the coldest quarter</b>	<b>-0.33</b>	0.10	-0.03
<b>Bio12</b>	<b>Annual precipitation amount</b>	-0.09	<b>-0.34</b>	-0.20
<b>Bio13</b>	<b>Precipitation amount of the wettest month</b>	-0.06	-0.25	<b>-0.38</b>
Bio14	Precipitation amount of the driest month	-0.12	-0.28	0.22
<b>Bio15</b>	<b>Precipitation seasonality</b>	0.08	0.08	<b>-0.45</b>
<b>Bio16</b>	<b>Mean monthly precipitation amount of the wettest quarter</b>	-0.06	-0.28	<b>-0.34</b>
Bio17	Mean monthly precipitation amount of the driest quarter	-0.12	-0.29	0.18
Bio18	Mean monthly precipitation amount of the warmest quarter	-0.17	-0.29	0.15
<b>Bio19</b>	<b>Mean monthly precipitation amount of the coldest quarter</b>	-0.07	<b>-0.30</b>	-0.32
<b>cmi_m</b>	<b>Mean monthly climate moisture index</b>	-0.07	<b>-0.35</b>	-0.18
<b>gdd5</b>	<b>Growing degree days heat sum above 5°C</b>	<b>-0.32</b>	0.15	-0.06
hurs_m	Mean monthly near-surface relative humidity	-0.12	-0.15	0.09
scd	Snow cover days	0.08	-0.05	0.05



**SUPPLEMENTARY 3.** Principal Component Analysis (PCA) of all forest plots, with PC1 (Continentality) against PC2 (precipitation) above and PC1 against PC3 (Precipitation seasonality) below. Plots are grouped by the three functional types of forests: Deciduous broadleaved forests (dark green), Evergreen broadleaved forests (orange) and Coniferous forests (blue). The black arrows represent CHELSA 2.1 bioclimatic variables.

**SUPPLEMENTARY 4.** Results of the pairwise PERMANOVA analysis carried out for all the EUNIS level-4 types of forests with the bioclimatic data obtained from CHELSA 2.1. R2 values are shown for all compared pairs. The value of those pairs with p value < 0.5 (i.e., non-significantly different between them, bioclimatically) are grey shaded.

	T111	T121	T172	T182	T197	T19A	T1Bx	T1By	T1D1	T1D7	T1E1	T1Fx	T211	T21x	T21y	T21z	T221	T27x	T3A1	T3C1
T121	0.188																			
T172	0.336	0.502																		
T182	0.301	0.376	0.055																	
T197	0.050	0.251	0.192	0.189																
T19A	0.170	0.352	0.105	0.109	0.058															
T1Bx	0.172	0.022	0.437	0.290	0.201	0.279														
T1By	0.446	0.435	0.009	0.039	0.362	0.155	0.346													
T1D1	0.196	0.131	0.153	0.079	0.178	0.119	0.062	0.316												
T1D7	0.579	0.577	0.064	0.134	0.500	0.310	0.500	0.060	0.451											
T1E1	0.084	0.070	0.301	0.182	0.089	0.143	0.029	0.238	0.024	0.390										
T1Fx	0.278	0.265	0.020	<b>0.007</b>	0.203	0.057	0.184	0.070	0.124	0.192	0.105									
T211	0.152	0.011	0.266	0.237	0.285	0.273	0.033	0.622	0.257	0.656	0.053	0.485								
T21x	0.290	0.037	0.491	0.429	0.427	0.467	0.089	0.694	0.362	0.756	0.130	0.553	0.030							
T21y	0.140	0.335	0.128	0.169	0.041	0.041	0.277	0.310	0.257	0.435	0.153	0.196	0.408	0.537						
T21z	0.035	0.096	0.260	0.208	0.072	0.129	0.071	0.379	0.089	0.515	0.024	0.206	0.104	0.221	0.164					
T221	0.380	0.095	0.600	0.533	0.497	0.556	0.174	0.702	0.420	0.773	0.228	0.567	0.043	0.032	0.582	0.304				
T27x	0.159	0.132	<b>0.002</b>	0.013	0.135	0.038	0.094	<b>0.007</b>	0.158	0.013	0.059	0.053	0.522	0.427	0.112	0.141	0.376			
T3A1	0.387	0.055	0.433	0.373	0.502	0.467	0.081	0.704	0.369	0.745	0.141	0.578	0.111	0.123	0.597	0.285	0.096	0.517		
T3C1	0.323	0.257	0.012	0.033	0.297	0.113	0.192	<b>0.029</b>	0.299	<b>0.001</b>	0.132	0.135	0.677	0.614	0.271	0.285	0.566	<b>0.029</b>	0.676	
T3D6	0.188	0.208	0.020	0.058	0.148	0.052	0.161	0.181	0.302	0.174	0.100	0.208	0.649	0.557	0.084	0.196	0.499	0.222	0.670	0.429