



# Life-form diversity across temperate deciduous forests of Western Eurasia: A different story in the understory

Javier Loidi<sup>1</sup> | Milan Chytrý<sup>2</sup> | Borja Jiménez-Alfaro<sup>3</sup> | Nicola Alessi<sup>4</sup> | Idoia Biurrun<sup>1</sup> | Juan Antonio Campos<sup>1</sup> | Andraž Čarni<sup>5,6</sup> | Eduardo Fernández-Pascual<sup>7</sup> | Xavier Font Castell<sup>8</sup> | Hamid Gholizadeh<sup>9</sup> | Adrian Indreica<sup>10</sup> | Ali Kavgacı<sup>11</sup> | Ilona Knollová<sup>2</sup> | Alireza Naqinezhad<sup>9</sup> | Pavel Novák<sup>2</sup> | Arkadiusz Nowak<sup>12,13</sup> | Željko Škvorc<sup>14</sup> | Ioannis Tsiripidis<sup>15</sup> | Kiril Vassilev<sup>16</sup> | Corrado Marcenò<sup>1,2</sup>

<sup>1</sup>Department of Plant Biology and Ecology, University of the Basque Country UPV/EHU, Bilbao, Spain

<sup>2</sup>Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic

<sup>3</sup>Research Unit of Biodiversity - CSIC/UO/PA, Universidad de Oviedo, Mieres, Spain

<sup>4</sup>UIBK Institute of Botany, University of Innsbruck, Innsbruck, Austria

<sup>5</sup>Research Centre of the Slovenian Academy of Sciences and Arts, Jovan Hadži Institute of Biology, ZRC-SAZU, Ljubljana, Slovenia

<sup>6</sup>University of Nova Gorica, School for Viticulture and Enology, Nova Gorica, Slovenia

<sup>7</sup>Department of Organisms and Systems Biology, University of Oviedo, C/ Catedrático Rodrigo Uría, Oviedo, Spain

<sup>8</sup>Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona, Barcelona, Spain

<sup>9</sup>Department of Biology, Faculty of Basic Sciences, University of Mazandaran, Babolsar, Mazandaran, Iran

<sup>10</sup>Department of Silviculture, Transilvania University of Brasov, Romania

<sup>11</sup>Southwest Anatolia Forest Research Institute, Antalya, Turkey

<sup>12</sup>Botanical Garden - Center for Biological Diversity Conservation, Polish Academy of Sciences, Warsaw, Poland

<sup>13</sup>Institute of Biology, University of Opole, Opole, Poland

<sup>14</sup>Forestry Section, University of Zagreb, Zagreb, Croatia

<sup>15</sup>Department of Botany, School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece

<sup>16</sup>Plant and Fungi Diversity and Resources, Institute of Biodiversity and Ecosystem Research Department, Sofia, Bulgaria

## Correspondence

Javier Loidi, Department of Plant Biology and Ecology, University of the Basque Country UPV/EHU, Bilbao, Spain.  
Email: javier.loidi@ehu.eus

## Funding information

Czech Science Foundation, Grant/Award Number: 19-28491X; Basque Government, Grant/Award Number: IT936-16

Handling Editor: Gerald Schneeweiss

## Abstract

**Aim:** To analyse the biogeographic patterns of Temperate Deciduous Forests (TDFs) in Western Eurasia based on different life-forms and forests layers and explore their relationships with the current climate, Last Glacial Maximum (LGM) climate and topography.

**Location:** Western Eurasia.

**Taxon:** Vascular plants.

**Methods:** We delimited nine regions encompassing the variability of TDFs in Western Eurasia and collected 1000 vegetation plots from each. We deconstructed the plant communities into three layers, tree, shrub and floor. We used (i) generalized linear

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2021 The Authors. *Journal of Biogeography* published by John Wiley & Sons Ltd.



mixed models (GLMM) to analyse the influence of current climate, historical climate and topography on species richness by accounting for regional effects and (ii) redundancy analysis (RDA) with variance partitioning to describe the variation in life forms along abiotic gradients. The three forest layers were analysed jointly and separately.

**Results:** The Balkans, Alps and Carpathians appeared to be the richest in plant species, whereas the British Isles and the Hyrcanian region were the poorest. Annual temperature range and annual mean temperature were the best predictors of species richness for the whole dataset and for the shrub layer. The tree layer richness was mainly explained by the annual temperature range and by elevation, whereas the forest floor richness was more related to the annual temperature range and the annual mean temperature differences between the LGM and current climate. The current climate was the main predictor of the composition of the whole community, the tree layer and the floor layer, while the shrub layer was also influenced by historical climate.

**Main conclusions:** Our overview of the diversity of temperate deciduous forests in Western Eurasia demonstrates different patterns and drivers across life-forms and forest layers. While the diversity of trees is mainly linked to current climatic conditions, the shrub layer is also driven by postglacial-glacial climatic stability, suggesting a different origin from forest trees.

#### KEYWORDS

Europe, Euxinian, forest diversity, forest floor, Hyrcanian, life form, shrub layer, species richness, tree layer

## 1 | INTRODUCTION

Forests are not only trees, although trees are the plants by which we define the forest ecosystem. They are formed of different types of organisms interacting across complex webs of matter and energy (Perry et al., 2009), and these interactions depend on regional evolutionary histories. Within any forest biome of the world (Moncrieff et al., 2016; Mucina, 2018), there are biogeographical differences among its regions depending on climate, substrate and history. Such differences are mainly reflected in the number and composition of vascular plants that co-occur in forest stands across regions (DRYFLOR et al., 2016; Večeřa et al., 2019). However, these patterns can differ among taxonomic groups or guilds of forest species. Vascular plants in the forest understory significantly depend on shading by the canopy (Mestre et al., 2017; Pardé, 1974; Valladares et al., 2016), yet this effect varies across forest types, depending on canopy density, the identity of the canopy species, ecological factors and regional evolutionary history (Royo & Carson, 2009).

In Western Eurasia, the understory flora of temperate deciduous forests (hereinafter TDFs) is highly specialized to shade conditions, including many species that avoid open habitats (Braun-Blanquet, 1964; Mucina et al., 2016; Schmid et al., 2011). This shade-adapted forest flora has been commonly used to differentiate deciduous forests (the phytosociological class *Quercus-Fagetum sylvaticae*, split up into several narrower classes by some authors; Mucina et al., 2016) from other forest types occurring in Western Eurasia. Across their

broad distribution range, European TDFs vary in their species and life-form composition. Recent studies (Jiménez-Alfaro et al., 2018; Padullés Cubino et al., 2021; Večeřa et al., 2019) demonstrated that the spatial patterns of species richness within European TDFs depend on climatic, edaphic and topographic drivers, but also on the evolutionary and glacial-postglacial history of the flora. Both ecology and history might also be reflected in the distribution of life forms among geographical regions, but relevant information is still missing. During the Pleistocene, the climate was changing dramatically, but different climatic factors did not follow the same trends (Brown et al., 2020). Consequently, the life forms adapted to a particular climatic feature, for example, summer drought, would react differently from the life forms adapted to another feature, for example, winter frost. This is expected to have left various imprints in the geographic and climatic distribution of the current life forms across the TDFs.

Usually, different life forms respond differently to specific environmental factors, e.g., therophytes are better adapted to the summer-dry Mediterranean climate than hemicryptophytes (Pfadenhauer & Klötzli, 2014). However, the occurrence of particular life forms in some regions can depend on historical refugia (Habel et al., 2010; Willis & Whittaker, 2000). Higher species richness of deciduous trees would be expected in southern areas as the historical climate was not so severe there, but in some of them, drought periods can have limited their diversity (Grossiord, 2020). Other examples are laurophyllous trees and shrubs, which dominated forests in the middle to late Tertiary across large areas of southern Europe



but now are relict in restricted climatically favourable regions (Alessi et al., 2019; Kovar-Eder et al., 2006). By deconstructing the forest plant communities into different life-forms and forest layers and assessing their distribution patterns separately, we intend to compare the geographic patterns in the understory and the tree layer of Western Eurasian TDFs to find out whether they respond differently to ecological and historical biogeographic drivers.

Specifically, we ask the following questions:

1. Do different life-forms and forest layers respond similarly to environmental factors?
2. Which biogeographical patterns of life-forms and forests layers are related to the current climate, past climate and topography?

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and region selection

Temperate deciduous forests currently occupy a vast area in Western Eurasia, extending from the Atlantic seaboard to the southern coastal fringes of the Black Sea (Euxinian area) and the Caspian Sea (Hyrceanian area) (Figure 1). They develop mostly under temperate climatic conditions (Rivas-Martínez, 2007) and occur between the boreal conifer forest biome in the north, the Mediterranean sclerophyllous forest biome in the south and the steppe biome in the southeast. We selected nine regions where such forests are the dominant potential natural vegetation (Jahn, 1991; Röhrig, 1991). These regions were chosen to encompass as much as possible of the biogeographical and bioclimatic variability of the TDFs of Western Eurasia. They are distributed across the north-south and west-east gradients of the Western Eurasian TDF distribution. They also include the most important mountain areas in which such forests dominate in piedmonts and at mid-elevations (Bohn et al., 2000–2003). An essential criterion for the region selection was the availability of a sufficiently large number of vegetation plots to permit the analysis (see below). The northwest Atlantic border is represented by the British Isles (1) region. The extensive low-elevation territories of Central Europe, including Germany and the Czech Republic are represented by the Central Europe region (2). The mountain ranges of Central Europe are represented by the Alps (3) and the Carpathians (4). Southern Europe is further represented by the Iberian Peninsula (5), Italy (6) and the Balkans (7). Finally, the isolated eastern occurrences of TDFs are represented by the Euxinian region (8), including the coastal parts of northern Turkey and Georgia, and the Hyrcanian region (9) in northern Iran (Figure 1).

