



Fagus sylvatica and *Quercus pyrenaica*: Two neighbors with few things in common



Sergio de Tomás Marín^{a,*}, Jesús Rodríguez-Calcerrada^b, Salvador Arenas-Castro^c, Iván Prieto^d, Guillermo González^b, Luis Gil^b, Enrique G. de la Riva^{a,d}

^a Department of Ecology, Brandenburgische Technische Universität Cottbus-Senftenberg, Konrad-Wachsmann-Allee 6, 03046, Cottbus, Germany

^b Forest Genetics and Ecophysiology Research Group, School of Forestry Engineering, Universidad Politécnica de Madrid, Madrid, Spain

^c Area of Ecology, Botany Department, Ecology and Plant Physiology, Faculty of Sciences, Universidad de Córdoba, Córdoba, Spain

^d Ecology Department, Faculty of Biology and Environmental Sciences, Universidad de León, León, Spain

ARTICLE INFO

Keywords:

Environmental niche
European beech
Forest dynamics
Functional niche
Hypervolume
Pyrenean oak
Species coexistence
Sub-Mediterranean community

ABSTRACT

Background: The Iberian Peninsula comprises one of the largest boundaries between Mediterranean and Euro-siberian vegetation, known as sub-Mediterranean zone. This ecotone hosts many unique plant species and communities and constitutes the low-latitude (warm) margin of numerous central European species which co-occur with Mediterranean vegetation. Two of the main species found in this region are the Eurosiberian European beech (*Fagus sylvatica* L.) and the Mediterranean Pyrenean oak (*Quercus pyrenaica* Willd.). It remains unclear how the different physiological and adaptive strategies of these two species reflect their niche partitioning within a sub-Mediterranean community and to what extent phenotypic variation (intraspecific variability) is driving niche partitioning across Eurosiberian and Mediterranean species.

Methods: We quantified functional niche partitioning, based on the n -dimensional hypervolume to nine traits related to resource acquisition strategies (leaf, stem and root) plus relative growth rate as an additional whole-plant trait, and the environmental niche similarity between Pyrenean oak and European beech. Further, we analyzed the degree of phenotypic variation of both target species and its relationship with relative growth rates (RGR) and environmental conditions. Plant recruitment was measured for both target species as a proxy for the average fitness.

Results: Species' functional space was highly segregated (13.09% overlap), mainly due to differences in niche breadth (59.7%) rather than niche replacement (25.6%), and beech showed higher trait variability, i.e., had larger functional space. However, both species shared the environmental space, i.e., environmental niches were overlapped. Most plant traits were not related to abiotic variables or RGR, neither did RGR to plant traits.

Conclusions: Both target species share similar environmental space, however, show notably different functional resource-use strategies, promoting a high complementarity that contributes to maintaining a high functionality in sub-Mediterranean ecosystems. Therefore, we propose that conservation efforts be oriented to preserve both species in these habitats to maximize ecosystem functionality and resilience.

1. Introduction

The southern two thirds of the Iberian Peninsula account for around 20% of the total surface of the Mediterranean region (Quézel, 1985), with the northernmost part of the Peninsula belonging to the Euro-siberian region. Thus, the Iberian Peninsula represents one of the largest boundaries between Mediterranean and Eurosiberian vegetation, known as the sub-Mediterranean zone (Sánchez de Dios et al., 2009). This transitional region constitutes the lower latitude margins of the

distribution ranges of numerous central European species that co-occur with Mediterranean vegetation (Quézel, 1985). Given their particular environmental conditions at the boundary between Mediterranean and Eurosiberian climates, sub-Mediterranean regions are of special conservation interest because of their high biodiversity. These ecotone regions host species from both Mediterranean and Eurosiberian climates and many endemic species forming unique plant communities (Sánchez de Dios et al., 2009; Vila-Viçosa et al., 2020a, 2020b; see Loidi (2017) for a detailed description of the sub-Mediterranean vegetation in the Iberian

* Corresponding author. Department of Ecology, Brandenburg University of Technology, Konrad-Wachsmann-Allee 6, 03046, Cottbus, Germany.

E-mail address: dtm.sergio@gmail.com (S. de Tomás Marín).

<https://doi.org/10.1016/j.fecs.2023.100097>

Received 21 October 2022; Received in revised form 7 February 2023; Accepted 9 February 2023

2197-5620/© 2023 The Authors. Publishing services by Elsevier B.V. on behalf of KeAi Communications Co. Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Peninsula).

Two of the main tree species inhabiting these mixed communities in the Iberian sub-Mediterranean regions are the Pyrenean oak (*Quercus pyrenaica* Willd.) and the European beech (*Fagus sylvatica* L.; Sánchez de Dios et al., 2009). Pyrenean oak and European beech (referred to as beech hereafter) are dominant key species in forest formations in Mediterranean and Eurosiberian regions, respectively (von Wühlisch, 2008; Packham et al., 2012; Quintano et al., 2016). Pyrenean oak is especially important in the Iberian Peninsula, which hosts 95% of Pyrenean oak's global distribution (Lorite et al., 2008; Quintano et al., 2016). This species has traditionally been of interest for silvo-pastoral uses: firewood, charcoal production and grazing for livestock in times of pasture scarcity (Jiménez et al., 1998). It also plays an important ecological role in the Iberian Peninsula for the species-rich ecosystems it creates (García and Jiménez, 2009; Quintano et al., 2016). In fact, Pyrenean oak forest formations are included in the European Habitats Directive—habitat 9230 subtype 41.61—as Sites of Community Importance (García and Jiménez, 2009; Interpretation Manual of European Habitats - EUR28). However, due to a long history of human activities, Pyrenean oak forests are nowadays seriously deteriorated (Calvo et al., 2003; Castro et al., 2006; Quintano et al., 2016; Salomón et al., 2017).

Beech is one of the most ecologically and culturally important trees in Europe (von Wühlisch, 2008; Packham et al., 2012); it is found throughout the continent, with its optimal distribution range around Central Europe (Bohn and Welß, 2003; Kramer et al., 2010). Beech is especially sensitive to drought stress (Aranda et al., 2013) and is being replaced by more drought-resistant species in lower altitudes in response to increasing drought events due to climate change (Peñuelas and Boada, 2003; Albert et al., 2017; Illés and Móríc, 2022). Further, at a continental scale, species distribution models predict a northward shift in beech distribution ranges (Kramer et al., 2010). Rear-edge (warmer) marginal populations are potentially more vulnerable to increasing drought conditions than populations at the core of its distribution range (Fréjaville et al., 2020; Camarero et al., 2021). However, contrary to these predictions, beech populations in the Iberian “Sistema Central” mountainous range are spreading, likely in response to the abandonment of traditional land uses that occurred after the middle twentieth century (Sánchez de Dios et al., 2021). It is important to develop appropriate management and conservation measures for this species that ensure its persistence and correct functioning in sub-Mediterranean habitats.

Although there is abundant information available in the literature on the distribution and ecology of both beech and Pyrenean oak (Aranda, 1998; Aranda et al., 1996, 2013, 2020; Kramer et al., 2010; Camisón et al., 2015; Quintano et al., 2016; Pérez-Luque et al., 2020), it still remains unclear how the different functional responses of these two species determine the composition and structure of mixed forests in sub-Mediterranean communities under a climate change scenario. In this context, a functional trait approach is a broadly-known, key tool to understand the mechanisms underlying species responses to changing environmental conditions and to assess niche differences among coexisting species (de la Riva et al., 2018b; Carvalho et al., 2020). Furthermore, a functional profiling approach allows to elucidate how individuals use the resources from their environment (Garnier and Navas, 2012), being the differences among species associated with specific functional strategies (Carvalho et al., 2020).

According to modern coexistence theory, differences in functional niche and fitness among species drive the outcome of competition under any combination of environmental conditions (Kraft et al., 2015). The differences in average species fitness in a community determine the competitive dominance of certain species in terms of per-capita growth rates (Chesson, 2000). On the other hand, the range of distribution of trait values within species, i.e. the intraspecific trait variation, may be considered a proxy of their realized niche (Helsen et al., 2020). In this regard, functional segregation among species in a community depends both on their mean trait values (i.e., functional distinctiveness) and the intraspecific variation of these trait values (i.e., functional diversity)

(Galán Díaz et al., 2021). In this framework, quantifying the functional niche space overlap based on plant traits defining multiple resource-use strategies improves the understanding of plant species coexistence within communities with varying resource availability (Carvalho and Cardoso, 2020). Functional trait convergence among coexisting species (low functional distinctiveness) may arise as a result of habitat filtering (McGill et al., 2006). By contrast, high functional distinctiveness allows coexisting species to minimize fitness differences and avoid interspecific competition through higher complementarity in the use of resources (Mao et al., 2018), a process known as limiting similarity (MacArthur and Levins, 1967). In this regard, high intraspecific variation enhances the competitive ability of plant species and stabilizes their niche differences with competitors (Bittebiere et al., 2019), leading to functional trait divergence within a given habitat, and ultimately determining community assembly processes (Jung et al., 2010). Thus, incorporating intraspecific trait variability will improve our understanding of how coexisting species exploit the available resources and the implications of coexisting strategies for ecosystem processes and functions.

Integrating functional strategies at the whole plant level is important since resource use strategies can be measured and defined at multiple organ levels (e.g. leaves, roots and stems; Wright et al., 2004; Chave et al., 2009; Prieto et al., 2015; Roumet et al., 2016; see de la Riva et al., 2016; Zhao et al., 2016 for the Plant Economics Spectrum). An integrated approach to the study of functional strategies at the whole plant level has been often overlooked within the conceptual framework of niche breadth. Previous studies have typically focused on a single attribute of the study species such as distribution or tree growth (i.e., Ruiz-Laburdette et al., 2012; Dorado-Liñán et al., 2017, 2019). Moreover, some recent studies have mainly focused on traits related only to water use (e.g., González-González et al., 2014; Vodnik et al., 2019; Gea-Izquierdo et al., 2021), overlooking the use of other resources. Most of these studies have explored the segregation of tree species based mainly on their sensitivity to climate and particularly to drought stress. However, additional factors that are often ignored, such as soil physicochemical properties or topographic attributes, also seem to determine species performance and composition of sub-Mediterranean ecosystems (Nanos et al., 2005).

Transition zones, such as the sub-Mediterranean ecotone, where species from two different biomes can coexist, are ideal to assess species coexistence across environmental gradients (Mao et al., 2018), but have received relatively limited attention to date. Our main goal was to determine whether coexistence of Pyrenean oak and beech trees in a mixed forest stand in central Spain, where beech reaches one of the southernmost populations in Europe (Hernández Bernejo et al., 1982; Aranda et al., 2000; Rubio-Cuadrado et al., 2018a), is driven by differences in niche partitioning. To address this aim, we first analyzed the functional distinctiveness and functional diversity of both species at the whole plant level using 9 leaf, stem and root traits, plus the relative growth rate measured in 51 individual trees, and identified which were the environmental drivers best associated with phenotypic variation along the forest. In addition, we also estimated the functional niche of both species using the multidimensional hypervolume concept proposed by Hutchinson (see Blonder et al., 2014; Blonder, 2018; and Carmona et al., 2016, 2019). In this approach, hypervolume overlap corresponds to the functional space shared by both species and hypervolume differentiation corresponds to the unique functional space of each species (Carvalho and Cardoso, 2020). Furthermore, we assessed plant recruitment as a proxy of average fitness. Moreover, given that environmental heterogeneity at local scale may also affect the coexistence of different species (Speziale and Ezcurra, 2011), we also compared the environmental niches of both species, that is, the environmental conditions that each species needs to meet its physiological and ecological requirements (Pearman et al., 2008; VanDerWal et al., 2009). The comparative study of the functional and environmental niches of beech and Pyrenean oak will improve our understanding of the ecology and assembly processes of sub-Mediterranean communities. Such information may provide

guidance for the conservation and restoration of these ecosystems in a climate change context (Cavender-Bares et al., 2016; Nock et al., 2016).

2. Materials and methods

2.1. Study area

This study was carried out in the “Hayedo de Montejo” forest (Montejo forest hereafter). This forest was traditionally managed as an open woodland, and it evolved into the current secondary forest since the abandonment of massive livestock grazing in the 1960s (Pardo and Gil, 2005). However, today it still is relatively easy to find a few cows grazing sporadically in the forest. Montejo forest is part of the “Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe”, a list of European beech forests included in the UNESCO World Heritage Sites List. Furthermore, Montejo is part of the “Sierra del Rincón”, which was designated as a Reserve of the Biosphere by UNESCO in 2005. Montejo is a sub-Mediterranean forest with a high diversity of plant species and communities coexisting in a relatively small area (Hernández Bermejo et al., 1982; Gil et al., 2010; Moreno et al., 2005). The forest species list includes some endangered herbaceous species such as *Paris quadrifolia* L., *Melica uniflora* Retz. and *Aconitum napellus* L., as well as tree species at the rear edge of their distribution in Europe such as *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. (Rodríguez-Calcerrada et al., 2011). Eurosiberian species coexist with typically Mediterranean plant species such as the already mentioned Pyrenean oak (*Q. pyrenaica*) and other small tree species such as hawthorne (*Crataegus monogyna* Jacq.), among others (Sánchez de Dios et al., 2009; Gil et al., 2010; Rivas-Martínez et al., 2011).

The Montejo forest has ca. 125 ha and is located in the Spanish “Sistema Central” range (41°7' N, 3°30' W), between 1250 and 1550 m a.s.l. Orientation is predominantly northeast, although it ranges from south to north in some locations. The area has a transitional climate between the Mediterranean climate in the east of the mountain range and more continental climate in the western side. The slope of the terrain varies between nearly flat at higher elevations to slopes of ca. 58% in the steepest areas. Soil depth ranges from 30 cm in upper areas to 1.5 m down in the valley. Mean annual precipitation in the study forest is 858.8 mm and mean annual temperature 9.7 °C for the 1994–2021 period. Summers are dry and hot, with a marked drought period (average rainfall and temperature in July are 23.9 mm and 19.1 °C, respectively) typical of the Mediterranean climate. Precipitation and temperature data were obtained from a weather station located in the Montejo forest that has been recording climatic data since 1994.

The geology of the area is dominated by schists (Moreno et al., 2005). Soils have a sandy loam texture with three well-marked horizons. They are fertile and moderately acidic with good permeability and moderate water-holding capacity (Gil et al., 2010).

2.2. Sampling design

From 1994 to 2015 three forest inventories (FIs) were made in Montejo by personnel from the Polytechnic University of Madrid, in 1994, 2005 and 2015. In these FIs, 125 circular plots with a 30-m diameter were established in a 100 m × 100 m grid. In each of the plots, all trees were counted to estimate total tree density (number of trees per ha) and identified at the species level. Moreover, basal area ($\text{m}^2 \cdot \text{ha}^{-1}$) and dominant height of 10 taller trees/plot (m) were estimated. Tree diameter at breast height (DBH) was measured in trees with DBH > 5 cm. In the FIs of the years 2005 and 2015, the center of the 125 plots as well as the adult trees (DBH > 5 cm) within each plot were georeferenced with a total station. See Appendix S6 Table S6.3 for mean values and variance of stem density, basal area, dominant tree height and DBH by each of the forest types detailed below.

