ASSESSING THE RESISTANCE AND RESILIENCE CAPACITY OF LOW ELEVATION MEDITERRANEAN WOODY VEGETATION TO FIRE AND CLIMATE CHANGE BASED ON PLANT TRAITS AND RECOMMENDATIONS FOR FORESTRY PRACTICES

ALÇAK RAKIM AKDENİZ ODUNSU VEJETASYONUNUN BİTKİ KARAKTERLERİNE DAYANARAK YANGINA VE İKLİM DEĞİŞİKLİĞİNE KARŞI DİRENÇ VE DİRENGENLİK KAPASİTESİNİN BELİRLENMESİ VE ORMANCILIK UYGULAMA ÖNERİLERİ

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to all women

who have to fight

for equal rights in education and career opportunities

ABSTRACT

ASSESSING THE RESISTANCE AND RESILIENCE CAPACITY OF LOW ELEVATION MEDITERRANEAN WOODY VEGETATION TO FIRE AND CLIMATE CHANGE BASED ON PLANT TRAITS AND RECOMMENDATIONS FOR FORESTRY PRACTICES

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Mediterranean Basin includes vegetation types most exposed to fire and climate change. Recently, studies on plant traits provide information on how ecosystems work at the species and community level. The aim of this study was developing suggestions on forestry implementations for low altitude Mediterranean woody vegetation by revealing species diversity, species richness, functional group classifications (i.e. growth form, regeneration strategy, resprouting ability), leaf trait variations (i.e. specific leaf area, leaf thickness, leaf area), resilience and resistances capacities to fire and climate change by using plant traits, at species and community level.

This thesis was conducted in Mediterranean vegetation dominated by Turkish red pine (*Pinus brutia* Ten.) and maquis species in Köyceğiz, Marmaris and Datça regions in Muğla province, southwestern Anatolia (Turkey). Fieldworks were conducted in semi-closed Turkish red pine forests, open Turkish red pine forests, closed maquis shrublands, open maquis shrublands and scrubland. A total of 28 study sites were selected, and in each study site three 10×40 m belt transects were sampled. All woody plants in each transect were identified, and their locations, height and coverage were measured. Saplings were counted in the 5×10 m subsections in each belt transect. Besides that, leaf samples

were collected from 857 individuals belonging to 38 woody plant species. Specific leaf area, leaf thickness and leaf area measurements of these samples were carried out in the field and laboratory. For assessing the resistance and resilience capacities of vegetation types to fire and climate change, 17 plant traits obtained from the field and literature were included in the analysis.

The most striking distinction was differences among forest-shrubland-scrubland vegetation types, and shrublands had highest value regarding to species diversity and richness. In addition, functional group classifications, non-metric multidimensional scaling analysis and indicator species analyzes also revealed a sharp difference between open and closed habitats. Regarding to leaf trait variations, differences were found among plant species, functional groups and plant communities. Based on the results from leaf trait measurements, forests and shrublands are more resistant to drought, however scrublands are more successful to disturbances. Findings on resistance and resilience capacities to fire and climate change showed that open habitats are more resilient to both fire and climate change compared to closed habitats, and the resistance capacity to climate change is ranked as forest > shrubland > scrubland from the highest to the lowest, considering coverage of individuals. Finally, resistance and resilience capacities were inversely related, i.e. scrubland has the highest resilience but the lowest resistance capacity.

Findings from this study revealed the differences among low altitude Mediterranean woody vegetations with respect to plant community parameters and plant functional traits. The results demonstrate the functional differences between open and closed vegetations in low altitude Mediterranean environments. This study provides new new insights for forestry implementations and conservation strategies to be applied in both maquis areas and Turkish red pine forests in Turkey by revealing the resistance and resilience potential of Mediterranean vegetation types to fire and climate change.

Keywords: open and closed states, *Pinus brutia* forests, shrubland, scrubland, functional group classification, plant community.

ÖZET

ALÇAK RAKIM AKDENİZ ODUNSU VEJETASYONUNUN BİTKİ KARAKTERLERİNE DAYANARAK YANGINA VE İKLİM DEĞİŞİKLİĞİNE KARŞI DİRENÇ VE DİRENGENLİK KAPASİTESİNİN BELİRLENMESİ VE ORMANCILIK UYGULAMA ÖNERİLERİ

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Akdeniz Havzası, yangın ve iklim değişikliği etkilerinin en çok hissedildiği vejetasyon tiplerine sahiptir. Son yıllarda bitki karakterleri kullanılarak yapılan çalışmalar, ekosistemlerin tür ve komünite düzeyinde nasıl çalıştığına dair bilgiler sunmaktadır. Bu tez kapsamında, alçak rakım Akdeniz odunsu vejetasyonunun tür çeşitliliği, tür zenginliği, fonksiyonel grup sınıflandırmaları (büyüme formu, rejenerasyon stratejisi, sürgün verme yeteneği) ve yaprak karakterleri (özgül yaprak alanı, yaprak kalınlığı, yaprak alanı) bakımından, ayrıca bitki karakterlerinin kullanılmasıyla yangın ve iklim değişikliğine karşı direnç ve direngenlik kapasiteleri bakımından hem tür hem komünite düzeyinde karşılaştırılması ve ormancılık uygulamalarına önerilerin geliştirilmesi amaçlanmıştır.

Bu tez çalışması, güneybatı Anadolu'da (Türkiye) Muğla İli sınırları içerisinde Köyceğiz, Marmaris ve Datça yörelerinde, Kızılçam (*Pinus brutia* Ten.) ve maki elemanlarının hakim olduğu Akdeniz vejetasyonunda gerçekleştirilmiştir. Arazi çalışmaları, yarı kapalı kızılçam ormanı, boşluklu kapalı kızılçam ormanı, kapalı çalılık, açık çalılık ve frigana sınıflarını kapsayacak şekilde yürütülmüştür. Toplamda 28 örnekleme alanında çalışılmış, her bir örnekleme alanında üçer adet 10×40 m büyüklüğündeki transektlerde örneklemeler yapılmıştır. Her bir transektte yer alan odunsu bitkiler teşhis edilmiş, konumları, boyları ve örtüş çapları ölçülmüştür. Transekte yer alan fideler, her bir transektin 5×10 m büyüklüğünde ayrılan alt bölümleri ölçeğinde sayılmıştır. Ayrıca bitki

fonksiyonel karakterleri için, 38 odunsu bitki türüne ait 857 bireyden yaprak örnekleri toplanarak özgül yaprak alanı, yaprak kalınlığı ve yaprak alanı ölçümleri arazide ve laboratuvarda gerçekleştirilmiştir. Beş farklı vejetasyon tipinin yangına ve iklim değişikliğine olan direnç ve direngenlik kapasitelerinin belirlenmesi için, arazi ve literatürden elde edilen 17 adet bitki fonksiyonel karakteri analize dahil edilmiştir.

