

## RESEARCH ARTICLE

# Shrub diversity in Mediterranean shrublands: Rescuer or victim of productivity?

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## Abstract

**Aims:** Unravelling the most prevalent causal direction between diversity and function in naturally recovered plant assemblages can greatly improve our understanding of the functional significance of diversity and its applications under the ongoing environmental changes. In this study, we apply a structural equation model framework to unravel the most plausible causal direction in the diversity–productivity relationship in subseral Mediterranean shrub-dominated communities.

**Methods:** Total shrub cover (as a proxy of productivity when controlled by the time since land use cessation or the last wildfire), the number of species, and the number of functional types based on the dominant life forms (phanerophytes vs. chamaephytes), and the dominant foliar syndromes (deciduous vs. evergreen, needled vs. broad-leaved), were sampled in 195 circular plots distributed along an elevation gradient ranging from 400 to 1400 m a.s.l. in the Central Iberian Peninsula. We first explored the distribution of functional types along the elevation gradient using a non-metric multidimensional scaling (NMDS). Secondly, a structural equation model (SEM) framework using mixed-effects models was defined to unveil the prevalent causal direction between diversity (species and functional types) and productivity at the landscape scale.

**Results:** Model selection using the Fisher's C information criterion supported a causal direction from total shrub cover to diversity in this landscape. Interestingly, the best supported model also supported a positive relationship between species richness and the number of functional types, which in turn is driven by the total shrub cover along the elevation gradient.

**Conclusions:** Our results suggest that more species might not necessarily boost productivity. On the contrary, ongoing warming temperatures and aridity, which are characteristic of low elevations compared to highlands, might significantly reduce the number of species (victim rather than rescuer) through deleterious effects on productivity.

## KEYWORDS

complementarity, energy–diversity theory, land use abandonment, Mediterranean shrublands, species richness, total shrub cover

## 1 | INTRODUCTION

Shrub species are major components of subseral vegetation in the Mediterranean bioclimatic region with important implications for nutrient cycling (Simões et al., 2012), soil loss prevention (García-Estringana et al., 2013), carbon sequestration (Pasalodos-Tato et al., 2015), livestock feeding (Papanastasis et al., 2008) and forest restoration (Gómez-Aparicio et al., 2004). Interestingly, functions such as productivity (Montès et al., 2008), water harvesting (Ursino & Callegaro, 2016), toxicity avoidance for livestock in natural landscapes (Rogosic et al., 2006), and carbon storage (Chen et al., 2018) of shrub-dominated communities are significantly and positively tied to species diversity: for example higher levels of function are yielded in species-rich communities. For this reason, the conservation/promotion of diversity is viewed as an efficient nature-based solution to mitigate the negative effects of the ongoing global climate change on ecosystem functioning (Mori et al., 2021). However, inferring mechanisms from diversity–function relationships in observational studies is challenging, especially when covariation of both diversity and function can be linked to the variability of shared environmental determinants driving species assembly (Bengtsson et al., 2002). Hence, promoting species diversity as a climate change mitigation strategy might not have the desirable consequences everywhere.

A positive relationship between diversity and productivity has been long reported since the 70s. For instance, experiments using artificial combinations of short-lived plant species and microcosms have shed light on the potential mechanisms underlying such a positive causal influence of diversity on productivity (Loreau, 2010). On the one hand, more species can increase ecosystem productivity through a more intensive and efficient exploitation of water and soil nutrients due to niche complementarity (Craven et al., 2016). On the other hand, more species can increase the probability of having the most productive taxon under certain environmental conditions (selection effects) (Loreau, 1998). Additionally, positive diversity effects can be linked to facilitation under the assumption that certain plants (namely nurse plants) can boost diversity and productivity simultaneously via amelioration of the physical environment and nitrogen fixation (Soliveres et al., 2015). Arguments in support of the opposite causal direction (i.e., productivity determines diversity), have nonetheless also been reported in the ecological literature. The energy–diversity theory sustains that productivity, as a metric of available energy in nature, controls the number of viable populations via abundance (e.g. higher productivity reduces extinction risks in natural populations by promoting abundance) and thus, diversity would be the consequence rather than the cause of productivity (Srivastava & Lawton, 1998).

