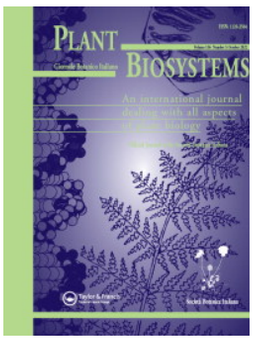

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Diversity and regeneration strategies in woody plant communities of the Mediterranean Basin: Vegetation type matters

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ABSTRACT

The Mediterranean Basin has distinct vegetation types shaped by fire, herbivory, and various human activities. Based on data from 83 belt transects of 10×40 m in 28 study sites for five physiognomic vegetation types (semi-closed forest, open forest, closed shrubland, open shrubland, and scrubland) in southwestern Anatolia (Turkey), we analyzed woody species diversity, woody community composition, and vegetation structure of study sites. We used the growth form and regeneration strategy for functional comparisons of physiognomic vegetation types. We found clear distinctions in diversity, species composition, and functional structure of woody plant community across five physiognomic vegetation types. The forest-shrubland-scrubland distinction was the most apparent one. Despite similarities in the woody species richness and Shannon diversity, open and closed vegetation states of forests and shrublands also differed regarding the density and cover of mature individuals and the density of saplings in different functional groups. Non-metric multidimensional scaling analyses and indicator species analyses also indicated clear distinctions among physiognomic vegetation types and openness states. Our findings indicate the necessity of a more complex description of vegetation types in the Mediterranean Basin. The results suggest that open and closed vegetation states of forests and shrublands are functionally distinct vegetation types.

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Pinus brutia forest; open vegetation; woody plant community; regeneration strategies; scrubland; shrubland; the Mediterranean Basin; NMDS; indicator species analysis

Introduction

The Mediterranean Basin includes various vegetation types that differ in their form, structure, diversity, and human use (Keeley et al. 2012). These distinct vegetation types have been shaped by summer drought, recurrent fires, and grazing during the Pleistocene since the onset of the Mediterranean climate (Suc 1984; Naveh and Carmel 2004). Consequently, plant communities resilient and/or resistant to fire, drought, and herbivory are dominated the Mediterranean (Lavorel 1999). Humans have also been a strong influence on Mediterranean landscapes in several ways, such as agro-pastoral activities, logging, and urbanization for millennia (Perevolotsky and Seligman 1998; Blondel and Aronson 1999; Naveh and Carmel 2004). The interactions of natural and anthropogenic drivers result in mosaic landscapes including different vegetation types across the Mediterranean Basin. In recent decades, however, the changes in land-use patterns, climate, and fire regimes increase the uncertainty about the trajectory of changes in these vegetation types (Pausas and Millán 2019; Baudena et al. 2020). Such vegetation shifts are of concern to the future biodiversity of the Mediterranean region (Sedlar et al. 2018), where has nearly 10% of the Earth's total plant diversity (Cowling et al. 1996) and is considered as a biodiversity hotspot (Myers et al. 2000).

Historically, vegetation types in the Mediterranean Basin were classified based on the vegetation structure and dominant growth form (Harshberger 1926; Zohary 1947). It is widely accepted that three distinct vegetation types exist in the Mediterranean Basin: forests (dominated by pines or oaks), shrublands (maquis, matorral, or garrigue), and scrublands (phrygana, tomillar, or batha) (Arianoutsou 1998; Blondel and Aronson 1999; Keeley et al. 2012; Kavgaci et al. 2017). Complex classifications of Mediterranean vegetation are also possible based on the dominant species (Demirbaş Çağlayan et al. 2020) or community assembly (Bonari et al. 2021; Kavgacı et al. 2021). Moreover, forests and shrublands (including both tall shrublands and scrublands) are considered as alternative biome states in the Mediterranean Basin mediated by fire disturbance (Pausas and Bond 2020). Fire and herbivory better predict biome boundaries in many parts of Earth in comparison to classical climate-based approaches (Bond 2005; Staver et al. 2011; Dantas et al. 2016). The alternative biome state approach brings forward the idea that open vegetation states are not early successional or degraded habitats, but on contrary they are stable systems (Pausas and Bond 2020). Therefore, defining alternative biome states based on disturbances to explain landscape mosaics has implications for our understanding of and management decisions on ecosystems (Pausas and Bond 2019). In the context of alternative stable states theory, Mediterranean forests and shrublands (*sensu lato*) represent closed and open vegetation states, respectively (Pausas and Bond 2020). On the other hand, the openness

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state of shrubland or forest vegetation has rarely been considered in the classification of Mediterranean vegetation (e.g., Levin et al. 2013), although it has recently been recognized as an essential part of the vegetation dynamics and ecosystem function in many biomes (Bond 2019).

Most conservation efforts are channeled toward undisturbed forest habitats in the Mediterranean Basin. However, open habitats such as shrublands, scrublands, and post-fire regeneration states of forests are also of conservation importance because they include ecologically important plant communities (Lombardo et al. 2020) and form suitable habitats for wildlife (Mangas et al. 2008; Soyumert et al. 2020). Furthermore, open and burned habitats harbor several herbaceous and dwarf shrub species that cannot survive in undisturbed forests and their existence across a forest-shrubland matrix increase biodiversity at the landscape level. Consequently, a lack of acknowledging well-defined vegetation types would limit our understanding of conservation and management in Mediterranean landscapes comprised of closed and open forests and shrublands.

Functional group-based descriptions and comparisons of Mediterranean vegetation types have not been made except in studies that examined post-disturbance vegetation dynamics (e.g., Kazanis and Arianoutsou 2004; Tavşanoğlu and Gürkan 2014). Consequently, no attention has been given to the differences and similarities in plant community assembly and vegetation structure among different Mediterranean vegetation types using a functional approach. Since post-fire recovery processes or old-field successions are well explained using functional groups based on regeneration strategy or growth form (Bonet and Pausas 2004; Kazanis and Arianoutsou 2004; Tavşanoğlu and Gürkan 2014), functional groups may also be efficiently used to describe and classify long-undisturbed vegetation types and alternative vegetation states in the Mediterranean Basin. Such an approach would help us classify vegetation types in a more sophisticated way for better conservation and management in the global change era.

In this study, we aimed to define vegetation and woody community structure in three major physiognomic vegetation types (forest, shrubland, and scrubland) of the Mediterranean Basin with a functional approach using growth form and post-fire regeneration strategies. Considering open and closed habitats can differ from each other regarding the ecological dynamics proceed within, we also included two openness states (closed and open) for forest and shrubland vegetation in the study. We ask the following specific question: Do the diversity patterns and functional structure of woody plant communities in these physiognomic vegetation types differ from each other? Regarding this question, we hypothesized that main physiognomic vegetation types and their openness states should differ in species diversity, species composition, dominant growth form, and dominant regeneration strategy regarding the woody plant community. To test this hypothesis, we counted mature individuals and saplings and estimated the cover of woody species in belt transects nested in study sites representing the vegetation types under question. Then, we compared the density and cover of each woody species and functional group (growth form and regeneration strategy) and diversity patterns of communities in different vegetation types.