Vejetasyon tiplerinde yer alan komüniteler arasındaki farklılıkların en göze çarpanı orman-çalılık-frigana arasında tespit edilmiş olup, tür çeşitliliği ve zenginliği bakımından çalılık sınıfları en yüksek değerlere sahip çıkmıştır. Buna ek olarak, yapılan fonksiyonel grup sınıflandırmaları, metrik olmayan çok boyutlu ölçekleme analizi ve indikatör tür analizleri açık ve kapalı habitatlar arasında da keskin bir farkın olduğunu ortaya koymuştur. Yaprak karakterleri ile yapılan karşılaştırmalarda bitki türleri, fonksiyonel gruplar ve vejetasyon tipleri arasında farklılıklara rastlanılmıştır. Ayrıca orman ve çalılıkların kuraklığa olan direncinin en fazla, friganaların ise yangın gibi müdahale etkileri altında daha yüksek direngenliğe sahip oldukları belirlenmiştir. Yangın ve iklim değişikliğine karşı direnç ve direngenlik kapasiteleri bakımından, açık habitatların kapalı habitatlara nazaran hem yangın hem iklim değişikliğine karşı daha direngen oldukları, iklim değişikliğine karşı direnç kapasitesinin ise bitki bireylerinin örtüş dereceleri göz önüne alındığında, en yüksekten en düşüğe doğru orman > çalılık > frigana olarak sıralandığı bulunmuştur. Ayrıca direnç ve direngenlik kapasitelerinin zıt ilişkili olduğu ve buna en iyi örnek olarak da frigana sınıfının en yüksek seviyede direngen, diğer yandan ise en düşük direnç kapasitesine sahip olduğu ortaya konmuştur.

Bu çalışmadan elde edilen bulgular, alçak rakım Akdeniz odunsu vejetasyonları arasındaki farklılıkları bitki komünite parametreleri ve fonksiyonel karakterleri bakımından ortaya koymuştur. Bulgular, Akdeniz alçak rakım ortamlarında açık ve kapalı vejetasyonların ekolojik ve fonksiyonel olarak farklılıklarını göstermiştir. Bu çalışma, Akdeniz vejetasyon tiplerinin yangın ve iklim değişikliğine karşı direnç ve direngenlik potansiyellerini ortaya koyarak, Türkiye'de gerek makilik alanlarda gerekse Kızılçam ormanlarında gelecek yıllarda uygulanabilecek ormancılık faaliyetleri ve koruma stratejileri için yeni bakış açıları sunmaktadır.

Anahtar Kelimeler: açık ve kapalı habitatlar, *Pinus brutia* kızılçam ormanı, maki, frigana, fonksiyonal grup sınıflandırması, bitki komünitesi.

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CHAPTER 1: GENERAL INTRODUCTION

The Mediterranean type ecosystems are located in five regions of the world: the Mediterranean Basin, Chile, California, the Cape Region of South Africa and Western & South Australia (Tavşanoğlu and Gürkan 2004). The Mediterranean Basin consists of different vegetation types in terms of both structure and diversity (Keeley et al. 2012). The most important reason for this differences is that the region has been shaped for centuries by anthropogenic disturbances such as agricultural activities, domestic grazing, and urbanization (Blondel and Aronson 1999) and natural disturbances such as drought, herbivory, and fires (Suc 1984; Naveh and Carmel 2004). The Mediterranean Basin contains 10% of the world's total plant diversity (Cowling et al. 1996) and is a one of the biodiversity hotspots (Myers et al. 2000). Besides that, the Mediterranean Basin will be most exposed to the effects of climate change (Cubash et al. 1996; Lavorel 1999) such as extreme drought and frequent fires (Giorgio and Lionello 2008; Enright et al. 2014). Recent studies have revealed that it is not possible to predict the structural changes that the effects of climate change will cause on vegetation types in this region (Pausas and Millån 2019; Baudena et al. 2020).

The most characteristic vegetation type in the Mediterranean Basin is called "maquis" and 73% of Mediterranean type ecosystems are located in this region (Cowling et al. 1996). Although there is conflicting information on the distribution of maquis vegetation in Turkey, according to the study of Kaya et al. (2009), there is a total of 7.5 million hectares of maquis area in the Marmara, Aegean and Mediterranean regions. The general definition of maquis, that dominates the low altitude Mediterranean vegetation belt, is a vegetation type consists of evergreen shrubs, small trees and trees with hard and small leaves that can reach up to 2-5 meters (Mayer and Aksoy 1998; Özalp 2000; Aksoy 2006). It is also known that maquis are adapted to limited water resources under arid conditions (Mereu et al. 2009; Hernåndez et al. 2010; Altieri et al. 2015). According to some sources, maquis were formed by the degeneration of Turkish red pine forests (*Pinus brutia* Ten.) as a result of anthropogenic effects (Tansley 1913; Semple 1919; Polunin-Huxley 1990). Moreover, as a result of the destruction of maquis shrublands, garrigue and phrygana vegetations assumed to emerge (Knapp 1965; Schmidt 1969; Yaltırık 1975). Tomaselli (1977), on the other hand, acknowledges maquis and garrigue vegetation types that have

not been damaged on the steep cliffs of the Mediterranean coast, and states that degradation is not always a cause and maquis are a level of progressive evolution.