For our study, we selected a subset of 60 plots and sampled 51 healthy adult trees from the FI with at least 10 cm of DBH scattered throughout

the forest in accordance with their distribution, both in areas where beech is more abundant than Pyrenean oak and in areas where Pyrenean oak is more abundant than beech, as well as in areas where both species have similar abundances and in areas where sessile oak (*Q. petraea*), the third most abundant species in Montejo forest, is the dominant tree species (see Appendix S6 Table S6.2 for the abundances of these three species in the different areas of the forest). These areas were classified based on the dominance of the species registered in the FI as follows: (I) *Fagus sylvatica*, (II) *Quercus pyrenaica*, (III) *Quercus petraea* (when >60% of the abundance corresponded to one of these three species, respectively), (IV) mixed forest 1 (transition areas between *F. sylvatica* and *Q. pyrenaica*) and (V) mixed forest 2 (transition area with codominance of *F. sylvatica*, *Q. pyrenaica* and *Q. petraea*). We selected 26 individuals of *F. sylvatica* and 25 of *Q. pyrenaica* that, according to FIs, are the main representatives of Eurosiberian and Mediterranean vegetation in Montejo, respectively. Five individuals from the FIs of each target species were sampled in each area, except in area V where 6 individuals of beech were sampled instead of five.

2.3. Measurements of abiotic variables

In a subset of 60 plots from the FIs, we determined soil organic matter content (SOM) and soil nitrate and phosphate concentrations. Three soil samples were collected between June and July 2021 with a hand trowel from the top 15 cm in each plot at three spots following the slope of the plot, one of the samples corresponding to the center of the plot and the other two approximately 5 m above and below the center. The three soil samples from each plot were then mixed in a plastic bag to homogenize the soil and taken to the lab where they were dried at 50 °C to constant weight (~72 h) and sieved at 2 mm. Soil organic matter content was estimated by the loss-on-ignition (LOI) method (Bensharada et al., 2022), soil nitrate concentration was determined using a UV/VI spectrophotometer at 218/228 nm after extraction with 0.01 mol·L⁻¹ calcium chloride (Houba et al., 2000), and soil phosphate concentration was estimated with the same spectrophotometer at 880 nm after extraction with Calcium-Acetate-Lactate (CAL) solution (Schüller, 1969). Slope, aspect and altitude of the plots where the trees were selected were estimated using the GIS software package Spatial Analyst (ArcGIS 10 Desktop 10.5.1) and the Digital Terrain Model of 5 m grid produced by the Spanish National Program for Aerial Orthophotography (PNOA). Soil depth was measured in four points 10-m apart from the center of the plot following cardinal directions by hammering a 1-m-long iron bar into the soil until reaching the bedrock. When the bedrock was deeper than 1 m, we assigned a value of 1 m soil depth to that specific location. Soil depth was then calculated as the mean depth of the four values per plot.

2.4. Plant trait sampling and measurements

Plant material (leaf, shoots and roots) was sampled for each tree between June and July 2021, when leaves were fully expanded. From each selected individual, leaves, stems and roots were sampled. We selected healthy, mature trees and collected south-oriented, two-year-old shoots with full-sun-exposed and expanded green leaves using a 4-m pole vault ensuring all the leaves were attached to the shoot section. Heights of sampled branches varied due to tree canopy structure and technical limitations. In the same trees, we excavated fine roots (<2 mm diameter) from the top 15–20 cm of soil near the trunk of the trees. Roots were stored fresh in the field and taken to the lab where they were rinsed in distilled water to eliminate adhered soil particles.

Six aboveground and three belowground key morphological and physicochemical functional traits associated with resource acquisition were measured (Table 1): leaf dry matter content (LDMC; leaf dry mass per unit of water-saturated fresh mass; $\text{mg} \cdot \text{g}^{-1}$), specific leaf area (SLA; leaf area per unit of leaf dry mass; $\text{m}^2 \cdot \text{kg}^{-1}$), leaf C isotopic ratio ($\delta^{13}\text{C}$; ‰), leaf carbon to nitrogen ratio (C:N), stem dry matter content (SDMC; stem dry mass per unit of water-saturated fresh mass; $\text{mg} \cdot \text{g}^{-1}$), Huber

Table 1

List of the 9 functional traits considered in this study, their abbreviations, units and functional roles.

Trait	Abbreviation	Unit	Functional role	References
Leaf morphology				
Leaf dry matter content	LDMC	mg·g ⁻¹	Physical resistance and stress tolerance	Pérez-Harguindeguy et al. (2013); de la Riva et al. (2017)
Specific leaf area	SLA	m ² ·kg ⁻¹	Leaf longevity, light capture and growth rate	Shipley and Vu (2002)
Stem morphology				
Stem dry matter content	SDMC	mg·g ⁻¹	Physical resistance	de la Riva et al. (2018b)
Root morphology				
Root dry matter content	RDMC	mg·g ⁻¹	Physical resistance	de la Riva et al. (2018b)
Specific root area	SRA	m ² ·kg ⁻¹	Water and nutrients acquisition	de la Riva et al. (2021b)
Average root diameter	Rdiam	mm	Water and nutrients acquisition	Freschet et al. (2021)
Physiology				
Huber value	H _v	cm ² ·cm ⁻²	Water transport capacity	Mencuccini et al. (2019)
Leaf chemistry				
Isotopic carbon fraction	δ ¹³ C	‰	Gas exchange and water use efficiency	Prieto et al. (2018)
Ratio C:N	C:N	‰/‰	Growth rate	Zhang et al. (2020)

Based on fresh mass.

value (H_v ; sapwood area:leaf area), root dry matter content (RDMC; root dry mass per unit of root fresh mass; mg·g⁻¹), specific root area (SRA; root area per unit of root dry mass; m²·kg⁻¹), average root diameter (Rdiam; mm), and tree main-stem relative growth rate (RGR; mm·mm⁻¹·year⁻¹). Leaves and roots were scanned with EPSON® V850 PRO scanner. Leaf area was measured from the scanned images with ImageJ software (Schneider et al., 2012). Root area and diameter were obtained by analyzing the scanned images with WinRHIZO 2009 (Regent Instruments and Win/MacRHIZO, 2001). Tissue collection, storing and processing of all leaf, stem and root material, as well as trait measurements, were carried out following the protocols detailed by Pérez-Harguindeguy et al. (2013). RDMC was measured following the same procedure as LDMC. For a detailed protocol of trait harvesting and measurements see also de la Riva et al. (2016).

Tree diameter at breast height (DBH) was used to calculate the tree relative growth rate (RGR) as the difference in DBH between the years 2021 and 2005 divided by the DBH in 2005 (to account for differences in tree size) and by the number of years elapsed between initial and final DBH, i.e., 16 years, to calculate it on a yearly basis.

Additionally, plant recruitment was measured for both target species and taken as a proxy of average fitness. As present recruitment may be highly determined by the dominance of the species in the plot (Perea et al., 2020), we divided the forest in the five different categories detailed above (Appendix S6 Table S6.2). Plots were then classified into one of the five categories and a minimum of three plots per category were then selected (a total of 22 plots). The selection of plots was made according to the topography of the terrain and the abundances recorded in the FI of the three main species in the different areas. In each of the plots, three 25-m long and 2-m wide parallel transects along the slope were drawn and all the individuals of both beech and Pyrenean oak with a DBH <5 cm were counted along this transect and classified as seedlings (<1 year old) or juveniles (≥1 year old) following the protocol of Lloret et al. (2016). For the purposes of our study we did not differentiate between juveniles being resprouts and juveniles grown from seeds. However, we assume the majority of juveniles of Pyrenean oak to be sprouts due to their proximity to adult trees and the high sprouting ability of this species (Valbuena-Carabaña and Gil, 2013). Juveniles of beech, on the other hand, were considered mostly trees from seed origin due to their usually relatively high distance to potential mother trees (personal observation) and because seed origin is the predominant form of regeneration of beech (Milios and Papalexandris, 2019). All individuals classified as seedling were individuals from seed origin.

2.5. Data analyses

2.5.1. Functional niche analyses

We analyzed the degree of functional dissimilitude between species using a two-tailed Wilcoxon test for each plant trait to detect significant

differences in mean trait values. When significant, one-tailed Wilcoxon tests were run to detect which species showed higher (or lower) trait values. To assess differences in the functional niche segregation and phenotypic diversity between beech and Pyrenean oak, we calculated their trait probability density function (TPD), which represents the probabilities of observing each possible trait value in a given ecological unit (*sensu* Carmona et al., 2016), and functional richness (FRic) — i.e., the functional trait space occupied by a species (Carmona et al., 2019)— for each trait independently. For each species its TPD was calculated using kernel density estimation based on trait averages and variances of the species (see Carmona et al., 2019 for mathematical details). FRic is the sum of the hypervolumes of cells in which TPD is greater than 0. FRic is conceptually similar to the volume obtained with the hypervolume method (Blonder 2018; see Appendix S2 Table S2.1 for values of FRic for each study trait of both target species). Both TPDs and FRic were calculated with the TPD R package with default parameters (Carmona et al., 2019). Additionally, we built the functional hypervolume of each species with the 9 leaf, stem and root traits plus RGR following the multidimensional kernel density estimation (KDE) procedure with default parameters from the HYPERVOLUME R package (Blonder et al., 2018b). In order to reduce the number of dimensions and improve axes orthogonality (recommended for this analysis), we first conducted a principal component analysis (PCA) including all study traits previously log-transformed, centered and scaled (Blonder et al., 2018b). We used the first three principal components to construct the hypervolumes, which explained 69.04% of the variance of trait values. This hypervolume represents the realized functional niche of the species (see Appendix S3 from Supporting Information for details of hypervolume construction). We assessed functional niche segregation between beech and Pyrenean oak by calculating the overlap/differentiation between the total hypervolume of each species (see Appendix S4 from Supporting Information for more details of overlap calculation).

As these metrics of phenotypic diversity, i.e., the range of values occupied by each trait and the functional space occupied by each species, may be strongly influenced by the effect of certain individuals with extreme trait values, to remove this confounding effect, we computed the size of the kernel density for each trait independently and for the total hypervolume using 100 randomizations and 15 individuals per species. This randomization allowed us to determine actual differences in the phenotypic diversity of each species and not the effect of potential individuals with extreme trait values. Then, we calculated the mean effect size (Hedges' *d*) and bias-corrected 95%-bootstrap confidence intervals (EFFECTSIZE R package, Torchiano, 2018) for differences in kernel densities between species, for each trait independently and for the hypervolume constructed with the 10 traits. Mean effect sizes were considered significant when their 95%-confidence interval did not overlap with zero.

To explore the influence of abiotic variables (SOM, soil nitrate and phosphate concentrations, soil depth and slope) in the phenotypic

variability of each species, we conducted maximum likelihood techniques with a linear function using the LIKELIHOOD package in R (Murphy, 2015). We only fitted two-factor models to avoid overestimating the models with spurious parameters with very poor weights (Grueber et al., 2011). The factors were added either additively or multiplicatively. We computed every possible model and models were then ranked by their Akaike Information Criterion corrected for small sample size (AICc, Barton and Barton, 2015). We selected the best-fitted model as the model with the lowest Akaike Information Criterion ($\Delta AIC < 2$). The best-fitted linear models were then re-run using REML and the slope of these models were used as an estimation of the variability of each trait in response to the corresponding environmental factors.

2.5.2. Environmental and geographic niche analyses

To compare the environmental requirements of each species we calculated the environmental niche segregation and their preferences for the geographical space with the subset of 60 plots from the FIs. To do that, two different approaches were used: i) the ECOSPAT framework that includes tools for the spatial analysis and modeling of species' realized niches (Broennimann et al., 2012; Di Cola et al., 2017) and ii) generalized linear regression models (GLMs). Both approaches are complementary, since the first one quantifies the environmental niche through the overlapping of niches between the two target species only based on the environmental values extracted for the presence records of each species; while the second one calculates both the environmental and the geographic niches for the two target species based on the abundance data in terms of total tree density (response variable) related to the five selected topographic and soil predictor variables (independent variable). The environmental and geographic niche calculations based on both the ECOSPAT and generalized linear regression model (GLMs) approaches are described in detail in Supporting Information Appendix S5. Prior to conducting statistical analyses, to spatialise the abiotic data (topographic attributes and soil properties) collected for each study plot, we performed

a geospatial interpolation through different steps: 1) we created and rasterized a grid template with the same pixel size as the plot diameter (30 m); 2) we fitted a model to return objects by using the Inverse Distance Weighting method; and 3) we interpolated by using the “interpolate” function from the RASTER R package. We then derived raster files corresponding to the original predictor variables (i.e. three topographic attributes and five soil attributes) that may play an important role in defining the environmental suitability for the two target species at fine scales. We measured collinearity effects with the pairwise Pearson's correlation coefficient and variance inflation factor (VIF) for these first eight predictors, and defined the final set considering the statistical tests, expert judgment, and scientific literature (Pardo et al., 1997; Gavilán et al., 2018). Thus, we considered only those variables having Pearson's pairwise correlation coefficients ≤ 0.75 and VIF < 4 and thus only five independent predictors: aspect (ASP), elevation (ELE), soil organic matter (SOM), slope (SLO), and soil depth (SDP).

2.5.3. Recruitment analyses

To compare the average fitness based on species recruitment, we used contingency tables and the chi-square test of independence. Recruits were separated by category (sites dominated by *Fagus sylvatica*, *Quercus pyrenaica*, *Quercus petraea* and a mixture of the species) and by age (seedlings and juveniles), and significance between these factors (p -value) was computed using a Monte Carlo simulation with 5000 repetitions (Hope, 1968).

All data analyses were conducted with the R Software v. 4.1.2 (R Core Team, 2021).

3. Results

Results from trait probability density analyses indicated that beech and Pyrenean oak are functionally dissimilar species with different trait values for each species for nine out of the 10 traits considered (Fig. 1).