Material and methods

Study area

The study area was located between Köyceğiz Lake and Datça Peninsula in southwestern Anatolia (Muğla province, Turkey) in the eastern Mediterranean Basin (36.686° N, 27.362° E at the westernmost point and 36.835° N, 28.640° E at the easternmost point; Figure 1). Dominating vegetation type was maquis shrubland and Turkish red pine (*Pinus brutia* Ten.) forests. The area has one of the highest forest and shrubland coverage in Anatolia and also includes Kermes oak (*Quercus coccifera* L.) garrigues and subshrub-dominated phrygana vegetation. The study area has served as a glacial refugium during Pleistocene glaciations, at least for the last glacial maximum. It also harbors forest stands of tree species of Tertiary origin (*Liquidambar orientalis* Mill. and *Phoenix theophrastii* Greuter). These biogeographical legacies make the area one of the major centers of biodiversity and endemism in the Mediterranean Basin and an important hotspot for conserving plant diversity (Médail and Quézel 1997).

The study area has a Mediterranean climate with wet winters and a prolonged summer-dry period (5 months). Since the long dry, and hot summer makes the vegetation fire-prone, the area is also a hotspot for wildfires in Turkey. As a result of frequent crown fires, forest habitats and maquis shrublands compose a fragmented mosaic landscape structure on vast areas (Tavşanoğlu and Gürkan 2014). Moreover, in the study area, forest stands and shrublands are found at different levels of open vegetation states, namely semi-closed and open forests, closed and open shrublands, or scrublands.

Studwy sites

We focused on three major vegetation types of the eastern Mediterranean Basin: thermo-Mediterranean pine forests (*Pinus brutia* forests in our case), sclerophyllous maquis shrublands, and phrygana vegetation (Keeley et al. 2012). Using forest management plans and digitalized maps prepared by the General Directorate of Forestry of Turkey, we identified five categories of vegetation types dominating the study area: semi-closed Turkish red pine (*P. brutia*) forest (hereafter; semi-closed forest), open Turkish red pine forest (hereafter; open forest), closed maquis shrubland (hereafter; closed shrubland), open maquis shrubland (hereafter; open shrubland), and phrygana scrubland (hereafter; scrubland) (Supplementary Table 1). Based on the information obtained from local forest management units and our field observations, possible sampling sites were evaluated by considering the accessibility of stands (roads, steep slopes, etc.), past forest management activities, and recent wildfire occurrences. We eliminated the managed and recently burned stands from our potential study site list to not consider the sites at different regeneration states of vegetation in the study. In this way, we provided that each vegetation type group represents a distinct vegetation state at its maturity.

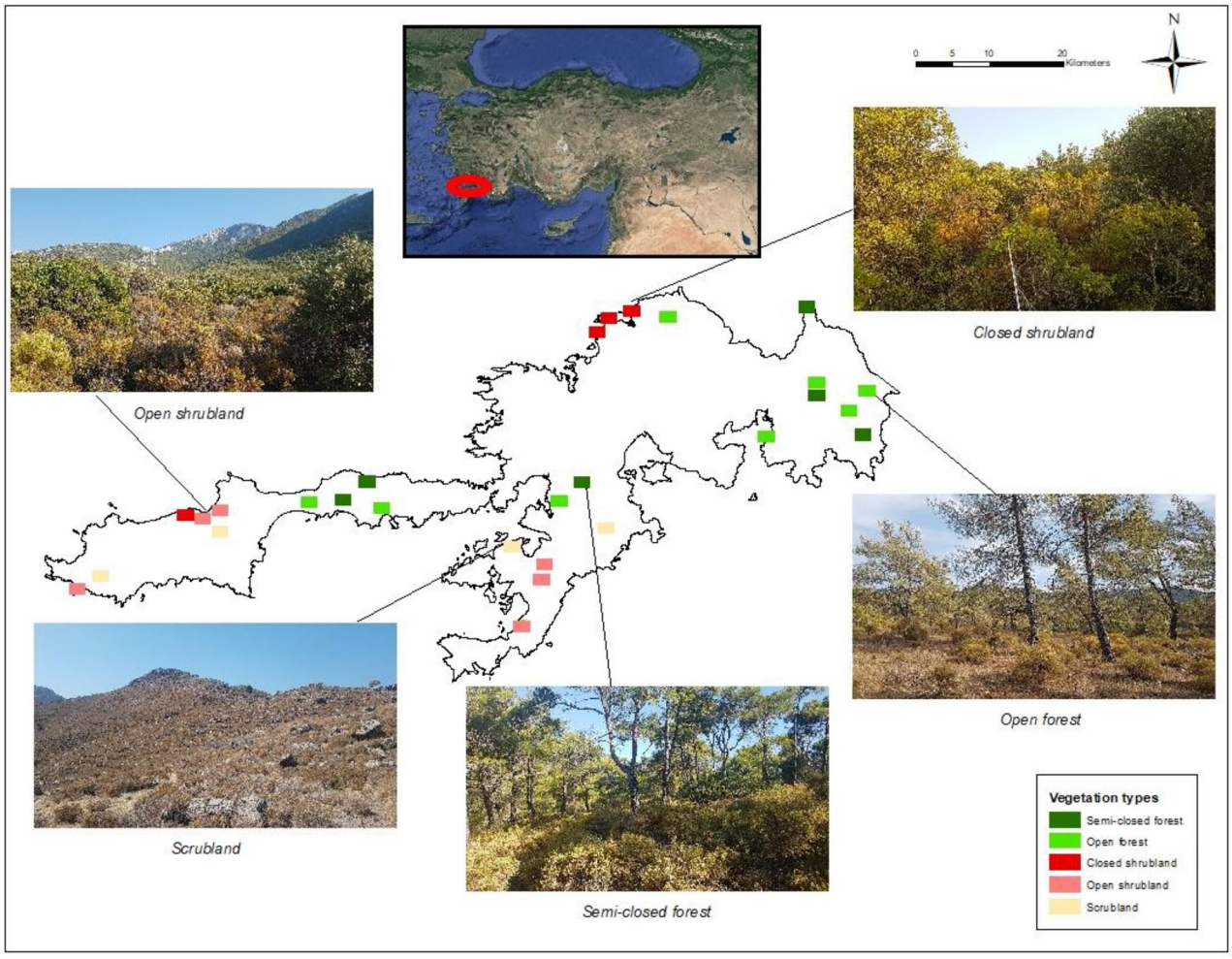

Figure 1. The study area and study sites. The minor map at the top indicates the location of the study area in Turkey, while the major map shows the locations of study sites. Study sites representing different vegetation types included in the study are given in different colors, and a general view of each vegetation type is also presented. Note that the scale is for the major map.

Table 1. Total number of individuals at mature and sampling stages sampled (only mature individuals) and counted (both matures and saplings) belonging to woody plant community in the studied physiognomic vegetation types.

	Mature		Sapling	
Study site	Individual	Species	Individual	Species
Semi-closed forest	3.347	33	5.359	36
Open forest	4.478	37	6.905	39
Closed shrubland	2.875	33	2.446	28
Open shrubland	5.399	39	4.097	34
Scrubland	3.042	22	1.022	20
Total	19.141	54	19.829	53

In total, we selected 28 study sites for five vegetation type categories. Since the total coverage area and the number of stands differ among vegetation types in the whole study area, we assigned the study sites in each vegetation type based on this information. Consequently, we selected different number of study sites for semi-closed forest (#6), open forest (#8), closed shrubland (#4), open shrubland (#6), and scrubland (#4).