### 2.2 | Data set filtering and resampling

We obtained a dataset of 132,447 vegetation plots from the European Vegetation Archive (EVA; Chytrý et al., 2016) and the

Hyrceanian Forest Vegetation Database (Gholizadeh et al., 2019). The vegetation plots were selected from other vegetation types in Turboveg 3 program using an Expert System (hereinafter ES) created specifically for this purpose (for more information about the ES procedure, see Appendix S1) and tailored to choose the deciduous non-riparian forest plots of the *Quercus-Fagetea* (Loidi, 2020). We excluded the riparian forests to deal with forests dependent more on climate and less on local soil moisture. We identified the plots recorded within the nine pre-defined regions using ArcGIS 10 (ESRI, Redlands, CA, USA). To have comparable and homogeneous datasets in terms of plot size, we selected, from each region, vegetation plots with sampled areas between 100 and 400 m<sup>2</sup>. Within this size range, effects of log(plot area) on the log(species richness) were negligible, as tested by an ordinary least squares linear model ( $r^2=0.0014$ ;  $p < 0.001$ ).

To reduce oversampling of specific areas and to maintain heterogeneity of species composition inside each region, we followed the resampling approach proposed by Knollová et al. (2005). The data set was geographically stratified using a grid of 2.5 longitudinal and 1.5 latitudinal minutes. Then it was resampled using the Heterogeneity-Constrained Random (HCR) resampling algorithm (Lengyel et al., 2011) with Bray–Curtis dissimilarity as resemblance measure, and we retained five plots per grid cell. Finally, we randomly selected 1000 vegetation plots per region. The resampled dataset consisted of 9000 vegetation plots (9 regions × 1000 plots) and 2063 vascular plant species (for the full species list, see Appendix S2). The data filtering, stratification and resampling procedures were run in the JUICE 7.1 software (Tichý, 2002).

### 2.3 | Species data

The taxonomic concepts and nomenclature were harmonized according to the Euro+Med PlantBase (<http://www.emplantbase.org>; see Appendix S2). We removed non-vascular plants, hybrids and the taxa identified only at the genus or family level. Subspecies were merged at the species level. Once we prepared the final species list, we assigned all species to life forms as follows (Tutin et al., 1964–1980):

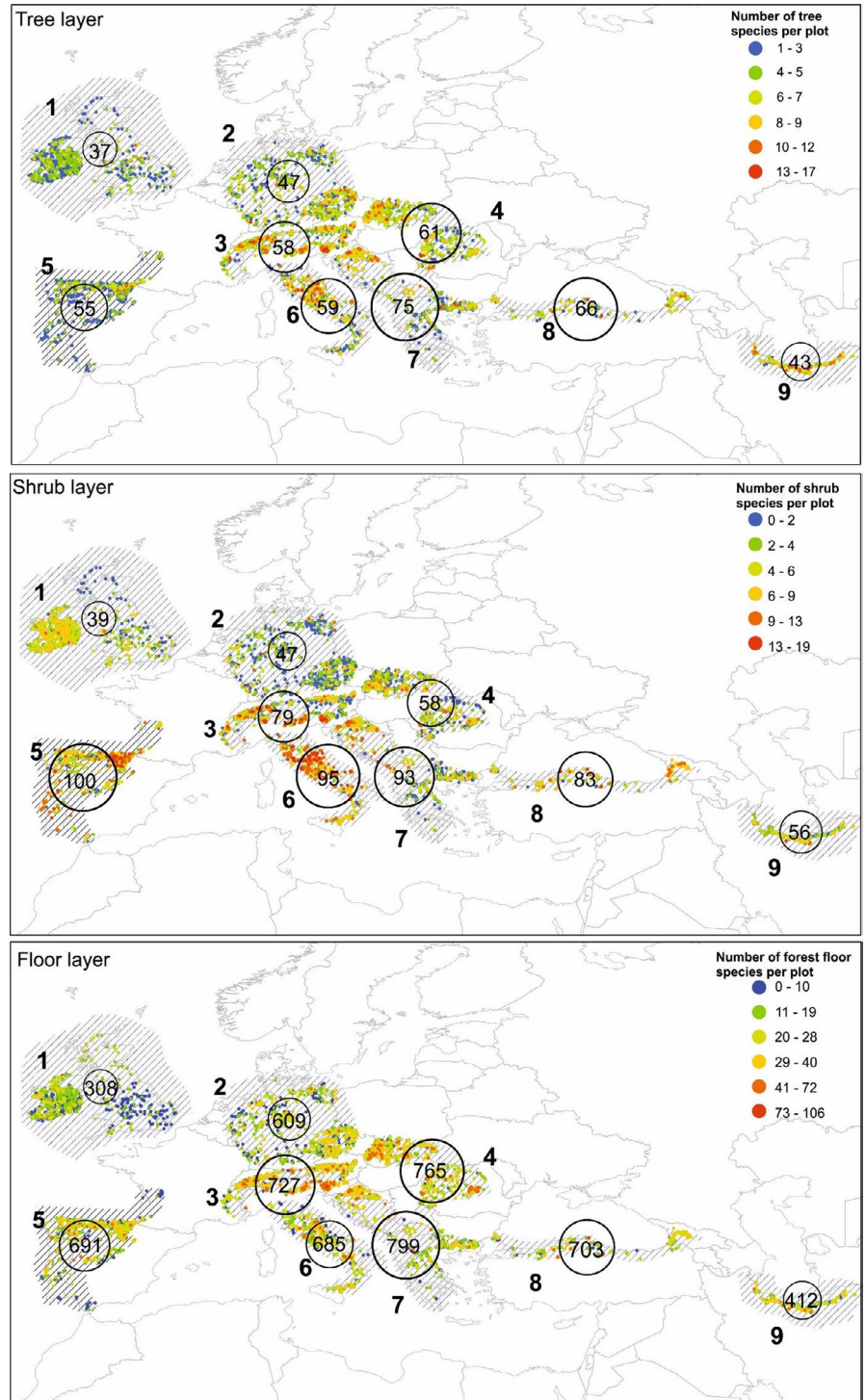
- Tree: woody species with usually a single trunk and with an average height over 10 m.
- Shrub: woody species with usually multiple trunks and with an average height from 0.3 to 10 m.

Both trees and shrubs were further divided into deciduous broadleaf, evergreen broadleaf and gymnosperm.

- Forest-floor: These species were further divided according to Raunkjær's life forms of chamaephyte, geophyte,



**FIGURE 1** Components of forest plant species richness for tree, shrub and floor layer in the nine studied regions. The richness was counted per plot and region. Colour scale indicates the number of species in plots. Numbers in the circles are the total species counts per region. The size of the circles is related to the number of species in each region recorded in its 1000 vegetation plots. The regions are: British Isles (1), Central Europe (2), Alps (3), Carpathians (4), Iberian Peninsula (5), Italy (6), Balkans (7), Euxinian (8) and Hyrcanian (9). The geographic coordinate system used to create these maps is unprojected WGS84.



hemipteryte and therophyte (Raunkiaer, 1934), and additionally into fern and liana. The representatives of the latter two groups belong to some of Raunkiaer's life forms, but they were classified separately because of their specific ecology.

Based on these categories, the species in the dataset were separated into three groups: tree layer, shrub layer and floor layer.

### 2.4 | Environmental variables

We considered three groups of variables: the first group (a) includes four variables characterizing current climate, which are putatively related to the variation in life forms along an abiotic environmental gradient: annual mean temperature, annual temperature range, annual precipitation and precipitation of the warmest quarter. The second group (b) represents the palaeoclimatic instability, defined

as the difference between the Last Glacial Maximum (hereinafter LGM) and the current climatic conditions. We defined climatic differences as the absolute value of the difference between the current climate and the LGM model for the above-mentioned climatic variables. The climatic variables were obtained by overlaying the individual plot coordinates and the CHELSA climate data set in ArcGIS 10. For the LGM, we used the PMIP3 model (Karger et al., 2017). Climatic data were downloaded in a raster of 30 arc-sec, corresponding to a spatial resolution of ~1 km. The third group of variables (c) is represented by elevation and terrain ruggedness, calculated as a vector ruggedness measure (VRM) according to Sappington et al. (2007).

We ran a pilot PCA with all the environmental variables and retained only those with an inflation factor < 8 and correlation < 0.6 for future analysis (for more details, see Appendix S3). The final variables to be used were annual mean temperature, annual temperature range, precipitation of the warmest quarter, differences in annual mean temperature between LGM and the present (hereinafter TdLGM), roughness and elevation. Spatial data were managed in ArcGIS 10 (ESRI).