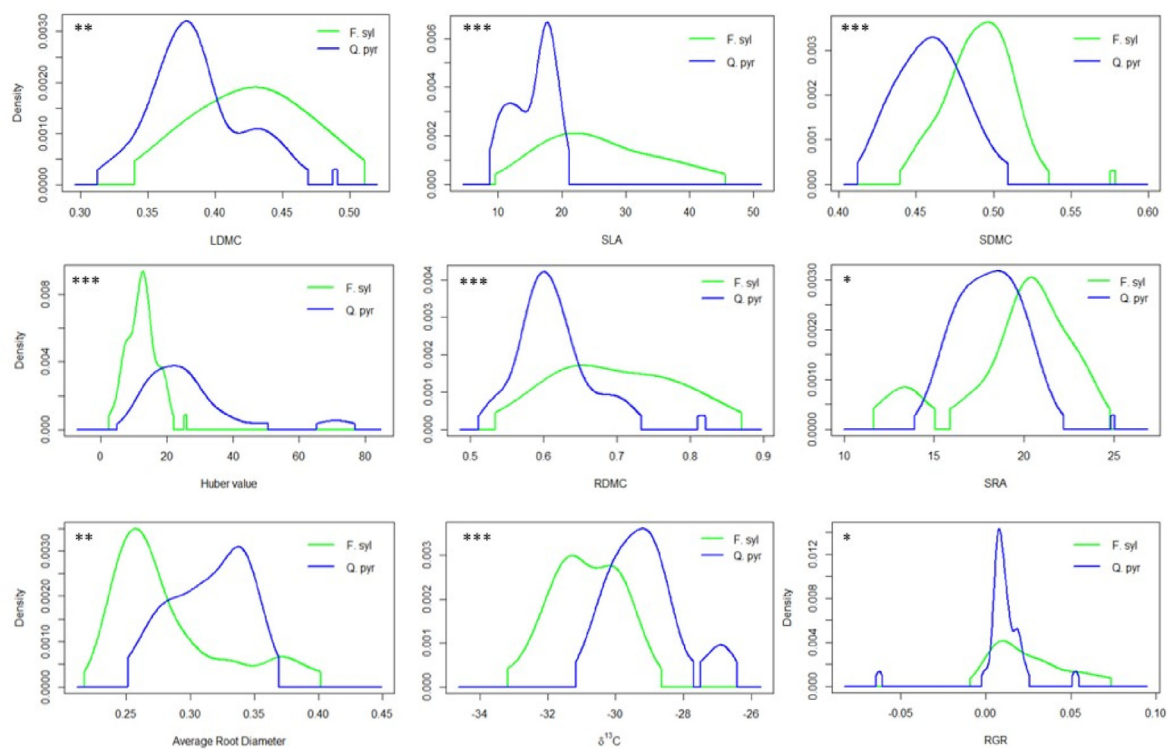


Fig. 1. Trait Probability density (TPD) functions for each of the study traits in *Fagus sylvatica* (F. syl, green) and *Quercus pyrenaica* (Q. pyr, blue). Only traits presenting significant differences between both species are shown. Note: H_v values are multiplied by 10^5 to facilitate comparisons. Trait abbreviations are in Table 1. Significant differences among the mean values (two-tailed Wilcoxon test analyses) are marked with an asterisk at the top left corner of each plot: $p < 0.001$ “***”; $p < 0.01$ “**” and $p < 0.05$ “*”. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Beech had on average higher LDMC, SLA, SDMC, RDMC, SRA and RGR, while Pyrenean oak showed higher leaf $\delta^{13}\text{C}$, Huber values (H_v) and Rdiam ($p < 0.05$ in all cases) (Fig. 1); foliar C:N showed marginal significant differences between species ($p = 0.081$). Descriptive statistics for the study traits of both species are shown in Table S1.1. FRic values are shown in Table S2.1.

Overall, results from the randomized analysis showed higher diversity in the trait space for beech than for Pyrenean oak. Mean effect sizes were positive and significantly different from 0, except for SDMC and $\delta^{13}\text{C}$, indicating that beech occupied a larger proportion of the functional space than Pyrenean oak by presenting higher phenotypic variability (except for H_v which showed the opposite pattern), an effect that was magnified when accounting for all traits together (Fig. 2).

Results from our linear modeling approach showed a predominant influence of altitude on three out of the 10 study traits. Beech trees growing at lower altitudes had higher H_v , leaf $\delta^{13}\text{C}$ and thicker Rdiam (Fig. 3), reflecting a more conservative and efficient use of water with decreases in altitude. Conversely, we found no significant relationships between abiotic variables and traits for Pyrenean oak.

Our results show that beech and Pyrenean oak present highly segregated functional niches, as shown by the low level of niche overlap (13.09%) between both hypervolumes (Fig. 4a; Supporting Information, Appendix S3, Fig. S3.1; see Appendix S4 in the Supporting Information for details on the calculation of niche overlap and partitioning).

We did not observe differences in the environmental niche between species (Fig. 4b). The PCA calculated by ECOSPAT explained 63.52% of the variability in the study area (first component: 42.78%; second component, 20.74%) (Supporting Information, Appendix S5, Fig. S5.3a). The equivalency and similarity tests showed that environmental niches were not less similar than expected by chance, with these tests exhibiting non-significant p -values (Supporting Information, Appendix S5, Fig. S5.3b). Moreover, the mean Schoener's D index, a measure of spatial niche overlap (Schoener, 1968; Warren et al., 2008, see Appendix S5 for details), indicated a high overlap between niches ($D = 0.71$), with high stability ($S = 0.98$; $I: 0.83$ n.s.) while the expansion and unfilling were low ($E = 0.02$ and $U = 0.13$, respectively).

Based on GLM results, topographic and soil-related models at local and finer scale showed a high performance in terms of abundance for beech and Pyrenean oak, being the latter the species that showed the highest performance for all metrics (Supporting Information, Appendix S5, Table S5.1). In addition to showing a high relationship of species

performance with elevation, which was highlighted in previous sections, both species also showed a high effect of aspect, but with opposite sign (Supporting Information, Appendix S5, Table S5.2). Although beech did not show a significant relationship with slope, Pyrenean oak showed a strong and significant relationship with this topographic variable. However, the highlight finding was that the abundance of both species showed opposite relationships with soil organic matter and soil depth, being highly significant in beech and not in Pyrenean oak.

The local correlation map between the GLM predictions for both species based on topographic and soil-related predictors (Fig. 5) shows pixels where correlation between model predictions is negative, null or positive over the study area. Positive correlations appear in moderate to low slope areas (i.e. areas with the wider contour lines), where both species coexist, while negative correlations are observed in areas where steep slopes and shallow soils are more suitable for Pyrenean oak than for beech (Fig. 5).

Plant recruitment was also non-randomly distributed across forest types and ages for both beech and Pyrenean oak ($p < 0.001$). We registered a higher number of seedlings of beech than expected by chance (null model), except in those plots dominated by Pyrenean oak, where beech seedlings were very scarce or absent and beech juveniles were found in relatively low numbers (Fig. 6; Supporting Information, Appendix S6, Table S6.1).

4. Discussion

4.1. Differences in functional strategies and phenotypic variability among beech and Pyrenean oak

In this study, we observed a clear functional distinctiveness at the whole plant level (leaf, stem and roots) between beech and Pyrenean oak that allows their coexistence in a bioclimatic boundary such as the sub-Mediterranean Hayedo de Montejo forest. Beech is a mesophytic shade tolerant species that is widely distributed in temperate climates (Maracchi et al., 2005; Durrant et al., 2016), and rare in the Mediterranean due to its high sensitivity to water stress across all its ontogenetic stages (Ellenberg, 1988; Hacke and Sauter, 1995; Aranda et al., 1996; Robson et al., 2009). On the other hand, Pyrenean oak is a Mediterranean species distributed at lower latitudes in southern Europe with a high tolerance to water stress (Lorite et al., 2008; Quintano et al., 2016). Although beech tends to show lower stomatal conductance and higher stomatal control

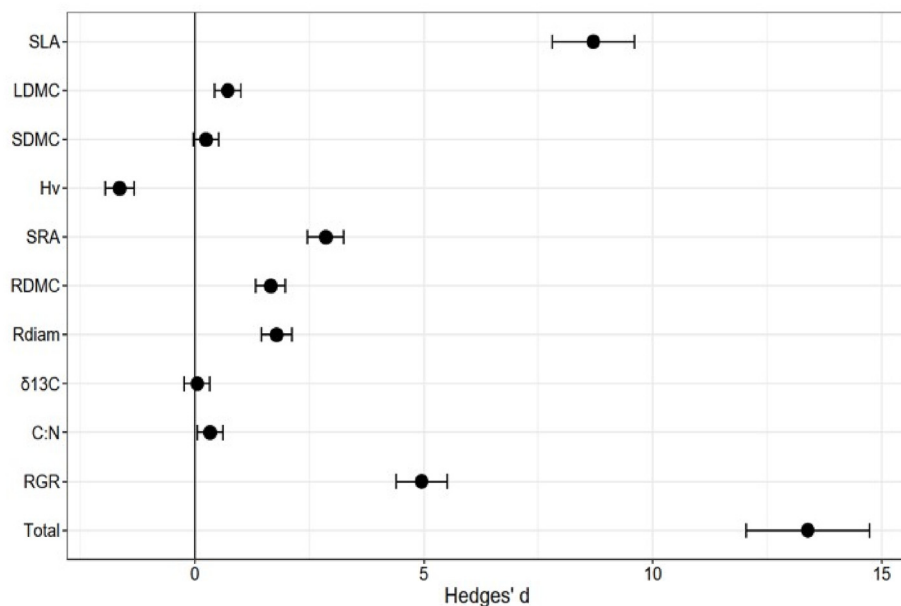


Fig. 2. Mean effect size (Hedges' d) and bias-corrected 95%-bootstrap confidence intervals for differences in the intraspecific variability (kernel density) of each trait independently and all together (Total) among *Fagus sylvatica* and *Quercus pyrenaica*. Positive mean effect sizes indicate that *F. sylvatica* presented on average larger intraspecific variability for a given trait than *Q. pyrenaica*. Size of the kernel density for each trait and for the 10 traits together (Total) were obtained by 100 randomizations composed of 15 individuals per species from the total pool. A mean effect size is considered significantly different from zero when its 95%-confidence interval does not overlap with zero (vertical solid line).

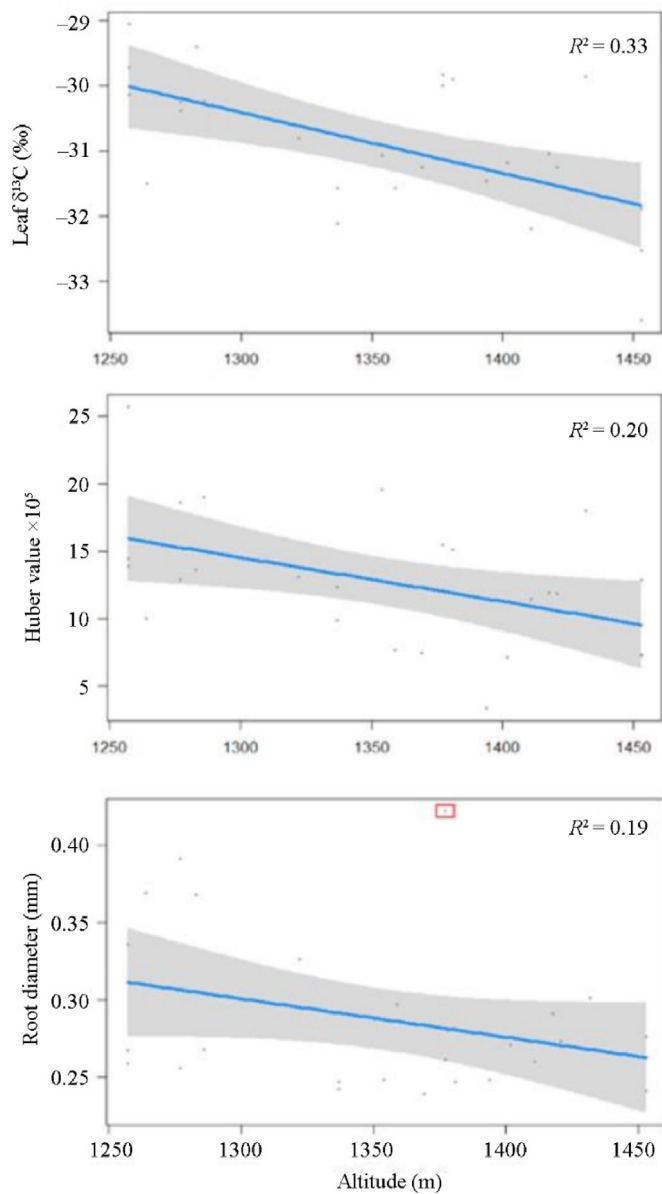


Fig. 3. Relationship of trait values of *Fagus sylvatica* in response to altitude (the best-fitted models supported by the Akaike Information Criterion ($\Delta AIC < 2$)). Root diameter was fitted to altitude after excluding one outlier with abnormally high root diameter (red square). R^2 of fitted models are shown in the upper-right corner of each plot. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

when water availability decreases than other temperate species such as *Q. petraea* (Aranda et al., 2005), it showed a greater resource acquisitive strategy than Pyrenean oak, i.e. higher resource uptake (higher SLA) and faster relative growth rates, in agreement with our expectations. Moreover, the lower foliar $\delta^{13}\text{C}$ and C:N ratios observed in beech in our study may be related to a more profligate use of water and nutrients (Poorter and de Jong, 1999; Prieto et al., 2018). In contrast, Pyrenean oak showed the opposite trend (Fig. 1), reflecting a higher efficiency in the use of nutrients and water, i.e. lower SLA and higher foliar $\delta^{13}\text{C}$ and C:N ratios, as expected for a xerophytic oak adapted to higher temperatures and insolation, and longer summer drought periods characteristic of Mediterranean conditions (Aranda et al., 1996; Hernández-Santana et al., 2008). These results partly agree with other studies showing higher C assimilation rates per unit leaf area and mesophyll conductance to CO_2 in sub-Mediterranean oak species compared to beech (Cano et al., 2013;

Peguero-Pina et al., 2015). Furthermore, the differences in stem-related traits observed between beech and Pyrenean oak are likely due to their different wood anatomy, with beech presenting a diffuse-porous anatomy (Steppe and Lemeur, 2007) and Pyrenean oak being a ring-porous species (Corcuera et al., 2006). These different wood anatomies have been shown to influence stem-related traits (Robert et al., 2017).

Species from the *Quercus* genus (oaks) are able to uptake water from deeper soil layers during summer drought (Leuschner et al., 2001; Zapater et al., 2011), a strategy associated with lower nutrient uptake given the vertical decoupling between water and nutrient uptake (Querejeta et al., 2021; Prieto et al., pers. comm. 2022). Beech trees generally show a shallower rooting habit and are more prone to exhibit water stress signs when shallow soil layers dry out in the early summer (Cocozza et al., 2016; Wang et al., 2021). Previous studies from Montejo forest support this view, as they have reported higher leaf relative water contents, faster relative growth rates and greater respiratory costs, i.e. higher metabolic activity, in beech than in Pyrenean oak trees (Aranda et al., 1996; Rodríguez-Calcerrada et al., 2019). The observed segregation in leaf traits of both species along the resource uptake trade-off can also be extended to roots (Root Economics Spectrum; de la Riva et al., 2021a, 2021b). Given the shallower rooting habit in beech (Wang et al., 2021), the higher SRA and lower root diameter probably allow the species to maximize water and nutrient uptake from shallow soil layers and maintain relatively high water potential, stomatal conductance and transpiration during dry conditions occurring in sub-Mediterranean zones (Prieto et al., 2018; Querejeta et al., 2021), and increase the potential to encounter and absorb relatively immobile soil resources (de la Riva et al., 2021a, 2021b). Indeed, beech trees are able to meet their high water demands in drier environments by increasing their SRA at the expense of a decrease in fine root biomass (Meier and Leuschner, 2008). They achieve this by a reduction in the average diameter of fine roots, likely as result of reducing C investment to fine roots (Meier and Leuschner, 2008); that is, by optimizing the amount of water absorbed per unit root biomass. Whether a higher dry matter content (as found here for beech) is advantageous for a species with an acquisitive resource strategy is less clear. The construction of plant tissues implies trade-offs between carbon costs, mechanical support, water transport efficiency and storage of water and assimilates (Pratt et al., 2007; de la Riva et al., 2021a). Higher tissue dry matter content can imply higher construction costs in tissues with higher C:N ratios (Villar and Merino, 2001; Villar et al., 2006; de la Riva et al., 2021b; but see Rodríguez-Calcerrada et al., 2019), features that are frequently observed in species with more conservative strategies (Laureano et al., 2008; Prieto et al., 2018; Querejeta et al., 2018; Delpiano et al., 2020).

