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 refugia 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 24 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.

**Key words**:

# 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 until that moment to certain areas with microclimatic conditions (e.g. shores, steep slopes, deep canyons, intramontane valleys, etc.) started to 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 NW 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 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 SW 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 km2. 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 (± 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 acidophilus and basiphilous forests in a preliminary test.

Additionally, we visited three native *Pinus sylvestris* forests in the southern Cantabrian Mountains, since all relevés collected from SIVIM with *Pinus sylvestris* as dominant tree species within our study area were, in fact, artificial plantations. We did a total of 15 relevés to have a representation of this natural formations in the Cantabrian Mixed Forest Ecoregion. These relevés were not used in the classification analysis, but added to the final classification.

**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 *Crocosmia* x *crocosmiiflora*, an invasive non-native nothotaxon whose parental species are not found in our territory (González Costales 2007) and *Populus* x *canadensis*, another non-native nothotaxon with just one of its parentals 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 2,897 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 s*outhern 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 this point, this classification analysis established 22 groups.

Finally, we added the *Pinus sylvestris* relevés we did, resulting in a final number of 24 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 80.47% of the variation. We interpreted PCA axis 1 (35.96% 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 (28.94%) as total precipitation, being negatively related to annual precipitation; and axis 3 (15.57%) as precipitation seasonality, being negatively related to precipitation seasonality and the amount of precipitation during the wettest season (Supplementary 2, 3). The values of the forest plots along the three PCA axes were then compared in a boxplot 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 type.

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 > 0.7, we kept those with the highest contribution to the PCA axes (Supplementary 2, 4). The variables finally selected were: Bio2 (mean diurnal air temperature range), Bio11 (mean daily mean air temperatures of the coldest quarter), Bio12 (annual precipitation amount), Bio15 (precipitation seasonality) and Bio17 (mean monthly precipitation amount of the driest quarter). 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. We carried the analysis with an unequal proportion of presences/absences, since each type of forest displayed a different number of plots. However, we ascribed these differences to the uneven distribution of forests in our study, i.e. forests with scarce plots are rarer and not undersampled. All the analyses were computed separately for the three major functional forest types and for the 24 compositional forest types.

# RESULTS

**Classification of the Cantabrian Mixed Forests**

We recognized 24 different types of natural and semi-natural forests and woodlands in our study area: 12 d*eciduous broadleaved forests*, 7 e*vergreen broadleaved forests* and 5 c*oniferous 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* and both *Pinus sylvestris* *forests* centroid within or close the deciduous zone, respectively; *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 ancient plantations within their original native range. Other coniferous forests would be semi-natural *Taxus woodlands* and relict *Juniperus* *woodlands* and *Pinus sylvestris forests*. The main characteristics of the forest types are described below, while diagnostic species for each type of forest is provided in Table 2 and Supplementary 5.

*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 alders (*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 *Physospermum cornubiense* 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, by 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 in the eastern part of the terriyory, 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*.

T22x Cantabrian *Laurus* forests. Mainly coastal low forests dominated by bay laurel (*Laurus nobilis*), with the occasional presence of common olive (*Olea europaea*) and a great richness of vines like *Smilax aspera*.

T22y Cantabrian *Prunus lusitanica* forests. Inland continental low forests dominated by Portuguese laurel cherry (*Prunus lusitanica*), being these forests relicts from the Tertiary.

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*

T37x Cantabrian *Pinus sylvestris* forests on non-acid soils. Forest dominated by Scots pine (*Pinus sylvestris*) growing on basic soil, with just a single representant in the southern margin of the Cantabrian Mountains, accompanies by base-loving shrubs like savin juniper (*Juniperus sabina*), bearberry (*Arctostaphylos uva-ursi*) or snowy mespilus (*Amelanchier ovalis*).

T37y Cantabrian *Pinus sylvestris* forests on non-acid soils. Acidophilous open forests dominated by Scots pine (*Pinus sylvestris*), represented by only a few relict remnants in southern continental valleys of the Cantabrian Mountains, with the presence of deciduous tree species such as sessile oak (Quercus petraea), orocantabrian oak (Quercus orocantabrica) or beech (Fagus sylvatica) and an understory dominated mainly by Vaccinium myrtillus or different heath species, like *Erica arborea* or *Daboecia cantabrica.*

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 analysed 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, being scarcer 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 Quercus forests on acid soils, mountain Betula forests, Pinus sylvestris forests on acid* and *non-acid soils, Taxus woodlands, Juniperus woodlands*) from forests that appear closer to the coast (e.g. *Quercus ilex forests, Laurus forests, Pinus pinaster forests*). The 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, Pinus sylvestris forests on acid-soils*) from low-rainfall forests (e.g. *thermophilous Quercus forests*, *Quercus pyrenaica forests*, *Quercus suber forests*, *Quercus rotundifolia* *forests on acid* and *non-acid soils ,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, Prunus lusitanica forests*), 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*, *Laurus 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 on the one hand *Juniperus* *woodlands* and *Pinus sylvestris forests on acid* and *non-acid soils*, with a low seasonality of precipitationk, and, on the other hand, *Pinus pinaster* forests, with a high seasonality due to the Mediterranean influence, while *Taxus* *woodlands* would have halfway values.

Adonis analysis showed significant but slight differences between functional forest types (*R2* = 0.076, *p* = 0.001, N = 3). In contrast, the dissimilarities were found stronger for the EUNIS level-4 types (*R2* = 0.494, *p* = 0.001, N = 24). This was consistent with the pairwise analysis results (Supplementary 6). Although some forest pairs showed low R2 values, we found that many of them were significantly different from each other, with few exceptions. On the one hand, *Laurus forests* were the more bioclimatically unique forest type, followed by *Pinus sylvestris forests on acid soils* and *mountain Betula forests*, with R2 values higher than 0.75 when compared with other forests (Fig. 4). On the other hand, the more similar forests (i.e. lowest R2 values) were *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*, *mountain Betula forests* or *Pinus sylvestris forests on non-acid soils*.

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 terms, the mean monthly precipitation amount of the driest quarter (Bio17) seems to be the most important bioclimatic variable to explain deciduous forests distribution, with a clear aversion for regions with scarce precipitation during the dry season. However, this variable was not found significant for broadleaved evergreen forests, while it was the second most important for coniferous forests, with the opposite trend shown by the deciduous ones, following an apparent preference for drier summers. Regarding broadleaved evergreen forests, both annual precipitation amount (Bio12) and mean daily mean air temperatures of the coldest quarte (Bio11) were found as the most important variables, with a negative and positive relation to them, respectively. Therefore, this type of functional forest would be more related to warmer winters and drier regions, while coniferous and deciduous forests would prefer colder winters and higher amount of precipitation; being the latter the most explicative variable for the occurrence of coniferous forests. This gets in conflict with their second most important variable (precipitation amount of the driest quarter, Bio17), with which they are negatively related.