Biodiversity–ecosystem functioning (BEF) experiments conducted in long-lived plant communities are at early ontogenetic stages, such that solid evidence of the mechanisms underlying diversity effects remains elusive (see Bruehlheide et al., 2014 for details on current BEF experiments in forests). Otherwise, it is still unclear whether experimental insights can resemble the reality of the diversity–productivity relationship in natural communities (Diaz

et al., 2003; Griffiths et al., 2008) where the combination of species is a product of deterministic and neutral processes driving species assembly in the long run (Chase & Myers, 2011). Hence, even if correlational studies are seemingly inconclusive because both causal directions can be inferred from the positive diversity–productivity relationship, they can still represent an important source of evidence in naturally assembled plant communities. Recently, a global-extent hypothesis testing conducted on forest data worldwide suggested that both types of mechanisms could be reconciled along the latitudinal productivity gradient: that is, niche complementarity being more likely towards the most productive forest biomes on Earth, and energy–diversity mechanisms towards limiting conditions in either dry or cold climates (Madrigal-González et al., 2020). Even if causality from pure correlational insights remains a major challenge, testing these hypotheses might represent a significant step forward to developing a reliable mechanistic frame for the functional significance of biodiversity in natural assemblages.

In this study, we conducted a model selection based on the Fisher's C information criterion on two structural equation models to discern which hypothesis (complementarity hypothesis, diversity causes productivity; diversity–energy hypothesis, productivity causes diversity) is more prevalent in shrub-dominated assemblages in the Central Iberian Peninsula. In doing so, we aim at unravelling whether promoting diversity could be an effective strategy for climate change mitigation through increased productivity and the ensuing biomass accretion and carbon sequestration. On the contrary, if productivity is the cause of species richness (diversity as a victim of productivity), diversity would be a victim of the ongoing climate change in the sense that by eroding productivity, harsher climatic conditions could lead to significant species loss eventually.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The study was conducted in a vast territory comprising two adjoining protected areas in central–western Spain. On the one hand, the Arribes del Duero peneplain (Arribes del Duero Natural Park) represents a flattish area on a granite plateau where soils are acidic and sandy, with low contents of organic matter and nitrogen. On the other hand, the western sector of the Spanish Sistema Central range represents a mountain territory comprising the Sierra the Candelario (Biosphere Reserve Sierra de Béjar–Sierra de Francia), Sierra de Francia (Sierra de Francia Natural Park) and Sierra de Gata (Natural Protected Site of El Rebollar y Los Agadones). Soils are in general acidic (granites, acidic slates and quartzites) and sandy with higher amounts of organic carbon and nitrogen with increasing altitude. The whole area is included in the bioclimatic Mediterranean region, and so a chronic summer water deficit is noticeable at every site considered. Climate thus ranges from subhumid Mediterranean in the lowlands to hyperhumid Mediterranean in the highlands. Accordingly, a marked turnover of dominant taxa along the elevation

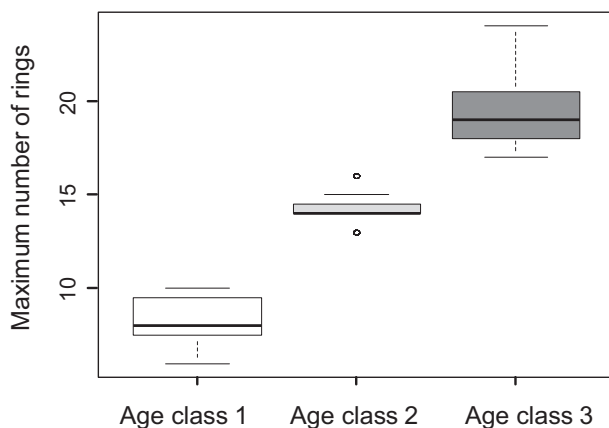


gradient has been reported in this area previously (Madrigal-González et al., 2007). Legume species such as *Cytisus multiflorus* and *Cytisus scoparius* tend to be dominant in lowlands, whereas heaths such as *Erica australis* and *Calluna vulgaris* are dominant taxa in highlands. At intermediate positions, communities dominated by *Cistus ladanifer* dominate soils on acidic slates and quartzites.

All shrub assemblages considered represent seral successional stages of different age established after wildfires occurred in post-agricultural lands. Land abandonment started during the 50s, reached its maximum over the 70s, and persists today as a consequence of depopulation of rural areas (Molino, 2020). This land abandonment has made a strong footprint on vegetation and landscape configuration. Interestingly, a large proportion of the territory is occupied by shrub-dominated communities as seral stages of *Quercus* forests: that is *Quercus pyrenaica* upwards and *Q. ilex* and *Q. faginea* towards lowlands (Madrigal-González et al., 2014).