There are different opinions about the Mediterranean vegetation classification. Some sources classifies in regards to the dominant species such as *Quercus coccifera* maquis and *Arbutus andrachne* maquis or their size such as high or low maquis (Mayer and Aksoy 1998; Aksoy 2006), however, some sources categorizes such as forests, shrubs and phrygana (Keeley et al. 2012; Kavgacı et al. 2017). Besides these, in recent years, as a result of the alternative biome state approach, which suggests that open states are permanent like closed states, the Mediterranean ecosystem is divided into open and closed vegetation types (Pausas and Bond 2020).

Maquis are not considered as forests in Turkey and do not have any protection status. Within the scope of "Official Instruction Regarding the Determination of Forest Boundaries at the Confluence of Maquis and Forest Fields", entered into force in 1950, maquis that could not produce any non-wood forest products were removed from the forest boundary (Ayanoğlu 1996). According to the changes made in Forest Law No. 6831 in 1973 and 1982, it was decided that the maquis areas lost their forest quality and were beneficial to be converted into agricultural areas should not be counted as forests. The instruction by the General Directorate of Forestry, published in 2012, promotes rehabilitation implementations to convert maquis into Turkish red pine forests. In 2022, the General Directorate of Forestry published an another instruction for clear cutting in maquis areas to prevent fires and support the production of non-wood forest products.

1.1. The Aim of the Study

The aim of this research are as follows:
- to present the structure of the low altitude Mediterranean woody vegetation types,
- to reveal the differences between vegetation types in terms of species diversity, species richness, growth form, regeneration strategies and resprouting,
- to determinate the differences of leaf traits in species and plant community level,
- to evaluate the resilience and resistance capacities of vegetation types to fire and climate change by using plant functional traits,

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- to develop recommendations for forestry implementations practices and conservation strategies.

1.2. The Importance of the Study:

This study will contribute to plant ecology and forest ecology fields by revealing structural and functional differences of the plant communities in the low altitude Mediterranean woody vegetation types. The results have potential to improve our understanding of Mediterranean vegetation dynamics and Mediterranean forestry. Besides that, knowing the resilience and resistance capacities of vegetation types to fire and climate change will guide to predict the state of Mediterranean vegetation after disturbances that will affect the Mediterranean Basin more and more with each passing day. Finally, the results of the study will help to develop suggestions on forestry implementations and conservation strategies applied in maquis areas of Turkey.

1.3. The Questions and Hypotheses of the Study:

In the study, low altitude Mediterranean woody vegetation types were compared in terms of species diversity and richness, plant community composition and structures, and their resilience and resistance capacities to fire and climate change were determined based on plant functional traits. In this context, the following questions were asked for woody plant communities in Mediterranean vegetation:

   a) Do the diversity and functional structure differ from each other,
   b) Do leaf traits vary at species, functional group and plant community levels,
   c) Do resilience and resistance capacity levels to fire and climate change differ from each other?

In the light of these research questions, the main hypotheses of the study are as follows:

   1) "Vegetation types should differ in species diversity and composition, and functional groups such as growth form, regeneration strategy and resprouting capacity",
   2) "Species, functional group and plant communities should vary in terms of leaf traits",

3) "Vegetation types should differ in resilience and resistance capacities to fire and climate change."

1.4. Study Area and Sites

The case study area is located within the borders of Muğla province, between Köyceğiz Lake and Datça peninsula (36.686° N, 27.362° E at the west and 36.835°N, 28.640°E at the east) and its dominant vegetation types are maquis shrubland and Turkish red pine forests. In the study area, has a Mediterranean climate type, long dry summer periods lasting about 5 months are observed. Moreover, as it is located in a fire-prone ecosystem, it has a fragmented mosaic landscape (Tavşanoğlu and Gürkan 2014). The study was carried out in five main vegetation types includes maquis, which are different from each other: semi-closed forest (*"1 kapalı Çz"* in Turkish), open forest (*"BÇz"* in Turkish), closed shrubland (*"Mak3"* in Turkish), open shrubland (*"BMak"* in Turkish), and scrubland (*"OT"* in Turkish).

Study sites were selected from within the Sultaniye Forestry Management Unit of the Köyceğiz Forestry Management Directorate and Bayır, Hisarönü, Çetibeli and Datça Forestry Management Units of the Marmaris Forestry Management Directorate. After the examining of related forest management plans, interviews with the local foresters and field observations, a total of 28 study sites were determined. Since the coverage lands of vegetation types in the study area are different from each other, the number of study sites selected for the correct representation is different: semi-closed forest (#6), open forest (#8), closed shrubland (#4), open shrubland (#6), and scrubland (#4). Within each study site, three 10×40 m (400 m^2) belt transects were established, with a distance of 30-50 m from each other and at least 5 m from any road (main road, forest road, pathway, etc.). All the field studies were carried out on transect basis, in other words in 83 transects.

1.5. The Structure of the Thesis

The thesis consists of 6 chapters in total, including the "Introduction" and "Conclusions" chapters, where the results of each chapter are briefly evaluated. The second, third, fourth and fifth chapters of the thesis are structured as scientific articles.

In the "Introduction" chapter, the purpose and importance of the study are mentioned in general, the research hypotheses and questions that form the main lines of the study are included, and information about the study area is also given.

In the second chapter of the thesis, we examined woody species diversity, community composition and vegetation structure of study sites. For this purpose, 28 study sites of five different low altitude Mediterranean woody vegetation types were selected and a total of 83 transects of 10×40 m were determined in each area. All woody mature and sapling individuals in each transect were identified. The height and diameter measurements of adult individuals were made and their positions were determined. In addition, the sapling were counted in the sub-quadrats of 5×10 m of the transects. Five different vegetation types were compared in terms of species diversity and species richness, growth forms, regeneration strategies and resprouting capacity, plant community composition and structure, both on the abundance and cover data of species. This chapter has already been published in the journal *"Plant Biosystems"* (https://doi.org/10.1080/11263504.2022.2036845).

In the third chapter, we analyzed the variation of leaf traits at woody species, functional group and woody plant community levels. For this purpose, leaf samples were collected from 857 individuals belonging to 38 species from the study sites. As a result of desk and laboratory studies with leaf samples, leaf area, leaf thickness and specific leaf area values of each individual sampled were measured. The results were compared between species, functional groups such as growth form, regeneration strategies and resprouting capacities, and plant communities in five different vegetation types.