Field measurements and counts

Field measurements and counts were performed within three belt transects 10 × 40 m (400 m^2) in size in each study site. These belt transects were located at the geographic center of study sites when possible and had 30 to 50 m distance from each other. If there is a road close to the center of the study site, the starting point of the transect was assigned to at least 5 m distance to the road. In total, we sampled 83 belt transects for the study nested in 28 study sites. One transect was missing in one study site, and the size of 13 belt transects was 10 × 30 m due to the extreme topographic conditions in sites. In latter cases, raw data was calculated proportionally to the size of the transect.

In each belt transect, we counted all mature individuals and saplings for each woody species. We measured two perpendicular diameter lengths of the canopy of each mature

individual within the belt transect. Thus, we determined the number of mature individuals and saplings in each belt transect and each study site. The canopy cover (hereafter; cover) of each mature individual was calculated as the area of the disk projected the canopy, using the average of two measured lengths as the diameter:

$$Cover = \pi \left(\frac{\left(Diameter1 + Diameter2 \right)}{2} \right)^2$$

To count saplings of each species, we divided each transect into eight 5 × 10 m quadrats, and then all saplings in each quadrat were counted. Since the main focus of our study is woody plant communities, we did not perform any count or measurements on herbaceous species.

We took samples from woody plant individuals that could not be identified in the field and then identified them in the herbarium. Nomenclature follows mainly the Turkish flora book (Davis, 1965–1985) and updated by considering recent taxonomic advances (The Plant List 2013).

Functional classifications

We classified woody species based on their growth form and regeneration strategy to identify functional similarities or differences in vegetation structure among the studied vegetation types. Studies on Mediterranean vegetation types are generally based only on tree and shrub growth forms (Sternberg and Shoshany 2001; Gritti et al. 2006; Malkinson et al. 2011). However, to reveal growth form differences more detailed especially between shrubland and scrubland, the woody species recorded in the study sites were classified using the descriptions in the BROT database: subshrub, shrub, large shrub, tree, and liana (Tavşanoğlu and Pausas 2018). Subshrubs refer dwarf plants typically less than 50 cm, shrubs are typically less than 1.5 m and frequently have several shoots from the soil level, large shrubs represent tall plants that may reach tree structure under optimal conditions, trees are very tall plants mostly with one main primary stem, and liana represents climber plants (Tavşanoğlu and Pausas 2018).

We also included the regeneration strategy of woody species in our functional classification since it is an important plant trait in fire-prone Mediterranean ecosystems and a determinant of the post-fire recovery of plants after the fire (Paula et al. 2009; Tavşanoğlu and Gürkan 2014). For regeneration strategy classification, we mainly followed Pausas et al. (2004), which adopted an approach based on the resprouting and propagule persistence of plant species. According to that, after %100 scorch by fire, resprouters (R+) can resprout, while non-resprouters (R-) have no capacity to resprout. Besides, seeds or fruits of propagule-persisters (P+) persist after the fire, but non-propagule-persisters (P-) cannot. In addition to this primary regeneration strategy classification, we further include seed bank locality for P + species in our classification system: canopy (c) or soil (s) seed bank. Seed bank location is an essential trait for the regeneration mode of Mediterranean species as the fate of the species with these strategies significantly differs in long-term vegetation dynamics (Tavşanoğlu and Gürkan 2014). In the end, each woody species was classified into one of the following regeneration strategy classes: (1) non-resprouter and propagule persister species with a canopy seed bank (R-P + c), (2) non-resprouter and propagule persister species with a soil seed bank (R-P + s), (3) resprouter and propagule-non-persister species (R + P-), and (4) "R + P+" species: resprouter and propagule-persister species with a soil seed bank (R + P+). Since no species is known for R + P + c strategy in the Mediterranean Basin, we did not include soil seed bank information in the acronym of R + P + strategy for simplicity. Regeneration strategy information of species were also obtained from the BROT database (Tavşanoğlu and Pausas 2018).

Data analysis

We used data from belt transects for all analyses. We calculated woody species richness and diversity of saplings and mature individuals to describe diversity patterns for each belt transect. Species richness was obtained as the total number of species found in a belt transect. Species diversity was calculated using Shannon's formula (hereafter, "Shannon diversity") based on the number of species and the number of individuals of each species in the belt transect. Before analyzing Shannon diversity data, a rarefaction analysis was performed to understand whether further analyses using the data are proper. The difference in species richness among vegetation types was tested using a generalized linear model (GLM) assuming the Poisson distribution since the response variable was count data. We performed a general linear model (LM) for comparing Shannon diversity among vegetation types. For each analysis, the residuals of the model results were checked using diagnostic plots.

We also calculated the mean cover and number (i.e., density) of saplings and mature individuals for each woody species in each belt transect. The frequency of occurrence of each woody species was also calculated for belt transects in each vegetation type. The difference in cover among vegetation types were tested using a general linear model assuming the Gaussian distribution. Since the number of individual data had excess zeros, the difference in the number of individuals among vegetation types was tested using a two-stage approach: a GLM assuming the Poisson distribution and a GLM assuming the binomial distribution. The former analysis was performed on data whose zeros were excluded, while the latter included only presence and absence data for each species created from the original number data. In this way, we were able to cope with zero-inflated number data in these analyses.

In addition to analyses on individual species, we classified woody plant species into different growth forms and regeneration strategies, then analyzed whether the cover and number of different functional groups differ among the studied vegetation types. In these functional group analyses, we used generalized linear models assuming Poisson distribution to compare the number of individuals (count data), while general

linear models to compare cover (continuous data). The multiple comparisons following the LM or GLM analyses were performed by estimating marginal means for different vegetation type pairs. A chi-square analysis was also performed to test whether the number of mature individuals and saplings and the cover of mature individuals belonging to different growth forms and regeneration strategies differ among vegetation types.

To understand how the structure and species composition of the woody plant community varies depending on the vegetation type, we implemented a non-metric multidimensional scaling (NMDS) and a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) for the presence, cover, and number data for mature individuals of woody species. To reveal differences in woody plant community composition and structure between vegetation type pairs, we performed PERMANOVA analysis for each pair separately. However, in these cases, we considered $\alpha = 0.01$ for detecting significant differences due to several pairwise comparisons. We also used the indicator value analysis (IndVal; Dufrene and Legendre 1997) to identify indicator woody plant species by using presence-absence data and the Pearson's phi coefficient of association (Chytry et al. 2002) to determine the ecological preferences of species by using density data for different vegetation types. These two indices are used to list species that specific to habitats (De Cáceres and Legendre 2009). Because of the unequal number of sites in different vegetation types, we used a specific function to correct index estimates by sample size.

All the analyses were performed in the R environment (R Core Team 2020). We used *diversity* function for Shannon diversity analysis, *rarefy* and *rarecurve* functions for rarefaction analysis, *metaMDS* and *adonis* functions for NMDS and PERMANOVA analysis (all in the *vegan* package; Oksanen et al. 2019) and *multipatt* function for indicator species analysis and Pearson's phi coefficient of association analysis (in the *indicspecies* package, De Cáceres 2020). Marginal means were estimated using *emmeans* function (in the *emmeans* package, Lenth 2020).

Results

Species richness and diversity

Overall, we recorded 19141 mature individuals belonging to 54 woody species in study sites. Besides that, in total, we also recorded 19829 saplings belonging to 53 woody species in study sites (Table 1, Supplementary Table 2). We recorded a higher number of saplings than mature individuals in semi-closed and open forests. However, the number of mature individuals was higher than that of saplings in the rest of the vegetation types (Table 1). Rarefaction analyses of species richness in belt transect showed that the species-sample size curves were asymptotic in most cases (**Supplementary** Figure 1), and therefore were satisfactory for further analysis of species richness and diversity.