## 2.2 | Sampling design and data collection

We defined a nested sampling design for data collection along an elevation gradient consisting of 13 sites ranging from 400 m a.s.l. to 1400 m a.s.l. (see Table S1). Within each site, we established three patches of 0.5 ha, each of them in a shrub community of different age (maximum age of the most dominant shrub individuals, see Figure 1 for shrub age distribution in each age class). Finally, five circular sampling plots of 5 m radius were randomly distributed in each of the shrub-dominated patches. A total of 195 sampling plots were thus surveyed across the study area. Cover in terms of the orthogonal projection of shrubs on the ground at the species level was visually estimated, always by the same researcher (JMG), in each sampling plot so that total shrub cover at the plot level, computed as the sum of species coverages, can exceed 100%. Total shrub cover has been proved to be a good proxy of above-ground biomass accretion in Mediterranean shrublands (Montès et al., 2008). Interestingly, total



**FIGURE 1** Boxplot for the distribution of the maximum shrub ages at the plot level aggregated by the three age classes considered in the field sampling design. Shrub age was estimated using dendrochronological techniques.

shrub cover can be transformed into productivity if shown to be related to time. In our study, total shrub cover was controlled by the age of shrub stands in the models so that total shrub cover might thus be considered a proxy of productivity.

The number of species was retrieved as the number of shrub species in each plot. To have a simple/meaningful proxy of richness of functional types we firstly classify species as phanerophytes and chamaephytes following the Raunkiaer classification system (see Table S2). After that, we group phanerophytes according to their dominant foliar syndrome: that is, broad-leaved deciduous, broad-leaved evergreen, needle-leaved evergreen and stem-photosynthesizing legumes. This way, we have every shrub species aggregated into one of five functional types. These leaf syndromes have been used previously to define tree functional types in diversity-functioning studies because of the implications of foliar traits for complementarity in space, time and the source of nitrogen (Madrigal-González et al., 2016; Ruiz-Benito et al., 2017; Feng et al., 2022).

We finally obtained geographical coordinates and elevation in the centre of each patch with the help of GPS technology. Climatic data (i.e. monthly precipitation and temperature) were retrieved from the Atlas Climático Digital de la Península Ibérica (Ninyerola et al., 2005).

The age of each shrubland patch was measured as the maximum age obtained in the biggest cohort of shrubs at each patch. We collected the thickest two basal sections in each of five shrub individuals in each patch. We sanded the basal sections with progressively finer sandpapers (280, 340, 500, 800) so as to allow clear visualization of every growth ring. Finally, we count the number of rings of each section with the help of a magnifying glass.

## 2.3 | Statistical analyses

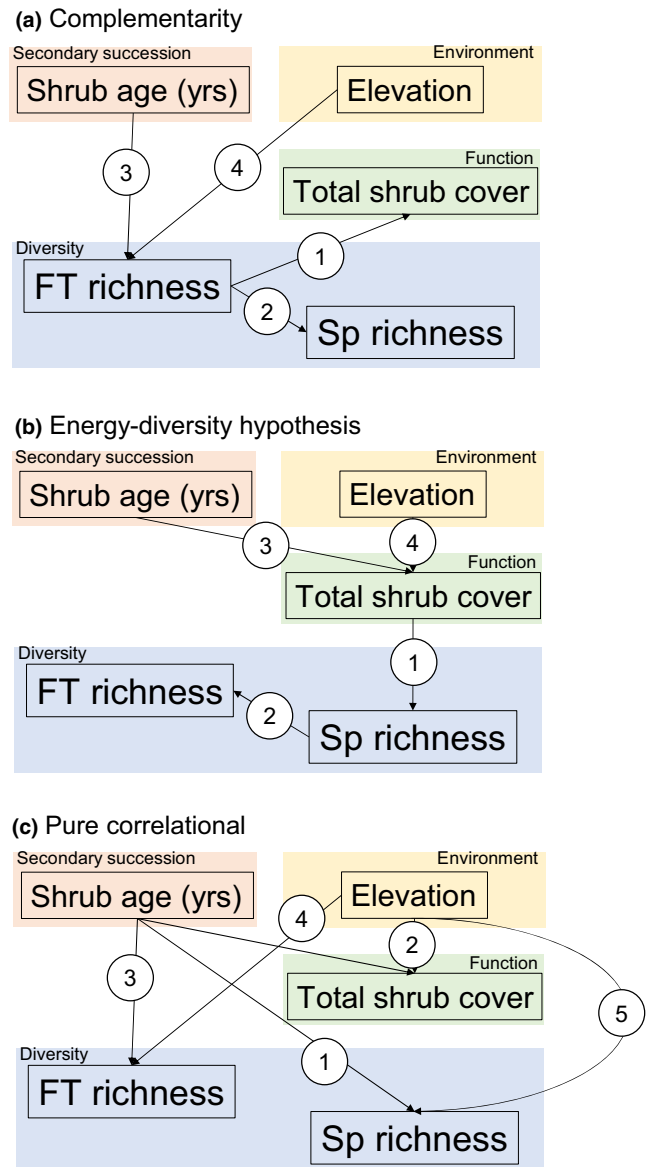
We firstly applied a non-metric multidimensional scaling (NMDS) analysis to the plot by functional types matrix as a descriptive evaluation of the distribution of functional types across the most conspicuous dimensions of environmental variability, namely elevation and land use cessation. We fitted a two-dimension model based on a Bray–Curtis distance matrix and used a stress value of 0.2 as the threshold to support/reject the model. To assist the interpretability of axes, we included environmental variables such as *elevation*, *mean annual temperature*, *mean maximum temperature*, *mean minimum temperature*, *minimum temperature of the coldest month*, *summer precipitation*, *daily temperature range of the coldest month* and *maximum shrub age* in the ordination plot by their correlation with the NMDS axes. The inclusion of these environmental variables in the NMDS helped us to cover a two-fold purpose: e.g. to analyse how temperatures and precipitation correlate with elevation on the one hand, and to explore how the distribution of functional types is responsive to shrub age and elevation/climatic variability. NMDS was fitted using the ‘metaMDS’ function and environmental variables were fitted using the ‘envfit’ function (999 random permutations) in the R package *vegan* (Oksanen et al., 2022).