## 2.5 | Analysis of richness of forest layers

We calculated species richness for each layer considering the number of species per plot and the total number of species per region, that is, the regional species pool (Figure 1). To analyse the influence of the environmental variables on species richness per plot, we used generalized linear mixed models (GLMM) computed for the whole data set and the three layers (tree, shrub and floor) separately. We computed the GLMMs using 'region' as the random factor to account for spatial autocorrelation of the data and to consider historical or stochastic factors related to regional idiosyncrasies. The analyses were conducted in R 3.6.3 (R Core Team 2019) with the *lme4* package (Bates et al., 2015) after scaling the variables with the 'scale' R function, using a Poisson error distribution fitted with a logit link function (McCullagh & Nelder, 1989). Model performance was addressed by the Akaike Information Criterion (AIC) and the marginal (m) and conditional (c)  $R^2$  estimated by the trigamma function in *MuMIn* R package (Barton, 2020) for calculating model fits without ( $mR^2$ ) or with ( $cR^2$ ) the random factor considered.

## 2.6 | Analysis of the distribution of life-form composition

To describe the variation in life forms along abiotic environmental gradients, we calculated the proportion of life-forms for each plot (hereinafter Wpli-fo), weighted by species abundance using CANOCO 5 (ter Braak & Šmilauer, 2012). The original Braun-Blanquet cover-abundance classes were transformed into percentage cover as follows:  $r = 0.5\%$ ;  $+ = 0.5\%$ ;  $1 = 3\%$ ;  $2 = 15\%$ ;  $3 = 38\%$ ;  $4 = 63\%$  and  $5 = 88\%$ . We ran constrained ordination using Redundancy Analysis

(RDA) to summarize the part of the variation in Wpli-fo explained by environmental variables. We used forward selection to select the best subset of the environmental variables ( $p_{adj} < 0.01$ ). The analysis was run for the whole dataset and the three layers separately. The response variables were centered and standardized, and a test of significance of all constrained axes was performed using 999 unrestricted permutations.

We used the subsets of the previously selected environmental variables to run a variation partitioning analysis and quantify (i) the effect of space, using 'region' as spatial variables, and (ii) the response of Wpli-fo to three groups of variables. The analysis was run for the whole data set and the three separated layers. A stepwise selection of the environmental variables ( $p_{adj} < 0.01$ ) was performed. As the amount of variation explained by a group of variables is expected to grow linearly with the number of variables of each group (Peres-Neto et al., 2006) we used the adjusted explained variation for the partitioned fraction following Legendre (2007) and Peres-Neto et al. (2006). All the analyses were performed using JUICE (Tichý, 2002) and CANOCO 5 (ter Braak & Šmilauer, 2012).

## 3 | RESULTS

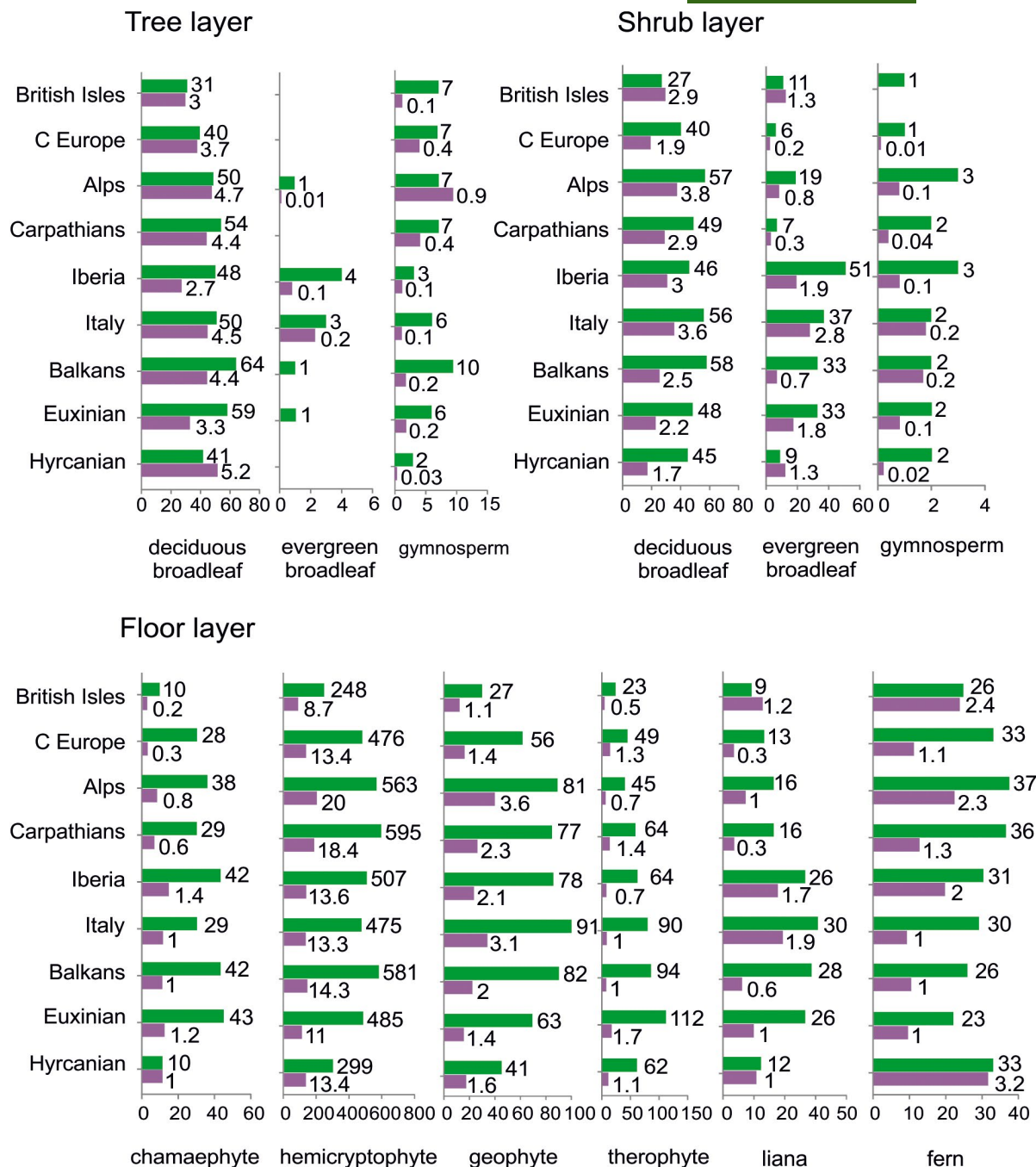
### 3.1 | Species richness

Species richness showed different patterns for each layer analysed, both for the number of species per plot and the total number of species per region (Figures 1 and 2). The species pool of the tree layer was not showing a clear pattern among the regions, with the Balkans being the most diverse both in the total tree species number (75), deciduous broadleaf tree species number (64) and gymnosperm tree species number (10). Evergreen trees were abundant in the southern regions, particularly the Iberian Peninsula, where this group reached the highest species number (4). In contrast, the most isolated regions, such as the British Isles and the Hyrcanian region, showed the lowest tree species richness.

The number of tree species per plot showed a different pattern. In this case, the most diverse regions were Hyrcanian and the Alps. The Hyrcanian region showed the highest mean number of deciduous tree species per plot (5.2), and the Alps the highest gymnosperm diversity (0.9). Italy was the most diverse in evergreen broadleaf trees (0.2).

In the shrub layer, the species pool size increased from the north to the south, with a more pronounced increase in evergreen broadleaf shrubs. Balkans was the most diverse region in deciduous broadleaf shrubs (58), whereas Iberian Peninsula showed the highest number of evergreen broadleaf (51) and gymnosperm shrubs. Lower numbers characterized peripheral regions such as the British Isles and the Hyrcanian. Concerning the number of species per plot, the Alps and Italy were the richest regions, the former with a mean number of deciduous shrubs per plot of 3.8 and the latter with a mean number of evergreen broadleaf and gymnosperm species per plot of 2.8 and 0.2, respectively.





**FIGURE 2** Number of species per region (green) and the average number of species per plot (violet) calculated per forest layer and life form. For better visualization, the bar lengths for average numbers of species per plot were multiplied by 10, while the numbers next to these bars are original values

In the species pool of the floor layer, hemicryptophytes were the most represented life form in all the regions with the highest number in the Carpathians (595 species) and the lowest number in the British Isles and the Hyrcanian region (248 and 299 species respectively). There was also a marked increase of therophytes from the north to the south. The Euxinian region was the most diverse in therophytes, both in the total species number (112 species) and species number per plot (1.7 species).

Regarding the number of species per plot, the regions with the highest numbers of forest-floor species were the Alps and the Carpathians, mainly due to the high numbers of hemicryptophytes (20.0 and 18.4 respectively). The number of ferns per plot was high in the Hyrcanian region, the British Isles and the Alps (3.2, 2.4 and 2.3 respectively). The Alps also contained the highest mean number of geophytes (3.6), followed by Italy (3.1). Iberian Peninsula contained the highest number of chamaephytes, whereas the British

Isles were characterized by the lowest number of all species on the floor layer. Chamaephytes, hemicryptophytes and geophytes had a similar abundance pattern, with lower numbers in the peripheral regions, except for the Hyrcanian region. In comparison, therophytes and lianas showed a tendency towards higher numbers in the southern regions.