For mature individuals, both woody species richness and Shannon diversity were higher in shrublands than forests and scrublands (Figure. 2, Supplementary Table 3). For saplings, however, these differences were less prominent (Figure 2). Indeed, the differences in species richness and diversity of saplings were insignificant between all vegetation type pairs except scrublands (Supplementary Table 3). The lowest woody diversity and richness values were obtained in scrublands, for both mature individuals and saplings, mainly due to the dominance of a few plant species such as *Sarcopoterium spinosum* (L.) Spach (Supplementary Tables 4 and 5).

Presence, density, and cover of individual species

Woody species differed in their frequency of occurrence, density, and cover among different vegetation types

Table 2. The mean density (ind./transect) of saplings and mature individuals and mean cover (%) of mature individuals in terms of different growth forms for each vegetation type. Generalized linear models assuming Poisson distribution and general linear models assuming Gaussian distribution were used to analyze the density (i.e., the number of saplings and mature individuals) and cover, respectively. *Dev.* is deviance. The same letters next to the values indicate no significant difference ($P > 0.05$) across vegetation types.

Growth form	Semi-closed forest	Open forest	Closed shrubland	Open shrubland	Scrubland	Poisson GLM	
						Dev.	P
Density of mature individuals							
subshrub	17.0a	27.1b	48.9c	114.5d	163.4e	3482.9	<0.0001
shrub	108.9a	137.6b	87.0c	158.7d	77.8c	598.3	<0.0001
large shrub	27.6a	20.1b	70.3c	35.1d	5.8e	917.7	<0.0001
tree	13.1a	10.1b	12.3ab	5.4c	4.3c	115.8	<0.0001
liana	3.9a	7.3b	21.1c	3.9a	2.3a	334.2	<0.0001
Density of saplings							
subshrub	30.9a	56.1b	29.1a	57.5b	38.8c	296.1	<0.0001
shrub	83.5a	141.7b	45.3c	129.4d	40.6c	1502.1	<0.0001
large shrub	85.9a	49.5b	105.6c	49.0b	3.5d	1739.4	<0.0001
tree	10.9a	15.6b	2.4c	0.8d	1.6 cd	477.5	<0.0001
liana	74.6a	35.4b	21.4c	4.3d	0.8e	2249.5	<0.0001
						Linear Model	
						F	P
Cover of mature individuals							
subshrub	1.9ab	2.9b	5.2bc	15.2c	42.5d	27.6	<0.0001
shrub	33.9ab	47.2a	20.1b	31.7ab	17.3b	3.9	0.0057
large shrub	39.4a	16.4ac	76.3b	36.5a	6.8c	12.7	<0.0001
tree	91.5a	63.1b	37.7bc	5.5c	2.8c	26.6	<0.0001

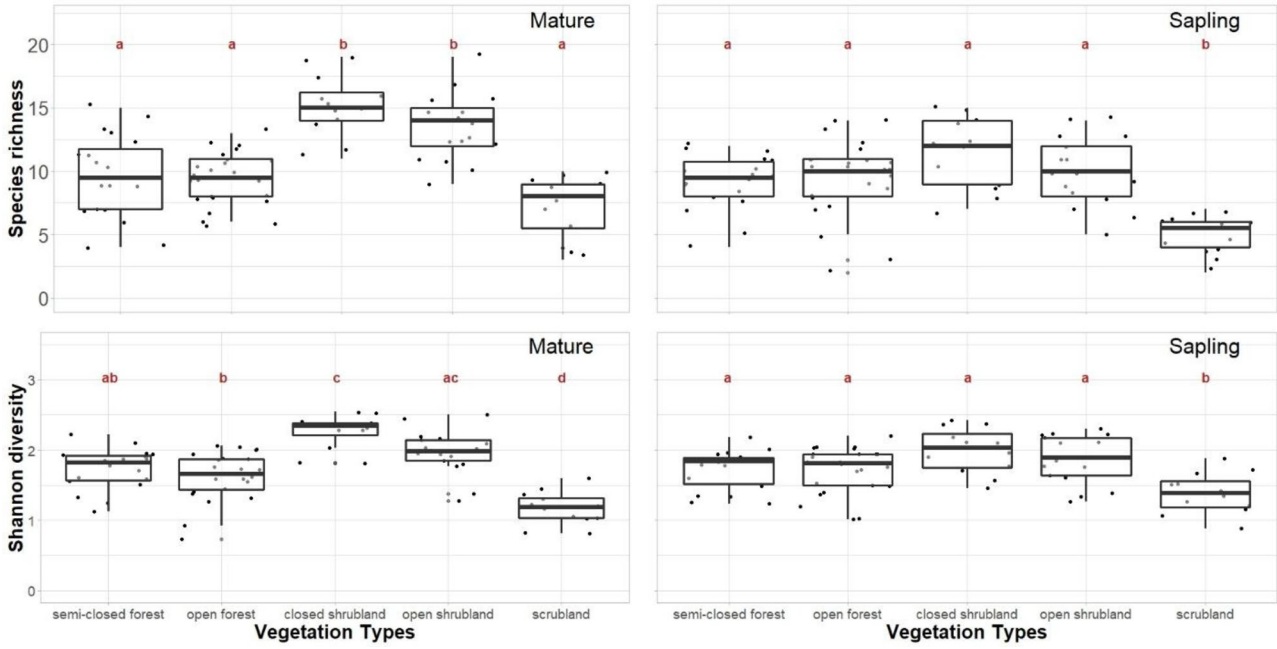

Figure 2. Species richness and Shannon diversity of saplings and mature individuals in different vegetation types. Data points are values obtained from belt transects. In boxplots, the horizontal black line is the median, the box extends from 25th to 75th percentiles, and whiskers show 1.5 interquartile ranges.

Table 3. The mean density (ind./transect) of saplings and mature individuals and mean cover (%) of mature individuals in terms of different regeneration strategies for each vegetation type. Generalized linear models assuming Poisson distribution and general linear models assuming Gaussian distribution were used to analyze the density (i.e., the number of saplings and mature individuals) and cover, respectively. *Dev.* is deviance. The same letters next to the values indicate no significant difference ($P > 0.05$) across vegetation types.

Reg. strategy	Semi-closed forest	Open forest	Closed shrubland	Open shrubland	Scrubland	Poisson Dev.	Poisson P
Density of mature individuals							
R-P+c	11.6a	9.1a	2.6b	0.1c	0.0c	349.9	<0.0001
R-P+s	78.3a	67.7b	68.7b	90.1c	35.4d	362.5	<0.0001
R+P-	32.8a	33.7a	146.6b	60.8c	12.3d	2255.3	<0.0001
R+P+	44.3a	80.1b	18.3c	101.7d	184.5e	2514.7	<0.0001
Density of saplings							
R-P+c	10.1a	15.0b	1.7c	0.0d	0.2cd	485.7	<0.0001
R-P+s	77.3a	97.5b	36.3c	93.4b	29.3d	929.1	<0.0001
R+P-	161.2a	88.9b	156.3a	65.5c	4.6d	3193.5	<0.0001
R+P+	30.5a	67.1b	3.9c	42.4d	45.5d	1030.6	<0.0001
						Linear Model F	Linear Model P
Cover of mature individuals							
R-P+c	90.4a	62.4b	18.8c	0.3c	0.0c	33.4	<0.0001
R-P+s	17.3a	12.7a	15.1a	14.8a	5.3a	1.2	0.3173
R+P-	40.3ac	17.8ac	100.7b	41.2a	8.6c	23.0	<0.0001
R+P+	18.2ab	35.4ac	4.1b	21.1ab	51.0c	7.8	<0.0001