We defined a frame of analyses based on three structural equation models, two of them representative of the mentioned hypotheses (niche complementarity and the energy–diversity hypothesis respectively), and the last one as a null hypothesis in which diversity and productivity are simply collinear variables along the elevational gradient (Figure 2). In the case of the niche complementarity model, we assumed that both total shrub cover and species richness should be a linear function of the number of functional types, along the elevation gradient and the time since land use cessation (Figure 2a). In the case of the energy–diversity hypothesis, total shrub cover is assumed to be directly determined by elevation and the time since land use cessation. Subsequently, total shrub cover rules the number of species per plot and indirectly, the number of functional types per plot (Figure 2b). In order to avoid collinearity in the regression models, we considered two environmental variables only, elevation and shrub age, which summarizes for the main sources of environmental variation in our sampling design: that is, climatic variability (elevation) and succession-related changes of vegetation (shrub stand age).

We evaluated each of the former structural equation models using Fisher's C, which is based on the missing paths (Lefcheck, 2016). Model selection was conducted using the derived Fisher's C information criterion (CIC sensu Cardon et al., 2011, see Lefcheck, 2016).

### 3 | RESULTS

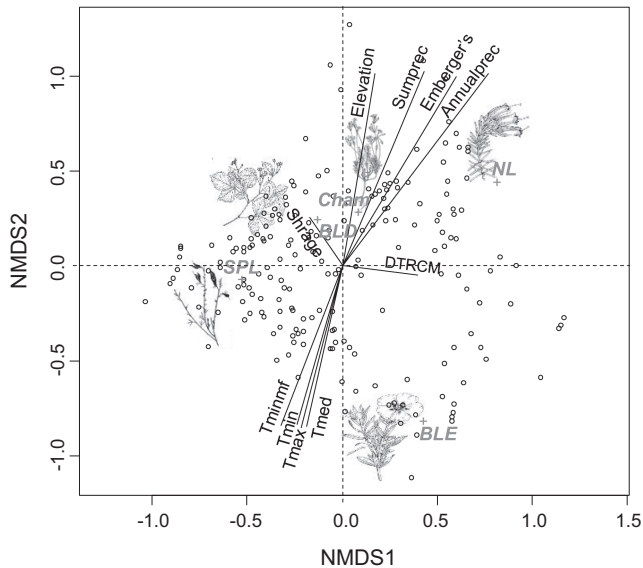
A total of 40 woody species belonging to five functional types were identified in the field survey from across the territory. The distribution of functional types was seemingly well correlated with elevation as shown by results of the NMDS (Figure 3; stress value = 0.14). The most dominant functional type at high-elevation sites was the needle-leaved evergreen, which includes species such as *Erica australis*, *E. arborea*, *E. umbellata* and *Calluna vulgaris*. On the opposite side of the elevation gradient (NMDS2), the dominant functional type was the broad-leaved evergreen including species such as *Cistus ladanifer*, *Phyllyrea angustifolia*, *Arbutus unedo* or *Quercus ilex*. In between, chamaephytes such as *Lavandula stoechas*, *Thymus mastichina* or *Halimium ocymoides* tend to be more abundant in the upper part of the gradient whereas photosynthetic stem legumes such as *Cytisus multiflorus*, *Cytisus scoparius* or *Retama sphaerocarpa* do so towards lower sites. Broad-leaved deciduous species such as *Rubus ulmifolius*, *Rosa canina* or *Quercus pyrenaica* tend to be more abundant at intermediate elevations. Curiously, the minimum and the maximum number of shrub species (one species and 12 species respectively) were recorded in plots located in early and intermediate successional stages of the same site (Mieza: 700 and 710 m a.s.l. respectively). The mean number of species per plot was 6 ( $\pm 2$  SD). Mean total shrub cover per plot was 90% ( $\pm 40$  SD) with maximum values (216% cover) in Mediterranean hyperhumid conditions ( $>1000$  m a.s.l.), and minimum values in the driest and warmest conditions nearby the village of La Fregeneda (429 m a.s.l.). The mean number of functional types per plot was 3 ( $\pm 0.8$  SD) with minimum



