

Living at the edge: the functional niche occupation of woody plant communities in the submediterranean ecotone

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- **Background and Aims** Submediterranean areas are rich ecotones, where slight modifications in environmental conditions can lead to substantial changes in the composition of plant communities. They thus offer an ideal scenario to examine plant community assembly. In this study, we followed a trait-based approach including intraspecific variability to elucidate (1) the relationship between niche occupancy components and species richness, (2) the processes governing the assembly of these communities and (3) the contribution of intraspecific trait variability in shaping the functional trait space.
- **Methods** We measured eight morphological and chemical traits in 405 individuals across 60 plots located in different forest communities (Mediterranean, Eurosiberian and Mixed) coexisting within a submediterranean ecosystem in central Spain. We calculated three niche occupancy components related to Hutchinson's n -dimensional hypervolumes: the total functional volume of the community, the functional overlap between species within the community and the average functional volume per species, and then used null models to explore the relative importance of habitat filtering, limiting similarity and intraspecific variability as assembly patterns.
- **Key Results** Both habitat filtering and niche differentiation drive the community assembly of Mediterranean communities, whereas limiting similarity and hierarchical competition shape Eurosiberian communities. Intraspecific responses were mostly explained by shifts in species niches across the functional space (changes in the position of the centroids of hypervolumes).
- **Conclusions** Different assembly mechanisms govern the structure of Mediterranean, Eurosiberian and Mixed plant communities. Combining niche occupancy components with a null model approach at different spatial scales offers new insights into the mechanisms driving plant community assembly. Consideration of intraspecific variability is key for understanding the mechanisms governing species coexistence in species-rich ecotones.

Key words: Community assembly, functional strategies, hypervolumes, mixed forests, intraspecific variability, root traits, woody plant communities.

INTRODUCTION

Understanding community assembly processes and the mechanisms of species coexistence has been a fundamental goal in ecology for decades (MacArthur and Levins, 1967; Diamond, 1975; Hubbell, 2001; Adler *et al.*, 2007; Turner, 2008; Mason *et al.*, 2011; Kraft *et al.*, 2015; Gross *et al.*, 2021). Much research has been devoted to analysing the patterns of biodiversity stemming from multiple assembly processes (e.g. trait convergence or divergence) with the aim to generalize community assembly rules from common emerging patterns (Gross *et al.*, 2021). The classical view in community assembly rules is that environmental stress selects the range of strategies that plant species can display, promoting a convergence of plant

trait values through habitat filtering. By contrast, divergent trait values among plant species, i.e. different plant strategies, allow species to use a wider range of resources, thus promoting species coexistence (Weiher and Keddy, 1995; Cornwell and Ackerly, 2009). In this regard, a classical approach for delineating species niches is Hutchinson's niche concept and the concepts of niche volume and niche overlap (Hutchinson, 1957). However, due to the difficulties in measuring resource axes for a large number of species, either within or across plant communities, one approximation to the Hutchinsonian niche is using a trait-based approach to investigate the n -dimensional functional niche space occupied by the set of species forming a plant community (e.g. Stevenson, 1982; Litvak and Hansell, 1990; Newsome *et al.*, 2007; Godsoe, 2010; D'Andrea and Ostling,

2016). This approach has been recently extended to describe the functional volume (hypervolume) occupied by a given community, with the axes representing the covariation among functional traits rather than resources (Blonder et al., 2018). Since plant functional traits are good proxies for plant resource use strategies (Wright et al., 2004; Prieto et al., 2018; de la Riva et al., 2021), this functional approach has enabled significant progress in our understanding of community assembly processes (de la Riva et al., 2017a, b; Carvalho and Cardoso, 2020; Lu et al., 2021; Conceição and Morimoto, 2022).

One caveat of most studies exploring community assembly processes using functional traits is that they have rarely considered intraspecific trait variability (e.g. Lamanna et al., 2014; Swenson and Weiser, 2014), or simplify it by using species mean trait values (e.g. Jung et al., 2014; de la Riva et al., 2016; Niu et al., 2020). However, intraspecific trait variability has important consequences for the assembly of species (Khalil et al., 2019; Galán Díaz et al., 2021; Jiang et al., 2022) because it strengthens the competitive abilities of species and stabilizes species niche differences within communities (Clark, 2010). There have been recent efforts to incorporate intraspecific trait variability at the individual level in niche space occupancy measurements to refine empirical quantifications of the functional volume and ecological theory (i.e. Benavides et al., 2019; Li and Shipley, 2019; Carvalho and Cardoso, 2020; de Tomás Marín et al., 2023). However, we still lack a proper understanding of the role of intraspecific variability in community assembly, particularly how it can shape niche space occupancy. Therefore, incorporating intraspecific trait variability can provide valuable insights into how the exploitation of available resources by coexisting species reflects habitat filtering, limiting similarity or simply pure stochasticity (Hubbel, 2001; Siefert, 2012; de la Riva et al., 2016; Khalil et al., 2019; Li and Shipley, 2019). In this regard, Li et al. (2018) defined three essential niche occupancy components related to Hutchinson's n -dimensional hypervolumes that, incorporating intraspecific trait variation, allow us to accurately estimate how species occupy functional niche space (Carvalho and Cardoso, 2020): the total functional volume of the community (T), the functional overlap between species within the community (O) and the average functional volume per species (A). These niche occupancy components proved useful in describing the functional niche occupation and assembly patterns in grassland communities along environmental gradients (Li and Shipley, 2019) but, to date, we do not know whether it can be useful to study community assembly processes in forest ecosystems subjected to contrasting environmental conditions.

The relationship between functional volumes and species richness is a promising path to better understand the assemblage of species across environmental gradients (Lamanna et al., 2014; Swenson and Weiser, 2014; Li and Shipley, 2019). Although it is often assumed that volumetric indices, e.g. the total functional volume, are positively correlated with species richness (Villéger et al., 2008; Swenson and Weiser, 2014; Li et al., 2018), some studies suggest that functional volumes could saturate as richness increases (Stegen and Swenson, 2009). Moreover, different responses of the niche occupancy components reveal different community assembly processes (see Li et al., 2018; Li and Shipley, 2019). Convergence among coexisting species resulting from strong habitat filtering would

be reflected by a more tightly packed functional volume (i.e. smaller T and/or A) and a greater functional redundancy (bigger O) between species. In contrast, limiting similarity would be reflected by bigger functional (T) and average (A) volumes of the entire community, at the expense of decreasing functional redundancy (i.e. smaller O). Moreover, recent studies also advocate for the relevance of understanding the response of individual species to changing environments, for instance assessing the relative importance of niche shifts (i.e. shifts in species mean trait values) and niche contractions/expansions (i.e. reductions/increases in species functional volumes) in response to changing environmental conditions (Benavides et al., 2019; Carvalho and Cardoso, 2020). We argue that the dual consideration of intraspecific trait variability at both the community- and species-levels can help to better describe the processes underlying community and species distribution patterns.