(Supplementary Tables 4–6). Some woody species were found in some specific vegetation types, whereas others were present with a high frequency, density, or cover in all vegetation types. Of the species recorded in the study, only 12 occurred across all vegetation types, from semi-closed forests to scrublands. These species were *Asparagus aphyllus* L., *Calicotome villosa* (Poir.) Link, *Cistus creticus* L., *C. salviifolius* L., *Genista acanthoclada* DC., *Olea europaea* L., *Phillyrea latifolia* L., *Phlomis lycia* D. Don, *Pistacia lentiscus* L., *Quercus coccifera*, *Sarcopoterium spinosum*, and *Thymbra capitata* (L.) Cav. (Supplementary Table 6). There was no general trend regarding the growth form or regeneration strategy of these species as they were in various groups (resprouters or non-resprouters, and subshrubs, shrubs, large shrubs, or liana) (Supplementary Table 2). Two of these species, namely *Cistus creticus* (12.3-29.2 ind./transect) and *Genista acanthoclada* (11.5-39.8 ind./transect), occurred with very high densities in all vegetation types, while others had relatively lower values (< 2.4 ind./transect) at least in one vegetation type (Supplementary Table 5). Mature *Cistus salviifolius* individuals reached their maximum densities (> 50 ind./transect) in both semi-closed forests and open shrublands (Supplementary Table 5), consequently, they were dominated not only open shrubland sites but also the understory of Turkish red pine forests.

Sarcopoterium spinosum had very high densities (52.2 and 146.2 ind./transect) in open shrublands and scrublands (Supplementary Table 5), respectively, and was a dominant component of these vegetation types. All these species with very high densities were propagule-persisters (P+) and shrubs or subshrubs (Supplementary Table 2). On the other hand, these species had relatively lower coverage in the vegetation than propagule-non-persisters (P-) except *S. spinosum* whose reach 40% coverage in scrublands. Indeed, *Phillyrea latifolia*, *Olea europea*, and *Arbutus andrachne* L., which all have R+P- strategy, had 29.6%, 18.3%, and 15.4% cover values in closed shrublands (Supplementary Table 6). As a species with the same strategy, *Quercus coccifera*, furthermore, reached 13.5% cover values in both closed and open shrublands.

As expected, the dominant figure of vegetation in forest sites was *Pinus brutia* with 96.1% and 61.2% coverage, and 12.2 and 8.9 ind./transect densities in semi-closed and open forests, respectively (Supplementary Tables 5 and 6). Although *P. brutia* had a relatively lower density in closed shrublands (2.1 ind./transect; Supplementary Table 5), this tree species also contributed to the vegetation markedly in closed shrublands as its cover value reaches 18% (Supplementary Table 6). *Erica manipuliflora* Salisb., a shrub species with R+P+ strategy, had its highest cover values in both semi-closed (11.4%) and open (24.1%) forests (Supplementary Table 6). Besides *E. manipuliflora*, the dominant species found in the understory of *P. brutia* trees differed markedly, as *C. salviifolius* (14.9%), *Phillyrea latifolia* (12.2%), and *Q. coccifera* (11.3%) had relatively high cover values in semi-closed forests. However, in open forests, *Genista acanthoclada* (9.4%) and *Cistus creticus* (6.6%) had higher coverage among others (Supplementary Table 6).

Growth form

There were significant differences in the density of mature individuals and saplings of woody species among vegetation types (Table 2, Supplementary Table 7). Consequently, the relative number of mature individuals and saplings significantly differed among vegetation types (χ^2 = 4595.4, d.f. = 16, $P < 0.0001$ for matures; χ^2 = 4670.5, d.f. = 16, $P < 0.0001$ for saplings; Figure 3). In a similar manner, the cover of growth forms significantly differed among vegetation types (χ^2 = 5314.0, d.f. = 16, $P < 0.0001$; Figure 3). Subshrubs occurred with the highest density (163.4 ind./transect) and cover (42.5%) in scrubland (mostly *Sarcopoterium spinosum*), although those of saplings were counted mostly in open forest and open shrubland (56.0 and 57.5 ind./transect, respectively, Table 2). Mature individuals of shrubs outnumbered other growth forms in all vegetation types except scrublands in which subshrubs had a higher density than shrubs (Figure 3a, Table 2). On the other hand, this was not the case when cover values were considered, as trees and large shrubs dominated forests and shrublands, respectively, and subshrubs had the highest coverage in scrublands. Albeit that, shrubs were still important components of the vegetation in all vegetation types by reaching cover values between 17.3% and 47.2% (Table 2).

Large shrubs dominated closed shrublands regarding the density of mature individuals and saplings and the cover of mature individuals (Table 2, Figure 3). Several species contributed to this dominance of large shrubs, most apparently *Arbutus andrachne*, *Pistacia lentiscus*, *Phillyrea latifolia,* and *Quercus coccifera* (Supplementary Tables 5 and 6). Closed shrublands also had a considerable number of mature *Olea europea* trees (9.4 ind./transect), whereas the dominant tree species of the region, *Pinus brutia* had relatively lower density in closed shrubland than forests (2.1 vs. >8.9 ind./transect, respectively, Supplementary Table 5). On the other hand, with a substantial contribution of *O. europea* and *P. brutia* to vegetation cover (~36% in total), trees were essential components of the closed shrubland vegetation type (Table 2, Figure 3, Supplementary Table 6). Tree cover gradually decreased from semi-closed forest (91.5%) to scrubland (2.8%) (Table 2, Figure 3). Although the density of mature trees, mainly *Pinus brutia*, was not significantly different between semi-closed forest (13.1%) and open forest (10.0%), the sapling density of trees was found higher in open forest in comparison to the semi-closed forest (15.6% and 10.9%, respectively, $P < 0.05$, Table 2). Liana density exhibited opposite trends for mature individuals and saplings, in which the density of mature individuals gradually increased, but that of saplings decreased from semi-closed forest to closed shrubland (Table 2, Figure 3).

Density and cover showed contrasting patterns between large shrubs and shrubs/subshrubs with respect to the closeness of vegetation. Large shrubs had higher density and cover in semi-closed forest and closed shrubland relative to open forest and open shrubland, respectively, while shrubs/subshrubs had vice versa (Table 2, Figure 3). A similar trend to that was observed for large shrubs also occurred in the density of mature trees, but this was not true for tree saplings between semi-closed forests and open forests (Table 2, Figure 3).