**FIGURE 2** Graphical representation of the hypotheses under evaluation using structural equation models. (a) The complementarity model poses both productivity (total shrub cover) and species richness (Sp richness) as function (paths 1 and 2) of the functional-type richness (FT richness), which will be in turn a function of elevation (path 4) and shrub age (path 3). (b) The energy–diversity hypothesis states that diversity is function (path 1) of productivity (Total shrub cover). Specifically, species richness is a function of total shrub cover and functional-type richness is in turn a function of species richness (path 2). (c) The pure correlational model states that species richness, functional-type richness and total shrub cover are a function of elevation (paths 5, 4, 2 respectively) and shrub age (1, 3, 2 respectively), and thus there is no room for a causal relationship among them.

(1) and maximum values (5) running in parallel to minimum and maximum values of species richness.

Model selection using CIC supported the energy–diversity theory over the complementarity effects hypothesis (CIC<sub>comp</sub> = 49.49; CIC<sub>div-ener</sub> = 45.79; CIC<sub>null</sub> = 147.92) in the SEM analyses.

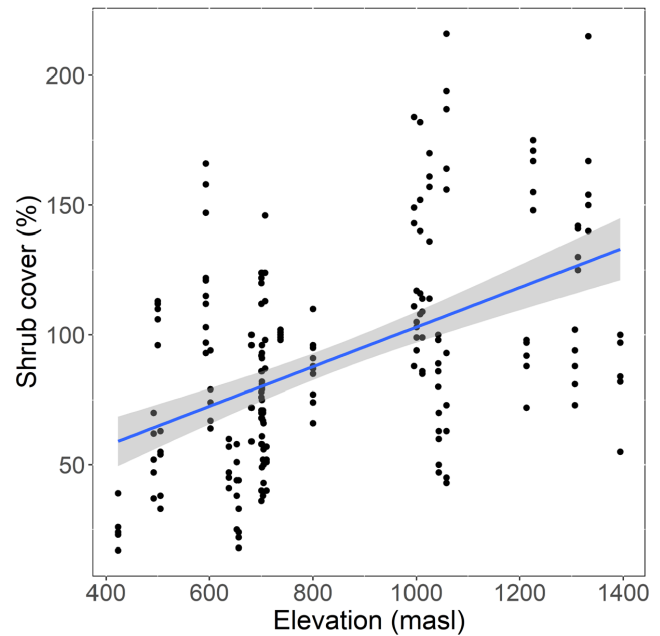


**FIGURE 3** Compositional biplot (non-metric multidimensional scaling, NMDS) applied to the functional types (grey crosses) × plots (empty circles) matrix. BLD, broad-leaved deciduous species; BLE, broad-leaved evergreen; Cham, chamaephytes; NL, needle-leaved species; SPL, stemmed photosynthetic legumes. Solid lines represent the environmental variables including climatic variables, elevation (elevation) and shrub age (Shrage). Length and direction of environmental variables are representative of the magnitude and sign of the correlation with axes. Legend of climatic variables: Annualprec, total annual precipitation; DTRCM, daily temperature range of the coldest month; Emberger's, humidity index of Emberger; Summprec, summer precipitation; Tmax, mean of maximum temperatures; Tmed, mean annual temperature; Tmin, mean of minimum temperatures; Tminmf, minimum temperature of the coldest month.

Importantly, both the complementarity and the diversity–energy models were interpretable as supported by the non-significant Fisher's *C* statistic (Fisher's *C* = 13.796, *p*-value = 0.183). On the contrary, significant missing paths between diversity and total shrub cover invalidated the null model as a suitable hypothesis (Fisher's *C* = 111.922, *p*-value < 0.001). The best supported model (energy–diversity) included a positive significant effect of elevation on total shrub cover and discarded shrub age as a significant determinant of total shrub cover (see [Figures 4](#) and [5a](#)). Total shrub cover, in turn, positively ruled the number of species at the plot level ([Figure 5b](#)) and indirectly the number of functional types through a significant path between the number of species and the number of functional types ([Figure 5c](#)). Neither elevation or shrub age directly affected the number of species nor the number of functional types per plot. Similarly, total shrub cover did not influence the number of functional types directly.