Nevertheless, not all compositional types of forests follow the same trends than the functional type they belong. While deciduous forests, as a whole, are positively related to rainfall during summer, particular forests such as *thermophilous Quercus forests* display the opposite trend. With regards to broadleaved evergreen forests, we found that this same variable is not explanatory for them in general terms, but it is at a particular level, with some of the forests positively related to the rainfall in summer (e.g. *Quercus ilex forests*) while others displays a negative relation to this variable (e.g. *Quercus rotundifolia forests* *on-non acid soils*). Unsurprisingly, coniferous forests follow this same pattern, with some of them preferring summer rainfall (e.g. *Taxus baccata woodlands*), while this functional type of forest is found negatively related to this variable. This same trend can be found for other variables and other forests (Table 3).

Respecting the soil pH, we found this variable non-significant or, in general, less explicative than bioclimatic variables. While broadleaved deciduous forests were found negatively related to this variable (i.e. they prefer acid soils), broadleaved evergreen forests showed a negative relation and coniferous forests were not determined by it. However, withing each functional forest we can find different forest types with an evident preference for acid or basic soils or no preference at all. Unexpectedly, some basic soil-loving forests were found negatively related to pH soil (e.g. *Fagus forests* *on basic soils*), also mostly acidophilous forests found positively related to this variable (e.g. *Quercus pyrenaica* *forests*) and soil-determined forests with no significant relation to this variable (e.g. *mixed forests on non-acid soils*).

# DISCUSSION

Our results indicate a wide climatic variation within 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. 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 is 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-Guitián *et al*. 2012, Mucina *et al*. 2016, Fernández Prieto *et al*. 2023). 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). A greater overlap was found between *Quercus suber forests* and 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-Guitián *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 some cases, 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 vegetation formations such as *Quercus ilex forests* have their optimum (Rivas-Martínez 2017a, Jiménez *et al*. 2003). Therefore, presence of calcareous substrate would play a key role in the dominance of *Cantabrian Quercus ilex forests* in the eastern coast of the ecoregion, explaining their absence in more acidic territories such as Western Asturias and Galicia, where they are mainly substituted by *Laurus forests*, *mixed forests* *on acid-soils* or *Pinus pinaster forests*. The opposite trend is found for *Quercus rotundifolia on acid-soils*, which find their space in regions with acid soils and low precipitation. Winter temperature seems to be another decisive driver in the differentiation between coastal-lowland and 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). The combination of these bioclimatic and edaphic drivers could be the major reason why almost all broadleaved evergreen forests have specific ecological spaces and are not able to become dominant in the territory.

Thus, 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 climatically 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 mesic *Quercus* forests, which had been restricted to intramontane valleys until then (Carrión *et al*. 2010). Therefore, 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, *Laurus 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 *Ilex woodlands* and *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 the dominant mountain forests (i.e. *Fagus*, *mountain Quercus, mountain Betula* and *Pinus sylvestris forests)*, since they have been widely reported as the replacement of *Fagus* formations in more degraded or recently perturbed areas (Costa *et al*. 1997). Additionally, both woodlands share diagnostic species with each other (*Galium rotundifolium* and *Sanicula europaea*) and with *Fagus forests* too(*Galium odoratum*) but not with *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 even though 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. Nevertheless, the cooccurrence of diagnostic species between *Pinus pinea* and *Quercus suber* forests is almost expected since both species can coexist and form mature forests, like the ones found in the coast of Pyrénées-Atlantiques and Landes French departments (Timbal& Savoie 1991, Rodríguez-Guitián *et al.* 2020). However, 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 a few locations in our ecoregion (García *et al.* 1997, Fernandes *et al.* 2015) 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).

To conclude, 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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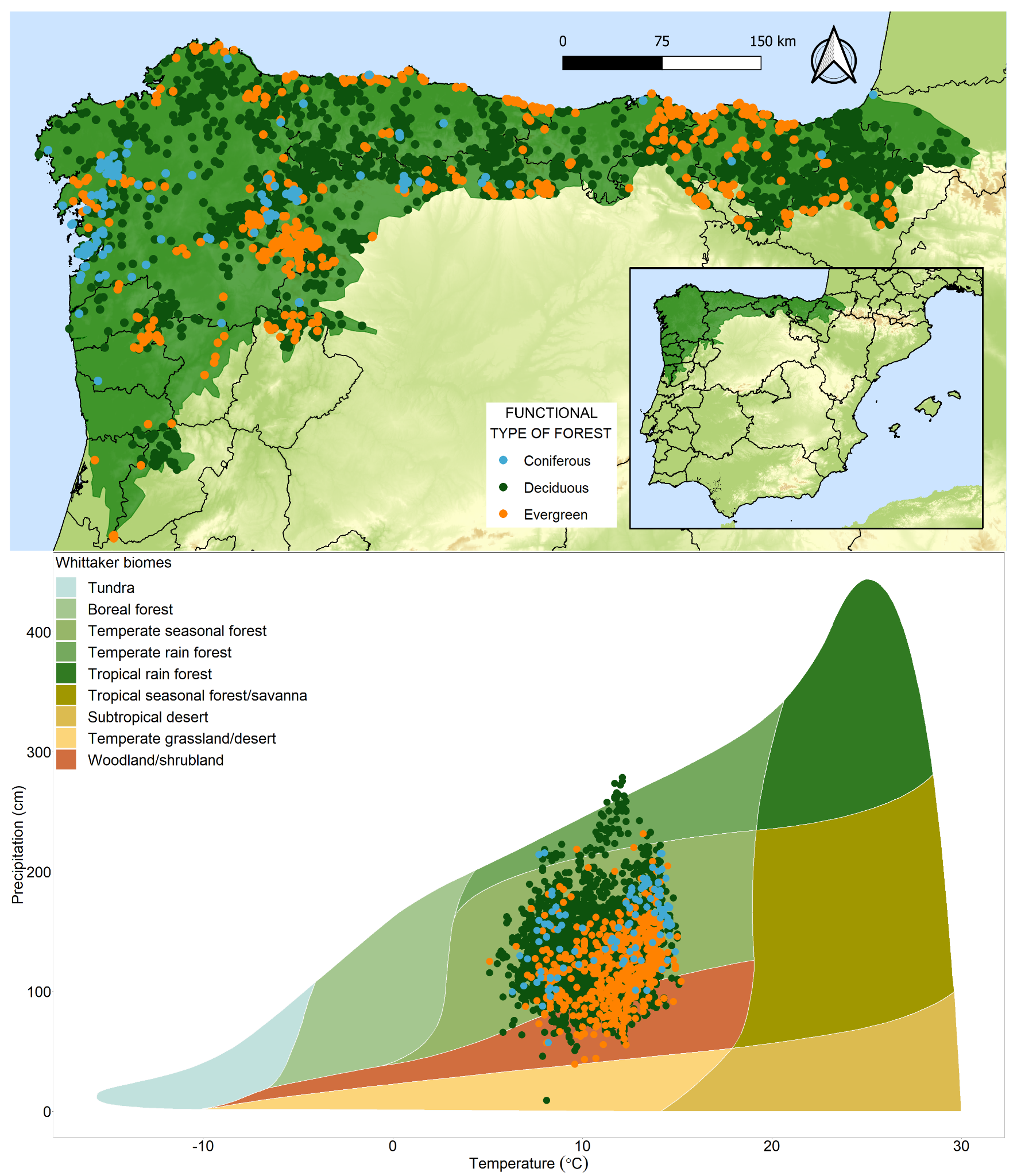
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# FIGURES