In the Iberian Peninsula, there is a large longitudinal edge between the Eurosiberian (northern) and Mediterranean (southern) biogeographical regions, forming one of the largest boundaries between Mediterranean and Eurosiberian vegetation (Sánchez de Dios et al., 2009). Many plant communities located along this border are subjected to climatic features between the Mediterranean and Eurosiberian biogeographical regions and are termed submediterranean. The low-latitude edges of the distribution ranges of many central European species frequently occur in submediterranean zones (Väre et al., 2003; Gil et al., 2010; Dorado-Liñán et al., 2017). This creates a mosaic of Mediterranean and Eurosiberian communities where slight modifications in environmental conditions can lead to substantial changes in plant composition (Ruiz-Labourdette et al., 2012). For instance, the variation of the hydric balance drives species turnover from xerophyllous drought-tolerant Mediterranean taxa (e.g. *Quercus ilex*, *Juniperus oxycedrus* or *Genista* spp.) growing in warmer and drier enclaves to cold-temperate drought-sensitive species (e.g. *Fagus sylvatica*, *Quercus petraea* or *Betula* spp.) that grow in wetter sites (Ruiz-Labourdette et al., 2012; Dorado-Liñán et al., 2017) with Mixed communities in between. These particularities make this submediterranean region an ideal scenario to test the relative importance of habitat filtering and limiting similarity along species richness gradients (de Bello et al., 2012; Li et al., 2018), as well as to explore the role of intraspecific variability in functional assembly (Violle et al., 2012). Specific pathways of community assembly rules in submediterranean ecosystems are still poorly known, although these areas are highly vulnerable to climate change, and priority areas for biodiversity conservation (Lionello et al., 2012; Ali et al., 2022). Therefore, deciphering assembly processes in submediterranean plant communities is not only crucial to expand our understanding of biodiversity patterns but also to predict the response of these communities to climate change.

In this study, we quantified the functional niche occupancy of 19 species in 60 plots located across different patches of vegetation (Mediterranean, Eurosiberian and Mixed communities) coexisting within a well-preserved submediterranean forest known as Hayedo de Montejo (UNESCO Natural World Heritage Site). Our aims were to (1) elucidate the relationship between niche occupancy components (T , O and A) and species richness, (2) elucidate the role of environmental variables in shaping plant community assembly processes,

(3) unveil general patterns in the assembly of coexisting species (habitat filtering vs niche differentiation) across different plant communities (Eurosiberian, Mediterranean and Mixed forests) and (4) address the contribution of intraspecific trait variability in shaping the functional trait space. To date, few studies have explored the patterns of segregation of dominant species along these climatic boundaries (e.g. Väre *et al.*, 2003; Ruiz-Labourdette *et al.*, 2012; Dorado-Liñán *et al.*, 2017) and we are the first to explore, using a functional trait-based approach, the extent to which local environmental conditions and/or biotic interactions shape the community assembly patterns of submediterranean forest.

MATERIAL AND METHODS

Study area

The study area is a 125-ha forest in central Spain named Hayedo de Montejo (hereafter Montejo), designated in 2017 as a World Natural Heritage site (UNESCO). Montejo is a Mixed forest of Mediterranean and Eurosiberian species located in the Sierra de Ayllón, on the Sistema Central Mountain range, in the upper basin of the Jarama river, between 1250 and 1500 m a.s.l. (41°07'N, 3°30'W). It has a continental submediterranean climate. Mean annual rainfall in Montejo is 900 mm, with a dry period that extends from June to August (Gil *et al.*, 2010). Mean annual temperature is 9.5 °C, with mean temperatures increasing up to 18.3 °C during summer months and decreasing to 3.3 °C during winter months (data for the 1994–2021 period). The soil has been categorized as a humic cambisol (Pardo *et al.*, 1997) with the topsoil (horizon A) reaching 50 cm depth on average, which allows for a rather large water storage capacity during dry periods (Rubio-Cuadrado *et al.*, 2020).

Montejo 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). Based on the 4th National Forestry Inventory (IFN4), the dominant tree species in Montejo are European beech (*Fagus sylvatica*), sessile oak (*Quercus petraea*) and the Mediterranean Pyrenean oak (*Quercus pyrenaica*) covering 27, 23 and 50 % of the total basal area, respectively (Rubio-Cuadrado *et al.*, 2020). Considering all the vascular plant species, species richness is high (with more than 458 species reported in the forest), and conditioned by microtopography and a variable mosaic of overstorey species (Hernández-Bermejo *et al.*, 1982; Rodríguez-Calcerrada *et al.*, 2011).

Species survey

According to the phytosociological characterization of the vegetation, several species contribute to the separation between Mediterranean and Eurosiberian communities, such as *Q. pyrenaica* (typically Mediterranean), or *F. sylvatica* and *Q. petraea* (absent in Mediterranean ecosystems) (Rivas-Martínez *et al.*, 2011). Based on this characterization and the information of the forest inventories (FIs) carried out in Montejo in 1994, 2005 and 2015 (Gil *et al.*, 2010), we divided the forest into six communities: two communities dominated by the Eurosiberian species (I) *F. sylvatica* and (II) *Q. petraea*, two

Mediterranean communities dominated by (III) *Q. pyrenaica* and (IV) Mediterranean shrublands (*Juniperus communis*, *Lavandula stoechas* and *Adenocarpus hispanicus*), and two transition communities without dominance of Eurosiberian or Mediterranean tree species: (V) communities co-dominated by both *F. sylvatica* and *Q. pyrenaica* (Fsy-Qpy Mixed forest) and (VI) communities with a codominance of *F. sylvatica*, *Q. pyrenaica* and *Q. petraea* (Fsy-Qpy-Qpe) (see Supplementary Data Appendix S1). We established ten circular plots with 15-m radius (706.85 m²) per community type (60 plots in total) from the FIs. All the woody plant species present in each plot were registered (19 species in total, see Appendix S2).

Trait measurements

In June and July 2020, during the maximum peak of plant growth in Montejo, five healthy adults per species and community (405 individuals in total) were randomly selected to measure eight morphological and chemical functional traits expected to represent niche differentiation and resource partitioning among species. A few branches with young, fully expanded leaves and a portion of stem of the previous year were collected from each individual plant. Fine roots (<2 mm in diameter) were sampled by excavating the first 20–30 cm of soil depth near the plant stem, thus ensuring that the sampling roots belonged to the selected individual. For a detailed protocol of leaf, stem and root sampling see de la Riva *et al.* (2016). For leaves, we determined their specific leaf area (SLA; leaf area per unit of leaf dry mass; m² kg⁻¹), leaf dry matter content (LDMC; dry mass per unit of water-saturated fresh mass; mg g⁻¹), leaf carbon-nitrogen ratio (C:N), and the carbon isotopic composition (δ¹³C; ‰) as a proxy for water use efficiency (Prieto *et al.*, 2018). In fine roots we determined their specific root area (SRA, root length per unit of root dry mass; m² kg⁻¹) and root diameter (Rdi; root mean diameter; mm). At the stem level, we measured the stem dry matter content (SDMC; dry mass per unit of water-saturated fresh mass; mg g⁻¹) and the Huber value (Hv; the ratio of sapwood cross-sectional area to the total leaf area in the distal part of the branch). Hv was measured in at least three individuals per species from different communities. All trait measurements were carried out following the protocol in Pérez-Harguindeguy *et al.* (2013).

Abiotic factors

Three soil samples from the top 15 cm were collected per plot using a hand trowel. One sample was collected in the centre of the plot and the other two 5 m above and below the centre following the terrain slope. The three soil samples per plot were mixed in a composite sample and taken to the laboratory where they were dried at 50 °C to constant weight over 72 h and finally sieved at 2 mm. Soil organic matter content (SOM) was estimated by the loss-on-ignition (LOI) method (Bensharada *et al.*, 2022), total soil nitrogen concentration (N) was determined by Kjeldahl digestion, and soil phosphate concentration (P) was estimated with a UV/VIS spectrophotometer at 880 nm after extraction with calcium–acetate–lactate (CAL) solution (Schüller, 1969). Slope, aspect and altitude in metres above sea level (hereafter elevation) of the plots were obtained

using the GIS software package Spatial Analyst (ArcGIS 10 Desktop 10.5.1) and the Digital Elevation Model with a 5-m grid produced by the Spanish National Program for Aerial Orthophotography (PNOA). Soil depth was measured in four cardinal points 10 m apart from the centre of the plot by hammering a 1.0-m-long iron bar into the soil until reaching the bedrock. When the bedrock was deeper than 1.0 m at a given point, it was assigned a depth of 1.0 m. Soil depth was calculated as the mean of the four values per plot.