One major challenge that remains unsolved is to understand how two species with different water use requirements are able to co-dominate a common geographical space. From an ecophysiological perspective, Pyrenean oak is more tolerant to drought and late frosts (Rubio-Cuadrado et al., 2021). From a biogeographical perspective, environmental conditions at Montejo forest are at the optimum for Pyrenean oak trees (Quintano et al., 2016). Furthermore, Pyrenean oak forests in this region have been historically managed and are well suited to resist human perturbations, which has favored the broad expansion of this oak species in the Sierra del Rincón mountain range (Pardo et al., 1997). In contrast, beech is at its southernmost distribution edge, where dry conditions strongly influence its physiological behavior and limit survival (Aranda, 1998; Aranda et al., 2000, 2002). However, beech trees at the Hayedo de Montejo have lower leaf osmotic potentials than other Eurosiberian species (e.g. *Q. petraea*), suggesting a certain degree of adaptation to seasonal summer drought (Aranda et al., 1996). Similarly, previous studies noted the great capacity of beech trees to acclimate to variable irradiance and low soil water availability conditions via integrated changes in SLA, SRA, blade thickness, stomatal densities or cavitation resistance (Aranda et al., 2001; Curt et al., 2005; Meier and Leuschner, 2008; Wortemann et al., 2011; Cano et al., 2013; Stojnic et al., 2015). The larger phenotypic variation observed in this study in beech than in

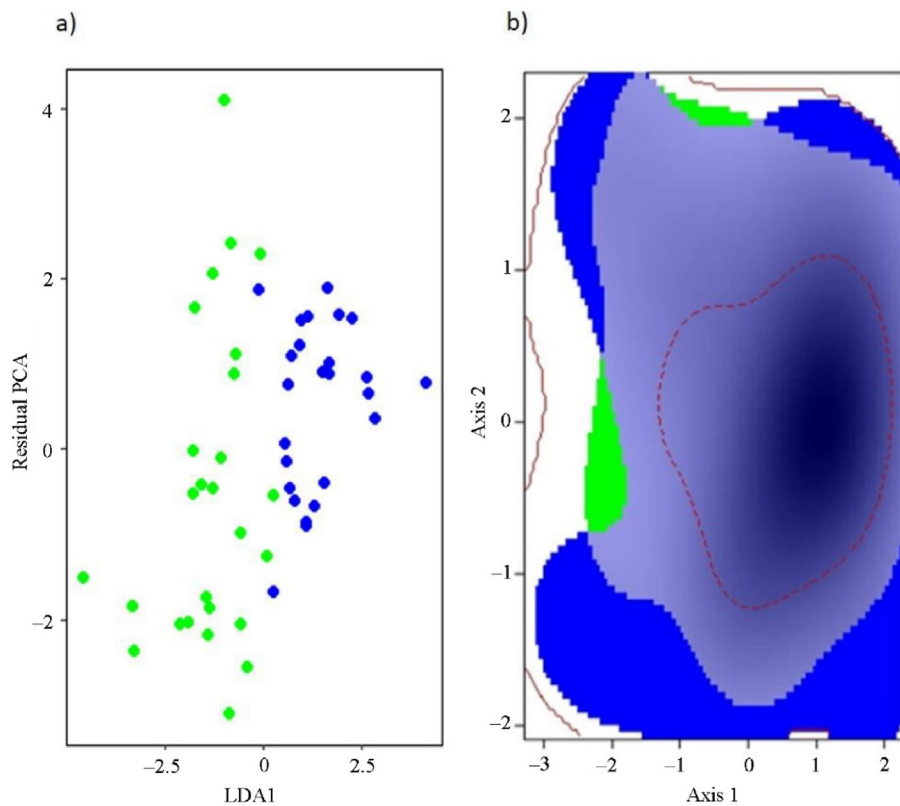


Fig. 4. Functional and environmental niche representations of *Fagus sylvatica* and *Quercus pyrenaica*: a) Estimated functional space occupancy of *F. sylvatica* (green) and *Q. pyrenaica* (blue) shown as 2D projections including all study traits (LDMC, leaf dry matter content; SLA, specific leaf area; SDMC, stem dry matter content; H_v , Huber value; RDMC, root dry matter content; SRA, specific root area; Rdiam, average root diameter; $\delta^{13}C$, leaf C isotopic ratio; C:N, leaf C:N ratio; and RGR, relative growth rate) created with the HYPEROVERLAP R package (Brown et al., 2020); b) Realized environmental niche overlap of *F. sylvatica* (blue) and *Quercus pyrenaica* (green) calculated by ECOSPAT R package. Grayish area indicates environmental niche overlap between both species. The external solid gray line represents the 100% environmental availability in the study area; the dashed line shows the 50% most frequent environmental conditions. Darker areas indicate higher density of occupancy of the environmental niche. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

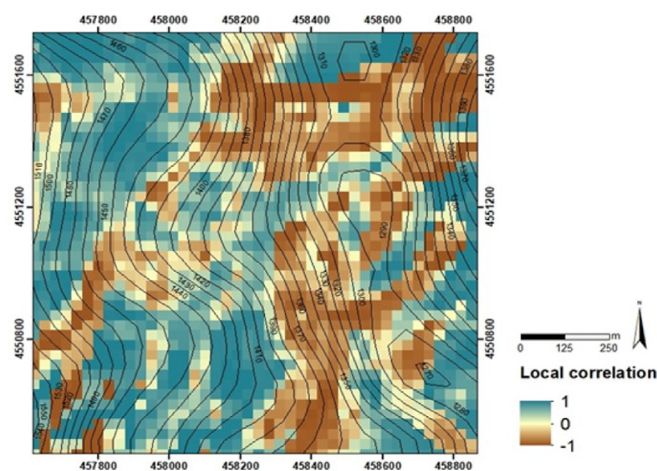


Fig. 5. Map of the spatial correlation between *Fagus sylvatica* and *Quercus pyrenaica* in Montejo forest: negative (brown), null (yellow) or positive (green) relationships are shown for each pixel (30 m \times 30 m) in the spatial model. Black continuous lines are iso-altitudinal contour lines, i.e. similar altitude, representing 10 m separation between consecutive lines. Altitude (m a.s.l.) is indicated next to each line. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Pyrenean oak trees at the plant level, i.e., including leaf and root traits, points to this direction, as high phenotypic variation likely contributes to optimize plant physiological performance under variable water supply, such as that found in sub-Mediterranean zones (Casson and Gray, 2008; Cano et al., 2013). These results emphasize the role of phenotypic variation in overcoming changes in abiotic conditions (Bittebiere et al., 2019), which could explain part of the unexpected beech success in a climatic border such as the Hayedo de Montejo.

Altitude is a particularly relevant variable regulating plant behavior because it is associated with steep changes in temperature and water availability over short distances (Vitasse et al., 2010; Schöb et al., 2013). As a general pattern, variation in morphological and physiological traits along altitudinal gradients are primarily developed to maintain plant carbon assimilation and balance (Bresson et al., 2011) and not so much to maintain the plant water balance (Vitasse et al., 2010). However, our results suggest that phenotypic variation in beech along the altitudinal gradient at Montejo forest (ca. 300 m) was mainly driven by traits associated with plant water balance. Indeed, altitude was negatively related to beech stem Huber values (H_v), foliar $\delta^{13}C$ and fine-root diameter, possibly as a result of increased water availability at higher altitudes, where the terrain is less steep. Similar decreases in H_v in response to increasing water availability have been found in other tree species (Carter and White, 2009). Lower foliar $\delta^{13}C$ at higher altitudes may be indicative of lower water use efficiency, i.e., less carbon fixed per unit water spent (Farquhar et al., 1989). Lower leaf $\delta^{13}C$ at high altitudes is probably the result of both a lower leaf C assimilation induced by lower temperatures (Farquhar et al., 1989) or an earlier leaf senescence (Vitasse et al., 2010). Nonetheless, it can also be a response to an enhanced stomatal conductance at higher altitudes driven by a higher water availability, as also found in other drought prone ecosystems (Prieto et al., 2018; Querejeta et al., 2022). This idea is further supported by previous evidence of changes in both temperature and soil water availability along an altitudinal gradient leading to a high beech plasticity in stomatal conductance (Psidová et al., 2018). Finally, smaller fine roots are typically more vulnerable to cavitation in response to drought and are less efficient in transporting water, so that thicker roots may prevent cavitation under potentially drier conditions at lower altitudes and increase root water transport (Jackson et al., 2000). Altogether, besides temperature, fine-scale water availability or biotic interactions with neighbors can explain beech phenotypic variability with altitude (Blonder et al., 2018a; van der Merwe et al., 2021). Further studies are required to

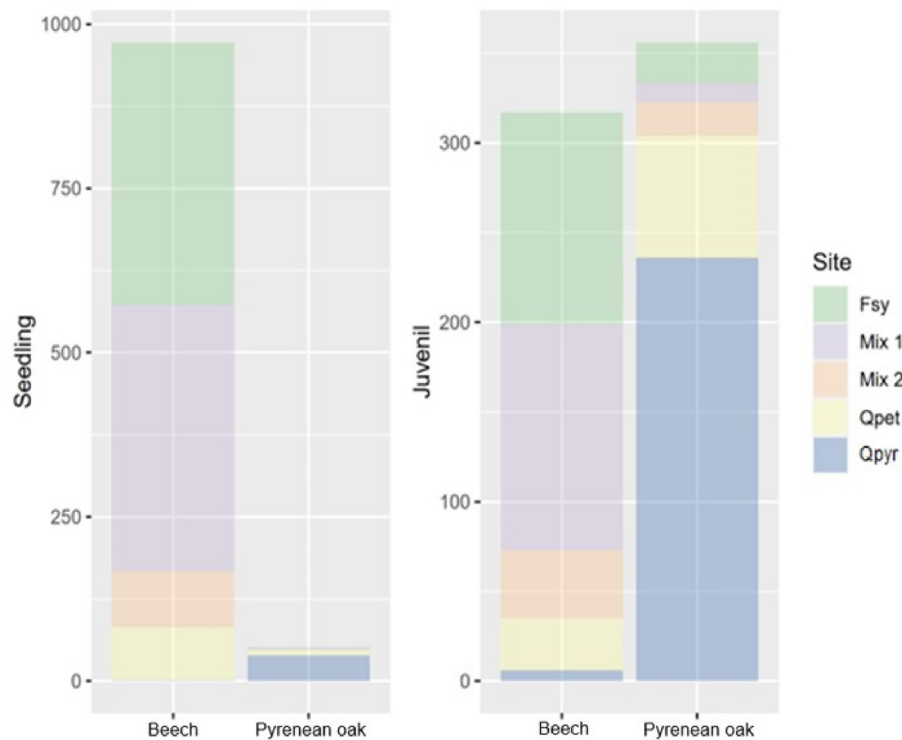


Fig. 6. Recruitment expressed as total number of seedlings (<1 year old individuals; left) and juveniles (≥ 1 year old individuals; right) of *Fagus sylvatica* and *Quercus pyrenaica* in each type of community named after the species with an abundance $\geq 60\%$. Fsy: *F. sylvatica*; Qpyr: *Q. pyrenaica*; Qpet: *Q. petraea*; Mix 1: transition area between *F. sylvatica* and *Q. pyrenaica*; Mix 2: transition area between *F. sylvatica*, *Q. pyrenaica* and *Q. petraea*.

clearly define the main drivers of phenotypic variation in beech trees in sub-Mediterranean zones.

4.2. Niche segregation and coexistence of beech and Pyrenean oak in Montejo

Our results point to consistent differences in the functional space between beech and Pyrenean oak at the Montejo forest. However, we did not observe differences in their realized environmental niche (Fig. 4), suggesting that there is not a clear niche partitioning related with the habitat suitability of the species. These results point to differences in the functional niche space between beech and Pyrenean oak allowing to reduce interspecific competition in a shared environment (de la Riva et al., 2017). This argument is held on the premise that the observed functional dissimilarities depict differences in resource use strategies (i.e., limiting similarity hypothesis; MacArthur and Levins, 1967). Therefore, beech and Pyrenean oak may compete for some resources in the same space with different intensity, which could stabilize their coexistence (de la Riva et al., 2017). However, the rapid acquisition of nutrients and water would allow beech trees to grow faster than Pyrenean oak trees. The dense shade created by beech tree canopies may induce a high competition for light (Van de Peer et al., 2017; Žemaitis et al., 2019), promoting an acquisitive set of traits as the most advantageous strategy to cope with competitive exclusion (Mayfield and Levine, 2010; de la Riva et al., 2018a). Thus, open areas resulting from different disturbance processes (for example, canopy tree death) may also be relevant for the coexistence of both species.

In addition, coexistence of beech and Pyrenean oak may also depend on their average fitness differences (Kraft et al., 2015). In this regard, tree recruitment success at the Montejo forest is currently clearly unbalanced between both species. Overall, the recruitment of beech was higher in most areas within the forest except in those already dominated by Pyrenean oak, but this result differed with the seedling recruitment stage. Beech showed a much higher recruitment at the seedling stage than

Pyrenean oak, but both species showed a similar recruitment at the juvenile stage. However, most juveniles from Pyrenean oak were found in areas dominated by Pyrenean oak adults, while juveniles of beech were abundant not only in areas dominated by beech but also in mixed areas co-dominated by beech and Pyrenean oak. The thicker and more closed tree canopy of beech forest patches may hinder the establishment and development of shade-intolerant Pyrenean oak recruits (Pardo et al., 2004), being the recruitment thus limited to more open-areas in forest patches dominated by Pyrenean oak. Indeed, the presence of young oaks in the Montejo forest was mainly relegated to forest patches in which oaks were already established before the 1960s (Rubio-Cuadrado et al., 2020). An additional factor that might favor a higher number of beech recruits could be that beeches are least preferred by large herbivores than oak recruits (Didion et al., 2011; Ohse et al., 2017; Perea et al., 2020). Furthermore, the earlier leaf phenology and synchrony with pollen emission of beech compared to that of Pyrenean oak probably hinders the pollination of Pyrenean oak trees within beech dominated-sites due to the physical barrier of beech canopies to oak pollen dispersal (Millerón et al., 2012). These features could explain the overall success of beech recruitment in the study area. Conversely, beech seedlings suffer from higher water stress under the canopy of Pyrenean oak trees as a result of the intense competition from grasses and the relatively high radiation in these rather open areas (Aranda et al., 2002; Pardo et al., 2004), thus hindering the recruitment of beech seedlings in these patches. Beech trees seem to produce more seedlings than Pyrenean oak, but their advancement to later ontogenetic stages appear to be highly compromised, probably as a result of the water stress induced by summer drought in these transition areas (Perea et al., 2020). On the other hand, the strong resprouting capacity of Pyrenean oak likely enhances the persistence of its recruits in those patches already colonized by the species (Valbuena-Carabaña and Gil, 2013).