In the fourth chapter of the study, we asked resilience and resistance capacities of woody plant communities to fire and climate change. For this purpose, resilience and resistance capacities of vegetation types to fire and climate change were determined by using plant functional traits. The trait values of the species recorded in the field study were compiled as a result of both field studies and literature research. The result of the study revealed the resilience and resistance capacities of both plant species and plant communities in five different vegetation types against fire and climate change.

In the fifth chapter, we quaried ecological function, importance and pressures over maquis vegetation in Turkey. For this purpose, definitions, legal status and forestry implementations of the maquis vegetation in Turkey are explained. Besides that, five different vegetation types were compared based on the findings of the chapters above, and suggestions were developed on the definition of maquis vegetation, forestry implementations and conservation strategies.

The last chapter, "Conclusions", briefly summarizes general results of the thesis presented in previous chapters.

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CHAPTER 2: DIVERSITY AND REGENERATION STRATEGIES IN WOODY PLANT COMMUNITIES OF THE MEDITERRANEAN BASIN: VEGETATION TYPE MATTERS*

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.

2.1. 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 20% 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; Kavgacı 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 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.

2.2. Material and Methods

2.2.1. 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; Fig. 2.1). 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.
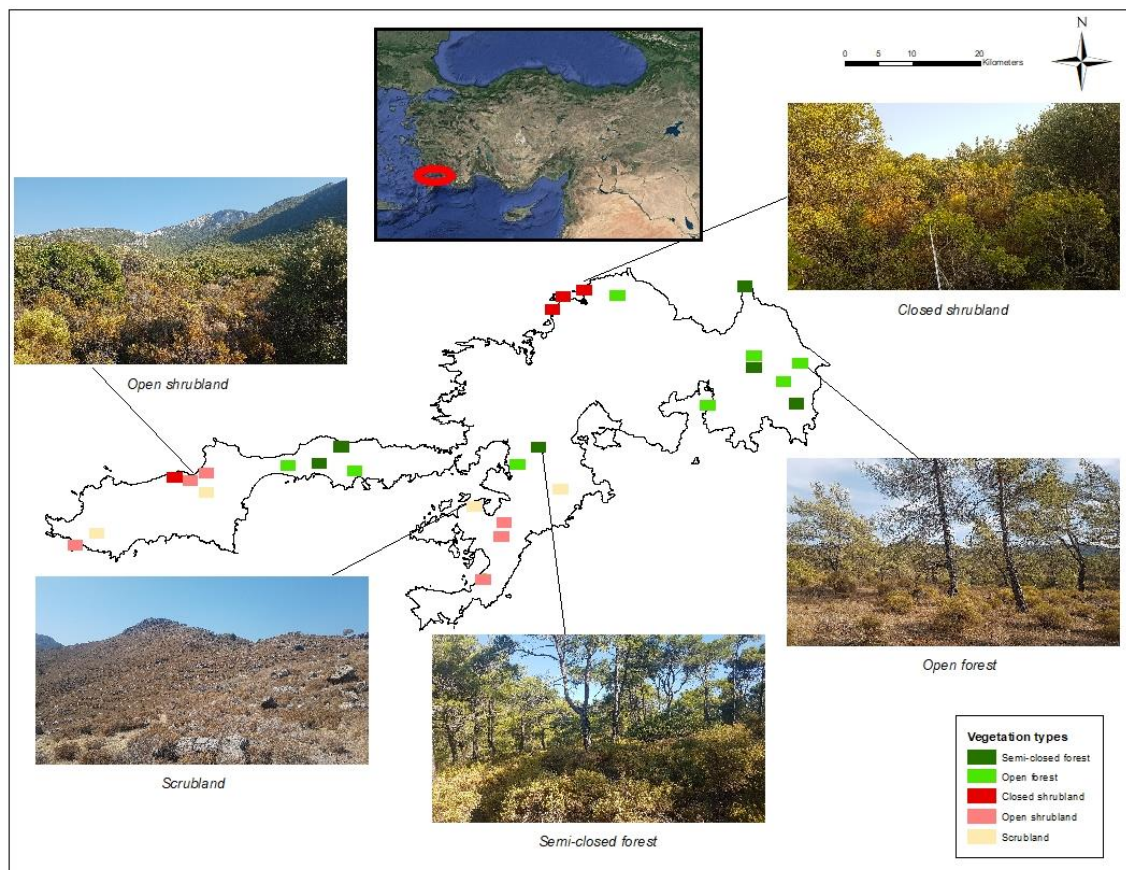
Figure 2.1. The study area and study sites. The minor map at the top indicates the location of the study area in Turkey, while the major map shows the locations of study sites. Study sites representing different vegetation types included in the study are given in different colors, and a general view of each vegetation type is also presented. Note that the scale is for the major map.

2.2.2. Study 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.

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).

2.2.3. Field Measurements and Counts

Field measurements and counts were performed within three belt transects 10×40 m (400 m²) 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:

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

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).

2.2.4. Functional classification

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 2001; Gritti et al. 2005; 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).

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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).

2.2.5. 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, Cáceres 2020). Marginal means were estimated using *emmeans* function (in the *emmeans* package, Lenth 2020).

2.3. Results

2.3.1. 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 2.1, 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 2.1). Rarefaction analyses of species richness in belt transects showed that the species-sample size curves were asymptotic in most cases (Supplementary Fig. 1), and therefore were satisfactory for further analysis of species richness and diversity.

Table 2.1. 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.