Regeneration strategy

Relative density of mature individuals and saplings of woody species and relative cover of mature individuals of woody species for different regeneration strategy classes differed from each other (χ^2 = 5287.4, d.f. = 12, $P < 0.0001$ for density of mature individuals; χ^2 = 3853.7, d.f. = 12, $P < 0.0001$ for density of saplings; χ^2 = 4770.6, d.f. = 12, $P < 0.0001$ for cover of mature individuals; Figure 4). Since *Pinus brutia* is the only dominant species with R-P+c strategy, trends in this regeneration strategy class strictly followed those of *P. brutia*. Thus, density and cover of mature individuals had significantly higher values in forest vegetation types than shrublands and the scrubland ($P < 0.05$; Table 3, Supplementary Table 8). Besides, although the cover of R-P+c strategy had higher in the semi-closed forest than open forest, sapling density of this regeneration strategy group was significantly higher in the open forest than semi-closed forest ($P < 0.05$; Table 3). The density of R-P+s species was high in all vegetation types except closed shrublands in which mature individuals of species with

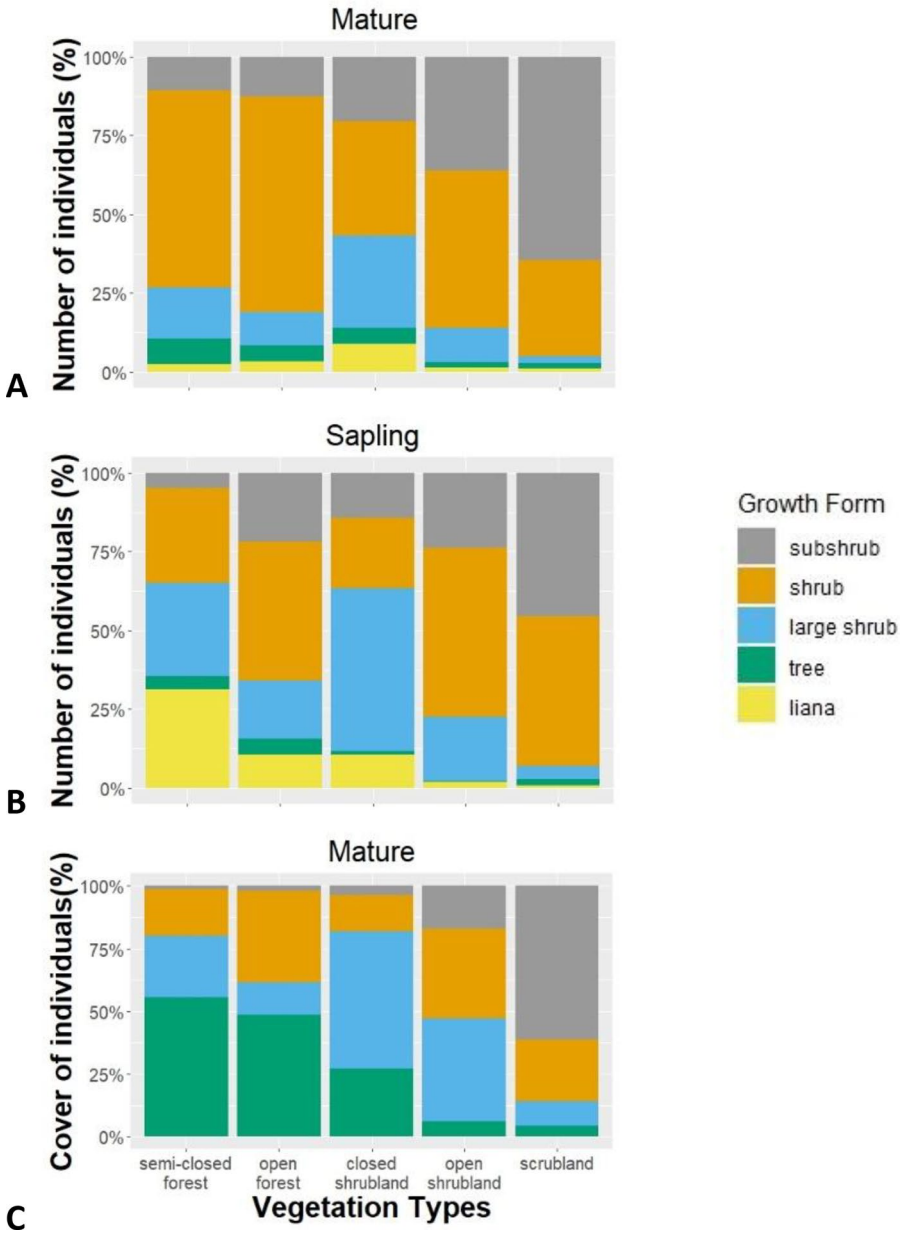

Figure 3. Relative total number of mature individuals (A) and saplings (B), and relative total cover mature individuals (C) for different growth forms in each vegetation type.

R + P- strategy outnumbered those with R-P + strategies (Table 3, Figure 4). Saplings of R-P + s strategy also had high numbers in all open habitats (open forest, open shrubland, and scrubland), but this was not the case in closed vegetation types (Table 3, Figure 4). Although they outnumbered many other regeneration strategies, the R-P + s strategy had not relatively high cover values in any vegetation type and had the lowest cover among other regeneration strategies in forests (Table 3, Figure 4).

The R + P- strategy that constitutes more than half of the species included in the study was recorded mainly in closed shrublands (146.6 ind./transect) and had 100% total cover value in this vegetation type (Table 3, Figure 4). Consequently, species with the R + P- strategy dominated closed shrublands. R + P- strategy was also a dominant group in semi-closed forest and open shrubland by reaching ~40% cover values. The density of saplings in the R + P- strategy was the highest among other regeneration strategies in semi-closed forest and closed shrubland and had a considerable contribution to the total density of woody plant saplings in open forest and open shrubland (Table 3, Figure 4). R + P + strategy had surprisingly low values of density (both mature individuals and saplings; 18.3 and 3.9 ind./transect, respectively) and cover (4.1%) in closed shrubland, but considerable contributed to the total density (>80 ind./transect) and cover (>20%) in open forest and open shrubland (Table 3). In scrubland vegetation, the R + P + strategy was the dominant figure in all aspects with 184.5 and 45.5 ind./transect values for mature and sapling density, respectively, and 51.0% cover (Table 3). Among the three most abundant species with R + P + strategy, *Sarcopoterium spinosum* dominated open shrubland and scrubland, whereas *Erica manipuliflora* was an essential component of forest vegetation types (Supplementary Table 5). The third species, *Genista acanthoclada* had a significant