Data analysis

Given the intrinsic correlation between traits (Wright *et al.*, 2004; Prieto *et al.*, 2018; de la Riva *et al.*, 2021), we ran a principal component analysis (PCA; Supplementary Data Appendix S3) to identify major axes of trait covariation and reduce the dataset into fewer functional dimensions (Laughlin, 2014). Prior to conducting the PCA, traits were mean-centred and scaled by dividing the centred values by their standard deviations. These traits largely occupied three key dimensions of plant ecological strategies, which were summarized by each of the three first principal components; that is, PC1, PC2 and PC3 indicated a clear gradient related to the Leaf Economic Spectrum (LES, Wright *et al.*, 2004), Root Economics Spectrum (RES, de la Riva *et al.*, 2021) and hydraulic architecture (HyArq, Tyree and Ewers, 1991), respectively. These principal components had eigenvalues over 1 (Villéger *et al.*, 2008); therefore, in further analysis, we used the scores of these PC axes.

Functional niche occupancy across communities in Montejo

Once axes were identified, we explored functional assembly patterns of woodland communities in Montejo by calculating niche occupancy components at the species level, i.e. taking into account intraspecific trait variability (Li *et al.*, 2018). This framework is based on the mathematical relationship of three niche occupancy metrics with species richness described by Li *et al.* (2018) (Equation 1):

$$S = \frac{T + O}{A} \quad (1)$$

where S corresponds to species richness, T is the total functional volume, O is the functional overlap between species and A is the average functional volume per species. For each plot, we calculated T , O and A on the scores of the first three PCA axes, using the ‘hypervolume_box’ function implemented in the ‘hypervolume’ R package (Blonder *et al.*, 2018). Total functional volume (T) was calculated as the sum of the individual functional volumes occupied by the species present in a community; O was quantified as the sum of the intersections among species hypervolumes considering the number of overlapping species, and A was calculated as the sum of all individual functional hypervolumes divided by the number of species. We used a fixed kernel bandwidth of 0.5 SD, a quantile threshold of 0.05 and 1000 Monte Carlo samples per data point (Li *et al.*, 2018; Li and Shipley, 2019). To avoid calculating hypervolumes on disjoint sets of observations, the bandwidth was optimized following the procedure of Barros *et al.* (2016) (Supplementary Data Appendix S4).

To investigate the relationship between the niche occupancy metrics and species richness, we ran generalized linear mixed models (GLMMs) using the ‘nlme’ package in R (Pinheiro *et al.*, 2017). In each case, we regressed each niche occupancy component (T , O , A) on species richness allowing for random variation in intercepts, where community was included as a random factor. In addition, to explore the differences in niche occupancy components and species richness between the communities, a one-way ANOVA was carried out, followed by post-hoc multiple pairwise comparisons (Tukey’s test). We tested for normality and homoscedasticity by examining the residuals plots and the normal q - q plots of the models.

Disentangling the role of environmental conditions in niche occupancy metrics and community composition

We explored the influence of abiotic variables (SOM, soil N and P concentrations, elevation, slope, aspect, and soil depth) in species richness and niche occupancy components using maximum-likelihood techniques with a linear mixed model function (‘likelihood’ package; Murphy and Murphy, 2015). We only fitted two-factor models to avoid overfitting the models with spurious parameters with very poor weights (Grueber *et al.*, 2011). The abiotic variables (fixed factors) were added either additively or multiplicatively, while community was included as a random factor. 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-fitting model as the model with the lowest AIC ($\Delta\text{AIC} < 2$). Next, we tested for normality and homogeneity of the variance by examining the residuals plots and the normal q - q plots of the best-fitted model. In addition, to investigate how species segregate along the study area, we used a stepwise model building for redundancy analysis (RDA), with the function `ordiR2step` implemented in the R package ‘vegan’ (Oksanen *et al.*, 2007). The function `ordiR2step` performs a forward model choice, based solely on adjusted R^2 and P -values, to determine which abiotic factors (SOM, soil N and P concentrations, elevation, aspect, soil depth, and slope) are best associated with community distribution.

All statistical analyses were performed in R v.4.2.1 (R Core Team, 2023). R code and the dataset used in this study are available at GitHub (https://github.com/galanze/montejo/tree/master/niche_occupancy) to ensure the reproducibility of the analyses.

Functional assembly patterns within plant communities

We explored the mechanisms that govern vegetation assembly at the local and regional scales since different rules may govern plant assembly at these scales as a result of habitat filtering (de Bello *et al.*, 2021). We used two null models to test whether the observed functional niche occupancy components differed from the null expectation at the two scales by defining two reference species pools in our dataset. The null model for the regional pool (hereafter called forest pool) (1) included the entire dataset, that is all the species measured in the study. This model assumes that any species within Montejo is able to inhabit any plot within the forest, i.e. there are no restrictions

for seed dispersal and seedling establishment. The null model for the community pool (hereafter called community pool) (2) included only the species present within each community, i.e. from the ten plots in each community type. This model makes the assumption that habitat filtering driven by competition from the dominant tree species and by site-specific abiotic constraints limits species establishment (Kraft *et al.*, 2015). Based on these criteria, we generated a null distribution for the three niche occupancy components (T , O and A) for each plot (100 permutations), maintaining the observed species richness in each plot and including five individuals per species. After generating null models, we calculated the standardized effect size (SES) for each niche occupancy component (T , O and A) for each plot as the observed value minus the average value of the null distribution divided by its standard deviation (Li *et al.*, 2018). A positive SES implies greater observed niche occupancy components than the null expectation and a negative SES represents smaller observed niche occupancy components than the null expectation. Methods that were applied to assemble null models and SES were adapted from Li *et al.* (2018). We used Wilcoxon signed-rank tests to detect significant SES among forest types. According to Li *et al.* (2018), if habitat filtering is the main driver of community assembly, T should have lower values than the null (neutral) expectation, while O and A could have higher or lower values. If limiting similarity prevails in communities, then O should have lower values than the null expectation; on the other hand, higher values of O could indicate hierarchical competition. If habitat filtering and limiting similarity jointly drive the functional niche occupancy (lower values of T and O than the null expectations), species should on average occupy smaller functional volumes (A).