## 4 | DISCUSSION

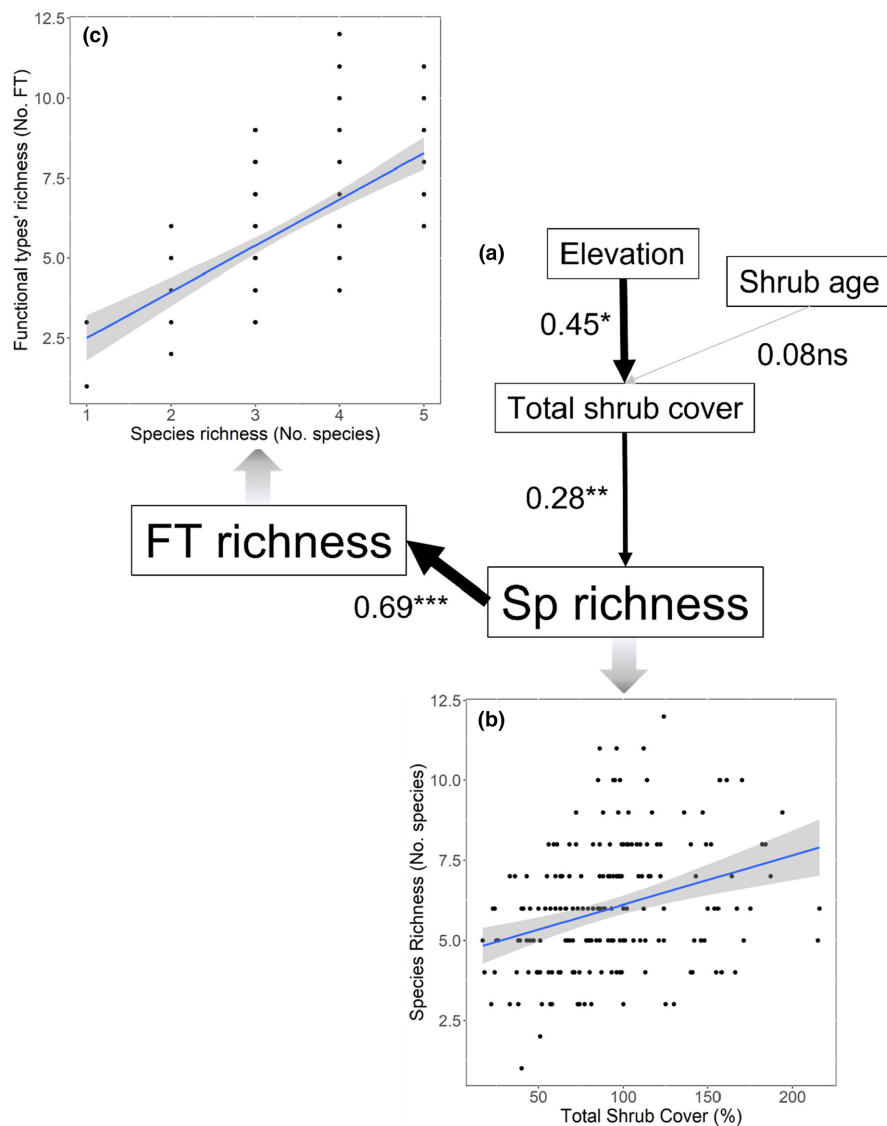
Our results suggest that the energy–diversity theory prevails over the complementarity hypothesis in these Mediterranean



**FIGURE 4** Relationship between elevation and shrub cover. The blue line represents the fitted regression line whereas the grey shadow denotes the 95% confidence interval around the marginal mean.

shrub-dominated communities. Thus, the environmental variability, through its control on productivity along the elevation gradient, determines the number of species assembled at the plot level, and subsequently, the number of functional types. This causal frame in the diversity–productivity relationship thus implies that more species might not necessarily represent an efficient mitigating strategy to face the ongoing climate warming through complementarity, even though a portfolio of more species can represent an insurance for productivity stability under changing environmental conditions (Schindler et al., 2015). On the contrary, the ongoing climate warming, through detrimental influences on productivity, would set both taxonomic and functional diversity as victims of impaired function under climate change.