In agreement with the observed patterns, the GLMMs showed different results for the whole dataset and the three subsets. The explained variation ( $cR^2$  and  $mR^2$ ) was the highest in the whole dataset and the shrub layer, followed by the tree and the floor layers (Table 1). In all cases, regional effects were important, as noted by substantially higher values in  $cR^2$  than  $mR^2$ , specially for the floor layer. The environmental variable most affecting total species richness in the whole dataset was the annual temperature range. The same variable was the best predictor for the tree and floor-layer species richness. In contrast, the shrub layer was mainly linked with annual mean temperature. The tree layer richness was influenced differently by the predictors of current climate, elevation and roughness (Table 1), while annual temperature range and temperature differences between the LGM and current climate had the strongest effects on the whole dataset and the floor layer.

### 3.2 | Drivers of life-form composition

Plot life-form proportion weighted by species abundances showed different patterns compared to species richness (see Figure 3 and Appendix S4a). According to RDAs, the explained variation was higher in the shrub layer, followed by the whole dataset, the tree layer and the floor layer (Table 2 and Appendix S4a). The shared effect between space and environmental variables was higher for the whole dataset than for the tree and floor layers (see Appendix S5). For the whole dataset, the most fitting variables were the annual mean

temperature, annual temperature range and the difference of temperature between the present and the LGM (TdLGM, see Appendix S4b). Axis 1 represents a gradient from the colder regions (Balkans, Carpathians, Alps and Central Europe) to the warmer regions (Hyrcanian, Euxinian, Italy and the Iberian Peninsula). Gymnosperm trees and hemicryptophytes prevailed in the colder regions, whereas the evergreen broadleaf shrubs and lianas prevailed in the warmer regions. Deciduous shrubs were abundant in the British Isles. Axis 2 represented a gradient from the regions with historically more stable climate (Balkans, Euxinian, Italy and Iberian Peninsula) to those with less stable climates (Carpathians, Alps, Central Europe and the British Isles). The deciduous trees were more abundant in the former than in the latter regions. The results of variation partitioning showed a larger effect of the current climate (stepwise selected variables: annual temperature range, annual mean temperature and precipitation of the warmest quarter) than historical (TdLGM) and topographic (elevation) variables (Appendix S4b).

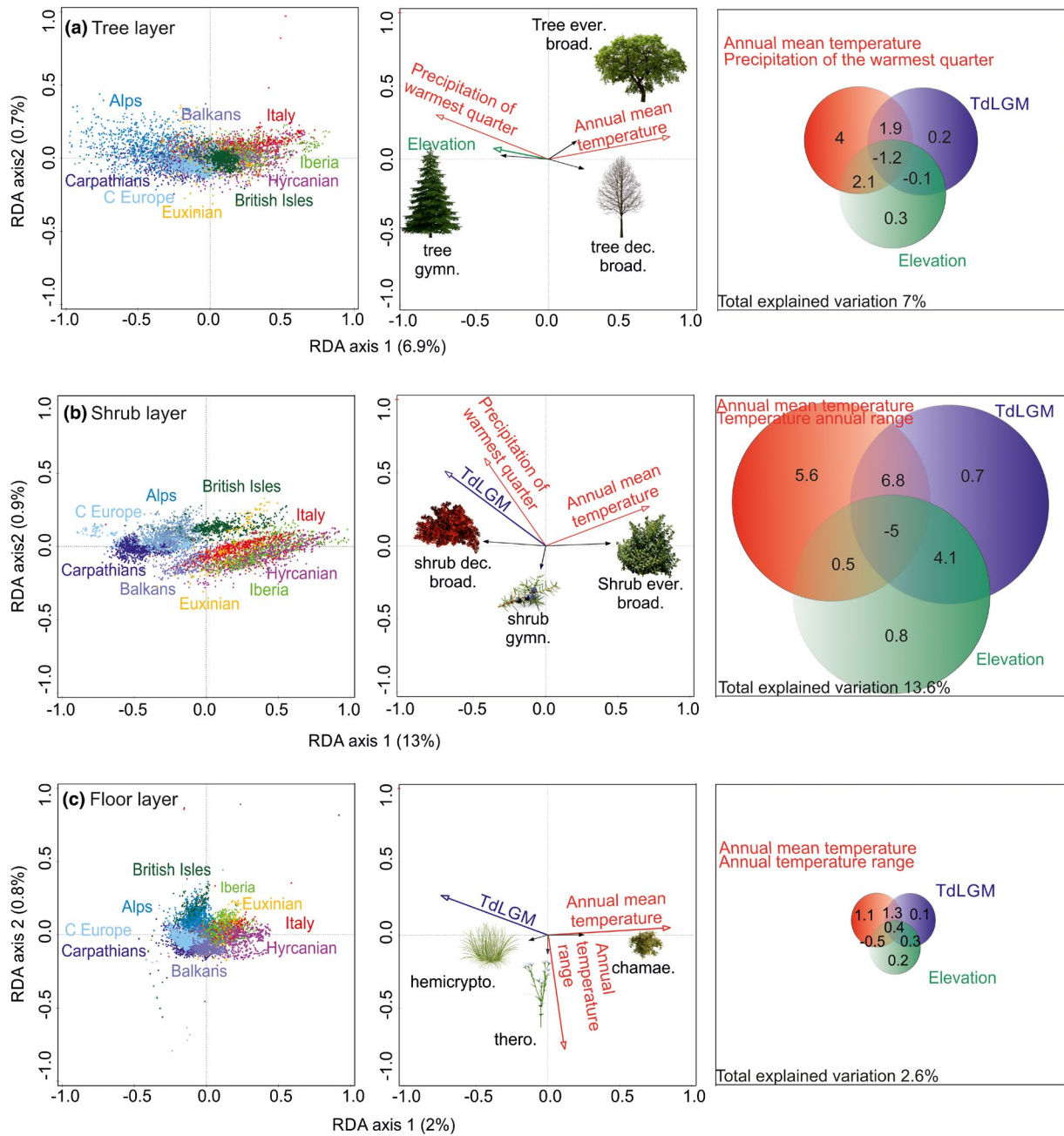
Regarding the tree layer, axis 1 had a higher pseudo-canonical correlation than axis 2 (Table 2). Axis 1 was a gradient from the warmest and driest regions (mainly Italy and Iberian Peninsula) to the wettest and coldest regions (the Alps and Carpathians). The abundance of evergreen broadleaf and deciduous trees was correlated with the warmest regions. Instead, the precipitation of the warmest quarter and elevation were positively correlated with the abundance of gymnosperm trees.

RDA of the shrub layer explained a higher proportion of variance than in the other two layers (Table 2). Axis 1 showed a climatic gradient from the warmest and driest regions to the coldest and wettest ones. The most fitting current climate variables were the annual mean temperature and the precipitation of the warmest quarter. Another important variable was the annual mean temperature difference between the current climate and the LGM climate (TdLGM). The regions with high summer precipitation and unstable

	The whole dataset	Tree layer	Shrub layer	Floor layer
AIC	90288	36945	36743	84370
R2m	0.22	0.13	0.21	0.12
R2c	0.53	0.20	0.48	0.44
Annual mean temperature	11.9***	3.6***	16.9***	0.8 ns
Annual temperature range	15.0***	14.0***	8.1***	8.4***
Precipitation of warmest quarter	11.2**	6.4***	5.2***	5.9***
TdLGM	-7.5***	-1.8 ns	-2.8**	-7.1***
Elevation	4.3***	-8.2***	-0.0 ns	6.7***
Terrain ruggedness	4.3***	3.1***	6.1***	0.9 ns

Parameters of different models considering the total species richness (the whole dataset) and the species richness of each layer are shown. AIC is the value of the Akaike Information Criterion. R2m and R2c show the marginal/conditional estimates of model fits (without/with the random factor) as estimated by the trigamma function in MuMIn R package. The numbers in the main part of the table are z values of the coefficients with significance levels (\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; ns not significant) for each explanatory variable. TdLGM is the annual mean temperature differences between the LGM and the current climate.

TABLE 1 Results of the generalized linear mixed models of species richness per plot, using region as the random factor



**FIGURE 3** RDA ordination separately for each layer. Only the three most fitting variables and life forms are shown. The total explained variance of each axis is reported in parentheses. The results of variation partitioning in RDA show the circle sizes in relation to the magnitude of the explained variation. Red circles: current climatic variables; blue: historical climatic variables; green: topographic variables. The stepwise selected variables of each subset are also reported. The explained variances are shown inside the circles, and the overlapping areas indicate the percentage shared effect of each fitted variable. The test in each analysis was significant at  $p < 0.01$ . TdLGM is the annual mean temperature difference between the Last Glacial Maximum (LGM) and the current climate. broad. = broadleaf; chamae. = chamaephyte; dec. = deciduous; ever. = evergreen; gymn. = gymnosperm; hemicropto. = hemicryptophyte; thero. = therophyte. The results of the RDA and variance partitioning of the whole dataset are shown in Appendix S4

post-LGM climate (Central Europe, Carpathians and Alps) were usually most abundant in deciduous shrubs. In contrast, warmer regions with stable temperature since the LGM (Euxinian, Iberian Peninsula, Italy and Hyrcanian) were richer in broadleaf evergreen shrubs. The variation partitioning, in this case, showed a lower influence on the current climate (stepwise selected variables: annual temperature range and annual mean temperature) compared to the historical

climate changes (TdLGM). Although the historical climate alone explained 0.7% of the total explained variation (13.6%), the sum of the shared effect with the current climatic (6.8%) and topographic variables (4.1%) suggested TdLGM be an important driver for the shrub layer (see Figure 3).