***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 (oC) 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. Forest plots are coloured according to the functional type they belong.

Gráfico, Gráfico de cajas y bigotes

Descripción generada automáticamente

***FIGURE 3*.** Boxplot of the three first axes from the Principal Component Analysis (PCA) for each type of forest. Each type of forest is coloured according to its correspondent functional type: dark green for deciduous broadleaved forests, orange for evergreen broadleaved forests and blue for coniferous forests.

Gráfico, Diagrama

Descripción generada automáticamente

***FIGURE 4.***Chord diagram representing bioclimatic dissimilarities (R2 from Pairwise ANOVA analysis) among the different types of EUNIS level-4 forests. More and wider links indicate higher dissimilarity. **A** All links. **B** Links with R2 > 0.25. **B** R2 > 0.5. **D** R2 > 0.75.

# TABLES

***TABLE 1*.** Classification for the present forests in our study area with the proposed Regional EUNIS Code and Name, the Number of plots (relevés), the Average number of vascular plant species, the Average number of tree species, the Number of diagnostic species (Φ ≥ 0.3), the Number of syntaxa (phytosociological associations) and the Evenness of each type of forest.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **EUNIS**  **Code** | **EUNIS Name** | **No. of plots** | **Average No. of species** | **Average No. of trees** | **No. of diagnostic species** | **No. of syntaxa** | **Evenness** |
| **Deciduous broadleaved forests** | | | | | | |  |
| T111 | Cantabrian *Salix* - *Populus* riparian forests | 231 | 32.7±12.9 | 6.9±2.5 | 26 | 10 | 0.708 |
| T121 | Cantabrian *Alnus* riparian forests | 387 | 23.9±10.5 | 4.7±2.0 | 10 | 8 | 0.644 |
| T172 | Cantabrian *Fagus* forests on non-acid soils | 703 | 22.4±8.7 | 2.9±2.1 | 4 | 4 | 0.601 |
| T182 | Cantabrian *Fagus* forests on acid soils | 380 | 18.2±6.5 | 3.3±2.0 | 3 | 5 | 0.609 |
| T197 | Cantabrian thermophilous *Quercus* forests | 170 | 24.7±9.1 | 4.1±2.0 | 4 | 4 | 0.739 |
| T19A | Cantabrian *Quercus pyrenaica* forests | 295 | 27.8±9.7 | 2.8±1.8 | 8 | 4 | 0.675 |
| T1Bx | Cantabrian mixed forests on acid soils | 437 | 22.9±8.0 | 4.7±2.0 | 2 | 6 | 0.677 |
| T1By | Cantabrian mountain *Quercus forests* on acid soils | 104 | 21.5±6.4 | 4.1±1.9 | 4 | 4 | 0.712 |
| T1D1 | Cantabrian lowland *Betula* forests | 113 | 23.8±10.9 | 4.8±2.0 | 6 | 5 | 0.708 |
| T1D7 | Cantabrian mountain *Betula* forests | 153 | 22.2±7.0 | 4.2±1.6 | 3 | 4 | 0.717 |
| T1E1 | Cantabrian mixed forests on non-acid soils | 379 | 34.1±10.3 | 6.7±2.1 | 1 | 12 | 0.771 |
| T1Fx | Cantabrian *Acer* - *Fraxinus* forests on acid-rich soils | 77 | 31.6±9.6 | 7.4±2.1 | 7 | 4 | 0.779 |
|  |  |  |  |  |  |  |  |
| **Evergreen broadleaved forests** | | | | | | |  |
| T211 | Cantabrian *Quercus suber* forests | 49 | 23.2±9.6 | 2.9±1.7 | 18 | 3 | 0.691 |
| T21x | Cantabrian *Quercus ilex* forests | 146 | 18.2±7.1 | 3.0±2.0 | 6 | 1 | 0.675 |
| T21y | Cantabrian *Quercus* *rotundifolia* forests on non-acid soils | 143 | 21.5±9.0 | 2.4±1.4 | 12 | 4 | 0.699 |
| T21z | Cantabrian *Quercus rotundifolia* forests on acid soils | 165 | 21.3±7.0 | 2.1±1.0 | 6 | 2 | 0.587 |
| T22x | Cantabrian *Laurus* forests | 187 | 17.9±7.3 | 2.3±1.7 | 11 | 6 | 0.641 |
| T22y | Cantabrian *Prunus lusitanica* forests | 24 | 20.4±11.3 | 4.8±1.9 | 2 | 2 | 0.670 |
| T27x | Cantabrian *Ilex* woodlands | 13 | 17.5±7.2 | 3.8±1.5 | 9 | 1 | 0.654 |
|  |  |  |  |  |  |  |  |
| **Coniferous forests** | | | | | | |  |
| T37x | Cantabrian *Pinus sylvestris* forests on non-acid soils | 4 | 21.0±3.1 | 2.5±0.6 | 27 | 0 | 0.524 |
| T37y | Cantabrian *Pinus sylvestris* forests on acid soils | 11 | 12.0±4.3 | 3.1±1.4 | 14 | 1 | 0.649 |
| T3A1 | Cantabrian *Pinus pinaster* forests | 86 | 16.7±5.5 | 1.9±0.9 | 13 | 0 | 0.619 |
| T3C1 | Cantabrian *Taxus* woodlands | 26 | 27.6±10.8 | 6.0±2.4 | 11 | 0 | 0.710 |
| T3D6 | Cantabrian *Juniperus* woodlands | 22 | 27.6±12.1 | 2.1±1.1 | 43 | 1 | 0.709 |