Study site	Mature		Sapling	
	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

For mature individuals, both woody species richness and Shannon diversity were higher in shrublands than forests and scrublands (Fig. 2.2, Supplementary Table 3). For saplings, however, these differences were less prominent (Fig. 2.2). 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 Table 4, Supplementary Table 5).
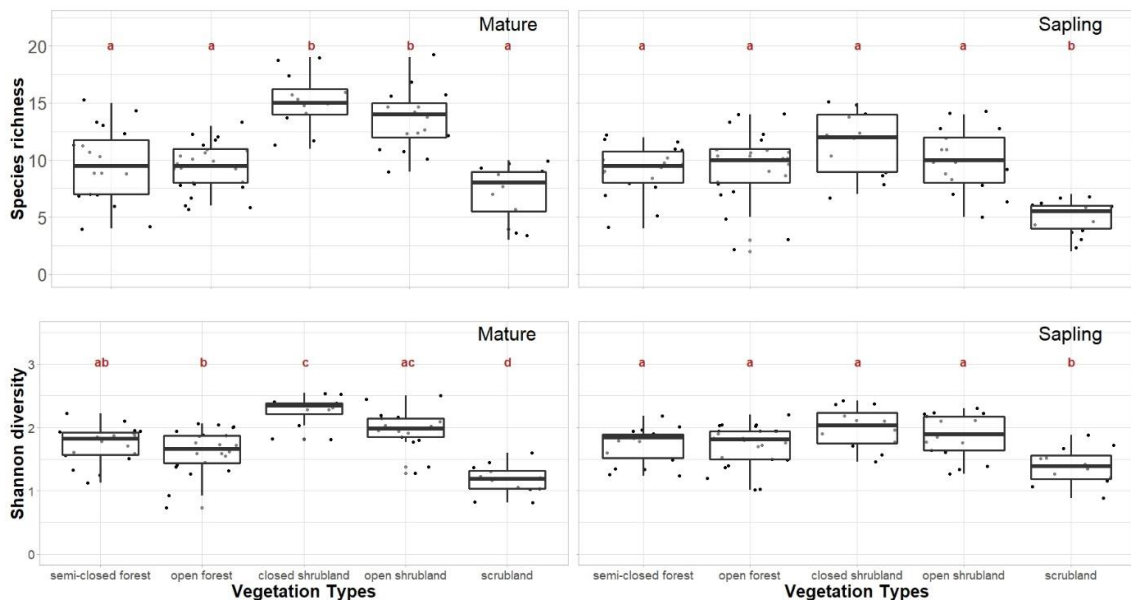
Figure 2.2. Species richness and Shannon diversity of saplings and mature individuals in different vegetation types. Data points are values obtained from belt transects. In

boxplots, the horizontal black line is the median, the box extends from 25th to 75th percentiles, and whiskers show 1.5 interquartile ranges.

2.3.2. Presence, Density, and Cover of Individual Species

Woody species differed in their frequency of occurrence, density, and cover among different vegetation types (Supplementary Table 4, Supplementary Table 5, Supplementary Table 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 Table 5; Supplementary Table 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).

2.3.3. Growth Form

There were significant differences in the density of mature individuals and saplings of woody species among vegetation types (Table 2.2, 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; Fig. 2.3). In a similar manner, the cover of growth forms significantly differed among vegetation types (χ^2 = 5314.0, d.f. = 16, P < 0.0001; Fig. 2.3). 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 2.2). Mature individuals of shrubs outnumbered other growth forms in all vegetation types except scrublands in which subshrubs had a higher density than shrubs (Fig. 2.3a, Table 2.2). 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 2.2).

Table 2.2. 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
lar. 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
lar. shrub	85.9a	49.5b	105.6c	49.0b	3.5d	1739.4	<0.0001
tree	10.9a	15.6b	2.4c	0.8d	1.6cd	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
lar. 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
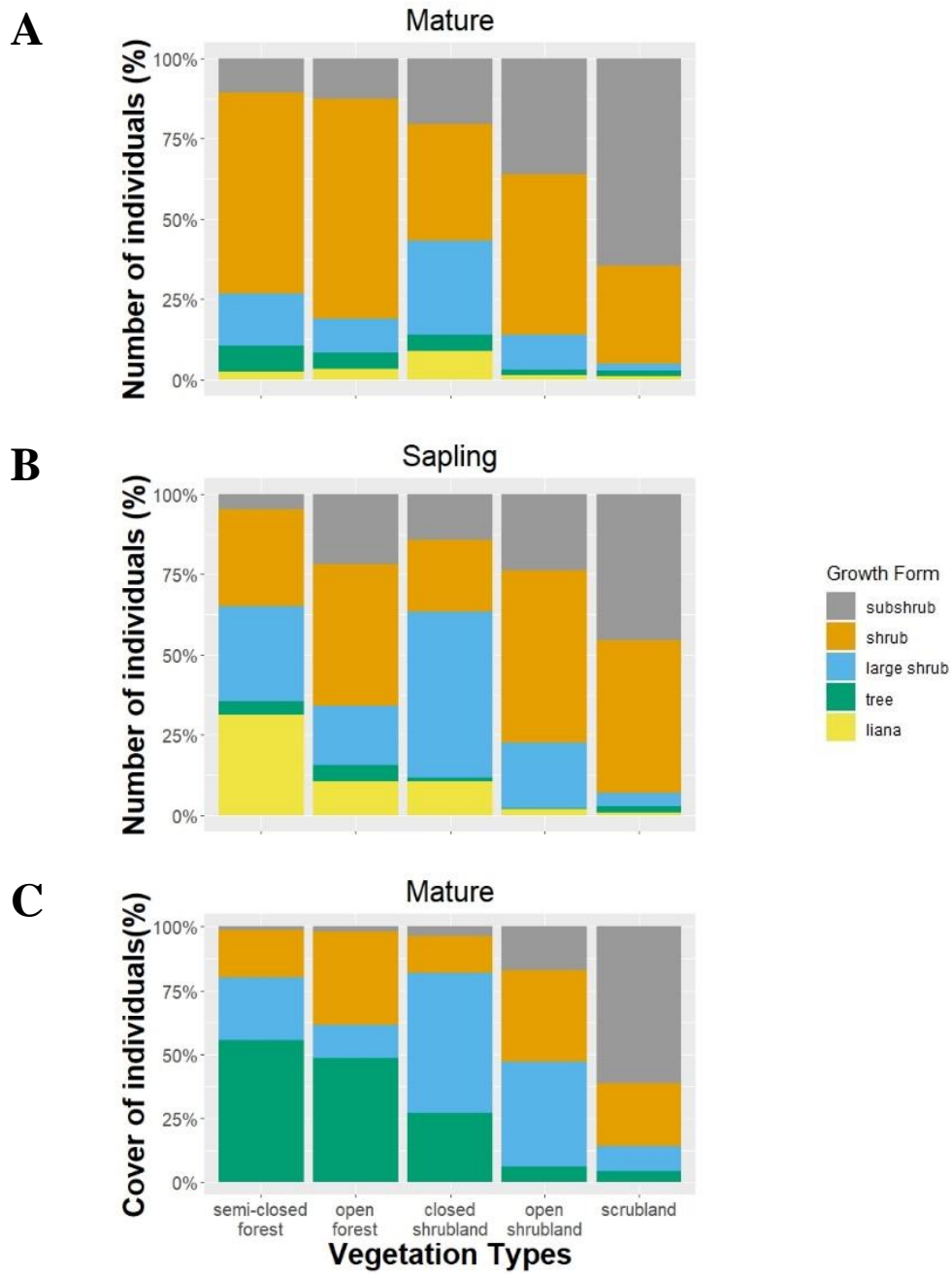
Figure 2.3. Relative total number of mature individuals (A) and saplings (B), and relative total cover mature individuals (C) for different growth forms in each vegetation type.