Finally, the floor layer showed a very low proportion of explained variance (Table 2). The most fitting environmental variables



TABLE 2 Results of the RDA for all the layers together and each layer separately

The whole dataset Axes	1	2
Eigenvalues	0.05	0.03
Explained variation (cumulative, %)	5.36	8.55
Pseudo-canonical correlation	0.58	0.48
Tree layer		
Eigenvalues	0.07	0.01
Explained variation (cumulative, %)	6.91	7.60
Pseudo-canonical correlation	0.36	0.12
Shrub layer		
Eigenvalues	0.13	0.01
Explained variation (cumulative, %)	13.05	13.93
Pseudo-canonical correlation	0.45	0.16
Floor layer		
Eigenvalues	0.02	0.01
Explained variation (cumulative, %)	2.06	2.82
Pseudo-canonical correlation	0.25	0.16

Only the cumulative explained variation of the first two axes is shown. The permutation test of all axes was significant for each analysis ( $p = 0.001$  with 999 permutations).

were annual mean temperature, annual temperature range and differences between the current and the LGM climate (TdLGM). The regions with unstable climate seemed to be richer in hemicryptophytes. In contrast, the warmest regions seemed to host more chamaephytes, whereas therophytes were more linked (positively) to a high annual temperature range.

## 4 | DISCUSSION

Analysing forests by means of their vascular plant species composition and abundance can be done by using the whole species lists or by deconstructing them into several subsets to analyse potential differences in their responses to a variety of drivers, as already shown by Jiménez-Alfaro et al. (2014) for alpine plant communities. Deconstructing into life-forms and vegetation layers can help characterize the relationships of vegetation to current environmental conditions and history by examining whether species in these groups follow similar or different patterns. In this study, we show that three main drivers are controlling the broad-scale distribution patterns of plant life forms and vegetation layers within the TDFs of Western Eurasia: current climate, topographic conditions and past climate. Considering the number of species per region in the different layers, that is, the regional species pools (Figure 1), the general trends show that the lowest richness is in the oceanic northwest and the highest in southern central Europe, where the climate has a higher annual temperature range (continentality), as shown in the

figure of Appendix S4b. It is known that terrain ruggedness is related to the number of vascular plants in the understory (Ewald, 2008) and the presence of mountain ranges enhances species richness (Perrigo et al., 2019). These results coincide with those obtained by Večeřa et al. (2019) for plot-level alpha diversity of the European forests.

We found that the British Isles are remarkable poor in their forest flora, consistently in most of the life-forms, which is also reflected in the low average number of species per plot. This can be related to the fact that most of this area was colonized recently, after the glaciers' retreat. During the LGM, all the flora disappeared in the northern part of the Isles, and only southwestern England and Ireland were ice-free and covered by treeless tundra-steppe communities with some small and scattered tree refugia (Bowen, 1999; Godwin, 1975; Kelly et al., 2010). The subsequent climatic amelioration in the Holocene resulted in a northward expansion of the woodland, initially of conifers (*Pinus sylvestris*) and then of deciduous trees and shrubs, such as *Betula* spp., *Corylus avellana* or *Ulmus* spp. (Bennett, 1984). It is possible that the current poverty in species of the British Isles was influenced by the opening of the English Channel, restricting the northward migration of species from the continent. This was possibly coupled with the progressive evolution of the climate with more oceanic features. In addition to this glacial and postglacial history, the British Isles have a low habitat heterogeneity because of their relatively flat topography with low mountains. Central Europe is also relatively poor in broad-leaf tree species, probably partly due to the legacy of glacial extinction, partly due to its lower habitat diversity and flat topography.

We also found that southern European regions are much richer in species, as expected from their warmer climate, their abundance of mountains and the presence of Pleistocene refugia for vascular plants, including many tree species (Brewer et al., 2002; Nieto Feliner, 2011; Svenning et al., 2008; Svenning & Skov, 2007), in comparison with central European areas where refugia existed (Birks & Willis, 2010; Willis & van Andel, 2004) but probably at lower magnitude. The Hyrcanian region is an exception, showing relatively modest numbers, which can be explained by its smaller extent and the position of that area at the margin of the TDF distribution range. It is noteworthy that although this region is one of the poorest regions in the total species number, it also has many species per plot of deciduous trees and ferns (but a low number of deciduous shrubs). This high alpha diversity is probably related to the refugial character of this area, supported by the stability of its mild climatic conditions in the late Pleistocene (Akhani et al., 2010). This area served as a refuge in which several species survived that went extinct elsewhere. The current climate of this area is mild, with only one dry month in summer (Djamali et al., 2011; Domroes et al., 1998). The Hyrcanian forest richness was documented in a recent vegetation survey (Gholizadeh et al., 2020). Areas with similar climatic conditions in southern Europe (Italy, Balkans) are covered by the richest forests containing a wide range of sub-Mediterranean species (Meusel & Jäger, 1989).

Considering the most relevant life-forms, if we focus on evergreen broadleaf woody plants (trees and shrubs), they are more represented in the southern regions: Italy, Balkans and Euxinian, reaching their



maximal number in the Iberian Peninsula. Alps and Carpathians, central and northwestern part of Europe and northern Iran have lower numbers or total absence of such trees and shrubs. This element is related to frost-free winters, typical of oceanic climates. This could explain its high representation in the Iberian Peninsula compared with the other southern areas, particularly the Hyrcanian region. Figure 3 shows a clear relation between the broadleaf evergreens and high temperatures, lower summer precipitation and lower continentality (annual temperature range) in the current climate; they are also related to lower difference when compared with LGM (TdLGM). This group is present in oceanic and warm areas with lower summer precipitation regimes, which have changed little since glacial times. This could be related to the refugial role of Mediterranean mountains during the Pleistocene (Alessi et al., 2019; Bennett et al., 1991; Franco Múgica et al., 1998; Ruiz-Labourdette et al., 2013), which allowed the survival of elements from the ancient evergreen laurophyllous forests. They occupied large areas of Europe in the Tertiary (Kovar-Eder et al., 2006) and were later replaced by TDFs (Barrón et al., 2010; Kovar-Eder et al., 2008; Mai, 1989). Their presence could be interpreted as a heritage from the remote past, surviving in a higher proportion in areas with relatively warmer and less severe climate in the Quaternary. Surprising is the scarcity of this group in the Hyrcanian region, which is in striking contrast with the Euxinian region. The latter region contains several endemic woody evergreen species, such as *Rhododendron* spp. and *Hypericum xylosteifolium*, as well as some Mediterranean taxa such as *Arbutus* spp. and *Erica arborea* (Browicz, 1989; Nakhutsrishvili et al., 2015). This could be explained by the fact that the most important environmental factor influencing the species richness of evergreen trees and shrub is the annual mean temperature, as shown by RDA analyses. Despite occurring at lower latitudes, most pristine parts of the Hyrcanian forests are located at elevations above 500 m, thus low temperatures could decrease evergreen species richness in this forest.

Gymnosperms are represented by few species and show higher numbers in the mountain areas such as the Alps and Carpathians. Most of them are species of temperate forests, such as *Abies alba*, *Juniperus communis*, *Pinus nigra* or *Taxus baccata*, not of boreal forests. In contrast, chamaephytes and therophytes show high numbers in the regions that have direct contact with Mediterranean areas, such as the Euxinian region, Iberian Peninsula, Italy and Balkans. The Hyrcanian region is an exception within the group of southern regions, but its isolation in the middle of highly continental summer-dry territories could explain this pattern. While ferns have a peak in the Alps, probably reflecting a wetter climate and a higher ecological diversity associated with their high ruggedness (Kreft et al., 2010), geophytes and hemicryptophytes show no deviation from the pattern of general poverty observed for the British Isles and the Hyrcanian region.

Our results show that among the environmental variables considered in this study, the annual temperature range is the main factor that affects species richness, except for the shrub layer, in which it mainly depends on annual mean temperature (Table 1). The evergreen species are more abundant in areas where the climate is drier in summer and warmer, but the annual temperature range is low and the differences from the LGM temperatures are also moderate

(TdLGM in Appendix S4b). This is consistent with the appreciation that oceanic climates favour laurophyllous evergreens with long growing seasons (Loidi, 2018). The low differences between the current and LGM climate could be due to milder conditions during the glacial maxima, a circumstance favouring the survival of these species during ice ages.

Conversely, the high annual temperature range, as an expression of the greater difference between seasons, combined with higher current temperatures, is coincident with higher numbers of deciduous trees (Appendix S4b). This tree richness in the southeastern regions is consistent also with the fact that they have been reported as their main refuge areas during ice ages (Bennet et al., 1991). The variation explained by the different groups of factors, current climatic, historical and topographic, is different across the three layers of the broadleaf deciduous forests of western Eurasia, similarly as has been reported from North America (McEwan et al., 2005) and east Asia (Wang et al., 2019). In the case of the tree layer, the most substantial influence stems from to the current climate compared to the other two layers, as indicated by the variation partitioning (Figure 3a). The current climate plays a relevant role in the shrub layer, but the variance partitioning also suggests a greater influence of the historical climate and topography (Figure 3b).