The importance of intraspecific variability in shaping the functional space

We adapted the framework proposed by Benavides *et al.* (2019) to explore the extent to which intraspecific trait variability was responsible for community assembly patterns within Montejo by testing whether intraspecific changes in niche position (hypervolume centroids) or niche breadth (hypervolume size) were driving community assembly. We analysed only the species present in at least four out of the six communities (13 species out of 19) to compare the observed patterns against a null expectation. For this, we compared the observed pairwise distances among centroids (niche position) and the observed variability in hypervolume size (niche breadth) of a given species across sites against a null distribution. To generate null distributions ($N = 499$), we shuffled rows in the plot \times principal components matrix, and recalculated the mean pairwise distance among centroids and the mean absolute pairwise differences in hypervolume size. We also calculated the mean pairwise distance among centroids for each functional axis to assess functional shifts for each particular strategy. These null assemblages represent communities where the functional space occupied by a species is not affected by local abiotic and/or biotic constraints (Benavides *et al.*, 2019). We computed the SES of the observed values with respect to the null distribution and used the Wilcoxon signed rank test to detect whether the SES differed from zero. Observed pairwise distances among centroids (niche position) and absolute differences in hypervolume

size (niche breadth) greater than expected by chance (i.e. $SES > 0$) reflect that species respond to the changing environment (i.e. vary across plots) by shifting their functional niche position and contracting/expanding their functional volume, respectively. Finally, we explored shifts in species niche shape among communities by measuring the contribution of each functional strategy axis (LES, RES, HyArq) to the overall volume with the ‘hypervolume_variable_importance’ function from the ‘hypervolume’ R package (Blonder *et al.*, 2018). For each randomization in the null model, we quantified the variability of the importance of each principal component relative to the hypervolume size of the null assemblage as the mean absolute pairwise difference. If a functional strategy axis reflects adaptability or responsiveness to the environment, we expect the observed variability in the importance of that axis to be greater than expected by chance.

RESULTS

Functional niche occupancy across submediterranean communities

The GLMMs showed that the increase in species richness across the 60 plots was associated with an increase in the total functional niche volume ($P < 0.001$; marginal $R^2 = 0.92$), an increase in the functional niche overlap ($P < 0.001$; marginal $R^2 = 0.80$) and a decrease in the average functional niche volume ($P = 0.009$; marginal $R^2 = 0.07$) (Fig. 1). We found differences in species richness and niche occupancy components among communities. Communities dominated by Eurosiberian species [*F. sylvatica* (Fsyl.) or *Q. petraea* (Qpet)] showed the lowest species richness whereas Mixed communities with *Q. petraea* (Fsy-Qpy-Qpe) and communities dominated by Mediterranean species [*Q. pyrenaica* (Qpyr) and shrubland (Shrub)] had the highest species richness (Fig. 2). Communities of Fsyl had on average the lowest T and O , and highest A . Communities dominated by Qpet and *F. sylvatica*–*Q. pyrenaica* Mixed communities (Fsy-Qpy) showed intermediate values of T and O , and the lowest A along with Mixed communities. Mixed communities with Qpet and communities dominated by Mediterranean species showed the highest values of T , and Mixed communities with Qpet and Shrub communities showed the highest O values. Mediterranean communities dominated by Qpyr showed the highest values of A along with Fsyl communities (Supplementary Data Appendix S5).

Disentangling the role of environmental conditions in niche occupancy metrics and community composition

The results from our modelling approach (the best-fitted linear model, $\Delta AICc < 2$) showed that the only abiotic factor that explained the niche occupancy components, and in particular the functional overlap (O), was soil N (marginal $R^2 = 0.07$) (Supplementary Data Appendix S6). In this model, the community type (random effects) accounted for a substantial amount of the variance, much higher than the abiotic factors (fixed effects) (conditional $R^2 = 0.61$). RDA for species composition showed two main axes of variation influenced by soil N, organic matter, soil depth and elevation,

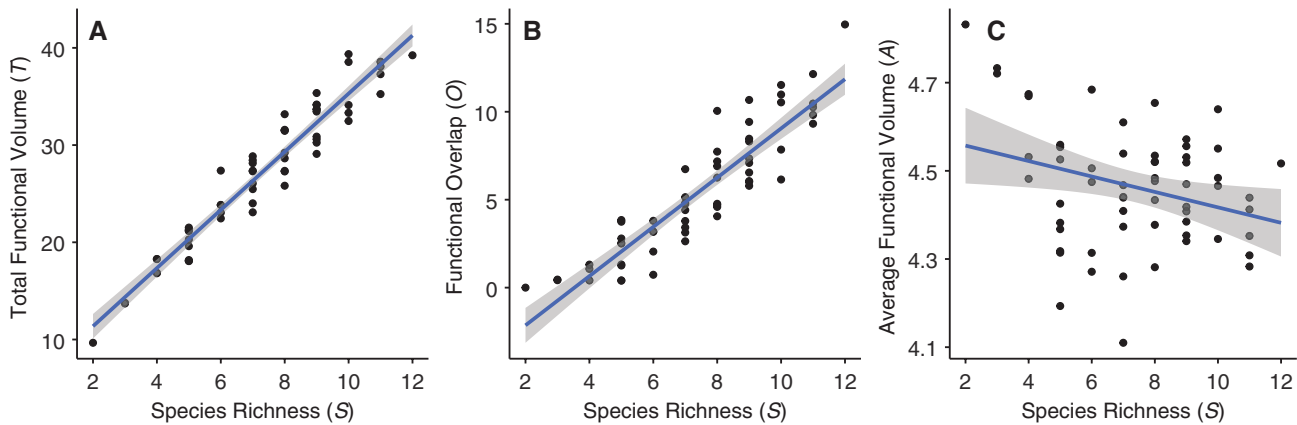


FIG. 1. Relationships between species richness (S) and niche occupancy components (T : total functional niche volume, O : functional niche overlap and A : average functional niche volume) across the 60 plots within the Hayedo de Montejo forest. Regression lines (solid) and 95 % confidence intervals (grey-shadowed areas) for the Mixed models are shown. Relationships were significant in all cases ($P < 0.01$).

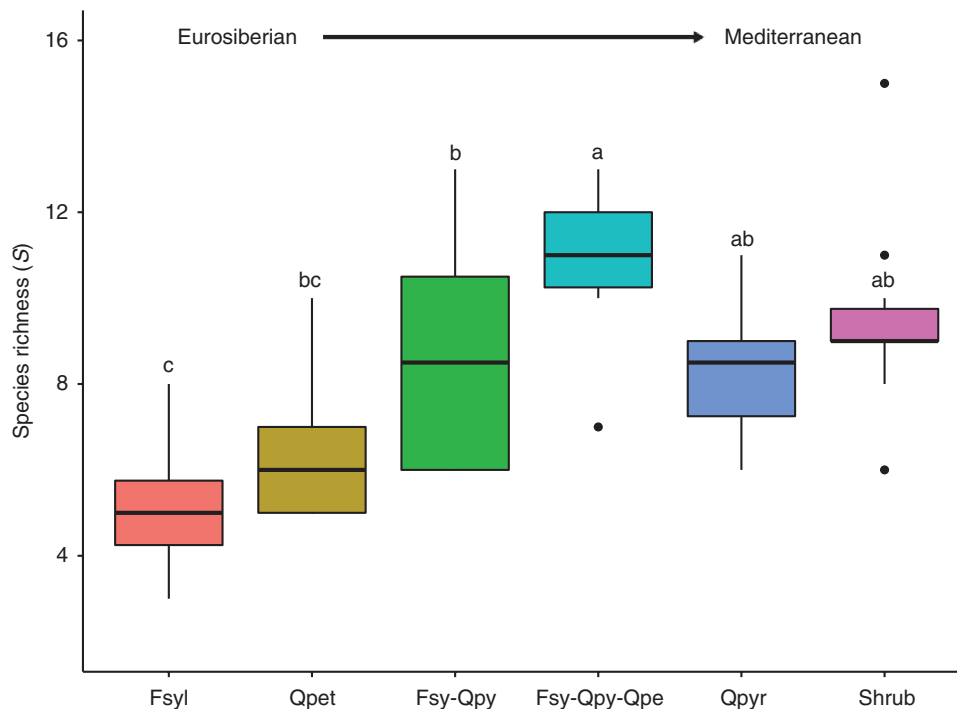


FIG. 2. Species richness (S) for each of the six communities considering all the species sampled in each plot. Lines inside the boxes represent median richness values, box limits are the 25th and 75th percentiles, error bars show the 10th and 90th percentiles, and filled symbols are outliers. Different letters indicate significant differences among communities (one-way ANOVA and post-hoc Tukey HSD; $P < 0.001$). FsyI: *Fagus sylvatica* (beech) community, Qpet: *Quercus petraea* (Eurosiberian oak) community, Qpyr: *Quercus pyrenaica* (Pyrenean oak) community, Shrub: shrubland community, Mixed transition communities (Fsy-Qpy-Qpe and Fsy-Qpy).