Large shrubs dominated closed shrublands regarding the density of mature individuals and saplings and the cover of mature individuals (Table 2.2, Fig. 2.3). Several species contributed to this dominance of large shrubs, most apparently *Arbutus andrachne*, *Pistacia lentiscus*, *Phillyrea latifolia,* and *Quercus coccifera* (Supplementary Table 5; Supplementary Table 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 2.2, Fig. 2.3, Supplementary Table 6). Tree cover gradually decreased from semi-closed forest (91.5%) to scrubland (2.8%) (Table 2.2, Fig. 2.3). 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 2.2). 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 2.2, Fig. 2.3).

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 2.2, Fig. 2.3). 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 2.2, Fig. 2.3).

2.3.4. Regeneration Strategies

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; Fig. 2.4). 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 2.3, 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 2.3). The density of R-P+s species was high in all vegetation types except closed shrublands in which mature individuals of species with R+P- strategy outnumbered those with R-P+ strategies (Table 2.3, Fig. 2.4). 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 2.3, Fig. 2.4). 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 2.3, Fig. 2.4).

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 2.3, Fig. 2.4). 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 2.3, Fig. 2.4). 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 2.3). 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 2.3). 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 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 Fig. 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 ($\chi^2 = 1155.2$, d.f. = 4, P < 0.0001 for density of mature individuals; $\chi^2 = 619.1$, d.f. = 4, P < 0.0001 for density of saplings; $\chi^2 = 1836.5$, d.f. = 4, P < 0.0001 for cover of mature individuals; Supplementary Fig. 2).

Table 2.3. 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.	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	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
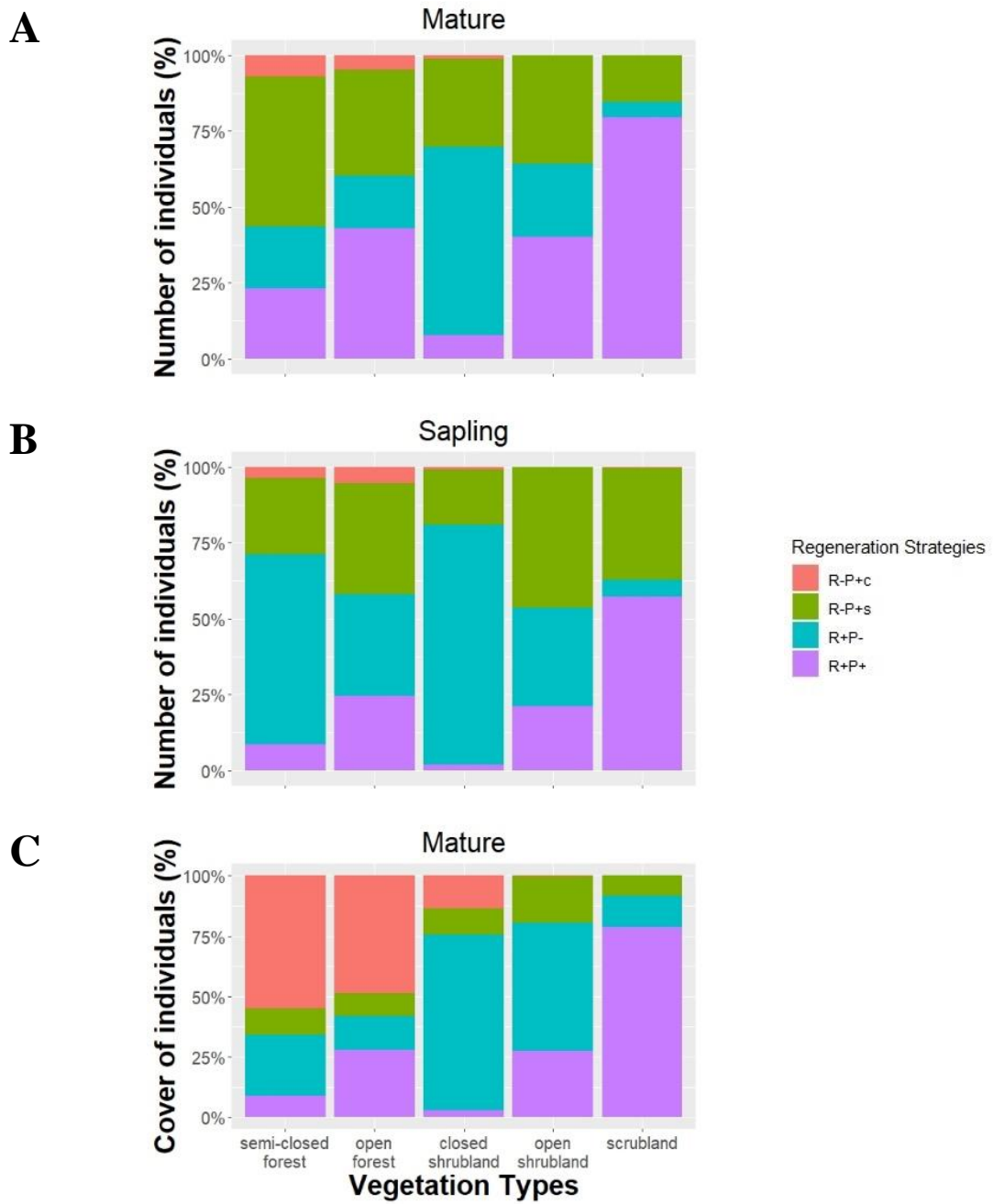
Figure 2.4. Relative total number of mature individuals (A) and saplings (B), and relative cover of mature individuals (C) for different regeneration strategies in each vegetation type.