The higher difference in temperatures with the LGM (higher TdLGM) is related to the abundance of the gymnosperm shrubs, deciduous shrub and hemicryptophytes. In particular, the TdLGM is the second most predictive variable of the shrub layer (Figure 3 and Appendix S4a). The shrub life form represents an integrated evolutionary response to environmental stress (Rundel, 1991), which is successful in many habitats (Götmark et al., 2016). Shrubs usually have higher growth rates than trees, higher survival in extreme conditions and weather, earlier seed set and dispersal, and also respond very fast to climatic changes.

Our results and the characteristics mentioned above suggest that the deciduous shrubs, due to their higher fitness and ecological plasticity, survived better than trees during the dramatic climatic variations of the Pleistocene. They probably replaced the forest communities offering, at the end of the LGM, a sort of natural 'nursery' for the tree recovery during the recolonization (Filazzola & Lortie, 2014). A complementary explanation for this point is that many of the shrubs can be regarded as initially external elements to the forests (Loidi, 2020). Some of them are actually heliophilous species that are not dependent on the shady forest ecosystems but survive under the shade due to the seed input commonly caused by birds. Many of these under-canopy shrubs constitute sink populations of individuals of low vitality, which are maintained through influx of propagules from populations that receive enough light to vigorously flower and form fruits. Actually, many shrub species live currently outside forests. This could explain the influence of the differences of the current mean temperature with that of the LGM (TdLGM) on shrubs in comparison to the trees. Many shrub populations were likely separated from the surviving forests during the LGM, and only during the Holocene the expansion of the forests resulted in the co-occurrence with shrublands.

The shrub layer shows this historical signal, whereas the current climate signal is predominant in the tree layer. For the floor layer, the current climate has a higher proportion of the variation showing a certain similarity with the trees, although the three groups of factors have low importance with a substantial overlapping of the influence attributed to them (Figure 3d). This can be due to other influences, not related to the climate, that may play a relevant role in masking the current or the past climate, such as nitrogen deposition and nutrient availability (Dirnböck et al., 2014), light regime (Helm et al., 2017), forest management (Horvat et al., 2017) or the regional species pool (Tscharncke et al., 2012).

Similar distributions and relationships with environmental factors of the trees and the forest-floor flora indicate their long-term coexistence. In some cases, they may have even experienced migrations and extinction episodes together, and share a common history since the late-Tertiary. It seems that there is a bond of the understory flora with that of the arboreal component forged during Pleistocene episodes. However, this is not the case for the shrub layer species composition.

## 5 | CONCLUSIONS

Separating forest plant communities into various functional elements, such as structural layers and life forms, provides more information on the historical and ecological profiles of the Western Eurasian temperate deciduous forests. If all the forest species are considered as a whole, the results confirm already known patterns, such as the floristic richness peaking in the southeast and its relationship with the annual temperature range or the refugial character of the southern peninsulas. However, when separating their vascular flora into these elements, it appears that not all of them have had an identical historical development during the Holocene. These differences are consistent with contrasting ecological affinities of these groups. The relationship of the arboreal element with that of the forest floor is detected, but blurred by other environmental factors that influence the herbaceous element. In contrast, the shrub element presents a clearly different signal, which suggests a separate origin from the forest.

## ACKNOWLEDGEMENTS

The authors are indebted to the custodians of the EVA databases for providing the vegetation-plot data, and to all the scientists who sampled these plots. MC, IK, PN and CM were funded by grant no. 19-28491X of the Czech Science Foundation and JL, IB, JAC and CM by grant no. IT936-16 of the Basque Government. The data used for this survey have been extracted with the permission of the EVA (European Vegetation Archive) and the Hyrcanian Forest Vegetation Database.

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary

materials. Plot data are available upon request in the Dryad repository: <https://datadryad.org/stash/share/7rVtXX4YUz7cAyAz4QNHqG7D7QyJz4Q4qzf2tr77ZE>.

## ORCID

Javier Loidi  <https://orcid.org/0000-0003-3163-2409>  
 Milan Chytrý  <https://orcid.org/0000-0002-8122-3075>  
 Borja Jiménez-Alfaro  <https://orcid.org/0000-0001-6601-9597>  
 Nicola Alessi  <https://orcid.org/0000-0002-4479-950X>  
 Idoia Biurrun  <https://orcid.org/0000-0002-1454-0433>  
 Juan Antonio Campos  <https://orcid.org/0000-0001-5992-2753>  
 Andraž Čarni  <https://orcid.org/0000-0002-8909-4298>  
 Eduardo Fernández-Pascual  <https://orcid.org/0000-0002-4743-9577>  
 Xavier Font Castell  <https://orcid.org/0000-0002-7253-8905>  
 Hamid Gholizadeh  <https://orcid.org/0000-0002-3694-368X>  
 Ali Kavğacı  <https://orcid.org/0000-0002-4549-3668>  
 Ilona Knollová  <https://orcid.org/0000-0003-4074-789X>  
 Alireza Naqinezhad  <https://orcid.org/0000-0002-4602-6279>  
 Pavel Novák  <https://orcid.org/0000-0002-3758-5757>  
 Arkadiusz Nowak  <https://orcid.org/0000-0001-8638-0208>  
 Željko Škvorc  <https://orcid.org/0000-0002-2848-1454>  
 Ioannis Tsiripidis  <https://orcid.org/0000-0001-9373-676X>  
 Kiril Vassilev  <https://orcid.org/0000-0003-4376-5575>  
 Corrado Marcenò  <https://orcid.org/0000-0003-4361-5200>

## REFERENCES

- Akhani, H., Djmal, M., Ghorbanalizadeh, A., & Ramezani, E. (2010). Plant biodiversity of Hyrcanian relict forests, N Iran: An overview of the flora, vegetation, palaeoecology and conservation. *Pakistan Journal of Botany (S.I. Ali Festschrift)*, 42, 231–248.
- Alessi, N., Těšitel, J., Zerbe, S., Spada, F., Agrillo, E., & Wellstein, C. (2019). Ancient refugia and present-day habitat suitability of native laurophylls in Italy. *Journal of Vegetation Science*, 30, 564–574. <https://doi.org/10.1111/jvs.12743>
- Barrón, E., Rivas-Carballo, R., Postigo-Mijarra, J. M., Alcalde-Olivares, C., Vieira, M., Castro, L., Pais, J., & Valle-Hernández, M. (2010). The Cenozoic vegetation of the Iberian Peninsula. A synthesis. *Review of Palaeobotany and Palynology*, 162, 382–402. <https://doi.org/10.1016/j.revpalbo.2009.11.007>
- Barton, K. (2020). *MuMIn: Multi-model inference. R package version 1.43.17*. Retrieved from <https://CRAN.R-project.org/package=MUMIn>
- Bates, D., Mälcher, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effect models using lme4. *Journal of Statistical Software*, 67, 1–48. Retrieved from <https://www.jstatsoft.org/article/view/v067i01>
- Bennett, K. D. (1984). The post-glacial history of *Pinus sylvestris* in the British Isles. *Quaternary Science Reviews*, 3, 133–155. [https://doi.org/10.1016/0277-3791\(84\)90016-7](https://doi.org/10.1016/0277-3791(84)90016-7)
- Bennett, K. D., Tzedakis, P. C., & Willis, K. J. (1991). Quaternary refugia of North European trees. *Journal of Biogeography*, 18, 103–115. <https://doi.org/10.2307/2845248>
- Birks, H. J. B., & Willis, K. J. (2010). Alpines, trees and refugia in Europe. *Plant Ecology and Diversity*, 1, 147–160. <https://doi.org/10.1080/17550870802349146>
- Bohn, U., Gollub, G., Hettwer, C., Neuhäuslová, Z., Schlüter, H., & Weber, H. (Eds.) (2000–2003). *Map of the natural vegetation of Europe. Scale 1: 2.5 million*. Bundesamt für Naturschutz.