***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 (Φ) for each type of forest, only species with Φ ≥ 0.3 are grey shaded. A maximum of seven unshared diagnostic species are shown for each forest. The complete list of diagnostic species is provided in Supplementary 6.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **EUNIS Code** | **T111** | **T121** | **T172** | **T182** | **T197** | **T19A** | **T1Bx** | **T1By** | **T1D1** | **T1D7** | **T1E1** | **T1Fx** | **T211** | **T21x** | **T21y** | **T21z** | **T22x** | **T22y** | **T27x** | **T37x** | **T37y** | **T3A1** | **T3C1** | **T3D6** |
| **No. of plots** | 231 | 387 | 703 | 380 | 170 | 295 | 437 | 104 | 113 | 153 | 379 | 77 | 49 | 146 | 143 | 165 | 187 | 24 | 13 | 4 | 11 | 86 | 26 | 22 |
| **Cantabrian *Salix - Populus* riparian forests** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Fraxinus angustifolia* | 61.1 | 17.8 | · | · | · | · | · | · | · | · | · | · | · | · | · | 3.4 | · | · | · | · | · | · | · | · |
| *Rubus caesius* | 54.1 | 0 | · | · | · | · | · | · | · | · | 2.4 | · | · | · | · | · | · | · | · | · | · | · | · | · |
| *Populus nigra* | 54 | 6.5 | · | · | · | · | · | · | · | · | 2.1 | 2 | · | · | · | · | · | · | · | · | · | · | · | · |
| *Ulmus minor* | 52.5 | 1.6 | · | · | · | · | · | · | · | · | 6 | · | · | · | · | · | · | · | · | · | · | · | · | · |
| *Salix fragilis* | 52.2 | 2.2 | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · |
| *Alliaria petiolata* | 49.6 | 1 | · | · | · | · | · | · | · | · | 5 | · | · | · | · | · | · | · | · | · | · | · | 6.1 | · |
| *Salix purpurea* | 49.5 | · | · | · | · | · | · | · | · | · | 0.1 | · | · | · | · | · | · | · | · | · | · | · | · | · |
| **Cantabrian *Alnus* riparian forests** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Lycopus europaeus* | 7.5 | 39.7 | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · |
| *Salix cinerea* | 12.5 | 37.6 | · | · | · | · | · | · | 29.5 | 6.7 | 2.4 | 12.2 | · | · | · | · | · | 18 | · | · | · | · | · | · |
| *Osmunda regalis* | · | 34.7 | · | · | · | · | · | · | 15.1 | · | 1.2 | 2.9 | · | · | · | · | · | 19.6 | · | · | · | · | · | · |
| *Oenanthe crocata* | 8.4 | 34 | · | · | · | · | · | · | 26.4 | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · |
| *Solanum dulcamara* | 25 | 31.6 | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · |
| *Lythrum salicaria* | 22.3 | 31.4 | · | · | · | · | · | · | 0.2 | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · |
| *Angelica sylvestris* | 18.5 | 31.3 | · | · | · | · | · | · | · | · | 10.2 | 2.9 | · | · | · | · | · | 11.5 | · | · | · | · | · | · |
| **Cantabrian *Fagus* forests on non-acid soils** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Helleborus viridis* | 0.7 | · | 39 | 4.1 | 4.5 | 1 | · | · | · | · | 20 | · | · | · | · | · | · | · | · | · | · | · | 2.5 | · |
| *Isopyrum thalictroides* | · | · | 33.7 | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · |
| **Cantabrian *Fagus* forests on acid soils** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Blechnumspicant* | · | 4 | · | 30.6 | · | · | 16.1 | · | 22.1 | 12.3 | 0.1 | 11.8 | · | · | · | · | · | 20.6 | 2 | · | · | · | 4 | · |
| **Cantabrian thermophilous *Quercus* forests** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Quercus pubescens* | · | · | · | · | 40.8 | · | · | · | · | · | 1.8 | · | · | 0 | 2.6 | · | · | · | · | · | · | · | · | · |
| *Viburnum lantana* | 19.9 | · | · | · | 40.8 | · | · | · | · | · | 6 | · | · | 0.2 | 9.1 | · | · | · | · | · | · | · | · | 9.7 |
| *Prunus spinosa* | 12.3 | · | · | · | 36.7 | 0.7 | · | · | · | · | 11.6 | · | · | 11.6 | 6.4 | 2.1 | 2.8 | · | · | · | · | · | · | · |
| Cantabrian *Quercus pyrenaica* forests | | | | | | | | | | | | | | | | | | | | | | | | |
| *Quercus pyrenaica* | · | · | · | · | 1.2 | 60.2 | 9 | · | · | · | 0.2 | · | 6.7 | · | · | 1.9 | · | · | · | · | · | · | · | 2.1 |
| *Cruciata glabra* | · | · | 0.5 | · | 3.6 | 47 | 1.1 | 0.1 | · | 0.9 | 3.7 | · | · | · | · | · | · | · | · | · | · | · | · | · |
| *Clinopodium vulgare* | · | · | · | · | 0.9 | 36.9 | · | · | · | · | · | · | 7.7 | · | 6.5 | 26.4 | · | 0.1 | · | · | · | · | · | 11 |
| *Physospermum cornubiense* | · | · | · | · | · | 36.9 | 7.7 | 20.7 | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · |
| *Festuca elegans* | · | · | · | · | · | 31.2 | · | · | · | 0.6 | · | · | · | · | · | 24 | · | 7 | · | · | · | · | · | · |
| *Prunella grandiflora* | · | · | · | · | 1.1 | 30.1 | 2.1 | · | 3.2 | · | 1.4 | · | · | · | · | · | · | 2.8 | · | · | · | · | · | · |