with plant communities located along this gradient showing some degree of overlap (Fig. 3). We detected strong variations between communities dominated by Eurosiberian tree species (*F. sylvatica* and *Q. petraea*) and those dominated by Mediterranean species (*Q. pyrenaica* and shrubland). Shrublands are situated in areas with higher nutrient content and shallow soils, contrasting with communities dominated by Eurosiberian tree species. *Quercus pyrenaica* communities were mostly situated in the areas with steeper slopes, whereas transitional communities of Eurosiberian and Mediterranean

species occupied intermediate positions in the environmental gradient space (Fig. 3).

Functional assembly patterns within plant communities

In comparison with the null model reflecting random species assembly, the observed functional metrics T , O and A showed different patterns depending on the community analysed. Plant communities dominated by *F. sylvatica* had higher values of T and A and lower values of O than expected

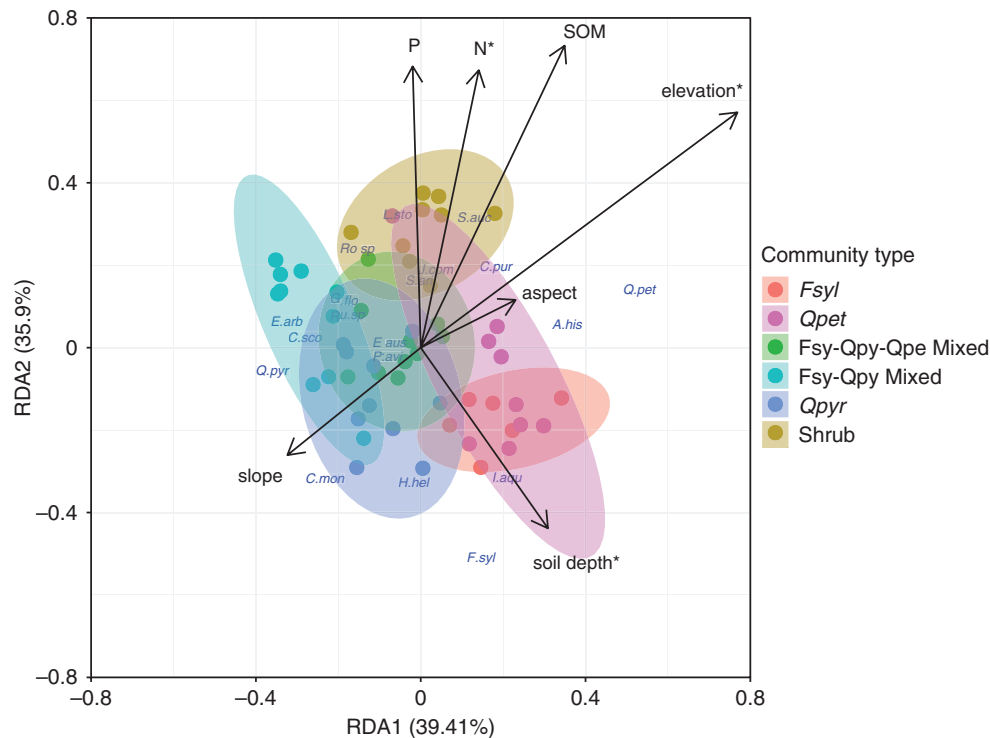


FIG. 3. Redundancy analysis (RDA) ordination diagrams for the six woodland communities and 19 woody species using the first two axes (RDA1 and RDA2) with and six environmental variables (N: soil N, P: soil P, SOM: soil organic matter, elevation, aspect, slope and soil depth). The communities are represented by coloured ellipses, the position of individual species in RDA space is represented by blue labels (see [Supplementary Data Appendix S2](#)) and coloured dots indicate the position of each plot in the RDA. Asterisks denote the variables selected in the best-fitted model ($\Delta AIC < 2$) in the stepwise RDA procedure (see [Material and Methods](#) for more details). F_{sy}: *Fagus sylvatica* (beech) community, Q_{pet}: *Quercus petraea* (Eurosiberian oak) community, Q_{py}: *Quercus pyrenaica* (Pyrenean oak) community, Shrub: shrubland community, Mixed transition communities (F_{sy}-Q_{py}-Q_{pe} and F_{sy}-Q_{py}).

by chance at both the regional and local scales. Shrubland communities had lower values of *T*, and higher values of *A* and *O* than expected at the regional scale but did not show any pattern at the community scale. Plots of the two Mixed areas showed similar results: lower values of *T* and higher values of *O* than the null expectations, and contrasting results for *A* among the two null models. Finally, communities dominated by *Q. petraea* showed lower values of *T* and *A* than the null model from the regional pool while the communities dominated by *Q. pyrenaica* exhibited the opposite results (higher values of *T* and *A*) (Fig. 4).

The importance of intraspecific variability in shaping the functional space

We found that intraspecific trait variability across communities was driven mainly by niche shifts (i.e. changes in species positions in trait space), as the observed distances between species hypervolume centroids across communities was significantly greater than expected by chance (Fig. 5). Niche shifts in trait space occurred in all three functional axes, LES, RES and HyArq, which suggests that the functional assembly patterns within plant communities are not only due to species turnover but also to intraspecific shifts in trait space. To a lesser extent, we detected small changes in niche total breadth among communities irrespective of the axis of variation, but no significant differences from zero in the SES of any particular axis (Fig. 5).

DISCUSSION

Functional niche occupancy across submediterranean communities

Understanding the contribution of species to a community's functional space as richness increases has broad implications for niche-based theory and for how and why species respond to community assembly processes (Lamanna *et al.*, 2014; Swenson and Weiser, 2014). Similar to other studies at global (Lamanna *et al.*, 2014; Li *et al.*, 2018; Benavides *et al.*, 2019), regional (Swenson and Weiser, 2014; Andrew *et al.*, 2021) and local scales (Le Bagousse-Pinguet *et al.*, 2014; Li and Shipley, 2019), we found that both functional diversity (*T*) and functional redundancy (*O*) increased as species richness increased in our communities, and did not saturate at a given richness as proposed by other authors (Stegen and Swenson, 2009). This suggests that, a priori, there are no boundaries constraining the functional volume as species richness increases (Swenson and Weiser, 2014), and that there are empty niche spaces that species with diverse nutrient-use strategies can occupy. This is probably the case in these transition zones (ecotones), where highly heterogeneous environmental conditions create a multitude of resource spaces that allow the coexistence of many species with divergent strategies (Mao *et al.*, 2018; Gulzar *et al.*, 2022). However, in contrast to results in Li *et al.* (2018) and Li and Shipley (2019), we found a negative relationship between the