2.3.5. 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 (Fig. 2.5; Supplementary Fig. 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 (Fig. 2.5, Supplementary Table 10).
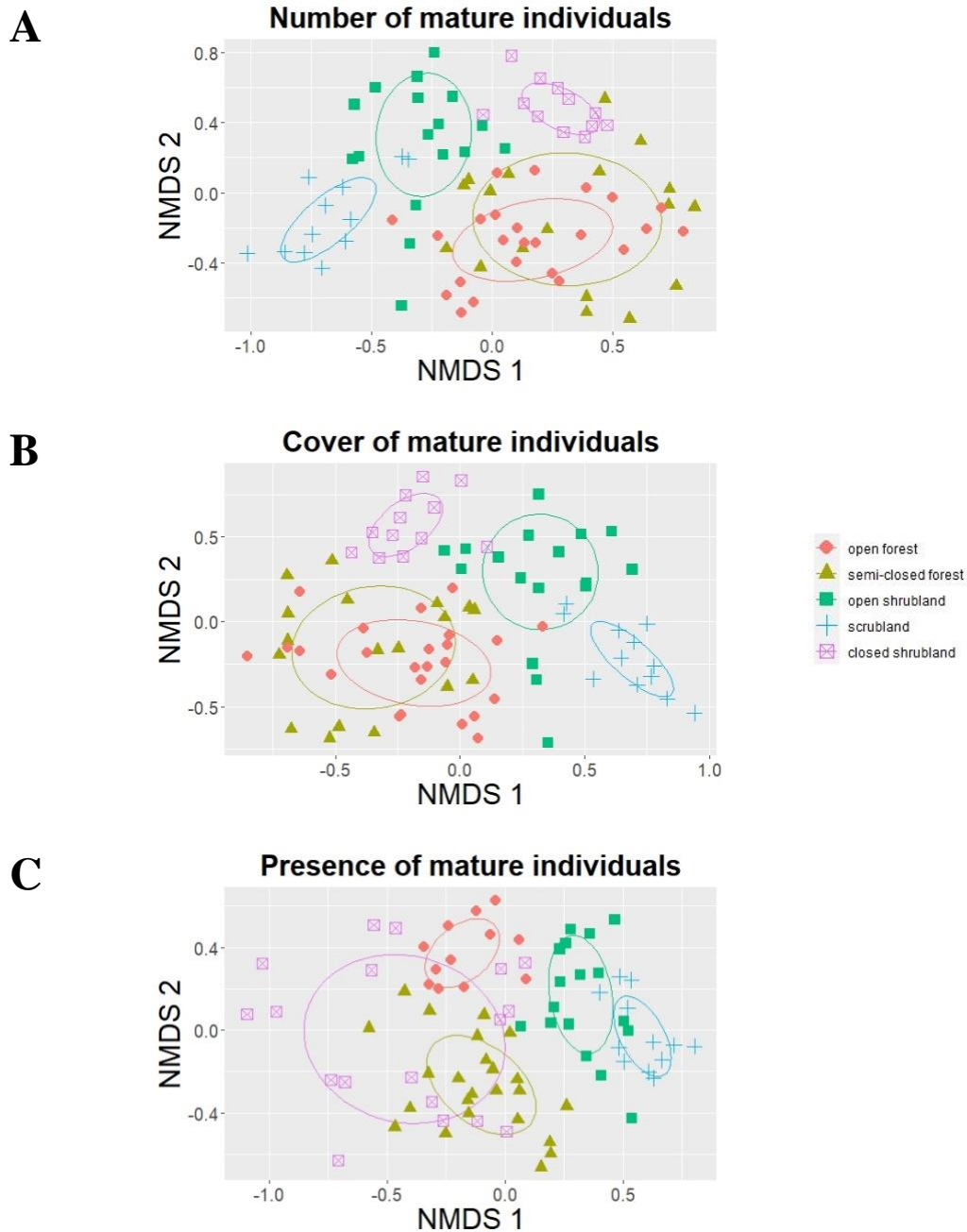
Figure 2.5. Non-metric multidimensional scaling graphs for (A) the number of individuals, (B) cover, and (C) presence of mature individuals. Different colors and shapes represent different vegetation types included in the study. Each data point symbolized a belt transect. Eclipses indicate the standard deviation of each vegetation type.

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 shrubland (#9) (Table 2.4). The analyses did not list any species for open forest, but two and one species for scrubland and semi-close forest, respectively (Table 2.4).

Table 2.4. 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 α = 0.05 for both analyses. Species are sorted by their IndVal values.

Species	Pearson's phi		IndVal	
	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 aphyllu*s	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	-	-

2.4. 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 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. 2003). 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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Supplementary Material to the Chapter 2

Supplementary Table 1. Vegetation type classes used in the study and their corresponding classes in forest management plans. Vegetation type classes were described according to the General Directorate of Forestry (2017).

Vegetation type classes		
In the study	**In forest management plans**	**Description**
Semi-closed forest	Turkish red pine forest	Mainly consists of mature Turkish red pine individuals with total coverage between 11% and 40%.
Open forest	Open Turkish red pine forest	Mainly consists of mature Turkish red pine individuals with total coverage < 10%.
Closed shrubland	Maquis	Mainly consists of large shrubs with total coverage between 11% and 100%.
Open shrubland	Open maquis	Mainly consists of large shrubs with total coverage < 10%.
Scrubland	Forest soil without any tree	Mainly consists of species that do not exceed 1 m height.

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Supplementary Table 2. The species recorded in the study and their taxonomic and some ecological properties. Regeneration strategy of a species (*sensu* Pausas 1999 and Pausas et al., 2004) includes information on both resprouting ability after the fire (resprouters: R+ or non-resprouters: R-), post-fire persistence ability via any propagule (propagule-persister: P+ or propagule-non-persister: P-), and the seed bank locality in propagule-persisters (canopy seed bank: c or soil seed bank: s). Growth form, resprouting ability, post-fire persistence via propagules, and seed bank locality information are based on the BROT database (Tavşanoğlu & Pausas, 2018) and field observations. Nomenclature follows Davis (1965-1985), but taxon and family names were updated according to The Plant List (2013).