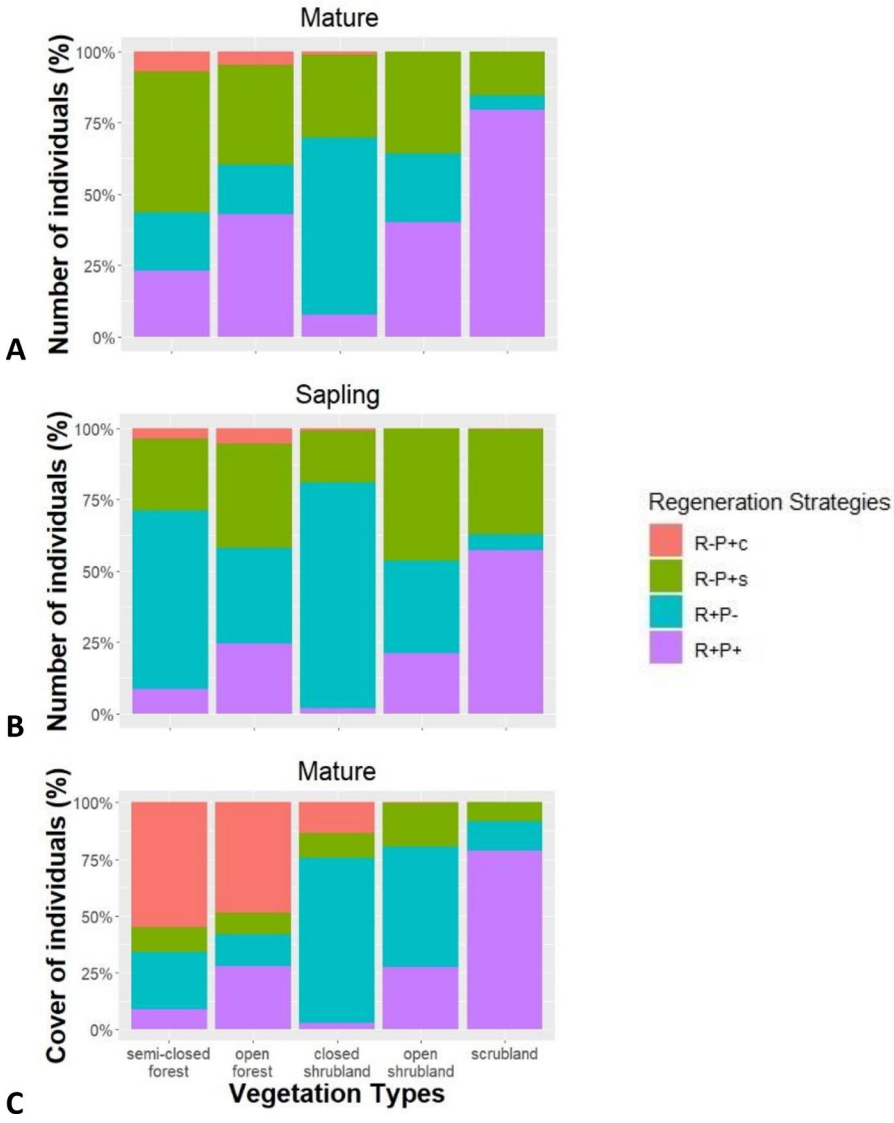

Figure 4. Relative total number of mature individuals (A) and saplings (B), and relative cover of mature individuals (C) for different regeneration strategies in each vegetation type.

contribution to all vegetation types, especially to open forest, open shrubland, and scrubland (Supplementary Table 5).

Analyzing the resprouting ability as a simple binary trait (yes/no) indicated that resprouters (R+) dominated shrubland and scrubland vegetation types, but non-resprouters (R-) were dominant in both two forest types (Supplementary Table 9, Supplementary Figure 2). Relative density of mature individuals and saplings and relative cover of mature individuals belonged to two resprouting ability groups were significantly different from each other (χ^2 = 1155.2, d.f. = 4, $P < 0.0001$ for density of mature individuals; χ^2 = 619.1, d.f. = 4, $P < 0.0001$ for density of saplings; χ^2 = 1836.5, d.f. = 4, $P < 0.0001$ for cover of mature individuals; Supplementary Figure 2).

Woody plant community composition and structure

Non-metric multidimensional scaling (NMDS) analyses showed that most vegetation types differed from each other regarding the density, cover, and presence of mature individuals of woody species (Figure 5; Supplementary Figure 3). Indeed, PERMANOVA analyses indicated significant differences among vegetation types (R^2 = 0.255 and $P = 0.001$ for density; R^2 = 0.422 and $P = 0.001$ for cover; and R^2 = 0.430 and $P = 0.001$ for presence). Additional PERMANOVAs comparing vegetation type pairs showed that all vegetation types differed from each other ($R^2 > 0.20$ and $P < 0.001$ in most cases, Supplementary Table 10) except the number of mature individuals between semi-closed forest and open forest (R^2 = 0.05, Supplementary Table 10). The most distinct separations were obtained among scrubland, open shrubland, and closed shrubland vegetation types, which differed clearly from each other and forest vegetation types (Figure 5, Supplementary Table 10).

Using indicator value analysis and Pearson's phi analysis, we identified 10 and 20 indicator woody species, respectively, in different vegetation types. The number of indicator woody species were the highest in closed shrubland (#10) and open

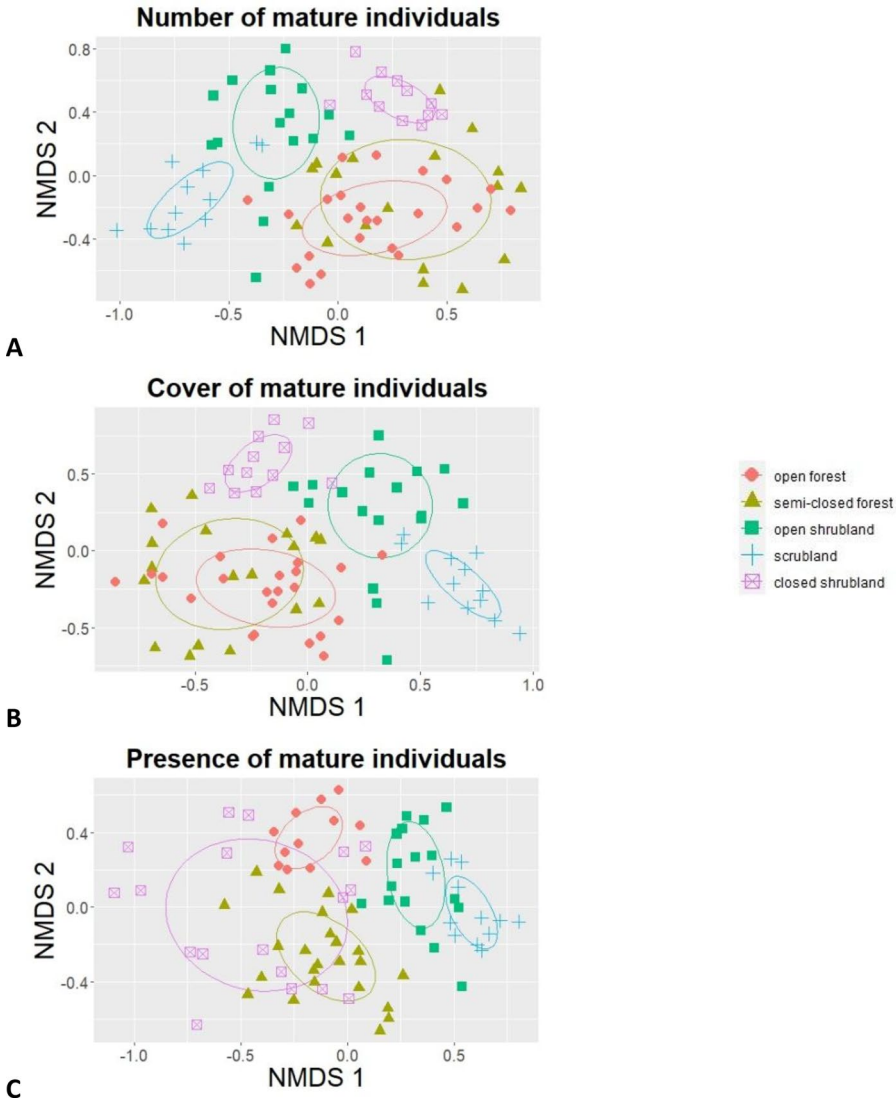

Figure 5. Non-metric multidimensional scaling graphs for (A) the number of individuals, (B) cover, and (C) presence of mature individuals. Different colors and shapes represent different vegetation types included in the study. Each data point symbolized a belt transect. Eclipses indicate the standard deviation of each vegetation type.

shrubland (#9) (Table 4). The analyses did not list any species for open forest, but two and one species for scrubland and semi-close forest, respectively (Table 4).