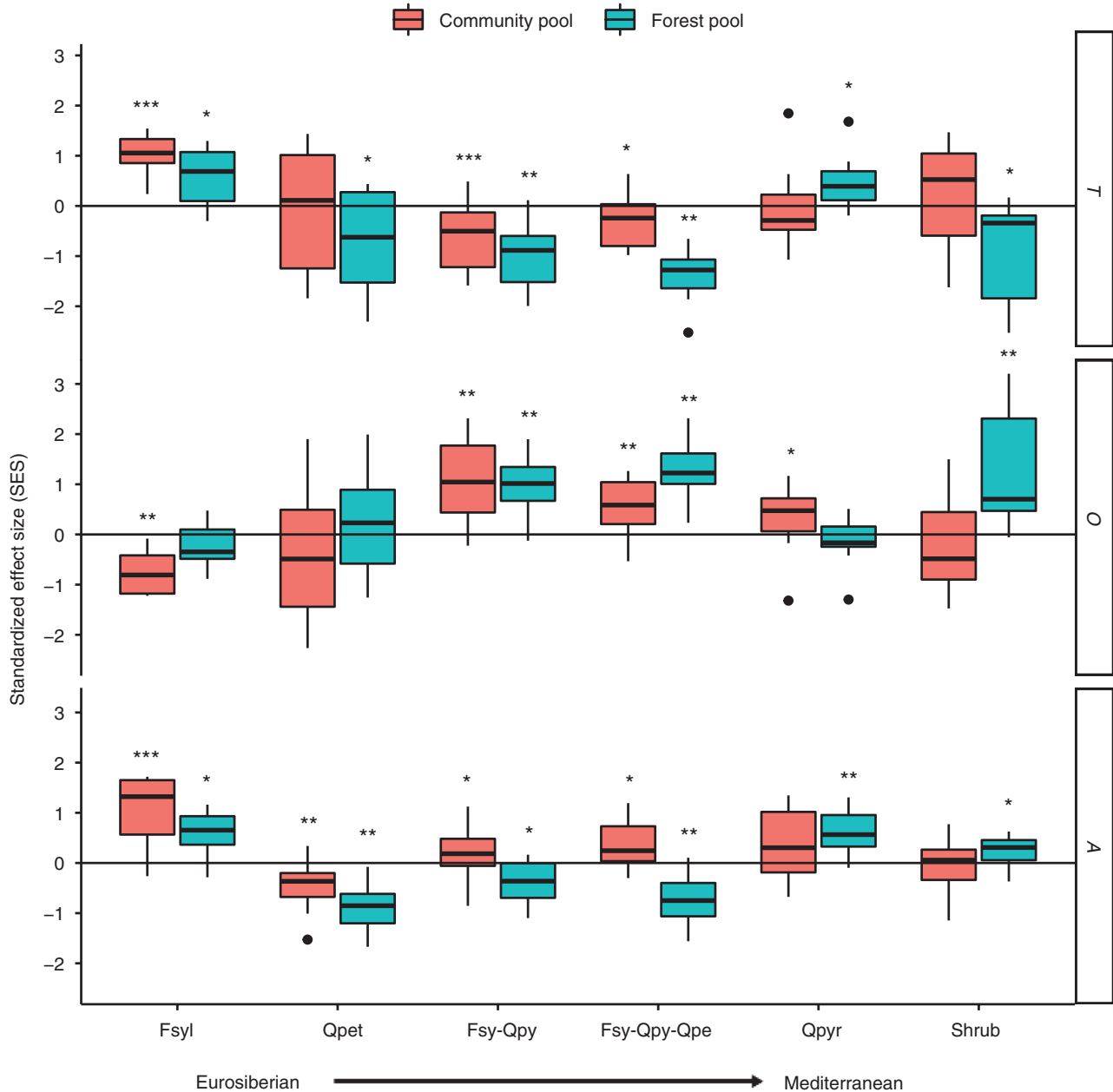


FIG. 4. Standardized effect sizes (SES) of niche occupancy components: total functional volume (T), functional overlap (O) and average functional volume (A). SESs greater or lower than 0 reflect that niche occupancy components (T , O or A) are greater or lower than expected by chance (null model, Wilcoxon tests; *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$). Forest pool: null model with the species pool within the whole forest; Community pool: null model with the species pool within each of the six communities. Fsyl: *Fagus sylvatica* (beech) community, Qpet: *Quercus petraea* (Eurosiberian oak) community, Qpyr: *Quercus pyrenaica* (Pyrenean oak) community, Shrub: shrubland community, Mixed transition communities (Fsy-Qpy-Qpe and Fsy-Qpy).

average functional volume (A) and species richness. Overall, our results show that, as species join the functional space of existing assemblages expanding the total functional volume (T), and because of increasing competition for the same resources (increases in O), some functionally specialized species are able to occupy empty niche spaces (decrease in A ; Swenson and Weiser, 2014). In agreement with limiting similarity theory (MacArthur and Levins, 1967), this specialization would allow the coexistence of multiple species in large

communities by alleviating interspecific competition, but at the expense of greater intraspecific competition derived from lower intraspecific variability (i.e. smaller A). These results support the idea that species from transition zones are able to stabilize their coexistence by modulating competition for available resources (i.e. water, nutrients or light), as previously observed in Mediterranean woody plant communities along gradients in resource availability (de la Riva et al., 2017a, b, 2018).

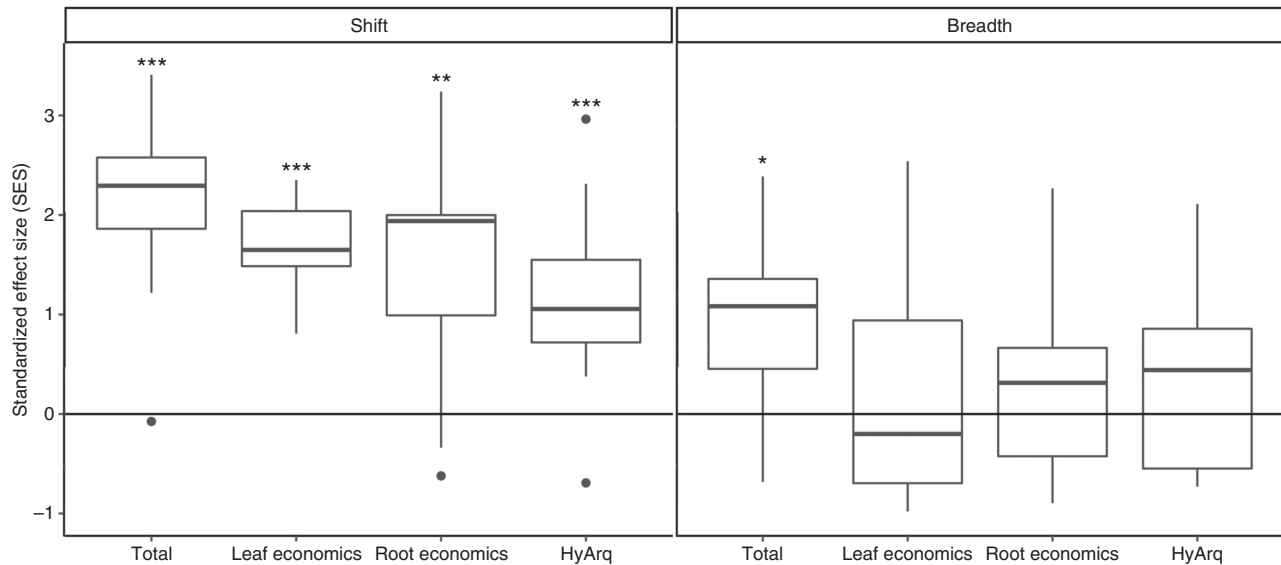


FIG. 5. Intraspecific responses to changing environment (i.e. forest type) measured as the standardised effect size (SES) between observed and null model expectations. Niche breadth is the variability in hypervolume sizes and niche shift refers to changes in hypervolume centroids. An SES significantly greater than 0 indicates greater observed distances among the hypervolume centroids of conspecific individuals in different patches (niche shift) than expected under the null model or greater variation among the hypervolume sizes of conspecific individuals in different patches (niche breadth) than expected under the null model (see Material and Methods for more details on null model calculations). Asterisks are shown above boxes when SES is significantly different from zero (Wilcoxon tests, *** $P < 0.001$, ** $P < 0.001$, * $P < 0.01$).