- Bowen, D. Q. (Ed.) (1999). *A revised correlation of Quaternary deposits in the British Isles*. Special report 23. Geological Society Publishing House.
- Braun-Blanquet, J. (1964). *Pflanzensoziologie. Grundzüge der Vegetationskunde* (3rd ed.). Springer.
- Brewer, S., Cheddadi, R., de Beaulieu, J. L., & Reille, M. (2002). The spread of deciduous *Quercus* throughout Europe since the last glacial period. *Forest Ecology and Management*, 156, 27–48. [https://doi.org/10.1016/S0378-1127\(01\)00646-6](https://doi.org/10.1016/S0378-1127(01)00646-6)
- Browicz, K. (1989). Chorology of the Euxinian and Hyrcanian element in the woody flora of Asia. *Plant Systematics and Evolution*, 162, 305–314. <https://doi.org/10.1007/BF00936923>
- Brown, J. L., Hill, D. J., & Haywood, A. M. (2020). A critical evaluation of the Oscillayers methods and datasets. *Global Ecology and Biogeography*, 29, 1435–1442. <https://doi.org/10.1111/geb.13103>
- Chytrý, M., Hennekens, S. M., Jiménez-Alfaro, B., Knollová, I., Dengler, J., Jansen, F., Landucci, F., Schaminée, J. H. J., Ačić, S., Agrillo, E., Ambarli, D., Angelini, P., Apostolova, I., Attorre, F., Berg, C., Bergmeier, E., Biurrun, I., Botta-Dukát, Z., Brisse, H., ... Yamalov, S. (2016). European Vegetation Archive (EVA): an integrated database of European vegetation plots. *Applied Vegetation Science*, 19, 173–180. <https://doi.org/10.1111/avsc.12191>
- Dirnböck, T., Grandin, U., Bernhard-Römermann, M., Beudert, B., Canullo, R., Forsius, M., Grabner, M.-T., Holmberg, M., Kleemola, S., Lundin, L., Mirtl, M., Neumann, M., Pompei, E., Salemaa, M., Starlinger, F., Staszewski, T., & Uziębło, A. K. (2014). Forest floor vegetation response to nitrogen deposition in Europe. *Global Change Biology*, 20, 429–440. <https://doi.org/10.1111/gcb.12440>
- Djamali, M., Akhiani, H., Khoshnavesh, R., Andrieu-Ponel, V., Ponel, P., & Brewer, S. (2011). Application of the global bioclimatic classification to Iran: implications for understanding the modern vegetation and biogeography. *Ecologia Mediterranea*, 37(1), 91–114. <https://doi.org/10.3406/ecmed.2011.1350>
- Domroes, M., Kaviani, M., & Schaefer, D. (1998). An analysis of regional and intra-annual precipitation variability over Iran using multivariate statistical methods. *Theoretical and Applied Climatology*, 61, 151–159. <https://doi.org/10.1007/s007040050060>
- DRYFLOR, Banda-R, K., Delgado-Salinas, A., Dexter, K. G., Linares-Palomino, R., Oliveira-Filho, A., Prado, D., Pullan, M., Quintana, C., Riina, R., Rodríguez, M. G. M., Weintritt, J., Acevedo-Rodríguez, P., Adarve, J., Álvarez, E., Aranguren B., A., Arteaga, J. C., Aymard, G., Castaño, A., Ceballos-Mago, N., ... Pennington, R. T. (2016). Plant diversity patterns in neotropical dry forests and their conservation implications. *Science*, 353, 1383–1387. <https://doi.org/10.1126/science.aaf5080>
- Ewald, J. (2008). Plant species richness in mountain forests of the Bavarian Alps. *Plant Biosystems*, 142, 594–603. <https://doi.org/10.1080/11263500802410942>
- Filazzola, A., & Lortie, C. J. (2014). A systematic review and conceptual framework for the mechanistic pathways of nurse plants. *Global Ecology and Biogeography*, 23, 1335–1345. <https://doi.org/10.1111/geb.12202>
- Franco Múgica, F., García Antón, M., & Sainz Ollero, H. (1998). Vegetation dynamics and human impact in the Sierra de Guadarrama, Central System, Spain. *The Holocene*, 8, 69–82. <https://doi.org/10.1191/095968398675691171>
- Gholizadeh, H., Naqinezhad, A., & Chytrý, M. (2019). Hyrcanian forest vegetation database. *Phytocoenologia*, 49, 209–210. <https://doi.org/10.1127/phyto/2018/0315>
- Gholizadeh, H., Naqinezhad, A., & Chytrý, M. (2020). Classification of the Hyrcanian forest vegetation, Northern Iran. *Applied Vegetation Science*, 23, 107–126. <https://doi.org/10.1111/avsc.12469>
- Godwin, H. (1975). *History of the British flora. A factual basis for phytogeography*. Cambridge University Press.
- Götmark, F., Götmark, E., & Jensen, A. M. (2016). Why be a shrub? A basic model and hypotheses for the adaptive values of a common growth form. *Frontiers in Plant Science*, 7, 1095. <https://doi.org/10.3389/fpls.2016.01095>
- Grossiord, C. (2020). Having the right neighbors: how tree species diversity modulates drought impacts on forests. *New Phytologist*, 228, 42–49. <https://doi.org/10.1111/nph.15667>
- Habel, J. C., Drees, C., Schmitt, T., & Assmann, T. (2010). Refugial areas and postglacial colonizations in the Western Palearctic. In J. C. Habel, & T. Assmann (Eds.), *Relict species: Phylogeography and conservation biology* (pp. 189–197). Springer. [https://doi.org/10.1007/978-3-540-92160-8\\_10](https://doi.org/10.1007/978-3-540-92160-8_10)
- Helm, N., Essl, F., Mirtl, M., & Dirnböck, T. (2017). Multiple environmental changes drive forest floor vegetation in a temperate mountain forest. *Ecology and Evolution*, 7, 2155–2168. <https://doi.org/10.1002/ece3.2801>
- Horvat, V., Biurrun, I., & García-Mijangos, I. (2017). Herb layer in silver fir-beech forests in the western Pyrenees: Does management affect species diversity? *Forest Ecology and Management*, 385, 87–96. <https://doi.org/10.1016/j.foreco.2016.11.037>
- Jahn, G. (1991). Temperate deciduous forests of Europe. In E. Röhrig, & B. Ulrich (Eds.), *Temperate deciduous forests. Ecosystems of the world*, (vol. 7, pp. 377–502). Elsevier.
- Jiménez-Alfaro, B., Girardello, M., Chytrý, M., Svenning, J.-C., Willner, W., Gégout, J.-C., Agrillo, E., Campos, J. A., Jandt, U., Kačák, Z., Šilc, U., Slezák, M., Tichý, L., Tsiripidis, I., Turtureanu, P. D., Ujházyová, M., & Wohlgemuth, T. (2018). History and environment shape species pools and community diversity in European beech forests. *Nature Ecology & Evolution*, 2, 483–490. <https://doi.org/10.1038/s41559-017-0462-6>
- Jiménez-Alfaro, B., Marcenò, C., Bueno, Á., Gavilán, R., & Obeso, J. R. (2014). Biogeographic deconstruction of alpine plant communities along altitudinal and topographic gradients. *Journal of Vegetation Science*, 25, 160–171. <https://doi.org/10.1111/jvs.12060>
- Karger, D. N., Conrad, O., Böhrner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, <https://doi.org/10.1038/sdata.2017.122>
- Kelly, A., Charman, D. J., & Newnham, R. M. (2010). A Last Glacial Maximum pollen record from Bodmin Moor showing a possible cryptic northern refugium in southwest England. *Journal of Quaternary Science*, 25, 296–308. <https://doi.org/10.1002/jqs.1309>
- Knollová, I., Chytrý, M., Tichý, L., & Hájek, O. (2005). Stratified resampling of phytosociological databases: some strategies for obtaining more representative data sets for classification studies. *Journal of Vegetation Science*, 16, 479–486. <https://doi.org/10.1111/j.1654-1103.2005.tb02388.x>
- Kovar-Eder, J., Jechorek, H., Kvaček, Z., & Parashiv, V. (2008). The integrated plant record: An essential tool for reconstructing Neogene zonal vegetation in Europe. *Palaios*, 23, 97–111. <https://doi.org/10.2110/palo.2006.p06-039r>
- Kovar-Eder, J., Kvaček, Z., Martinetto, E., & Roiron, P. (2006). Late Miocene to Early Pliocene vegetation of southern Europe (7–4Ma) as reflected in the megafossil plant record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 238, 321–339. <https://doi.org/10.1016/j.palaeo.2006.03.031>
- Kreft, H., Jetzt, W., Mutke, J., & Barthlott, W. (2010). Contrasting environmental and regional effects on global pteridophyte and seed plant diversity. *Ecography*, 33, 408–419. <https://doi.org/10.1111/j.1600-0587.2010.06434.x>
- Legendre, P. (2007). Studying beta diversity: Ecological variation partitioning by multiple regression and canonical analysis. *Journal of Plant Ecology*, 1, 3–8. <https://doi.org/10.1093/jpe/rtm001>
- Lengyel, A., Chytrý, M., & Tichý, L. (2011). Heterogeneity-constrained random resampling of phytosociological databases. *Journal of Vegetation Science*, 22, 175–183. <https://doi.org/10.1111/j.1654-1103.2010.01225.x>