| **Cantabrian mixed forests on acid soils** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Quercus robur* | · | 0.2 | · | 2.3 | · | · | 35.8 | · | 28.6 | · | 16.7 | · | · | 1.3 | · | · | · | 16.6 | · | · | · | 12.7 | · | · |
| *Castanea sativa* | · | · | · | 2.8 | · | 1.2 | 33.1 | · | 15.1 | · | 18.6 | 9.2 | · | · | · | · | 0 | · | · | · | · | · | · | · |
| **Cantabrian mountain *Quercus* forests on acids oils** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Eragrostis atrovirens* | · | · | · | · | · | · | · | 30.4 | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · |
| **Cantabrian lowland *Betula* forests** |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Deschampsia cespitosa* aggr. | 13.5 | 4.3 | · | · | · | · | · | · | 42.8 | · | 3.8 | · | · | · | · | · | · | · | · | · | · | · | · | · |
| *Senecio nemorensis* aggr. | · | 17.3 | · | · | · | · | · | · | 37.6 | · | · | 6.2 | · | · | · | · | · | · | · | · | · | · | · | · |
| *Holcus mollis* | · | · | · | 8.1 | · | 25.1 | 9 | 16.2 | 37.1 | 0.3 | 0.9 | 10.5 | · | · | · | · | · | · | · | · | · | · | 5.9 | · |
| *Crocus serotinus* | · | · | 6.3 | · | 0 | · | 0.4 | · | 30.4 | · | 0.8 | 0.3 | · | · | · | · | · | · | · | · | · | · | · | · |
| **Cantabrian mountain *Betula* forests** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Sorbus aucuparia* | · | · | · | 5 | · | · | · | 21.1 | · | 35.2 | · | 19.7 | · | · | · | · | · | · | 16.6 | · | 26.3 | · | 28.4 | · |
| **Cantabrian mixed forests on non-acid soils** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Fraxinus excelsior* | 11.3 | 19.9 | · | · | 0.5 | · | · | · | · | · | 35.7 | 24.6 | · | · | · | · | · | · | · | · | · | · | · | · |
| **Cantabrian *Acer-Fraxinus* forests on acid-rich soils** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Hacer pseudoplatanus* | 1.4 | 3.2 | · | · | · | · | · | 1.8 | 3.4 | · | 10.8 | 43.1 | · | · | · | · | · | 0.6 | 12.4 | · | · | · | 12.4 | · |
| *Valeriana pyrenaica* | · | 12.3 | · | · | · | · | · | · | 0.9 | 0.5 | 9.6 | 35.5 | · | · | · | · | · | · | · | · | · | · | 1.2 | · |
| *Corylus avellana* | 6.5 | 0.8 | · | · | 2.1 | · | 0.1 | 9.7 | · | 3.1 | 25.9 | 34 | · | · | · | · | · | · | 12.4 | · | · | · | 25 | · |
| *Saxifraga clusii* | · | 2.8 | · | · | · | · | · | · | 8.1 | · | · | 33.3 | · | · | · | · | · | · | · | · | · | · | · | · |
| *Chrysosplenium oppositifolium* | · | · | · | · | · | · | · | · | · | · | · | 32.8 | · | · | · | · | · | · | · | · | · | · | · | · |
| *Luzula sylvatica* | · | 1.4 | · | 16.2 | · | · | · | 12.9 | 1.5 | 26.7 | 0 | 32.1 | · | · | · | · | · | 5.8 | · | · | · | · | 19.1 | · |
| **Cantabrian *Quercus suber* forests** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Quercus suber* | · | · | · | · | · | · | · | · | · | · | · | · | 73.9 | · | 4.3 | 0.8 | · | 6.9 | · | · | · | · | · | · |
| *Anarrhinum duriminium* | · | · | · | · | · | · | · | · | · | · | · | · | 42.1 | · | · | · | · | · | · | · | · | · | · | · |
| *Vulpia myuros* | · | · | · | · | · | · | · | · | · | · | · | · | 40.8 | · | · | · | · | · | · | · | · | 5.2 | · | · |
| *Cistus salviifolius* | · | · | · | · | · | · | · | · | · | · | · | · | 40.4 | 9.8 | 12.8 | 20.9 | · | · | · | · | · | · | · | · |
| *Phillyrea angustifolia* | · | · | · | · | · | · | · | · | · | · | · | · | 35.6 | · | 2.4 | 28.1 | · | · | · | · | · | · | · | · |
| *Sesamoides purpurascens* | · | · | · | · | · | · | · | · | · | · | · | · | 35.6 | · | · | · | · | · | · | · | · | 1.4 | · | · |
| *Pimpinella villosa* | · | · | · | · | · | · | · | · | · | · | · | · | 34.1 | · | · | 4.3 | · | · | · | · | · | · | · | · |
| **Cantabrian *Quercus ilex* forests** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Quercus ilex* | · | · | · | · | · | · | · | · | · | · | 3.7 | · | · | 89.3 | · | · | · | · | · | · | · | · | · | · |
| *Phillyrea latifolia* | · | · | · | · | 1.9 | · | · | · | · | · | · | · | · | 62.1 | 10.9 | · | · | · | · | · | · | · | · | · |
| *Rhamnus alaternus* | · | · | · | · | 10.4 | · | · | · | · | · | · | · | · | 46.3 | 23.9 | · | 14.7 | · | · | · | · | · | · | · |
| *Rubia peregrina* | · | · | · | · | 20.3 | · | · | · | · | · | 1.4 | · | 7.7 | 36.4 | 24.6 | 20.2 | 28.3 | 2.6 | · | · | · | · | · | · |
| *Rosa arvensis* | · | · | 1.3 | · | 25.2 | · | · | · | · | · | 18.2 | · | · | 36.1 | · | · | · | · | · | · | · | · | · | · |
| ***Cantabrian* Quercus rotundifolia *forests on non-acid soils*** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Spiraea hypericifolia* | · | · | · | · | 11.7 | · | · | · | · | · | · | · | · | · | 49.1 | · | · | · | · | · | · | · | · | · |
| *Carex halleriana* | · | · | · | · | 1.9 | · | · | · | · | · | · | · | · | · | 48.5 | · | · | · | · | · | · | · | · | · |