Land-use changes during the 20th century have probably affected forest dynamics and species coexistence in Montejo, as has been previously observed in other mountain ranges in southern Europe (Kouba

et al., 2012; Palombo et al., 2013; Peña-Angulo et al., 2019). Although we acknowledge that more data collected at other spatial and temporal scales than those of this study are needed to extract proper conclusions, our data allow us to suggest that human legacy is likely a factor shaping spatial niche partitioning between the two studied species. Historically, human management of forest areas has favored the broad expansion of Pyrenean oak in transition areas in the Iberian Peninsula at the expense of Eurosiberian temperate species like beech (Pardo et al., 1997). Our results show a negative spatial correlation between both species on steeper areas and shallow soils of the forest where management was less intense (Fig. 5). According to satellite images and the first forest inventory in 1994 (Gil et al., 2010), Pyrenean oak patches were already well established in steeper areas long before the Montejo forest became a restricted area and traditional forest management activities were banned. In fact, Pyrenean oak shows a higher resprouting capacity than beech in disturbed areas with steep slopes (Pardo et al., 1997). Thus, the currently observed spatial niche segregation between both species in the Montejo forest could be more related to historical legacy management than actual differences in their realized niche, a question that warrants further attention in future studies.

4.3. Coexistence of beech and Pyrenean oak in the future and management implications

Future forest dynamics in Montejo will depend on the extent of climate change and its variable impact across microsites (e.g., sites with different soil depth or tree densities). After the abandonment of traditional land uses in Montejo during the 1960s, and the ensuing legal protection by national and European initiatives, an unexpected expansion of beech areas is occurring (see Appendix S7 from Supporting Information, and Gil et al., 2010). Similarly, previous studies have observed an expansion of beech at the expense of oaks in rear-edge populations (Martínez del Castillo et al., 2015; Rubio-Cuadrado et al., 2018b) as a result of the abandonment of traditional land uses (Améztegui et al., 2010; Kouba et al., 2012; Sánchez de Dios et al., 2021). Therefore, and despite beech being considered highly sensitive to drought stress, its ability to establish in better regeneration sites (Pardo et al., 2004) and its great competitive ability in moderately wet microsites seems to compensate for this limitation. This could explain its continuous increase at the expense of other drought adapted species such as Pyrenean oak (Perea et al., 2020). It is worth noting that despite both beech and Pyrenean oak have been considered to represent the latest successional stage in different ecological situations, they could also belong to different stages within the same successional process (Pardo et al., 1997). According to Meyer et al. (2003), mixed stands are not stable communities in beech forests. In the Iberian Peninsula, beech forests are mainly monospecific under low anthropogenic pressure (Castaño-Santamaría et al., 2021), being oaks usually excluded to sites with poor growing conditions (Rubio-Cuadrado et al., 2018b). Based on previous evidence and current forest dynamics in Montejo, asymmetric competition may theoretically occur between both species, promoting the competitive exclusion of Pyrenean oak in the long term. However, the projected increases in temperatures and lower rainfall in sub-Mediterranean areas for this century are expected to increase drought conditions and reduce the competitive ability and regeneration success of beech in southern populations (Aranda et al., 2002; Peuke et al., 2006). Furthermore, models predicting the future geographical distribution of sub-Mediterranean territories show a dramatic reduction in size (Sánchez de Dios et al., 2009; Ruiz-Labourdette et al., 2012). Also, several studies have already reported a negative impact of climate change on the current distribution and productivity of beech forests (e.g. Kramer et al., 2010; Falk and Hempelmann, 2013), with an expansion of Mediterranean oak species in sub-Mediterranean regions (Peñuelas et al., 2007; Benito Garzón et al., 2008; Hernández et al., 2017). The number of years with climatic conditions for optimal oak growth has increased in the last decades compared to those for beech in Montejo

(Rubio-Cuadrado et al., 2020), mostly associated to an increase in the number of late-spring frost events and severe summer droughts that could potentially offset the current expansion of beech (Castaño-Santamaría et al., 2021; Rubio-Cuadrado et al., 2021).

Nevertheless, negative climate change projections do not necessarily entail the total extinction of sensitive populations (Hampe, 2004; Gray and Hamann, 2013). Therefore, there is a need for adaptive management strategies that address the coexistence of both species under climate change scenarios in the Hayedo de Montejo. Silvicultural practices should be oriented to foster diverse forest formations that provide multiple ecosystem services (Brockerhoff et al., 2017; Jonsson et al., 2019; Bongers et al., 2021; Mey et al., 2022). For instance, the maintenance of different microsites, such as patches of shrub cover in open microsites, will enhance suitable regeneration niches for both species, promoting their future coexistence (Perea et al., 2020). Integrating information on the patterns of coexistence of Pyrenean oak and beech will help identify forest dynamics unbalances, allowing decision-makers to develop appropriate forest management plans to prevent or mitigate the negative impacts of climate change in this sub-Mediterranean region.

Funding

This work was financially supported by the German Research Foundation (Deutsche Forschungsgemeinschaft), being part of the project “the Functional Frontier among Mediterranean and Eurosiberian Plant Communities” (ECOFUMER, 441909701). Enrique G. de la Riva and Salvador Arenas-Castro are supported by María Zambrano fellowships funded by the Spanish Ministry of Universities and European Union-Next Generation Plan. Iván Prieto acknowledges funding from the Fundación Séneca (project 20654/JLI/18), co-funded by European Union ERDF funds.

Authors' contributions

Enrique G. de la Riva: funding acquisition, study design, data analyses, first draft writing. **Iván Prieto:** study design. **Jesús Rodríguez-Calcerrada:** study design, forest inventory data. **Sergio de Tomás Marín:** sample harvesting, data analyses, first draft writing. **Salvador Arenas-Castro:** data analyses. **Guillermo González:** forest inventory data. **Luis Gil:** Planning of and funding acquisition for forest inventories. All authors have reviewed and edited subsequent versions of the manuscript.

Data availability statement

The data will be archived in a public repository.

Declaration of competing interest

The authors declare that they have no conflict of interests that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors of this study would like to thank Mario Vega and all the technical staff of the “Hayedo de Montejo” for their always good willingness to facilitate our works in the forest and the interest shown in this study. Many thanks to Claudia Buchwald for her help and guidance in the lab analysis carried out for this research. Also thanks to Diego Alejandro Melo Prieto for his great help both in the field and in the lab, and to Pardis Golabvand and Marina Tsioli for their help with the lab analyses. We would also like to thank Professor Dr. Francisco Lloret for his advice on field ecological methodology and to his biology student at the time of the performance of this study Anna Ticó i Pifarré for her great help and support with the field work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2023.100097>.

References

- Albert, R.E.I.F., Xystrakis, F., Gaertner, S., Sayer, U., 2017. Floristic change at the drought limit of European beech (*Fagus sylvatica* L.) to downy oak (*Quercus pubescens*) forest in the temperate climate of central Europe. *Not. Bot. Horti. Agrob. 45* (2), 646–654. <https://doi.org/10.15835/nbha45210971>.
- Améztegui, A., Brotons, L., Coll, L., 2010. Land-use changes as major drivers of mountain pine (*Pinus uncinata* Ram.) expansion in the Pyrenees. *Global Ecol. Biogeogr. 19* (5), 632–641. <https://doi.org/10.1111/j.1466-8238.2010.00550>.
- Aranda, I., 1998. Comportamiento ecofisiológico de *F. sylvatica* L. y *Q. petraea* (Matt) Liebl. en el «Hayedo de Montejo de la Sierra» (CAM). Doctoral dissertation, Universidad Politécnica de Madrid, Madrid.
- Aranda, I., Gil, L., Pardos, J., 1996. Seasonal water relations of three broadleaved species (*Fagus sylvatica* L., *Quercus petraea* (Mattuschka) Liebl. and *Quercus pyrenaica* Willd.) in a mixed stand in the centre of the Iberian Peninsula. *For. Ecol. Manag. 84* (1–3), 219–229. [https://doi.org/10.1016/0378-1127\(96\)03729-2](https://doi.org/10.1016/0378-1127(96)03729-2).
- Aranda, I., Gil, L., Pardos, J.A., 2000. Water relations and gas exchange in *Fagus sylvatica* L. and *Quercus petraea* (Mattuschka) Liebl. in a mixed stand at their southern limit of distribution in Europe. *Trees (Berl.) 14* (6), 344–352. <https://doi.org/10.1007/s004680050229>.
- Aranda, I., Bergasa, L.F., Gil, L., Pardos, J.A., 2001. Effects of relative irradiance on the leaf structure of *Fagus sylvatica* L. seedlings planted in the understory of a *Pinus sylvestris* L. stand after thinning. *Ann. For. Sci. 58* (6), 673–680. <https://doi.org/10.1051/forest:2001154>.
- Aranda, I., Gil, L., Pardos, J.A., 2002. Physiological responses of *Fagus sylvatica* L. seedlings under *Pinus sylvestris* L. and *Quercus pyrenaica* Willd. overstories. *For. Ecol. Manag. 162* (2–3), 153–164. [https://doi.org/10.1016/S0378-1127\(01\)00502-3](https://doi.org/10.1016/S0378-1127(01)00502-3).
- Aranda, I., Gil, L., Pardos, J.A., 2005. Seasonal changes in apparent hydraulic conductance and their implications for water use of European beech (*Fagus sylvatica* L.) and sessile oak [*Quercus petraea* (Matt.) Liebl.] in South Europe. *Plant Ecol. 179* (2), 155–167. <https://doi.org/10.1007/s11258-004-7007-1>.
- Aranda, I., Rodríguez Calcerrada, J., Robson, T.M., Cano, F.J., Sánchez Gómez, D., 2013. Revisión de los aspectos funcionales de la respuesta a la sequía en *Fagus sylvatica*. *Sociedad Española de Ciencias Forestales, 6º Congreso Forestal Español*, ISBN 978-84-937964-9-5.
- Aranda, I., Cadahía, E., de Simón, B.F., 2020. Leaf ecophysiological and metabolic response in *Quercus pyrenaica* Willd seedlings to moderate drought under enriched CO₂ atmosphere. *J. Plant Physiol. 244*, 153083. <https://doi.org/10.1016/j.jplph.2019.153083>.
- Barton, K., Barton, M.K., 2015. Package ‘MuMIn’; version 1.43.17. <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf>. (Accessed 5 January 2022).
- Benito Garzón, M., Sánchez de Dios, R., Sainz Ollero, H., 2008. Effects of climate change on the distribution of Iberian tree species. *Appl. Veg. Sci. 11* (2), 169–178. <https://doi.org/10.3170/2008-7-18348>.
- Bensharada, M., Telford, R., Stern, B., Gaffney, V., 2022. Loss on ignition vs. thermogravimetric analysis: a comparative study to determine organic matter and carbonate content in sediments. *J. Paleolimnol. 67* (2), 191–197. <https://doi.org/10.1007/s10933-021-00209-6>.
- Bittebiere, A.K., Saiz, H., Mony, C., 2019. New insights from multidimensional trait space responses to competition in two clonal plant species. *Funct. Ecol. 33* (2), 297–307. <https://doi.org/10.1111/1365-2435.13220>.
- Blonder, B., 2018. Hypervolume concepts in niche- and trait-based ecology. *Ecography 41* (9), 1441–1455. <https://doi.org/10.1111/ecog.03187>.
- Blonder, B., Lamanna, C., Violle, C., Enquist, B.J., 2014. The *n*-dimensional hypervolume. *Global Ecol. Biogeogr. 23* (5), 595–609. <https://doi.org/10.1111/geb.12146>.
- Blonder, B., Kaps, R.E., Dalton, R.M., Graae, B.J., Heiling, J.M., Opedal, Ø.H., 2018a. Microenvironment and functional-trait context dependence predict alpine plant community dynamics. *J. Ecol. 106* (4), 1323–1337. <https://doi.org/10.1111/1365-2745.12973>.
- Blonder, B., Morrow, C.B., Maitner, B., Harris, D.J., Lamanna, C., Violle, C., Enquist, B.J., Kerkhoff, A.J., 2018b. New approaches for delineating *n*-dimensional hypervolumes. *Methods Ecol. Evol. 9* (2), 305–319. <https://doi.org/10.1111/2041-210X.12865>.
- Bohn, U., Weiß, W., 2003. Die potenzielle natürliche Vegetation. Klima, Pflanzen- und Tierwelt. In: *LEIBNITZ-INSTITUT FÜR LÄN-DERKUNDE [Hrsg.]: Nationalatlas Bundesrepublik Deutschland 3*, 84–87.
- Bongers, F.J., Schmid, B., Bruehlheide, H., Bongers, F., Li, S., von Oheimb, G., Li, Y., Cheng, A., Ma, K., Liu, X., 2021. Functional diversity effects on productivity increase with age in a forest biodiversity experiment. *Nat. Ecol. Evol. 5* (12), 1594–1603. <https://doi.org/10.1038/s41559-021-01564-3>.
- Bresson, C.C., Vitasse, Y., Kremer, A., Delzon, S., 2011. To what extent is altitudinal variation of functional traits driven by genetic adaptation in European oak and beech? *Tree Physiol. 31* (11), 1164–1174. <https://doi.org/10.1093/treephys/tpr084>.
- Brockerhoff, E.G., Barbaro, L., Castagneyrol, B., Forrester, D.I., Gardiner, B., González-Olabarria, J.R., Lyver, P.O.B., Meurisse, N., Oxbrough, A., Taki, H., Thompson, I.D., van der Plas, F., Jactel, H., 2017. Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodivers. Conserv. 26* (13), 3005–3035. <https://doi.org/10.1007/s10531-017-1453-2>.
- Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.J., Randin, C., Zimmermann, N.E., Graham, C.H., Guisan, A., 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecol. Biogeogr. 21* (4), 481–497. <https://doi.org/10.1111/j.1466-8238.2011.00698.x>.
- Brown, M.J., Holland, B.R., Jordan, G.J., 2020. HYPEROVERLAP: detecting biological overlap in *n*-dimensional space. *Methods Ecol. Evol. 11* (4), 513–523. <https://doi.org/10.1111/2041-210X.13363>.
- Calvo, L., Santalla, S., Marcos, E., Valbuena, L., Tárrega, R., Luis, E., 2003. Regeneration after wildfire in communities dominated by *Pinus pinaster*, an obligate seeder, and in others dominated by *Quercus pyrenaica*, a typical resprouter. *For. Ecol. Manag. 184* (1–3), 209–223. [https://doi.org/10.1016/S0378-1127\(03\)00207-X](https://doi.org/10.1016/S0378-1127(03)00207-X).
- Camarero, J.J., Gazol, A., Sangüesa-Barreda, G., Vergarechea, M., Alfaro-Sánchez, R., Cattaneo, N., Vicente-Serrano, S.M., 2021. Tree growth is more limited by drought in rear-edge forests most of the times. *For. Ecosyst. 8*, 25. <https://doi.org/10.1186/s40663-021-00303-1>.
- Camisón, Á., Miguel, R., Marcos, J.L., Revilla, J., Tardáguila, M.Á., Hernández, D., Lakićević, M., Jovellar, L.C., Silla, F., 2015. Regeneration dynamics of *Quercus pyrenaica* Willd. in the central system (Spain). *For. Ecol. Manag. 343*, 42–52. <https://doi.org/10.1016/j.foreco.2015.01.023>.
- Cano, F.J., Sánchez-Gómez, D., Rodríguez-Calcerrada, J., Warren, C.R., Gil, L., Aranda, I., 2013. Effects of drought on mesophyll conductance and photosynthetic limitations at different tree canopy layers. *Plant Cell Environ. 36* (11), 1961–1980. <https://doi.org/10.1111/pce.12103>.
- Carmona, C.P., de Bello, F., Mason, N.W., Lepš, J., 2016. Traits without borders: integrating functional diversity across scales. *Trends Ecol. Evol. 31* (5), 382–394. <https://doi.org/10.1016/j.tree.2016.02.003>.
- Carmona, C.P., de Bello, F., Mason, N.W., Lepš, J., 2019. Trait probability density (TPD): measuring functional diversity across scales based on TPD with R. *Ecology 100* (12), e02876. <https://doi.org/10.1002/ecy.2876>.
- Carter, J.L., White, D.A., 2009. Plasticity in the Huber value contributes to homeostasis in leaf water relations of a mallee Eucalypt with variation to groundwater depth. *Tree Physiol. 29* (11), 1407–1418. <https://doi.org/10.1093/treephys/tpp076>.
- Carvalho, J.C., Cardoso, P., 2020. Decomposing the causes for niche differentiation between species using hypervolumes. *Front. Ecol. Evol. 8*, 243. <https://doi.org/10.3389/fevo.2020.00243>.
- Carvalho, B., Bastias, C.C., Escudero, A., Valladares, F., Benavides, R., 2020. Intraspecific perspective of phenotypic coordination of functional traits in Scots pine. *PLoS One 15*, e0228539. <https://doi.org/10.1371/journal.pone.0228539>.
- Casson, S., Gray, J.E., 2008. Influence of environmental factors on stomatal development. *New Phytol. 178* (1), 9–23. <https://doi.org/10.1111/j.1469-8137.2007.02351.x>.
- Castañó-Santamaría, J., López-Sánchez, C.A., Obeso, J.R., Barrío-Anta, M., 2021. Structure, environmental patterns and impact of expected climate change in natural beech-dominated forests in the Cantabrian Range (NW Spain). *For. Ecol. Manag. 497*, 119512. <https://doi.org/10.1016/j.foreco.2021.119512>.
- Castro, J., Zamora, R., Hódar, J.A., 2006. Restoring *Quercus pyrenaica* forests using pioneer shrubs as nurse plants. *Appl. Veg. Sci. 9* (1), 137–142. <https://doi.org/10.1111/j.1654-109X.2006.tb00663.x>.
- Cavender-Bares, J., Ackerly, D.D., Hobbie, S.E., Townsend, P.A., 2016. Evolutionary legacy effects on ecosystems: biogeographic origins, plant traits, and implications for management in the era of global change. *Annu. Rev. Ecol. Syst. 47*, 433–462. <https://doi.org/10.1146/annurev-ecolsys-121415-032229>.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. *Ecol. Lett. 12* (4), 351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285>.
- Chesson, P., 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Systemat. 31* (1), 343–366. <https://doi.org/10.1146/annurev.ecolsys.31.1.343>.
- Cocozza, C., De Miguel, M., Pšidová, E., Ditmarová, L.U., Marino, S., Maiuro, L., Alvino, A., Czajkowski, T., Bolte, A., Tognetti, R., 2016. Variation in ecophysiological traits and drought tolerance of beech (*Fagus sylvatica* L.) seedlings from different populations. *Front. Plant Sci. 7*, 886. <https://doi.org/10.3389/fpls.2016.00886>.
- Corcuera, L., Camarero, J.J., Sisó, S., Gil-Pelegrín, E., 2006. Radial-growth and wood-anatomical changes in overaged *Quercus pyrenaica* coppice stands: functional responses in a new Mediterranean landscape. *Trees (Berl.) 20* (1), 91–98. <https://doi.org/10.1007/s00468-005-0016-4>.
- Curt, T., Coll, L., Prévosto, B., Balandier, P., Kunstler, G., 2005. Plasticity in growth, biomass allocation and root morphology in beech seedlings as induced by irradiance and herbaceous competition. *Ann. For. Sci. 62* (1), 51–60. <https://doi.org/10.1051/forest:2004092>.
- de la Riva, E.G., Tosto, A., Pérez-Ramos, I.M., Navarro-Fernández, C.M., Olmo, M., Anten, N.P., Marañón, T., Villar, R., 2016. A plant economics spectrum in Mediterranean forests along environmental gradients: is there coordination among leaf, stem and root traits? *J. Veg. Sci. 27* (1), 187–199. <https://doi.org/10.1111/jvs.12341>.
- de la Riva, E.G., Marañón, T., Violle, C., Villar, R., Pérez-Ramos, I.M., 2017. Biogeochemical and ecomorphological niche segregation of Mediterranean woody species along a local gradient. *Front. Plant Sci. 8*, 1242.
- de la Riva, E.G., Marañón, T., Pérez-Ramos, I.M., Navarro-Fernández, C.M., Olmo, M., Villar, R., 2018a. Root traits across environmental gradients in Mediterranean woody communities: are they aligned along the root economics spectrum? *Plant Soil 424* (1), 35–48. <https://doi.org/10.1007/s11104-017-3433-4>.
- de la Riva, E.G., Violle, C., Pérez-Ramos, I.M., Marañón, T., Navarro-Fernández, C., Olmo, M., Villar, R., 2018b. A multidimensional functional trait approach reveals the imprint of environmental stress in Mediterranean woody plant communities. *Ecosystems 21*, 248–262. <https://doi.org/10.1007/s10021-017-0147-7>.
- de la Riva, E.G., Prieto, I., Marañón, T., Pérez-Ramos, I.M., Olmo, M., Villar, R., 2021a. Root economics spectrum and construction costs in Mediterranean woody plants: the