Functions such as biomass accretion in shrub-dominated assemblages increase at higher elevations in water-limited regions (Mata-González et al., 2002). On the one hand, climatic harshness associated with drought in Mediterranean-type climates decreases with elevation (Latron et al., 2009). Specifically, summer rainfall, which is critical for woody plants to endure the chronic summer drought, is commonly tied to adiabatic cooling in Mediterranean mountains, as confirmed in our study area by the strong correlation between summer rainfall and elevation ( $r = 0.82$ ). Accordingly, above-ground productivity in mediterranean bioclimatic regions is highly sensitive to water inputs during the dry season (Cotrufo et al., 2011) particularly in lowlands, where increased transpiration demands imposed by higher temperatures can aggravate drought-prone stresses due to rainfall scarcity (Latron et al., 2009). More research, nonetheless, would be needed to incorporate differences in water retention capacity due to soil physical properties to fully



**FIGURE 5** Graphical representation of variables and standardized coefficients in the supported structural equation model. (a) Results of the best supported structural equation model. (b) Species richness (Sp richness) as a positive linear function of total shrub cover (%). (c) Functional-type diversity (FT richness) as linear positive function of species richness.

understand hydrological dynamics along the elevation gradient. On the other hand, the ordination of functional types indicates a strong environmental filtering generating a convergence in leaf strategy to cope with the variation in conditions and resources along our altitudinal gradient. Needle-leaved evergreen species dominate cold environments at high altitudes, where multilayered deep canopies are able to yield higher photosynthetic rates than broad-leaved species with shallower canopies (Sprugel, 1989), especially under the overcast conditions created by convection clouds in mountain environments (Ishii et al., 2012; Sanchez et al., 2016). At the warmer and driest part of the gradient, the dominant functional types corresponded to broad-leaved evergreens and stem-photosynthesizing legumes. Broad-leaved evergreen species in the Mediterranean are characterized by leaf traits such as low specific leaf area (SLA), dense mesophyll layer, and cells with thick cell walls, maximizing water use efficiency and avoiding wilt under drought conditions (Poorter et al., 2009; Campetella et al., 2019). In turn, stem-photosynthesizing legumes with short leaf lifespans can extend the carbon gain under periodic droughts and high irradiance conditions (Valladares &

Pugnaire, 1999; Valladares et al., 2003). This environmental filtering on the primary foliar syndromes along the elevation gradient sets the number of species per plot and subsequently the number of functional types (Wardle et al., 2000).

Total shrub cover was significantly related to both species and functional type richness. Specifically, the best supported causal direction in such a relationship suggests that the available energy, expressed ecologically as productivity, is the cause of the number of species directly, and the number of functional types indirectly. The More Individuals Hypothesis (MIH) has been defined as a mechanistic support for the energy–diversity theory in ecological communities (Srivastava & Lawton, 1998). The MIH states that more available energy in ecological communities allows for the existence of a greater number of individuals and with this, for a larger number of viable populations and species (Gaston, 2000). Interestingly, a recent revisiting of the MIH suggests that this prevalent causal direction between productivity and diversity does not deny the existence of complementarity or facilitation linked to niche segregation, but proposes that, in case they exist, they would play a secondary role



in the global causal frame (Storch et al., 2018). Studies on woody plant communities have reported significant positive influences of species diversity on different surrogates of productivity worldwide (Liang et al., 2016). In European forests, radial growth, stand basal area and above-ground biomass proxies significantly relate to diversity (Georgi et al., 2021; Madrigal-González et al., 2016; Ratcliffe et al., 2016; van der Plas, 2019). However, most of the studies did not test the causal direction from productivity to diversity and so only niche complementarity is commonly discussed as a reliable mechanism underpinning such relationship along large-scale environmental gradients (Madrigal-González et al., 2016; Ratcliffe et al., 2016; Ruiz-Benito et al., 2017).