| *Quercus coccifera* | · | · | · | · | 9.3 | · | · | · | · | · | · | · | · | · | 40.2 | · | · | · | · | · | · | · | · | · |
| *Juniperus phoenicea* | · | · | · | · | 2.4 | · | · | · | · | · | · | · | · | · | 38.1 | · | · | · | · | · | · | · | · | · |
| *Dorycnium pentaphyllum* | · | · | · | · | 5.8 | · | · | · | · | · | · | · | 0.6 | 7.2 | 38 | 0.2 | · | · | · | · | · | · | · | · |
| *Lavandula latifolia* | · | · | · | · | 2.7 | · | · | · | · | · | · | · | · | · | 35.4 | · | · | · | · | · | · | · | · | · |
| *Juniperus oxycedrus* aggr*.* | · | · | · | · | 12.3 | · | · | · | · | · | · | · | 3.3 | 0.2 | 32.1 | 0.8 | · | · | · | · | · | · | · | 4 |
| ***Cantabrian* Quercus rotundifolia *forests on acid soils*** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Pistacia terebinthus* | · | · | · | · | · | · | · | · | · | · | · | · | 8.8 | 11.9 | 4.1 | 34.9 | · | · | · | · | · | · | · | · |
| *Genista hystrix* | · | · | · | · | · | · | · | · | · | · | · | · | 10.3 | · | · | 33.5 | · | · | · | · | · | · | · | · |
| **Cantabrian *Laurus* forests** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Parietaria judaica* | · | · | · | · | · | · | · | · | · | · | · | · | · | 3.4 | · | · | 60.2 | · | · | · | · | · | · | · |
| *Laurus nobilis* | · | 6 | · | · | · | · | 3.5 | · | · | · | 2.6 | · | 5.3 | 17.3 | · | · | 55.9 | 2.5 | · | · | · | · | · | · |
| *Olea europaea* | · | · | · | · | · | · | · | · | · | · | · | · | · | 5.2 | · | · | 40.1 | · | · | · | · | · | · | · |
| *Digitaria sanguinalis* | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 35.9 | · | · | · | · | · | · | · |
| *Crithmum maritimum* | · | · | · | · | · | · | · | · | · | · | · | · | · | 12.2 | · | · | 33.6 | · | · | · | · | · | · | · |
| *Asplenium adiantum-nigrum* | · | · | · | · | · | · | 1.7 | · | · | · | 2.4 | · | 13 | 9.3 | · | 24.7 | 32.9 | · | · | · | · | · | · | · |
| *Iris foetidissima* | 18.6 | · | · | · | 2.5 | · | · | · | · | · | 9.7 | · | · | 0 | · | · | 31.4 | · | · | · | · | · | · | · |
| **Cantabrian *Prunus lusitanica* forests** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Prunus lusitanica* | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 83.3 | · | · | · | · | · | · |
| *Frangula alnus* | 1.9 | 10.9 | · | · | · | 2.7 | 20.2 | 4.2 | 17.6 | · | 0.2 | 2.5 | · | · | · | · | · | 32.8 | · | · | · | · | · | · |
| **Cantabrian *Ilex* woodlands** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Stellaria nemorum* | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 65.8 | · | · | · | 6.4 | · |
| *Veronica montana* | 3.5 | 1.5 | 8.2 | · | · | · | · | · | · | · | 4.6 | 1.2 | · | · | · | · | · | · | 44.5 | · | · | · | 3.9 | · |
| *Thelypteris limbosperma* | · | 0.3 | · | 10.4 | · | · | · | 1.4 | 4.9 | 6.2 | · | 1.8 | · | · | · | · | · | · | 39.1 | · | · | · | · | · |
| *Dryopteris dilatata* | · | · | 0.2 | 15 | · | · | · | 5 | 3.9 | 14.6 | · | 21.8 | · | · | · | · | · | · | 38.8 | · | · | · | 21.4 | · |
| *Paris quadrifolia* | · | · | 5.2 | · | · | · | · | · | · | 2.3 | · | 4.4 | · | · | · | · | · | · | 37.9 | · | · | · | 25.3 | · |
| *Scrophularia scorodonia* | 1.6 | 1.5 | · | · | · | · | · | · | · | · | · | · | · | · | · | 1.3 | 1.7 | 4.1 | 35.2 | · | · | · | · | · |
| *Ilex aquifolium* | · | · | 0.1 | 11.5 | · | · | 4.6 | 16.5 | · | 8.3 | 1.9 | 18.8 | · | · | · | · | · | 20.4 | 31.8 | · | · | · | 28.3 | · |
| **Cantabrian *Pinus sylvestris* forests on non-acid soils** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Campanula cantabrica* | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 86.1 | · | · | · | · |
| *Arctostaphylos uva-ursi* | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 86.1 | · | · | · | · |
| *Potentilla crantzii* | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 82.5 | · | · | · | 1.3 |
| *Hieracium glaucinum* | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 80.3 | 6.2 | · | · | · |
| *Hippocrepis comosa* | · | · | · | · | 0.5 | · | · | · | · | · | · | · | · | · | 0.7 | · | · | · | · | 73.1 | · | · | · | 5 |
| *Galium pumilum* | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 5.6 | 3 | · | · | · | 72.5 | · | · | · | · |
| *Linum appressum* | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 70 | · | · | · | · |
| **Cantabrian *Pinus sylvestris* forests on acid soils** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Erica australis* | · | · | · | · | · | 1.7 | · | 1.4 | · | · | · | · | 4.4 | · | · | 1.2 | · | · | · | · | 54.8 | · | · | · |
| *Luzula lactea* | · | · | · | · | · | 4.8 | · | 10.2 | · | · | · | · | · | · | · | · | · | · | · | · | 47.3 | · | · | · |