Disentangling the role of environmental conditions in niche occupancy metrics and community composition

Despite the large environmental heterogeneity in our study, we did not observe a strong effect of the environmental variables on the functional niche occupancy components among communities. Nonetheless, we did detect an increase in the functional niche overlap with increasing soil N, which was similar to the increase observed in response to higher species richness. The shrubland was one of the communities with higher species richness, functional volume and overlap, and higher soil N concentration, while the opposite was true for pure *F. sylvatica* stands. This enrichment in soil N in shrublands is explained by the presence of the N-fixing shrub *A. hispanicus* (Andrews and Andrews, 2017), which dominated the shrubland communities. In contrast, in pure *F. sylvatica* stands, the low light reaching the understorey would reduce the rate of organic matter mineralization reducing the amount of N in the soil (Rodríguez-Calcerrada et al., 2011).

Community distribution modelling revealed that the abiotic variables separated different plant communities in Montejo, which suggests that the first strong mechanism of species segregation and niche partitioning was related to environmental suitability. We observed a clear segregation among Mediterranean (Shrubland and *Q. pyrenaica*) and Eurosiberian (*F. sylvatica* and *Q. petraea*) communities, while the Mixed Forest occupied an intermediate environmental position. Our results are in agreement with the patterns reported by other authors (i.e. Gazol et al., 2017; Mason et al., 2011; Gulzar et al., 2022), who found that ecotones are dynamic areas where small changes in environmental conditions produce strong responses in plant communities. It is important to note that Montejo's dynamics and species coexistence have probably been affected by historical changes in land use during the 20th century (Gil et al., 2010).

For instance, *Q. pyrenaica* patches were mostly relegated to steeper areas with shallower soils where historical forest management was less intense (Dorado-Liñán et al., 2017), while *F. sylvatica* patches have shown an unexpected expansion since Montejo became a protected area and traditional forest management activities were banned (Gil et al., 2010). Moreover, the patches dominated by *F. sylvatica* were mainly distributed on lower, less steep, deeper soils, which are usually recognized as productive environments in Mediterranean ecosystems (de la Riva et al., 2016, 2018), where species segregation would be driven by competition (Ulrich et al., 2017; see below). Conversely, the shrubland community was in a high-elevation area with shallower and stony soils, which probably limited water availability and constrained the successful establishment of tree species despite the high N and organic matter content. We argue that soil depth and elevation are probably determining factors in terms of water availability in Montejo, which may affect plant responses to nutrient availability (Drenovsky et al., 2012). Therefore, both the historical legacy management and the high environmental heterogeneity in Montejo are probably driving the structure and spatial distribution of plant communities within short distances (Gulzar et al., 2022).

Functional assembly patterns within plant communities

In shrubland communities, the total functional volume was smaller and the functional overlap bigger than expected under the forest null model, which is consistent with a significant role for abiotic filtering in the assembly of these communities regionally (de la Riva et al., 2018). This suggests a strong pressure and convergence of resource strategies within this pool of species (Mason et al., 2011). However, when considering the local species pool within the shrubland, the absence of patterns

suggests that stochastic processes were influencing community assembly patterns (Hubbell, 2001), driven by the stochastic variation of seed dispersal and seedling demographic dynamics (Munoz and Huneman, 2016).

The communities dominated by the two *Quercus* species present in Montejo, *Q. petraea* and *Q. pyrenaica*, showed different assembly processes at the forest and community levels, with a clear segregation in their taxonomic composition and functional niche patterns. The functional segregation of both species under similar regional environmental conditions indicates different selection pressures at lower spatial scales (Valbuena-Carabaña et al., 2005). This functional segregation may be related to a more conservative resource-use strategy of *Q. pyrenaica* than *Q. petraea* (Rodríguez-Calcerrada et al., 2008; de Tomás Marín et al., 2023). The significantly higher species richness and functional diversity in areas dominated by *Q. pyrenaica* suggests that niche partitioning may be the main driver of the assembly at the regional scale. However, at the same time, the significantly higher overlap among co-occurring species within communities dominated by *Q. pyrenaica* indicates that different filters may act at different scales (Cingolani et al., 2007). With regard to the forest species pool, the lower competitive pressure exerted by *Q. pyrenaica* (Rodríguez-Calcerrada et al., 2011) would favour the presence of different complementary species functional profiles, as suggested by the greater average functional volume per species without increasing their overlap (Biswas and Mallik, 2010; Benavides et al., 2019). However, the stressful abiotic conditions in habitats dominated by *Q. pyrenaica* (i.e. higher slopes and shallower soils) would favour the functional redundancy among species at a local scale. Therefore, even though different functional profiles are able to establish within the community, these profiles would be represented by species with conservative strategies, i.e. species with low specific leaf and root areas, that tend to dominate in this community (our unpublished data), as previously observed in other communities dominated by Mediterranean *Quercus* species (de la Riva et al., 2018).

Further, we found contrasting patterns in the niche occupancy components of *Q. petraea* and *F. sylvatica* (both Eurosiberian trees), but they did not differ in their habitat suitability, suggesting that the strength of habitat filtering and community assembly processes in these communities depend on the asymmetric competition exerted between these two species. In general, *F. sylvatica* is a better competitor than *Q. petraea* and frequently outcompetes the former when co-occurring (Leushner et al., 2001; Ligot et al., 2013). The species within *Q. petraea* communities would thus assemble according to a competitive hierarchy related to functional traits, where species with functional profiles that differ from those conferring high competitive advantage are excluded (Gross et al., 2013; Carmona et al., 2019). However, this community does not show a higher than-expected overlap among species despite experiencing a higher constriction of the total functional space (i.e. smaller than expected total functional volumes). We suggest that hierarchical competition is probably acting at different levels. First, competition for resources may act as a convergence force clustering the functional space of co-occurring species from the forest pool (Mason et al., 2011). Second, there is a shift in the species functional profiles in a direction consistent with that expected to reduce competition, i.e. reducing overlap

(Carmona et al., 2019). These results are supported by other studies in Mediterranean environments where both processes have been shown to act simultaneously at regional and local levels (Gross et al., 2013; de Bello et al., 2009). Likewise, communities dominated by highly competitive species, such as *F. sylvatica*, frequently promote the loss of species by competitive exclusion (Mayfield and Levine, 2010; Rodríguez-Calcerrada et al., 2011; Castaño-Santamaría et al., 2021). Despite this, we found an overall higher than expected functional diversity and a lower than expected functional redundancy within plots dominated by *F. sylvatica*. This implies that, in agreement with the limiting similarity hypothesis (MacArthur and Levins, 1967; Wilson and Stubbs, 2012), only a few species with functional profiles different from those conferring higher competitive advantage are able to establish in these communities.