- Loidi, J. (2018). Plant eco-morphological traits as adaptations to environmental conditions: some comparisons between different biomes across the world. In: A. M. Grellier, K. Fujiwara, & F. Pedrotti (Eds.), *Geographical changes in vegetation and plant functional types*, (pp. 59–71). Springer. [https://doi.org/10.1007/978-3-319-68738-4\\_3](https://doi.org/10.1007/978-3-319-68738-4_3)
- Loidi, J. (2020). The concept of vegetation class and order in phytosociological syntaxonomy. *Vegetation Classification and Survey*, 1, 163–167. <https://doi.org/10.3897/VCS/2020/59977>
- Mai, D. H. (1989). Development and regional differentiation of the European vegetation during the Tertiary. *Plant Systematics and Evolution*, 162, 79–91. [https://doi.org/10.1007/978-3-7091-3972-1\\_4](https://doi.org/10.1007/978-3-7091-3972-1_4)
- McCullagh, P., & Nelder, J. (1989). *Generalized linear models*, (2nd ed.). Chapman & Hall/CRC.
- McEwan, R. W., Muller, R. N., & McCarthy, M. C. (2005). Vegetation-environment relationships among woody species in four canopy-layers in an old-growth mixed mesophytic forest. *Castanea*, 70, 32–46.
- Mestre, L., Toro-Manríquez, M., Soler, R., Huertas-Herrera, A., Martínez-Pastur, G., & Lencinas, M. V. (2017). The influence of canopy-layer composition in understory plant diversity in southern temperate forests. *Forest Ecosystems*, 4, e6. <https://doi.org/10.1186/s40663-017-0093-z>
- Meusel, H., & Jäger, E. J. (1989). Ecogeographical differentiation of the Submediterranean deciduous forest flora. In F. Ehrendorfer (Ed.), *Woody plants – evolution and differentiation since the Tertiary* (pp. 315–329). Springer Verlag. [https://doi.org/10.1007/978-3-7091-3972-1\\_17](https://doi.org/10.1007/978-3-7091-3972-1_17)
- Moncrieff, G. R., Bond, W. J., & Higgins, S. I. (2016). Revising the biome concept for understanding and predicting global change impacts. *Journal of Biogeography*, 43, 863–873. <https://doi.org/10.1111/jbi.12701>
- Mucina, L. (2018). Biome: evolution of a crucial ecological and biogeographical concept. *New Phytologist*, 222, 97–114. <https://doi.org/10.1111/nph.15609>
- Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A., Šumberová, K., Willner, W., Dengler, J., Gavilán García, R., Chytrý, M., Hájek, M., Di Pietro, R., Iakushenko, D., Pallas, J., Daniëls, F. J. A., Bergmeier, E., Santos Guerra, A., Ermakov, N., ... Tichý, L. (2016). Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science*, 19(Suppl 1), 1–264. <https://doi.org/10.1111/avsc.12257>
- Nakhutsrishvili, G., Zazanashvili, N., Batsatsashvili, K., & Montalvo, C. S. (2015). Colchic and Hyrcanian forests of the Caucasus: similarities, differences and conservation status. *Flora Mediterranea*, 25(Special Issue), 185–192. <https://doi.org/10.7320/FIMedit25SI.001>
- Nieto Feliner, G. (2011). Southern European glacial refugia: a tale of tales. *Taxon*, 60, 365–372. <https://doi.org/10.1002/tax.602007>
- Padullés Cubino, J., Lososová, Z., Bonari, G., Agrillo, E., Attorre, F., Bergmeier, E., Biurrun, I., Campos, J. A., Čarni, A., Čuk, M., De Sanctis, M., Indreica, A., Jiménez-Alfaro, B., Khanina, L., Knollová, I., Lenoir, J., Pielech, R., Rašomavičius, V., Škvorc, Ž., ... Chytrý, M. (2021). Phylogenetic structure of European forest vegetation. *Journal of Biogeography*, 48, <https://doi.org/10.1111/jbi.14046>
- Pardé, J. (1974). Le microclimat de la forêt. In P. Pesson (Ed.), *Écologie forestière. La forêt: son climat, son sol, ses arbres, sa faune* (pp. 29–46). Gauthier-Villars.
- Peres-Neto, P. R., Legendre, P., Dray, S., & Borcard, D. (2006). Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology*, 87, 2614–2625.
- Perrigo, A., Hoorn, C., & Antonelli, A. (2019). Why mountains matter for biodiversity. *Journal of Biogeography*, 47, 315–325. <https://doi.org/10.1111/jbi.13731>
- Perry, C. H., Woodall, C. W., Amacher, M. C., & O'Neill, K. P. (2009). An inventory of carbon storage in forest soil and down woody material of the United States. *Geophysical Monograph Series*, 183, 101–116. <https://doi.org/10.1029/2006GM000341>
- Pfadenhauer, J. S., & Klötzli, F. A. (2014). *Die Vegetation der Erde. Grundlagen, Ökologie, Verbreitung*. Springer. <https://doi.org/10.1007/978-3-642-41950-8>
- Raunkjær, C. (1934). *The life forms of plants and statistical plant geography*. Oxford University Press.
- Rivas-Martínez, S. (2007). Mapa de series, geoseries y geopermaseries de vegetación de España. Memoria del mapa de vegetación potencial de España. *Itinera Geobotanica*, 17, 5–436.
- Röhrig, E. (1991). Deciduous forests of the Near East. In E. Röhrig, & B. Ulrich (Eds.), *Temperate deciduous forests. Ecosystems of the world*, (Vol. 7, pp. 527–537). Elsevier.
- Royo, A. A., & Carson, W. P. (2009). *The formation of dense understory in forests worldwide: Consequences and implications for forest dynamics, biodiversity and succession. Advances in Threat Assessment and Their Application to Forest and Rangeland Management*. General Technical Report PNW-GTR-802: 469–496. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest and Southern Research Stations.
- Ruiz-Labourdette, D., Schmitz, M. F., & Pineda, F. D. (2013). Changes in tree species composition in Mediterranean mountains under climate change: Indicators for conservation planning. *Ecological Indicators*, 24, 310–323. <https://doi.org/10.1016/j.ecolind.2012.06.021>
- Rundel, P. W. (1991). Shrub life forms. In H. A. Mooney, W. E. Winner, & E. J. Pell (Eds.), *Response of plants to multiple stress*, (pp. 345–371). Academic Press.
- Sappington, J. M., Longshore, K. M., & Thompson, D. B. (2007). Quantifying landscape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave Desert. *Journal of Wildlife Management*, 71, 1419–1426. <https://doi.org/10.2193/2005-723>
- Schmidt, M., Kriebitzsch, W.-U., & Ewald, J. (2011). Waldartenlisten der Farn- und Blütenpflanzen, Moose und Flechten Deutschlands. *BfN-Skripten*, 299, 1–111.
- Svenning, J.-C., Normand, S., & Kageyama, M. (2008). Glacial refugia of temperate trees in Europe: insights from species distribution modelling. *Journal of Ecology*, 96, 1117–1127. <https://doi.org/10.1111/j.1365-2745.2008.01422.x>
- Svenning, J.-C., & Skov, F. (2007). Ice age legacies in the geographical distribution of tree species richness in Europe. *Global Ecology and Biogeography*, 16, 234–245. <https://doi.org/10.1111/j.1466-8238.2006.00280.x>
- ter Braak, C. J. F., & Šmilauer, P. (2012). *Canoco 5, Windows release (5.00). Software for multivariate data exploration, testing, and summarization*. Biometris.
- Tichý, L. (2002). JUICE, software for vegetation classification. *Journal of Vegetation Science*, 13, 451–453. <https://doi.org/10.1111/j.1654-1103.2002.tb02069.x>
- Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., ... Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes – eight hypotheses. *Biological Reviews*, 87, 661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>
- Tutin, T. G., Heywood, V. H., Burges, N. A., Valentine, D. H., Walters, S. M., & Webb, D. S. (Eds.) (1964–1980). *Flora Europaea*, (Vol. 1–5). Cambridge University Press.
- Valladares, F., Laanisto, L., Niinemets, U., & Zavala, M. A. (2016). Shedding light on shade: ecological perspectives of understory plant life. *Plant Ecology & Diversity*, 9, 237–251. <https://doi.org/10.1080/17550874.2016.1210262>
- Večeřa, M., Divišek, J., Lenoir, J., Jiménez-Alfaro, B., Biurrun, I., Knollová, I., Agrillo, E., Campos, J. A., Čarni, A., Crespo Jiménez, G., Čuk, M., Dimopoulos, P., Ewald, J., Fernández-González, F., Gégout, J.-C., Indreica, A., Jandt, U., Jansen, F., Kačák, Z., ... Chytrý, M. (2019).





- Alpha diversity of vascular plants in European forests. *Journal of Biogeography*, 46, 1919–1935. <https://doi.org/10.1111/jbi.13624>
- Wang, H., Zhang, M., & Nan, H. (2019). Abiotic and biotic drivers of species diversity in understory layers of cold temperate coniferous forest in North China. *Journal of Forest Research*, 30, 2213–2225. <https://doi.org/10.1007/s11676-018-0795-2>
- Willis, K. J., & van Andel, T. H. (2004). Trees or not trees? The environment of central and western Europe during the last Glaciation. *Quaternary Science Reviews*, 23, 2369–2387. <https://doi.org/10.1016/j.quascirev.2004.06.002>
- Willis, K. J., & Whittaker, R. J. (2000). The refugial debate. *Science*, 287, 1406–1407. <https://doi.org/10.1126/science.287.5457.1406>

#### BIOSKETCH

**Javier Loidi, Milan Chytrý, Borja Jiménez-Alfaro and Corrado Marcenò** are working on vegetation surveys and macroecology of plant communities basically in mountain ecosystems, coastal sand dunes, dry grasslands, heathlands and temperate broad-leaved forests of the world.

**Author contributions:** JL and CM conceived the idea and wrote the manuscript, with substantial input from MC and BJ-A. BJ-A and CM conducted the analysis.

#### SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**How to cite this article:** Loidi, J., Chytrý, M., Jiménez-Alfaro, B., Alessi, N., Biurrun, I., Campos, J.A., Čarni, A., Fernández-Pascual, E., Font Castell, X., Gholizadeh, H., Indreica, A., Kavgacı, A., Knollová, I., Naqinezhad, A., Novák, P., Nowak, A., Škvorc, Ž., Tsiripidis, I., Vassilev, K., & Marcenò, C. (2021). Life-form diversity across temperate deciduous forests of Western Eurasia: A different story in the understory. *Journal of Biogeography*, 48, 2932–2945. <https://doi.org/10.1111/jbi.14254>