***TABLE 2***. (Continued).

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| *EUNIS Code* | T111 | T121 | T172 | T182 | T197 | T19A | T1Bx | T1By | T1D1 | T1D7 | T1E1 | T1Fx | T211 | T21x | T21y | T21z | T22x | T22y | T27x | T37x | T37y | T3A1 | T3C1 | T3D6 |
| *Daboecia cantabrica* | · | · | · | · | · | 2.3 | 13.9 | 4.2 | 0.9 | · | · | · | 7 | · | · | · | · | · | · | · | 43 | 22.6 | · | · |
| *Genista polygaliphylla* | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 41.9 | · | · | · |
| *Cuscuta epithymum* | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 38.1 | 5.7 | · | · |
| *Asphodelu salbus* | · | · | · | · | · | 8 | 10 | 20.6 | · | · | · | · | · | · | · | · | 2.9 | 0.6 | · | · | 37.1 | 4.2 | · | · |
| *Gentiana lutea* | · | · | · | · | · | · | · | · | · | 8.4 | · | · | · | · | · | · | · | · | · | · | 34.5 | · | · | · |
| **Cantabrian *Pinus pinaster* forests** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Pinus pinaster* | · | · | · | · | · | · | · | · | · | · | · | · | 8.7 | · | · | · | · | · | · | · | · | 90 | · | · |
| *Neoschischkinia truncatula* | · | · | · | · | · | · | · | · | · | · | · | · | 4.5 | · | · | · | · | · | · | · | · | 49.5 | · | · |
| *Agrostis curtisii* | · | · | · | · | · | 3 | 7.3 | 4.2 | · | · | · | · | 1 | · | · | · | · | 1.1 | · | · | · | 47.1 | · | · |
| *Ulex minor* | · | · | · | · | · | 0.2 | 4.6 | · | · | · | · | · | 29.5 | · | · | · | · | · | · | · | · | 41.4 | · | · |
| *Corynephorus canescens* | · | · | · | · | · | · | · | · | · | · | · | · | 27.8 | · | · | · | · | · | · | · | · | 40.2 | · | · |
| *Erica cinerea* | · | · | · | · | · | 3.4 | 6.7 | · | · | · | · | · | 24.1 | · | 4.9 | 6.2 | · | · | · | · | · | 38.6 | · | · |
| *Pedicularis sylvatica* | · | · | · | · | · | · | · | · | · | 1.3 | · | · | 3 | · | · | · | · | · | · | · | · | 34.2 | · | · |
| **Cantabrian *Taxus* woodlands** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Taxus baccata* | · | · | · | · | · | · | · | · | · | 2.8 | · | 0.1 | · | · | · | · | · | 3.8 | 18.2 | · | · | · | 72.7 | · |
| *Aconitum lycoctonum* | · | · | 0.9 | · | · | · | · | · | · | 10.9 | 1.1 | · | · | · | · | · | · | · | · | · | · | · | 40.5 | · |
| *Milium effusum* | · | · | 9.6 | · | · | · | · | · | · | 0.7 | 3.4 | 19 | · | · | · | · | · | · | 3.2 | · | · | · | 38 | · |
| *Poa chaixii* | · | · | 2.6 | 1.8 | · | · | · | · | · | 15.6 | · | 0.6 | · | · | · | · | · | · | · | · | · | · | 35.5 | · |
| *Lilium martagon* | · | · | 12.6 | · | · | 0.8 | · | · | · | 7.4 | 3.5 | 7.3 | · | · | · | · | · | 2.9 | · | · | · | · | 34.8 | · |
| *Valeriana montana* | · | · | 1.6 | 0.5 | · | · | · | 7.4 | · | 16.8 | · | 9.8 | · | · | · | · | · | · | · | · | · | · | 32.1 | · |
| *Polygonatu mverticillatum* | · | · | 5.4 | 5.7 | · | · | · | 8.1 | · | 17.5 | · | 13.9 | · | · | · | · | · | · | 1.4 | · | · | · | 31.6 | · |
| **Cantabrian *Juniperus* woodlands** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Juniperus thurifera* | · | · | · | · | 1.5 | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 96.7 |
| *Koeleria vallesiana* | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 6.9 | · | · | · | · | · | · | · | · | 70.2 |
| *Thymus mastichina* | · | · | · | · | · | · | · | · | · | · | · | · | 2.7 | · | 1.3 | 13.3 | · | · | · | · | · | · | · | 61.1 |
| *Berberis vulgaris* | · | · | · | · | 2.6 | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 19.3 | · | · | 6.3 | 60.8 |
| *Anthyllis vulneraria* | · | · | · | · | 2.1 | · | · | · | · | · | · | · | · | 0.9 | 4.1 | 2.3 | · | · | · | · | · | 3.3 | · | 59.3 |
| *Erysimum duriaei* aggr. | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 58.4 |
| *Helianthemum canum* | · | · | · | · | 1.5 | · | · | · | · | · | · | · | · | · | 4.3 | · | · | · | · | · | · | · | 7.2 | 52.3 |
| **Other common species** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Alnus glutinosa* | 34.1 | 65.3 | · | · | · | · | · | · | 6.7 | · | 3.2 | · | · | · | · | · | · | · | · | · | · | · | · | · |
| *Carex reuteriana* | 1.3 | 31.4 | · | · | · | · | · | · | 32.6 | · | · | · | · | · | · | · | · | 6 | · | · | · | · | · | · |
| *Fagus sylvatica* | · | · | 41.8 | 41.8 | · | · | · | 0.1 | · | 0.5 | 2.1 | 8.6 | · | · | · | · | · | · | 5.7 | 15.7 | 3.8 | · | 3.7 | · |
| *Galium odoratum* | · | · | 32 | · | · | · | · | · | · | · | · | 13.2 | · | · | · | · | · | · | 8.4 | · | · | · | 39.1 | · |
| *Quercus faginea* | · | · | · | · | 39.6 | · | · | · | · | · | · | · | 2.5 | · | 11.9 | · | · | · | · | · | · | · | · | 49.6 |
| *Melampyrum pratense* | · | · | · | · | · | 31.8 | 9.4 | 25.2 | 0.5 | 9.9 | · | · | · | · | · | · | · | · | · | · | 35.6 | · | · | · |
| *Quercus petraea* | · | · | · | · | · | · | · | 44 | · | · | 2.7 | 31.3 | · | · | · | · | · | · | 3.1 | · | 17.3 | · | 5.7 | · |
| *Quercus orocantabrica* | · | · | · | · | · | · | · | 35.9 | · | · | · | · | · | · | · | · | · | · | · | · | 30.8 | · | · | · |
| *Betula celtiberica* | · | · | · | · | · | · | · | 10.5 | 45.3 | 43.9 | · | 17.5 | · | · | · | · | · | · | · | · | 10.4 | · | 9.4 | · |
| *Vaccinium myrtillus* | · | · | · | 24.9 | · | · | 1.2 | 29.5 | · | 32.1 | · | 7 | · | · | · | · | · | 7.6 | 9.8 | · | 35.5 | · | 7.9 | · |
| *Halimium alyssoides* | · | · | · | · | · | · | · | · | · | · | · | · | 45.1 | · | · | · | · | · | · | · | · | 43.5 | · | · |
| *Lavandula pedunculata* | · | · | · | · | · | · | · | · | · | · | · | · | 38.1 | · | · | 35.1 | · | · | · | · | · | · | · | · |
| *Daphne gnidium* | · | · | · | · | · | · | · | · | · | · | · | · | 37.5 | · | · | 37.8 | · | · | · | · | · | 12.8 | · | · |
| *Ulex europaeus* | · | · | · | · | · | 2.4 | 6.9 | · | 0.2 | · | · | · | 34.6 | · | · | · | 2.7 | · | · | · | · | 42.2 | · | · |
| *Cistus psilosepalus* | · | · | · | · | · | 0.7 | · | · | · | · | · | · | 32.1 | · | · | 0.7 | · | · | · | · | · | 30.9 | · | · |
| *Erica umbellata* | · | · | · | · | · | · | · | · | · | · | · | · | 30.7 | · | · | · | · | · | · | · | 5.5 | 50.5 | · | · |
| *Smilax aspera* | · | · | · | · | · | · | · | · | · | · | 3.5 | · | · | 60 | 0.1 | · | 45 | · | · | · | · | 0.3 | · | · |
| *Quercus rotundifolia* | · | · | · | · | 7.8 | · | · | · | · | · | · | · | 14.7 | · | 52.2 | 55.9 | · | · | · | 8.4 | · | · | · | · |
| *Genista scorpius* | · | · | · | · | 7.8 | · | · | · | · | · | · | · | · | · | 35.7 | · | · | · | · | · | · | · | · | 41.5 |
| *Amelanchier ovalis* | · | · | · | · | 9.4 | · | · | · | · | · | · | · | · | · | 32.1 | · | · | · | · | 46.7 | · | · | · | · |
| *Galium rotundifolium* | · | · | 0.5 | · | · | 1 | · | 0.9 | · | · | · | 8.6 | · | · | · | · | · | 4.9 | 33.2 | · | · | · | 33.2 | · |
| *Sanicula europaea* | · | · | 9.4 | · | · | · | · | · | · | · | 8.9 | 14.6 | · | · | · | · | · | 2.2 | 31.8 | · | · | · | 37.2 | · |
| *Pimpinella tragium* | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 0.2 | · | · | · | · | 77.7 | · | · | · | 36 |
| *Juniperus sabina* | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 4.4 | · | · | · | · | 69.7 | · | · | · | 55.9 |
| *Pinus sylvestris* | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | · | 67.6 | 67.6 | · | · | · |
| *Avenella flexuosa* | · | · | 0.9 | 32.1 | · | · | 3.9 | 30.8 | · | 13.5 | · | · | · | · | · | · | · | · | · | 3.4 | 43.6 | · | · | · |
| *Teucrium chamaedrys* | · | · | · | · | 1.6 | · | · | · | · | · | · | · | · | · | 36.5 | · | · | · | · | 60.7 | · | · | · | 42.2 |