- role of symbiotic associations and the environment. *J. Ecol.* 109 (4), 1873–1885. <https://doi.org/10.1111/1365-2745.13612>.
- de la Riva, E.G., Quejreja, J.I., Villar, R., Pérez-Ramos, I.M., Marañón, T., Galán Díaz, J., de Tomás Marín, S., Prieto, I., 2021b. The economics spectrum drives root trait strategies in Mediterranean vegetation. *Front. Plant Sci.* 12, 773118. <https://doi.org/10.3389/fpls.2021.773118>.
- Delpiano, C.A., Prieto, I., Loayza, A.P., Carvajal, D.E., Squeo, F.A., 2020. Different responses of leaf and root traits to changes in soil nutrient availability do not converge into a community-level plant economics spectrum. *Plant Soil* 450 (1), 463–478. <https://doi.org/10.1007/s11104-020-04515-2>.
- Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F.T., d'Amen, M., Randin, C., Engler, R., Pottier, J., Pio, D., Dubuis, A., Pellissier, L., Mateo, R.G., Hordijk, W., Salamin, N., Guisan, A., 2017. ecospat: an R package to support spatial analyses and modeling of species niches and distributions. *Ecography* 40 (6), 774–787. <https://doi.org/10.1111/ecog.02671>.
- Didion, M., Kupferschmid, A.D., Wolf, A., Bugmann, H., 2011. Ungulate herbivory modifies the effects of climate change on mountain forests. *Clim. Change* 109 (3), 647–669. <https://doi.org/10.1007/s10584-011-0054-4>.
- Dorado-Liñán, I., Zorita, E., Martínez-Sancho, E., Gea-Izquierdo, G., Di Filippo, A., Gutiérrez, E., Levanic, T., Piovesan, G., Vacchiano, G., Zang, C., Zlatanov, T., Menzel, A., 2017. Large-scale atmospheric circulation enhances the Mediterranean East-West tree growth contrast at rear-edge deciduous forests. *Agri. For. Meteorol.* 239, 86–95. <https://doi.org/10.1016/j.agrformet.2017.02.029>.
- Dorado-Liñán, I., Piovesan, G., Martínez-Sancho, E., Gea-Izquierdo, G., Zang, C., Cañellas, I., Castagneri, D., Di Filippo, A., Gutiérrez, E., Ewald, J., Fernández-de-Uña, L., Hornstein, D., Jantsch, M.C., Levanic, T., Mellert, K.H., Vacchiano, G., Zlatanov, T., Menzel, A., 2019. Geographical adaptation prevails over species-specific determinism in trees' vulnerability to climate change at Mediterranean rear-edge forests. *Global Change Biol.* 25 (4), 1296–1314. <https://doi.org/10.1111/gcb.14544>.
- Durrant, T.H., De Rigo, D., Caudullo, G., 2016. *Fagus sylvatica* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayza, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg.
- Ellenberg, H.H., 1988. *Vegetation Ecology of Central Europe*. Cambridge University Press.
- Falk, W., Hempelmann, N., 2013. Species favourability shift in Europe due to climate change: a case study for *Fagus sylvatica* L. and *Picea abies* (L.) Karst. based on an ensemble of climate models. *J. Climatol.* 2013, 787250. <https://doi.org/10.1155/2013/787250>.
- Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Biol.* 40 (1), 503–537. <https://doi.org/10.1146/annurev.pp.40.060189.002443>.
- Fréjaville, T., Vizcaíno-Palomar, N., Fady, B., Kremer, A., Benito Garzón, M., 2020. Range margin populations show high climate adaptation lags in European trees. *Global Change Biol.* 26 (2), 484–495. <https://doi.org/10.1111/gcb.14881>.
- Freschet, G.T., Roumet, C., Comas, L.H., Weemstra, M., Bengough, A.G., Rewald, B., Bardgett, R.D., De Deyn, G.B., Johnson, D., Klimesova, J., Lukac, M., McCormack, M.L., Meier, I.C., Pagès, L., Poorter, H., Prieto, I., Wurzbarger, N., Zadowny, M., Bagniewska-Zadworna, A., Blancaflor, E.B., Brunner, I., Gessler, A., Hobbie, S.E., Iversen, C.M., Mommer, L., Picon-Cochard, C., Postma, J.A., Rose, L., Ryser, P., Scherer-Lorenzen, M., Soudzilovskaia, N.A., Sun, T., Valverde-Barrantes, O.J., Weigelt, A., York, L.M., Stokes, A., 2021. Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. *New Phytol.* 232 (3), 1123–1158. <https://doi.org/10.1111/nph.17072>.
- Galán Díaz, J., de la Riva, E.G., Funk, J.L., Vilà, M., 2021. Functional segregation of resource-use strategies of native and invasive plants across Mediterranean biome communities. *Biol. Invasions* 23 (1), 253–266. <https://doi.org/10.1007/s10530-020-02368-5>.
- García, I., Jiménez, P., 2009. *Robledales de Quercus pyrenaica y robledales de Quercus robur y Quercus pyrenaica del Noroeste Ibérico*. En: VV. AA., *Bases Ecológicas Preliminares para la Conservación de los Tipos de Hábitat de Interés Comunitario en España*. Madrid: Ministerio de Medio Ambiente y Medio Rural y Marino, p. 66. ISBN: 978-84-491-0911-9.
- Garnier, E., Navas, M.L., 2012. A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review. *Agron. Sustain. Dev.* 32 (2), 365–399. <https://doi.org/10.1007/s13593-011-0036-y>.
- Gavilán, R.G., Vilches, B., Gutiérrez-Girón, A., Blanquer, J.M., Escudero, A., 2018. Sclerophyllous versus deciduous forests in the Iberian Peninsula: a standard case of Mediterranean climatic vegetation distribution. In: Grellier, A.M., Fujiwara, K., Pedrotti, F. (Eds.), *Geographical Changes in Vegetation and Plant Functional Types*. Springer, Cham, pp. 101–116. https://doi.org/10.1007/978-3-319-68738-4_5.
- Gea-Izquierdo, G., Aranda, I., Cañellas, I., Dorado-Liñán, I., Olano, J.M., Martín-Benito, D., 2021. Contrasting species decline but high sensitivity to increasing water stress on a mixed pine–oak ecotone. *J. Ecol.* 109 (1), 109–124. <https://doi.org/10.1111/1365-2745.13450>.
- Gil, L., Näger, J.A., González Doncel, I., Aranda García, I., Gonzalo Jiménez, J., López de Heredia, U., Millerón, M., Nanos, N., García-Calvo, R.P., Rodríguez Calcerrada, J., Valbuena Carabana, M., 2010. El hayedo de Montejo: una Gestión Sostenible. Dirección General de Medio Ambiente, Universidad Politécnica de Madrid, Madrid. ISBN:978-84-451-3218-0.
- González-González, B.D., Rozas, V., García-González, I., 2014. Earlywood vessels of the sub-Mediterranean oak *Quercus pyrenaica* have greater plasticity and sensitivity than those of the temperate *Q. petraea* at the Atlantic–Mediterranean boundary. *Trees (Berl.)* 28 (1), 237–252. <https://doi.org/10.1007/s00468-013-0945-2>.
- Gray, L.K., Hamann, A., 2013. Tracking suitable habitat for tree populations under climate change in western North America. *Clim. Change* 117 (1), 289–303. <https://doi.org/10.1007/s10584-012-0548-8>.
- Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* 24 (4), 699–711. <https://doi.org/10.1111/j.1420-9101.2010.02210.x>.
- Hacke, U., Sauter, J.J., 1995. Vulnerability of xylem to embolism in relation to leaf water potential and stomatal conductance in *Fagus sylvatica* f. *purpurea* and *Populus balsamifera*. *J. Exp. Bot.* 46 (9), 1177–1183. <https://doi.org/10.1093/jxb/46.9.1177>.
- Hampe, A., 2004. Bioclimate envelope models: what they detect and what they hide. *Global Ecol. Biogeogr.* 13 (5), 469–471. <https://doi.org/10.1111/j.1466-822X.2004.00090.x>.
- Helsen, K., Van Cleemput, E., Bassi, L., Graae, B.J., Somers, B., Blonder, B., Honnay, O., 2020. Inter-and intraspecific trait variation shape multidimensional trait overlap between two plant invaders and the invaded communities. *Oikos* 129 (5), 677–688. <https://doi.org/10.1111/oik.06919>.
- Hernández Bermejo, J.E., Costa Tenorio, M., Sáinz Ollero, H., Clemente Muñoz, M., 1982. *Catálogo florístico del hayedo de Montejo de la Sierra (provincia de Madrid)*. *Lagascalia* 11 (1), 3–65.
- Hernández, L., Sánchez de Dios, R., Montes, F., Sainz-Ollero, H., Cañellas, I., 2017. Exploring range shifts of contrasting tree species across a bioclimatic transition zone. *Eur. J. For. Res.* 136 (3), 481–492. <https://doi.org/10.1007/s10342-017-1047-2>.
- Hernández-Santana, V., Martínez-Fernández, J., Morán, C., Cano, A., 2008. Response of *Quercus pyrenaica* (melojo oak) to soil water deficit: a case study in Spain. *Eur. J. For. Res.* 127 (5), 369–378. <https://doi.org/10.1007/s10342-008-0214-x>.
- Hope, A.C., 1968. A simplified Monte Carlo significance test procedure. *J. Roy. Stat. Soc. Ser. B Methodol.* 30 (3), 582–598. <https://doi.org/10.1111/j.2517-6161.1968.tb00759.x>.
- Houba, V.J.G., Temminghoff, E.J.M., Gaikhorst, G.A., Van Vark, W., 2000. Soil analysis procedures using 0.01 M calcium chloride as extraction reagent. *Commun. Soil Sci. Plant Anal.* 31 (9–10), 1299–1396. <https://doi.org/10.1080/00103620009370514>.
- Illés, G., Móríz, N., 2022. Climate envelope analyses suggests significant rearrangements in the distribution ranges of Central European tree species. *Ann. For. Sci.* 79, 35. <https://doi.org/10.1186/s13595-022-01154-8>.
- Jackson, R.B., Sperry, J.S., Dawson, T.E., 2000. Root water uptake and transport: using physiological processes in global predictions. *Trends Plant Sci.* 5 (11), 482–488. [https://doi.org/10.1016/S1360-1385\(00\)01766-0](https://doi.org/10.1016/S1360-1385(00)01766-0).
- Jiménez, P., Díaz-Fernández, P., Martín, S., Gil, L., 1998. *Regiones de procedencia de Quercus pyrenaica Willd., Q. faginea Lam. y Q. canariensis Willd.* Organismo Autónomo Parques Nacionales. Madrid, ES 311-98-007-4.
- Jonsson, M., Bengtsson, J., Gamfeldt, L., Moen, J., Snäll, T., 2019. Levels of forest ecosystem services depend on specific mixtures of commercial tree species. *Native Plants* 5 (2), 141–147. <https://doi.org/10.1038/s41477-018-0346-z>.
- Jung, V., Violle, C., Mondy, C., Hoffmann, L., Muller, S., 2010. Intraspecific variability and trait-based community assembly. *J. Ecol.* 98 (5), 1134–1140. <https://doi.org/10.1111/j.1365-2745.2010.01687.x>.
- Kouba, Y., Camarero, J.J., Alados, C.L., 2012. Roles of land-use and climate change on the establishment and regeneration dynamics of Mediterranean semi-deciduous oak forests. *For. Ecol. Manag.* 274, 143–150. <https://doi.org/10.1016/j.foreco.2012.02.033>.
- Kraft, N.J., Godoy, O., Levine, J.M., 2015. Plant functional traits and the multidimensional nature of species coexistence. *Proc. Natl. Acad. Sci. USA* 112 (3), 797–802. <https://doi.org/10.1073/pnas.1413650112>.
- Kramer, K., Degen, B., Buschbom, J., Hickler, T., Thuiller, W., Sykes, M.T., de Winter, W., 2010. Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change—range, abundance, genetic diversity and adaptive response. *For. Ecol. Manag.* 259 (11), 2213–2222. <https://doi.org/10.1016/j.foreco.2009.12.023>.
- Laureano, R.G., Lazo, Y.O., Linares, J.C., Luque, A., Martínez, F., Seco, J.I., Merino, J., 2008. The cost of stress resistance: construction and maintenance costs of leaves and roots in two populations of *Quercus ilex*. *Tree Physiol.* 28 (11), 1721–1728. <https://doi.org/10.1007/s11104-012-1296-2>.
- Leuschner, C., Backes, K., Hertel, D., Schipka, F., Schmitt, U., Terborg, O., Runge, M., 2001. Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. *For. Ecol. Manag.* 149 (1–3), 33–46. [https://doi.org/10.1016/S0378-1127\(00\)00543-0](https://doi.org/10.1016/S0378-1127(00)00543-0).
- Lloret, F., de la Riva, E.G., Pérez-Ramos, I.M., Marañón, T., Saura-Mas, S., Díaz-Delgado, R., Villar, R., 2016. Climatic events inducing die-off in Mediterranean shrublands: are species' responses related to their functional traits? *Oecologia* 180 (4), 961–973. <https://doi.org/10.1007/s00442-016-3550-4>.
- Loidi, J., 2017. *The Vegetation of the Iberian Peninsula*. Springer, Cham. <https://doi.org/10.1007/978-3-319-54867-8>.
- Lorite, J., Salazar, C., Peñast, J., Valle, F., 2008. Phytosociological review on the forests of *Quercus pyrenaica* Willd. *Acta Bot. Gall.* 155 (2), 219–233. <https://doi.org/10.1080/12538078.2008.10516105>.
- MacArthur, R., Levins, R., 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* 101 (921), 377–385.
- Mao, W., Zhao, X., Sun, Z., Felton, A.J., Zhang, T., Li, Y., Smith, M.D., 2018. Limiting similarity mediates plant community niche hypervolume across a desert-steppe ecotone of Inner Mongolia. *Environ. Exp. Bot.* 153, 320–326. <https://doi.org/10.1016/j.envexpbot.2018.06.011>.
- Maracchi, G., Sirotenko, O., Bindi, M., 2005. Impacts of present and future climate variability on agriculture and forestry in the temperate regions: Europe. *Clim. Change* 70 (1), 117–135. <https://doi.org/10.1007/s10071-004-0166-7>.
- Martínez del Castillo, E., García-Martín, A., Aladrén, L.A.L., de Luis, M., 2015. Evaluation of forest cover change using remote sensing techniques and landscape metrics in Moncayo Natural Park (Spain). *Appl. Geogr.* 62, 247–255. <https://doi.org/10.1016/j.apgeog.2015.05.002>.