Discussion

Our results indicate that diversity, species composition, and functional structure of woody plant community significantly differ among Mediterranean vegetation types. The forest-shrubland-scrubland distinction was the most apparent one, as can be expected from the traditional approach to Mediterranean vegetation classification. However, besides this distinction, open and closed states of forests and shrublands were also functionally distinct vegetation types. Consequently, our study suggests that Mediterranean Basin vegetation is more diverse regarding functional structure and composition than previously thought.

We found clear distinctions in woody plant community and vegetation structure patterns across five vegetation types included in the study. Despite similarities in the woody species richness and Shannon diversity, open and closed vegetation states of forests and shrublands substantially differed regarding the density and cover of mature individuals and the density of saplings in different functional groups. However, we found that open and closed forests also have differences in the number of mature and immature individuals and plant cover regarding growth form, resprouting ability, and regeneration strategy. In contrast, shrublands and scrublands had more prominent differences in a similar manner, moreover, they both strongly differed from forests. Non-metric multidimensional scaling analyses, indicator species analysis, and Pearson's phi analysis also indicated clear distinctions among vegetation types and openness states. Thus, our study showed that vegetation type is an important determinant of the functional structure of Mediterranean Basin plant communities.

Alternative stable state theory predicts that open and closed vegetation types are alternative to each other in

Table 4. Species associated to vegetation types according to indicator value analysis (IndVal) and Pearson's phi coefficient of association. The number of random permutations was computed 9999 to precise the p-value, and $\alpha = 0.05$ for both analyses. Species are sorted by their IndVal values.

	Pearson's phi		IndVal	
Species	Estimate	P	Estimate	P
Closed shrubland				
Hypericum empetrifolium	0.593	0.0001	0.823	0.0001
Arbutus andrachne	0.586	0.0001	0.773	0.0001
Ruscus aculeatus	0.556	0.0001	0.772	0.0001
Arbutus unedo	0.438	0.0002	0.574	0.0006
Pistacia terebinthus	–	–	0.476	0.0309
Rubia tenuifolia	0.352	0.0403	0.408	0.0369
Phillyrea latifolia	0.699	0.0001	–	–
Olea europaea	0.556	0.0001	–	–
Smilax aspera	0.526	0.0001	–	–
Asparagus aphyllus	0.423	0.0034	–	–
Open shrubland				
Cistus parviflorus	0.399	0.0058	0.562	0.0009
Teucrium chamaedrys ssp. *syspirense*	0.464	0.0008	0.540	0.0114
Asperula brevifolia	0.337	0.0344	0.417	0.0309
Teucrium polium	–	–	0.378	0.0343
Daphne gnidioides	0.470	0.0005	–	–
Euphorbia acanthothamnos	0.374	0.0147	–	–
Phlomis lycia	0.354	0.0178	–	–
Quercus aucheri	0.344	0.0235	–	–
Phlomis grandiflora	0.308	0.0336	–	–
Scrubland				
Sarcopoterium spinosum	0.650	0.0001	–	–
Pyrus elaeagnifolia	0.358	0.0175	–	–
Semi-closed forest				
Styrax officinalis	0.334	0.0429	–	–

bimodal or multimodal stable state systems from tropical to boreal regions (Scheffer et al. 2012; Pausas 2015; Dantas et al. 2016; Pausas and Bond 2020). In the Mediterranean Basin, forests and shrublands, representing closed and open states, respectively, are known to be alternative biome states driven by fire regimes (Pausas and Bond 2020). These alternative states differ in many aspects, including species diversity and composition, plant height, and vegetation structure. Unsurprisingly, our results also revealed clear distinctions in diversity, species composition, and functional structure of woody plant community between forests and shrublands. Moreover, scrublands in our study appeared as a different vegetation type differing both from forests and shrublands in many aspects comparable with the difference between forests and shrublands.

Beyond these vegetation types (forest, shrubland, and scrubland), our study also suggests that two more categories based on the openness of forest and shrubland vegetation are distinguishable in the Mediterranean Basin as functionally distinct vegetation types. Especially closed and open shrublands differ each other in species composition, several indicator species, growth form, and regeneration strategy. This distinction was relatively looser, especially between open and closed forests, in comparison to that was present for shrublands versus forests. Blondel and Aronson (1999) stated that "open woodlands or park-like glades alternate with very dense and much lower stature vegetation types" in some low-altitude parts of the Mediterranean Basin and suggested that these vegetation formations often occur due to human activity. On the other hand, the total burnt area is much higher in open shrublands than in closed shrublands globally (Bond 2019), suggesting that fire is a significant driver shaping these vegetation states. Herbivory is another factor in forming open shrublands in the Mediterranean Basin (Perevolotsky and Haimov 1992). It is often hard to define the relative role of natural and anthropogenic drivers shaping local vegetation in the Mediterranean Basin as Mediterranean vegetation has been shaped by complex interactions among climate, fire, and herbivory (Naveh and Carmel 2004). A long-term study focusing on the transition among maquis vegetation types at various openness states indicates closed Mediterranean shrublands are irreversible stable states while open shrublands develop towards closed shrublands when there is no disturbance (Kadmon and Harari-Kremer 1999). Increasing aridity with climate change coupled with fires is expected to be a driver of the vegetation shift from forests to shrublands, but not to open forests in the Mediterranean Basin (Baudena et al. 2020). Since we selected our study sites based on minimum or zero human activity to avoid such confusion, by acknowledging open vegetation as a natural part of landscapes (Bond 2019), it is likely to consider these open and closed states of forest and shrublands as transition states between forests, shrublands, and scrublands in which bearing significant differences in terms of diversity and functional structure, but not degraded habitats.

Habitat mosaics comprising forests, shrublands, and scrublands or different post-disturbance regeneration stages increase the heterogeneity and diversity at the landscape level in the Mediterranean Basin (Trabaud and Galtié 1996; Romero-Alcaraz and Ávila 2000; Amici et al. 2013). Our results on differences in woody species composition and functional structure among forest, shrubland, and scrubland vegetation types support this idea. Furthermore, apparent differences in the relative abundance and cover among functional groups

across five vegetation types in our study suggest that the openness state of Mediterranean forests and shrublands may also contribute to plant functional diversity in Mediterranean landscapes and should be considered as a separate component of habitat mosaics in the Mediterranean Basin. Therefore, considering the openness state of vegetation may contribute to better conservation and management of Mediterranean landscapes (e.g., Levin et al. 2013).

Our study provides novel insights on the physiognomic vegetation types and woody plant communities in low altitude coniferous forest-shrubland systems of the Mediterranean Basin. Furthermore, our findings provide evidence for the necessity of a more complex description of vegetation types in the Mediterranean Basin and suggest that the openness state of forests and shrublands are worth considering as functionally distinct vegetation types. Such an awareness would enhance our understanding of the dynamics of Mediterranean vegetation and contribute to better conservation and management practices in the Mediterranean Basin. Finally, the further examination of alternative stable systems for the Mediterranean vegetation beyond forest versus shrubland states and the potential drivers of open and closed woody vegetation types are promising for a better understanding of the dynamics and patterns of vegetation in the Mediterranean Basin.

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Author contributions

Ç.T. conceived the idea and designed the research; İ.T. performed field studies with the contribution from Ç.T.; İ.T. conducted the data entry and management; İ.T. and Ç.T. performed statistical analyses and wrote the paper.

Disclosure statement

No potential conflict of interest was reported by the authors.

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