***TABLE 3***. Results of the Generalized Linear Models (GLMs) for each type of forests. For every model, the z value of each variable (Bio2 = mean diurnal air temperature range, Bio11 = mean daily mean air temperatures of the coldest quarter, Bio12 = annual precipitation amount, Bio15 = precipitation seasonality, Bio17 = mean monthly precipitation amount of the driest quarter) and its significance (\*\*\* = 0.001, \*\* = 0.01, \* = 0.05, . = 0.1) are shown, as well as the explained deviance (%).

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Bio2** | | **Bio11** | | **Bio12** | | **Bio15** | | **Bio17** | | **Soil pH** | | **Explained**  **deviance (%)** |
| **Deciduous** | 8.501 | \*\*\* | -7.46 | \*\*\* | n. s. |  | n. s. |  | 12.072 | \*\*\* | -7.52 | \*\*\* | 14.6 |
| T111 | 6.573 | \*\*\* | 6.156 | \*\*\* | -5.583 | \*\*\* | n. s. |  | 2.976 | \*\* | 6.838 | \*\*\* | 23.1 |
| T121 | 6.715 | \*\*\* | 13.875 | \*\*\* | -1.861 | . | 2.702 | \*\* | 2.57 | \* | -2.007 | \* | 16.3 |
| T172 | 2.069 | \* | -20.04 | \*\*\* | n. s. |  | -13.245 | \*\*\* | n. s. |  | -4.053 | \*\*\* | 23.7 |
| T182 | -1.922 | . | -9.839 | \*\*\* | 3.536 | \*\*\* | -5.542 | \*\*\* | -2.898 | \*\* | -8.332 | \*\*\* | 19.2 |
| T197 | 3.119 | \*\* | n. s. |  | n. s. |  | -8.473 | \*\*\* | -4.672 | \*\*\* | 4.207 | \*\*\* | 16.0 |
| T19A | 5.76 | \*\*\* | -4.285 | \*\*\* | -3.294 | \*\*\* | 3.798 | \*\*\* | 2.27 | \*\*\* | 1.605 | \* | 18.1 |
| T1Bx | 7.929 | \*\*\* | 12.708 | \*\*\* | -2.692 | \*\* | 2.249 | \* | 4.111 | \*\*\* | -8.053 | \*\*\* | 14.9 |
| T1BY | n. s. |  | -8.771 | \*\*\* | 3.247 | \*\* | n. s. |  | -3.297 | \*\*\* | -2.749 | \*\* | 12.3 |
| T1D1 | -2.503 | \* | -1.705 | . | 1.794 | . | n. s. |  | -4.346 | \*\*\* | -8.115 | \*\*\* | 13.4 |
| T1D7 | -3.415 | \*\*\* | -14.25 | \*\*\* | 7.227 | \*\*\* | n. s. |  | 1.589 |  | -5.148 | \*\*\* | 34.1 |
| T1E1 | 3.908 | \*\*\* | 6.108 | \*\*\* | 3.206 | \*\* | -9.718 | \*\*\* | n. s. |  | n. s. |  | 5.5 |
| T1Fx | n. s. |  | -4.479 | \*\*\* | 3.358 | \*\*\* | n. s. |  | -4.11 | \*\*\* | -2.657 | \*\* | 6.8 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| **Evergreen** | -6.112 | \*\*\* | 8.34 | \*\*\* | -8.581 | \*\*\* | 7.746 | \*\*\* | n. s. |  | 7.056 | \*\*\* | 15.2 |
| T211 | 4.476 | \*\*\* | 6.7 | \*\*\* | -1.996 | \* | 2.526 | \* | 1.673 | . | n. s. |  | 32.9 |
| T21x | -13.45 | \*\*\* | n. s. |  | -6.631 | \*\*\* | n. s. |  | 7.349 | \*\*\* | 1.703 | . | 31.3 |
| T21y | 1.908 | . | -2.991 | \*\* | 2.456 | \* | -5.42 | \*\*\* | -4.16 | \*\*\* | 1.589 |  | 23.0 |
| T21z | 4.764 | \*\*\* | 4.412 | \*\*\* | -5.377 | \*\*\* | 7.099 | \*\*\* | 5.756 | \*\*\* | -4.55 | \*\*\* | 24.9 |
| T22x | -1.757 | . | 7.405 | \*\*\* | 3.817 | \*\*\* | -5.184 | \*\*\* | -5.486 | \*\*\* | n. s. |  | 53.6 |
| T22y | 1.658 | . | 1.607 |  | 3.826 | \*\*\* | -2.219 | \* | -2.6 | \*\* | n. s. |  | 22.0 |
| T27x | -3.983 | \*\*\* | n. s. |  | 1.933 | . | -1.917 | . | -2.244 | \* | -2.493 | \* | 16.7 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| **Coniferous** | -5.523 | \*\*\* | -2.148 |  | 10.338 | \*\*\* | n. s. |  | -9.083 | \*\*\* | n. s. |  | 12.8 |
| T37x | -2.061 | \* | -3.177 | \*\* | n. s. |  | n. s. |  | -2.189 | \* | n. s. |  | 28.9 |
| T37y | n. s. |  | -4.6 | \*\*\* | 3.418 | \*\*\* | -3.048 | \*\* | -3.183 | \*\* | n. s. |  | 33.8 |
| T3A1 | 2.494 | \* | 7.201 | \*\*\* | 4.73 | \*\*\* | n. s. | \*\*\* | -4.171 |  | -2.604 | \*\* | 36.5 |
| T3C1 | n. s. |  | -5.374 | \*\*\* | n. s. |  | 4.16 | \*\*\* | 2.553 | \* | n. s. |  | 18.0 |
| T3D6 | -5.52 | \*\*\* | -6.218 | \*\*\* | n. s. |  | n. s. |  | -6.15 | \*\*\* | 3.192 | \*\* | 44.8 |