Finally, both Mixed communities (FsyL-Qpet and FsyL-Qpet-Qpyr) showed the same niche occupancy patterns and habitat suitability, which suggests that, overall, they could be considered similar from a functional perspective. These communities showed lower than expected functional diversity and higher than expected overlap at both the forest and the community scales, indicating that habitat filtering played a major role in assembling these communities. These results suggest that competition among species with similar functional profiles rather than abiotic filtering is the main underlying process. According to the ‘environmental filtering’ scenario, competitive interactions may have the strongest impact on community assembly at intermediate levels of environmental stress (Lehman and Tilman, 2000; Ulrich et al., 2017). Moreover, Mixed communities have a higher than expected average functional diversity at the community level, despite experiencing higher constriction of the total functional space (smaller T). This scenario would be possible if dominant species have the highest intraspecific variability within the community. These results reinforce the notion that intraspecific variability may drive species interactions by changing trait hierarchies and may increase species dissimilarities (Bennett et al., 2016; Carmona et al., 2019).

The importance of intraspecific variability in shaping the functional space

Intraspecific trait variability is a key driver of plant community dynamics (i.e. Carmona et al., 2019; Niu et al., 2020; Cardou et al., 2022), achieving a relatively high importance in shaping species functional niche space in this submediterranean region. When looking at individual species responses across communities, niche shifts (i.e. changes in the position of the hypervolume centroids), in addition to species turnover, explain the observed functional assembly patterns within plant communities in Montejo. Notably, each functional dimension (LES, RES and hydraulic) was significantly different from null model expectations, providing evidence of whole-plant variation within species across environments, even at the local scale. We also found that variability in total niche breadth (i.e. hypervolume size) across conspecific individuals from the same community was higher than expected by chance, suggesting that species increase their competitive ability by modifying the size of their functional niche space (Bittebiere et al., 2019). However, individual functional dimensions (related to the LES and RES, and plant hydraulic architecture) did not deviate from

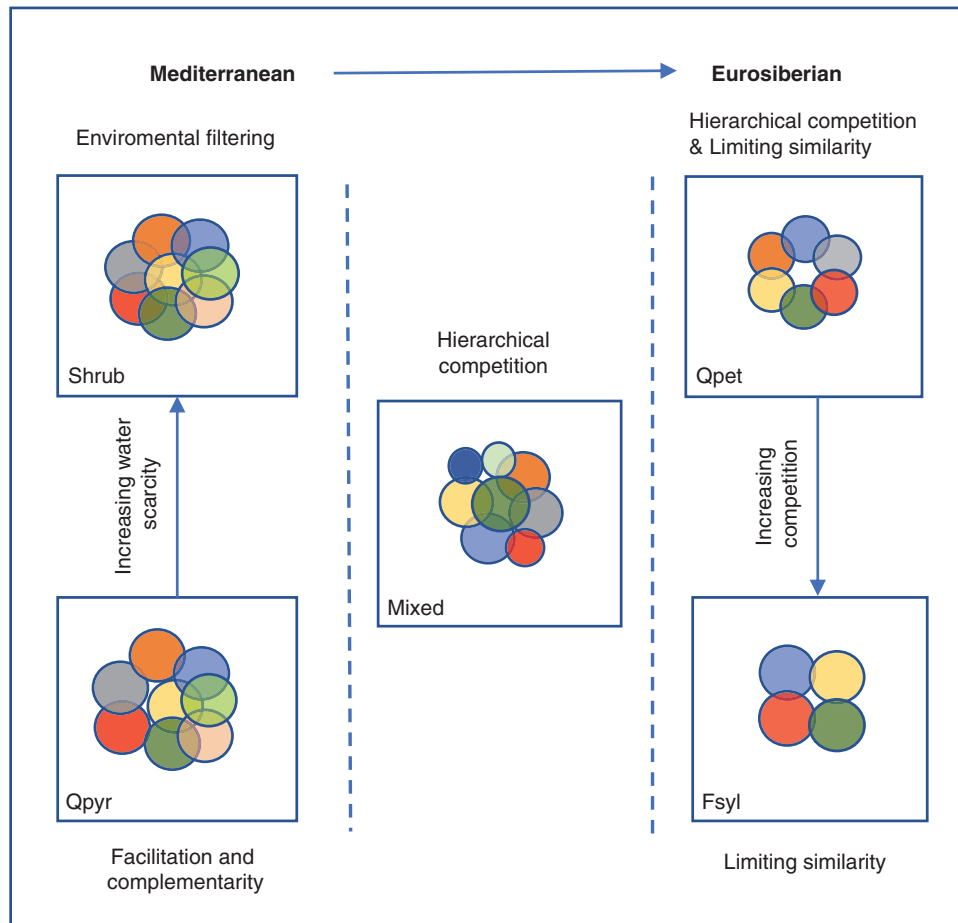


FIG. 6. Conceptual illustration of the results showing the main community assembly processes taking place at Hayedo de Montejo forest. Mean species richness per community type is reflected by the number of bubbles. The size of the bubbles and overlap is an estimation based on the total metrics values (Supplementary Data Appendix 5) and null model expectations (Fig. 4). Fsyl: *Fagus sylvatica* (beech) community, Qpet: *Quercus petraea* (Eurosiberian oak) community, Qpyr: *Quercus pyrenaica* (Pyrenean oak) community, Shrub: shrubland community, Mixed transition communities (Fsy-Qpy-Qpe and Fsy-Qpy).

null expectations, indicating that all three functional axes have a similar importance in shaping the functional space regionally. Thus, slight modifications in resource uptake strategies may help species to reach empty niche spaces and buffer conspecific competition (Bennet *et al.*, 2016; Carmona *et al.*, 2019). Altogether, our results highlight that incorporating intraspecific variability clearly allows the identification of community assembly patterns (Violle *et al.*, 2012; Benavides *et al.*, 2019) that would otherwise not emerge using mean functional trait values, highlighting the limitations of using global databases to study functional diversity. Thus, only better knowledge of how intraspecific trait variability modulates species coexistence and community assembly patterns globally will greatly advance our understanding of ecological systems.

CONCLUSIONS

Variable habitat conditions in submediterranean ecotones lead to a mosaic of plant communities with different species richness, composition, functional diversity and contrasting assembly processes (Fig. 6). In communities dominated by Mediterranean species, resource scarcity selects species with

similar ecological tolerances from the forest pool through habitat filtering. However, an alleviation of environmental stress in *Q. pyrenaica* communities promotes the diversification of functional strategies and niche differentiation among coexisting species, probably as a result of facilitation and complementarity. In contrast, two mechanisms operate in plant communities dominated by temperate trees; strong competition promotes niche diversification in *F. sylvatica* forests, in line with the limiting similarity hypothesis, while hierarchical competition constrains species richness and functional diversity in *Q. petraea* forests, a forced space sharing that can be buffered to a certain degree by niche differentiation. Similarly, hierarchical competition constrains coexisting species in Mixed communities to share similar functional profiles, promoting phenotypic clustering. We demonstrate here that combining niche occupancy components with a null model approach at two spatial scales could offer new insights into the mechanisms driving functional convergence and divergence in plant communities and allows a better understanding of the assembly processes and coexistence of species. We also emphasize that considering intraspecific trait variability is crucial for understanding the mechanisms of species coexistence in ecotones rich in microhabitats and species.

SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following.

Appendix S1. Aerial photograph of the study area at the ‘Hayedo de Montejo’. Appendix S2. Mean values and standard deviation for leaf, stem, specific root area and root diameter traits for the different woody species studied in each plant community. Appendix S3. Principal component analysis and weight of the variables in the two-dimensional plane created by PCA1 and PCA2. Appendix S4. Bandwidth optimization following two different procedures. Appendix S5. Boxplots of observed functional niche space components for each community. Appendix S6. Relationships between soil nitrogen, functional overlap and species richness.

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