A significant positive relationship between productivity and diversity might be a consequence of shared environmental drivers acting as confounding factors (Vilà et al., 2007). Our statistical frame also rejected this possibility, posing the hypothesis of a shared environmental driver as the less supported model. Rey Benayas and Scheiner (2002) found that the number of individuals, as function of the available energy, is among the most important determinants of species diversity at the site level in woody plant communities from across the Iberian Peninsula. Interestingly, the authors posed diversity as the response variable and so the interpretation of results was unidirectionally focused on energy as the cause of diversity. On the contrary, local studies in the Mediterranean have demonstrated the existence of positive diversity effects on the functioning of woody plant species (shrubs and trees). Using a local spatial approach, Montès et al. (2008) demonstrated the role of complementarity as the most likely mechanism involved in overyielding for combinations of two to three species in southeastern France. However, as the authors point out, positive diversity–function relationships mostly rely on the presence of *Cistus albidus* in the species combinations, probably due to the existence of strong negative intraspecific interactions in this species. Similarly, research conducted in tree species assemblages revealed that overyielding is contingent upon the species and trait composition rather than diversity per se (Jucker et al., 2014; Yuan et al., 2018). This suggests that, even if complementarity plays a role at the community level in woody plant communities in the Mediterranean, the energy–diversity hypothesis can attain a prevalent role if the focus is posed on landscape scales in which sources of environmental variability can determine disparate successional trajectories and species combinations. In this regard, mechanisms of species assembly reveal critical for unveiling the actual functional significance of species diversity in Mediterranean woody plant assemblages. Madrigal-González et al. (2020) proposed that species diversity will be the cause of abundance in highly productive areas where competition has acted as a major evolutionary force pushing natural selection towards minimization of limiting similarity among species (Schluter, 1994). Under such conditions, complementarity plays a two-fold role allowing for species coexistence via spatial clustering (Bastias et al., 2020) on the one hand and maximizing productivity through a more efficient resource uptake and use on the other (Forrester, 2017). On the opposite side of the climatic gradient, either cold or dry environments, environmental filtering has a

major role limiting functional trait values and the number of species able to persist (Diaz et al., 1998). Consequently, the available energy (productivity) gains a prevalent role driving the number of species through control on the demographic viability of populations. Following this reasoning, environmental filtering (mostly climatic variability) has been shown to drive shrub species assembly along elevation gradients in temperate latitudes (Bello et al., 2013). A meta-analysis on the role of environmental filters along elevation gradients supports this idea globally and states that climatic filters associated to elevation can dictate the composition of plant species locally through convergent effects on foliar functional traits (Read et al., 2014).

Unexpectedly, total shrub cover did not depict any significant pattern along the shrub age chronosequence. Research conducted in NW Spain to evaluate recovery in shrub communities after different disturbance treatments suggested that shrub cover maintains a low, yet constant, increment of cover after burning and ploughing over a 15-year time period (Calvo et al., 2002a). From then on, total shrub cover is expected to be arrested by the most dominant species that exert strong competitive influences on the accompanying species at late subseral stages (Calvo et al., 2002b). Hence, the lack of trend in our study might be attributed to the time lags considered in the design of the spatial chronosequence: that is, the youngest age class (7–10 years old) might be close to the threshold for shrub cover stabilization in successional time. Otherwise, using spatial chronosequences as surrogates of temporal variability is challenging even if the successional species turn-over is expected to be rapid, as might be the case in our study area. For instance, spatial chronosequences might poorly represent temporal successional changes when successional trajectories among sites have disparate velocities (Walker et al., 2010). Previous studies on successional recovery of shrublands in the Cantabrian Mountains suggested that velocities of shrub recovery after fire and cutting treatments vary along an elevation gradient at a 10-year time lag (Calvo et al., 2005). Current available information is unfortunately insufficient to affirm that successional dynamics are neither simultaneous nor convergent along the elevation gradient considered in this study. Further research is therefore needed to shed light on this uncertainty. Specifically, evaluating the validity of shrub stand age as a solid proxy of successional time in such a heterogeneous mountain territory will require long-term field monitoring schemes (>25 years) based on surveys of permanent plots along the elevation gradient.

## 5 | CONCLUSIONS

Our findings represent a step forward towards inferring the actual functional significance of diversity in Mediterranean shrub-dominated assemblages using observational data. A significant positive relationship between productivity and diversity can be interpreted in one causal direction or the other, or even in both directions if a third variable exerts control on both simultaneously. Nonetheless, using the statistical frame applied in this study, we can

affirm that diversity might not necessarily act as a primary mitigating factor in the face of global warming but rather as a victim of productivity due to its dependence on the available energy (productivity) in these Mediterranean shrubland communities. Therefore, efforts under global change should be primarily focused on maintaining productivity to preserve biodiversity rather than the other way around. Importantly, shrub age seems to be negligible for productivity in these shrub communities at the age levels considered here. Further research should be planned to extend the current scheme of age classes to earlier stages in which productivity thresholds could be detected and evaluated.


#### AUTHOR CONTRIBUTIONS

Jaime Madrigal-González conceived the idea and did the statistical analyses. Jaime Madrigal-González and José Antonio García Rodríguez participated in the field work; all authors discussed the results and commented on the manuscript. All authors wrote the paper.

#### DATA AVAILABILITY STATEMENT

Data are available at <https://figshare.com/articles/dataset/Matorral/21382686> (<https://doi.org/10.6084/m9.figshare.21382686.v1>).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Descriptive information of the study area.

**Appendix S2.** Species classification into functional types.

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