- Mayfield, M.M., Levine, J.M., 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol. Lett.* 13 (9), 1085–1093. <https://doi.org/10.1111/j.1461-0248.2010.01509>.
- McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21 (4), 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>.
- Meier, I.C., Leuschner, C., 2008. Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. *Global Change Biol.* 14 (9), 2081–2095. <https://doi.org/10.1111/j.1365-2486.2008.01634.x>.
- Mencuccini, M., Rosas, T., Rowland, L., Choat, B., Cornelissen, H., Jansen, S., Kramer, K., Lapenis, A., Manzoni, S., Niinemets, Ü., Reich, P.B., Schrodt, F., Soudzilovskaia, N., Wright, I.J., Martínez-Vilalta, J., 2019. Leaf economics and plant hydraulics drive leaf wood area ratios. *New Phytol.* 224 (4), 1544–1556. <https://doi.org/10.1111/nph.15998>.
- Mey, R., Zell, J., Thürig, E., Stadelmann, G., Bugmann, H., Temperli, C., 2022. Tree species admixture increases ecosystem service provision in simulated spruce-and beech-dominated stands. *Eur. J. For. Res.* 141, 801–820. <https://doi.org/10.1007/s10342-022-01474-4>.
- Meyer, P., Tabaku, V., Von Lupke, B., 2003. Die Struktur albanischer Rotbuchen-Urwälder – Ableitungen für eine naturnahe Buchenwirtschaft. Structural characteristics of Albanian beech (*Fagus sylvatica* L.) virgin forests — deductions for semi-natural forestry. *Forstwiss. Cent.blatt* 122 (1), 47–58. <https://doi.org/10.1046/j.1439-0337.2003.02041.x>.
- Milios, E., Papalexandris, C., 2019. Height growth of sprouts emerged from small stumps and seed origin saplings under shade, in low elevation *Fagus sylvatica* L. s.l. stands in Greece. *Dendrobiology* 82, 1–7. <https://doi.org/10.12657/denbio.082.001>.
- Millerón, M., López de Heredia, U., Lorenzo, Z., Perea, R., Dounavi, A., Alonso, J., Gil, L., Nanos, N., 2012. Effect of canopy closure on pollen dispersal in a wind-pollinated species (*Fagus sylvatica* L.). *Plant Ecol.* 213 (11), 1715–1728. <https://doi.org/10.1007/s11258-012-0125-2>.
- Moreno, J.A.C., de las Heras Puñal, P., Estébanez, N.L., Martín, M.J.R., 2005. Caracterización paisajística y ecológica de la Sierra del Rincon (Madrid). Centro de Investigaciones Ambientales de la Comunidad de Madrid, Comunidad de Madrid. <https://doi.org/10.13140/2.1.4707.2322>.
- Murphy, L., 2015. Package ‘likelihood’; version 1.7. <https://cran.r-project.org/web/packages/likelihood/likelihood.pdf>. (Accessed 5 January 2022).
- Nanos, N., Pardo, F., Nager, J.A., Pardos, J.A., Gil, L., 2005. Using multivariate factorial kriging for multiscale ordination: a case study. *Can. J. For. Res.* 35 (12), 2860–2874. <https://doi.org/10.1139/x05-211>.
- Nock, C.A., Vogt, R.J., Beisner, B.E., 2016. Functional traits. eLS 1–8. <https://doi.org/10.1002/9780470015902.a0026282>.
- Ohse, B., Seele, C., Holzwarth, F., Wirth, C., 2017. Different facets of tree sapling diversity influence browsing intensity by deer depending on spatial scale. *Ecol. Evol.* 7 (17), 6779–6789. <https://doi.org/10.1002/ece3.3217>.
- Packham, J.R., Thomas, P.A., Atkinson, M.D., Degen, T., 2012. Biological Flora of the British Isles: *Fagus sylvatica*. *J. Ecol.* 100 (6), 1557–1608. <https://doi.org/10.1111/j.1365-2745.2012.02017.x>.
- Palombo, C., Chirici, G., Marchetti, M., Tognetti, R., 2013. Is land abandonment affecting forest dynamics at high elevation in Mediterranean mountains more than climate change? *Plant Biosyst.* 147 (1), 1–11. <https://doi.org/10.1080/11263504.2013.772081>.
- Pardo, F., Gil, L., 2005. The impact of traditional land use on woodlands: a case study in the Spanish Central System. *J. Hist. Geogr.* 31 (3), 390–408. <https://doi.org/10.1016/j.jhg.2004.11.002>.
- Pardo, F., Gil, L., Pardos, J.A., 1997. Field study of beech (*Fagus sylvatica* L.) and melojo oak (*Quercus pyrenaica* Willd.) leaf litter decomposition in the centre of the Iberian Peninsula. *Plant Soil* 191 (1), 89–100. <https://doi.org/10.1023/A:1004237305438>.
- Pardo, F., Gil, L., Pardos, J.A., 2004. Structure and composition of pole-stage stands developed in an ancient wood pasture in central Spain. *Forestry* 77 (1), 67–74. <https://doi.org/10.1007/s13595-020-01004-5>.
- Pearman, P.B., Guisan, A., Broennimann, O., Randin, C.F., 2008. Niche dynamics in space and time. *Trends Ecol. Evol.* 23 (3), 149–158. <https://doi.org/10.1016/j.tree.2007.11.005>.
- Peguero-Pina, J.J., Sisó, S., Sancho-Knapik, D., Díaz-Espejo, A., Flexas, J., Galmés, J., Gil-Pelegrín, E., 2015. Leaf morphological and physiological adaptations of a deciduous oak (*Quercus faginea* Lam.) to the Mediterranean climate: a comparison with a closely related temperate species (*Quercus robur* L.). *Tree Physiol.* 36 (3), 287–299. <https://doi.org/10.1093/treephys/tpv107>.
- Peña-Angulo, D., Khorchani, M., Errea, P., Lasanta, T., Martínez-Arnáiz, M., Nadal-Romero, E., 2019. Factors explaining the diversity of land cover in abandoned fields in a Mediterranean mountain area. *Catena* 181, 104064. <https://doi.org/10.1016/j.catena.2019.05.010>.
- Peñuelas, J., Boada, M., 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biol.* 9 (2), 131–140. <https://doi.org/10.1046/j.1365-2486.2003.00566.x>.
- Peñuelas, J., Ogaya, R., Boada, M., Jump, S.A., 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). *Ecography* 30 (6), 829–837. <https://doi.org/10.1111/j.2007.0906-7590.05247.x>.
- Perea, R., López-Sánchez, A., Pallares, J., Gordaliza, G.G., González-Doncel, I., Gil, L., Rodríguez-Calcerrada, J., 2020. Tree recruitment in a drought-and herbivory-stressed oak-beech forest: implications for future species coexistence. *For. Ecol. Manag.* 477, 118489. <https://doi.org/10.1016/j.foreco.2020.118489>.
- Pérez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., van der Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* 61, 167–234. <https://doi.org/10.1071/BT12225>.
- Pérez-Luque, A.J., Benito, B.M., Bonet-García, F.J., Zamora, R., 2020. Ecological diversity within rear-edge: a case study from mediterranean *Quercus pyrenaica* Willd. *Forests* 12 (1), 10. <https://doi.org/10.3390/f12010010>.
- Peuke, A.D., Gessler, A., Rennenberg, H., 2006. The effect of drought on C and N stable isotopes in different fractions of leaves, stems and roots of sensitive and tolerant beech ecotypes. *Plant Cell Environ.* 29 (5), 823–835. <https://doi.org/10.1111/j.1365-3040.2005.01452.x>.
- Poorter, H., De Jong, R.O.B., 1999. A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytol.* 143 (1), 163–176. <https://doi.org/10.1046/J.1469-8137.1999.00428.X>.
- Pratt, R.B., Jacobsen, A.L., Ewers, F.W., Davis, S.D., 2007. Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. *New Phytol.* 174 (4), 787–798. <https://doi.org/10.1111/j.1469-8137.2007.02061>.
- Prieto, I., Roumet, C., Cardinael, R., Dupraz, C., Jourdan, C., Kim, J.H., Maeght, J.L., Mao, Z., Pierret, A., Portillo, N., Rounsard, O., Thammahacksa, C., Stokes, A., 2015. Root functional parameters along a land-use gradient: evidence of a community-level economics spectrum. *J. Ecol.* 103 (2), 361–373. <https://doi.org/10.1111/1365-2745.12351>.
- Prieto, I., Querejeta, J.I., Segrestin, J., Volaire, F., Roumet, C., 2018. Leaf carbon and oxygen isotopes are coordinated with the leaf economics spectrum in Mediterranean rangeland species. *Funct. Ecol.* 32 (3), 612–625. <https://doi.org/10.1111/1365-2435.13025>.
- Pšidová, E., Živčák, M., Stojnič, S., Orlovič, S., Gómory, D., Kučerová, J., Ditmarová, L., Strelcová, K., Brestič, M., Kalaji, H.M., 2018. Altitude of origin influences the responses of PSII photochemistry to heat waves in European beech (*Fagus sylvatica* L.). *Environ. Exp. Bot.* 152, 97–106. <https://doi.org/10.1016/j.envexpbot.2017.12.001>.
- Querejeta, J.I., Prieto, I., Torres, P., Campoy, M., Alguacil, M.M., Roldán, A., 2018. Water-spender strategy is linked to higher leaf nutrient concentrations across plant species colonizing a dry and nutrient-poor epiphytic habitat. *Environ. Exp. Bot.* 153, 302–310. <https://doi.org/10.1016/j.envexpbot.2018.06.007>.
- Querejeta, J.I., Ren, W., Prieto, I., 2021. Vertical decoupling of soil nutrients and water under climate warming reduces plant cumulative nutrient uptake, water-use efficiency and productivity. *New Phytol.* 230 (4), 1378–1393. <https://doi.org/10.1111/nph.17258>.
- Querejeta, J.I., Prieto, I., Armas, C., Casanoves, F., Diémé, J.S., Diouf, M., Yossi, H., Pugnaire, F.I., Rusch, G.M., 2022. Higher leaf nitrogen content is linked to tighter stomatal regulation of transpiration and more efficient water use across dryland trees. *New Phytol.* 235, 1351–1364. <https://doi.org/10.1111/nph.18254>.
- Quézel, P., 1985. *Definition of the Mediterranean Region and the Origin of its Flora*. Geobotany, Dordrecht.
- Quintano, P.N., Caudullo, G., de Rigo, D., 2016. *Quercus pyrenaica* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg, p. e01f807+.
- R Core Team, 2021. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Regent Instruments, Win/MacRHIZO, V, 2001. *5.0A User's Guide, Regent Instruments*. Québec, QC.
- Rivas-Martínez, S., Penas, Á., Díaz González, T.E., Ladero Álvarez, M., Asensi Marfil, A., Díez Garretas, B., Molero Mesa, J., Valle Tendo, F., Cano, E., Costa Talens, M., López, M.L., Fernández Prieto, J.A., Llorens, L., del Arco, M., Pérez de Paz, P.L., Wildpret de la Torre, W., Sánchez Mata, D., Fernández, F., Masalles Raurell, R., Ladero Fernández, M., Izco Sevillano, J., Amigo, J., Loidi Arregui, J., Alcaraz Ariza, F., del Río, S., Herrero, L., 2011. Mapa de series, geoserías y geopermaserías de vegetación de España (Memoria del mapa de vegetación potencial de España). Parte II. *Itenera Geobot* 18 (2), 425–800.
- Robert, E.M., Mencuccini, M., Martínez-Vilalta, J., 2017. The anatomy and functioning of the xylem in oaks. In: Gil-Pelegrín, E., Peguero-Pina, J.J., Sancho-Knapik, D. (Eds.), *Oaks Physiological Ecology. Exploring the Functional Diversity of Genus Quercus*. L. Springer, Cham, pp. 261–302. https://doi.org/10.1007/978-3-319-69099-5_8.
- Robson, T.M., Rodríguez-Calcerrada, J., Sánchez-Gómez, D., Aranda, I., 2009. Summer drought impedes beech seedling performance more in a sub-Mediterranean forest understory than in small gaps. *Tree Physiol.* 29 (2), 249–259. <https://doi.org/10.1093/treephys/tpn023>.
- Rodríguez-Calcerrada, J., Nanos, N., Del Rey, M.C., de Heredia, U.L., Escibano, R., Gil, L., 2011. Small-scale variation of vegetation in a mixed forest understory is partly controlled by the effect of overstorey composition on litter accumulation. *J. For. Res.* 16 (6), 473–483. <https://doi.org/10.1007/s10310-010-0237-2>.
- Rodríguez-Calcerrada, J., Salomón, R.L., Gordaliza, G.G., Miranda, J.C., Miranda, E., de la Riva, E.G., Gil, L., 2019. Respiratory costs of producing and maintaining stem biomass in eight co-occurring tree species. *Tree Physiol.* 39 (11), 1838–1854. <https://doi.org/10.1093/treephys/tpz069>.
- Roumet, C., Birouste, M., Picon-Cochard, C., Ghestem, M., Osman, N., Vriignon-Brenas, S., Cao, K., Stokes, A., 2016. Root structure–function relationships in 74 species: evidence of a root economics spectrum related to carbon economy. *New Phytol.* 210 (3), 815–826. <https://doi.org/10.1111/nph.13828>.

- Rubio-Cuadrado, Á., Camarero, J.J., del Río, M., Sánchez-González, M., Ruiz-Peinado, R., Bravo-Oviedo, A., Gil, L., Montes, F., 2018a. Long-term impacts of drought on growth and forest dynamics in a temperate beech-oak-birch forest. *Agri. For. Meteorol.* 259, 48–59. <https://doi.org/10.1016/j.agrformet.2018.04.015>.
- Rubio-Cuadrado, Á., Camarero, J.J., del Río, M., Sánchez-González, M., Ruiz-Peinado, R., Bravo-Oviedo, A., Gil, L., Montes, F., 2018b. Drought modifies tree competitiveness in an oak-beech temperate forest. *For. Ecol. Manag.* 429, 7–17. <https://doi.org/10.1016/j.foreco.2018.06.035>.
- Rubio-Cuadrado, Á., Camarero, J.J., Gordaliza, G.G., Cerioni, M., Montes, F., Gil, L., 2020. Competition overrides climate as trigger of growth decline in a mixed Fagaceae Mediterranean rear-edge forest. *Ann. For. Sci.* 77, 94. <https://doi.org/10.1007/s13595-020-01004-5>.
- Rubio-Cuadrado, Á., Camarero, J.J., Rodríguez-Calcerrada, J., Perea, R., Gómez, C., Montes, F., Gil, L., 2021. Impact of successive spring frosts on leaf phenology and radial growth in three deciduous tree species with contrasting climate requirements in central Spain. *Tree Physiol.* 41 (12), 2279–2292. <https://doi.org/10.1093/treephys/tpab076>.
- Ruiz-Labourdette, D., Nogués-Bravo, D., Ollero, H.S., Schmitz, M.F., Pineda, F.D., 2012. Forest composition in Mediterranean mountains is projected to shift along the entire elevational gradient under climate change. *J. Biogeogr.* 39 (1), 162–176. <https://doi.org/10.1111/j.1365-2699.2011.02592>.
- Salomón, R., Rodríguez-Calcerrada, J., González-Doncel, I., Gil, L., Valbuena-Carabana, M., 2017. On the general failure of coppice conversion into high forest in *Quercus pyrenaica* stands: a genetic and physiological approach. *Folia Geobot.* 52 (1), 101–112. <https://doi.org/10.1007/s12224-016-9257-9>.
- Sánchez de Dios, R., Benito-Garzon, M., Sainz-Ollero, H., 2009. Present and future extension of the Iberian submediterranean territories as determined from the distribution of marcescent oaks. *Plant Ecol.* 204 (2), 189–205. <https://doi.org/10.1007/s11258-009-9584-5>.
- Sánchez de Dios, R., Gómez, C., Aullo, I., Canellas, I., Gea-Izquierdo, G., Montes, F., Sainz-Ollero, H., Velázquez, J.C., Hernández, L., 2021. *Fagus sylvatica* L. peripheral populations in the mediterranean Iberian Peninsula: climatic or anthropic relicts? *Ecosystems* 24 (1), 211–226. <https://doi.org/10.1007/s10021-020-00513-8>.
- Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9 (7), 671–675. <https://doi.org/10.1038/nmeth.2089>.
- Schöb, C., Armas, C., Guler, M., Prieto, I., Pugnaire, F.I., 2013. Variability in functional traits mediates plant interactions along stress gradients. *J. Ecol.* 101 (3), 753–762. <https://doi.org/10.1111/1365-2745.12062>.
- Schoener, T.W., 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49 (4), 704–726.
- Schüller, H., 1969. Die CAL-Methode, eine neue Methode zur Bestimmung des pflanzenverfügbaren Phosphates in Böden. *Z. für Pflanzenernährung Bodenkunde* 123 (1), 48–63. <https://doi.org/10.1002/jpln.19691230106>.
- Shipley, B., Vu, T.T., 2002. Dry matter content as a measure of dry matter concentration in plants and their parts. *New Phytol.* 153 (2), 359–364. <https://doi.org/10.1046/j.0028-646X.2001.00320.x>.
- Speziale, K.L., Ezcurra, C., 2011. Patterns of alien plant invasions in northwestern Patagonia, Argentina. *J. Arid Environ.* 75 (10), 890–897. <https://doi.org/10.1016/j.jaridenv.2011.04.014>.
- Steppe, K., Lemeur, R., 2007. Effects of ring-porous and diffuse-porous stem wood anatomy on the hydraulic parameters used in a water flow and storage model. *Tree Physiol.* 27 (1), 43–52. <https://doi.org/10.1093/treephys/27.1.43>.
- Stojnic, S., Orlovic, S., Trudic, B., Zivkovic, U., von Wuehlisch, G., Miljkovic, D., 2015. Phenotypic plasticity of European beech (*Fagus sylvatica* L.) stomatal features under water deficit assessed in provenance trial. *Dendrobiology* 73, 163–173. <https://doi.org/10.12657/denbio.073.017>.
- Torchiano, M., 2018. Effsize: efficient effect size computation. <https://doi.org/10.5281/zenodo.1480624>.
- Valbuena-Carabana, M., Gil, L., 2013. Genetic resilience in a historically profited root sprouting oak (*Quercus pyrenaica* Willd.) at its southern boundary. *Tree Genet. Genomes* 9 (5), 1129–1142. <https://doi.org/10.1007/s11295-013-0614-z>.
- Van de Peer, T., Verheyen, K., Kint, V., Van Cleemput, E., Muys, B., 2017. Plasticity of tree architecture through interspecific and intraspecific competition in a young experimental plantation. *For. Ecol. Manag.* 385, 1–9. <https://doi.org/10.1016/j.foreco.2016.11.015>.
- van der Merwe, S., Greve, M., Olivier, B., le Roux, P.C., 2021. Testing the role of functional trait expression in plant–plant facilitation. *Funct. Ecol.* 35 (1), 255–265. <https://doi.org/10.1111/1365-2435.13681>.
- VanDerWal, J., Shoo, L.P., Johnson, C.N., Williams, S.E., 2009. Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. *Am. Nat.* 174 (2), 282–291. <https://doi.org/10.1086/600087>.
- Vila-Viçosa, C., Arenas-Castro, S., Marcos, B., Honrado, J., García, C., Vázquez, F.M., Almeida, R., Gonçalves, J., 2020a. Combining satellite remote sensing and climate data in species distribution models to improve the conservation of Iberian white oaks (*Quercus* L.). *ISPRS Int. J. Geo-Inf.* 9 (12), 735. <https://doi.org/10.3390/ijgi9120735>.
- Vila-Viçosa, C., Gonçalves, J., Honrado, J., Lomba, A., Almeida, R.S., Vázquez, F.M., García, C., 2020b. Late Quaternary range shifts of marcescent oaks unveil the dynamics of a major biogeographic transition in southern Europe. *Sci. Rep.* 10, 21598. <https://doi.org/10.1038/s41598-020-78576-9>.
- Villar, R., Merino, J., 2001. Comparison of leaf construction costs in woody species with differing leaf life-spans in contrasting ecosystems. *New Phytol.* 151 (1), 213–226. <https://doi.org/10.1046/j.1469-8137.2001.00147.x>.
- Villar, R., Robleto, J.R., De Jong, Y., Poorter, H., 2006. Differences in construction costs and chemical composition between deciduous and evergreen woody species are small as compared to differences among families. *Plant Cell Environ.* 29 (8), 1629–1643. <https://doi.org/10.1111/j.1365-3040.2006.01540.x>.
- Vitasse, Y., Bresson, C.C., Kremer, A., Michalet, R., Delzon, S., 2010. Quantifying phenological plasticity to temperature in two temperate tree species. *Funct. Ecol.* 24 (6), 1211–1218. <https://doi.org/10.1111/j.1365-2435.2010.01748.x>.
- Vodnik, D., Gričar, J., Lavrič, M., Ferlan, M., Hafner, P., Eler, K., 2019. Anatomical and physiological adjustments of pubescent oak (*Quercus pubescens* Willd.) from two adjacent sub-Mediterranean ecosystems. *Environ. Exp. Bot.* 165, 208–218. <https://doi.org/10.1016/j.envexpbot.2019.06.010>.
- von Wühlisch, G., 2008. *Fagus sylvatica*-Technical guidelines for genetic conservation and Use for European beech. EUFORGEN Technical Guidelines for Genetic Conservation and Use. Bioversity International, Rome, Italy, p. 6. ISBN 978-92-9043-787-1.
- Wang, F., Israel, D., Ramírez-Valiente, J.-A., Sánchez-Gómez, D., Aranda, I., Aphalo, P.J., Robson, T.M., 2021. Seedlings from marginal and core populations of European beech (*Fagus sylvatica* L.) respond differently to imposed drought and shade. *Trees (Berl.)* 35, 53–67. <https://doi.org/10.1007/s00468-020-02011-9>.
- Warren, D.L., Glor, R.E., Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evol. Int. J. Org. Evol.* 62 (11), 2868–2883. <https://doi.org/10.1111/j.1558-5646.2008.00482.x>.
- Wortemann, R., Herbette, S., Barigah, T.S., Fumanal, B., Alia, R., Ducouso, A., Gomory, D., Roedel-Drevet, P., Cochard, H., 2011. Genotypic variability and phenotypic plasticity of cavitation resistance in *Fagus sylvatica* L. across Europe. *Tree Physiol.* 31 (11), 1175–1182. <https://doi.org/10.1093/treephys/tp101>.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. *Nature* 428 (6985), 821–827. <https://doi.org/10.1038/nature02403>.
- Zapater, M., Hossann, C., Bréda, N., Bréchet, C., Bonal, D., Granier, A., 2011. Evidence of hydraulic lift in a young beech and oak mixed forest using ¹⁸O soil water labelling. *Trees (Berl.)* 25 (5), 885–894. <https://doi.org/10.1007/s00468-011-0563-9>.
- Žemaitis, P., Gil, W., Borowski, Z., 2019. Importance of stand structure and neighborhood in European beech regeneration. *For. Ecol. Manag.* 448, 57–66. <https://doi.org/10.1016/j.foreco.2019.05.066>.
- Zhang, J., He, N., Liu, C., Xu, L., Chen, Z., Li, Y., Wang, R., Yu, G., Sun, W., Xiao, C., Chen, H.Y.H., Reich, P.B., 2020. Variation and evolution of C:N ratio among different organs enable plants to adapt to N-limited environments. *Global Change Biol.* 26 (4), 2534–2543. <https://doi.org/10.1111/gcb.14973>.
- Zhao, N., Yu, G., He, N., Xia, F., Wang, Q., Wang, R., Xu, Z., Jia, Y., 2016. Invariant allometric scaling of nitrogen and phosphorus in leaves, stems, and fine roots of woody plants along an altitudinal gradient. *J. Plant Res.* 129 (4), 647–657. <https://doi.org/10.1007/s10265-016-080>.