Species	Family	Growth form	Resprouting ability	Regeneration strategy
Arbutus andrachne L.	Ericaceae	large shrub	yes	R+P-
Arbutus unedo L.	Ericaceae	large shrub	yes	R+P-
Asparagus aphyllus L.	Asparagaceae	liana	yes	R+P-
Asperula brevifolia Vent.	Rubiaceae	subshrub	no	unknown
Calicotome villosa (Poir.) Link	Leguminosae	shrub	yes	R+P+
Celtis australis L.	Cannabaceae	tree	yes	R+P-
Ceratonia siliqua L.	Leguminosae	tree	yes	R+P-
Cistus creticus L.	Cistaceae	shrub	no	R-P+s
Cistus parviflorus Lam.	Cistaceae	shrub	no	R-P+s
Cistus salviifolius L.	Cistaceae	shrub	no	R-P+s
Cotinus coggygria Scop.	Anacardiaceae	large shrub	yes	R+P-
Crataegus monogyna Jacq.	Rosaceae	large shrub	yes	R+P-
Cupressus sempervirens L.	Cupressaceae	tree	no	R-P+c
Cytisopsis pseudocytisus (Boiss.) Fertig	Leguminosae	subshrub	no	R-P+s
Daphne gnidioides Jaub. & Spach	Thymelaeaceae	shrub	unknown	unknown
Daphne sericea Vahl	Thymelaeaceae	shrub	variable	unknown
Dittrichia viscosa (L.) Greuter	Compositae	subshrub	yes	R+P+
Erica manipuliflora Salisb.	Ericaceae	shrub	yes	R+P+
Euphorbia acanthothamnos Heldr. & Sart. ex Boiss.	Euphorbiaceae	subshrub	yes	R+P+
Genista acanthoclada DC.	Leguminosae	shrub	yes	R+P+
Hypericum empetrifolium Willd.	Hypericaceae	subshrub	unknown	R+P+
Juniperus oxycedrus L.	Cupressaceae	large shrub	yes	R+P-
Laurus nobilis L.	Lauraceae	large shrub	yes	R+P-
Lavandula stoechas L.	Lamiaceae	subshrub	no	R-P+s
Myrtus communis L.	Myrtaceae	large shrub	yes	R+P-

Olea europaea L.	Oleaceae	tree	yes	R+P-
Origanum onites L.	Lamiaceae	subshrub	yes	R+P-
Osyris alba L.	Santalaceae	large shrub	yes	R+P-
Paliurus spina-christi Mill.	Rhamnaceae	large shrub	yes	R+P-
Phillyrea latifolia L.	Oleaceae	large shrub	yes	R+P-
Phlomis grandiflora H. S. Thomps.	Lamiaceae	shrub	unknown	unknown
Phlomis lycia D. Don	Lamiaceae	shrub	yes	unknown
Pinus brutia Ten.	Pinaceae	tree	no	R-P+c
Pistacia lentiscus L.	<u>Anacardiaceae</u>	large shrub	yes	R+P-
Pistacia terebinthus L.	<u>Anacardiaceae</u>	large shrub	yes	R+P-
Populus nigra L.	Salicaceae	tree	yes	R+P-
Ptilostemon chamaepeuce (L.) Less.	Compositae	shrub	yes	unknown
Pyrus elaeagnifolia Pall.	Rosaceae	tree	unknown	unknown
Quercus aucheri Jaub. & Spach	Fagaceae	large shrub	yes	R+P-
Quercus coccifera L.	Fagaceae	large shrub	yes	R+P-
Quercus infectoria subsp. *veneris* (A.Kern.) Meikle	Fagaceae	large shrub	yes	R+P-
Quercus ithaburensis Decne.	Fagaceae	tree	yes	R+P-
Rhamnus punctata Boiss.	Rhamnaceae	large shrub	unknown	unknown
Rhamnus pyrella O. Schwarz	Rhamnaceae	shrub	yes	R+P-
Rubia tenuifolia d´Urv.	Rubiaceae	liana	yes	R+P-
Ruscus aculeatus L.	Asparagaceae	subshrub	yes	R+P-
Sarcopoterium spinosum (L.) Spach	Rosaceae	subshrub	yes	R+P+
Satureja thymbra L.	Lamiaceae	subshrub	variable	unknown
Smilax aspera L.	Smilacaceae	liana	yes	R+P-
Spartium junceum L.	Leguminosae	large shrub	yes	R+P+
Styrax officinalis L.	Styracaceae	large shrub	yes	R+P-
Teucrium chamaedrys subsp. *syspirense* (C. Koch) Rech. f.	Lamiaceae	subshrub	yes	R+P-
Teucrium divaricatum Sieber ex Heldr.	Lamiaceae	subshrub	yes	R+P+
Teucrium polium L.	Lamiaceae	subshrub	yes	R+P+
Teucrium sandrasicum O. Schwarz	Lamiaceae	subshrub	unknown	unknown
Thymbra capitata (L.) Cav.	Lamiaceae	subshrub	variable	unknown

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Supplementary Table 3. Mean species richness and Shannon diversity values for each vegetation type estimated from the transect data. Model results for differences in species richness (Poisson GLM) and Shannon diversity (linear model) among different vegetation types. The same letters next to the values indicate no significant difference ($P > 0.05$) across vegetation types.

	Semi-closed forest	Open forest	Closed shrubland	Open shrubland	Scrubland	Poisson GLM	
						Dev.	P
Species richness							
Mature individuals	9.6a	9.4a	15.3b	13.5b	7.3a	53.6	< 0.0001
Saplings	9.2a	9.5a	11.4a	10.0a	5.0b	34.9	< 0.0001
						Linear model	
Shannon diversity						F	P
Mature individuals	1.7ab	1.6b	2.3c	1.9ac	1.2d	23.1	< 0.0001
Saplings	1.7a	1.7a	1.9a	1.9a	1.4b	6.5	0.0001

Supplementary Table 4. The frequency of occurrence of each species in the belt transects in each vegetation type. Values are the percentage of transects in which mature individuals of the species were recorded.

Species	Vegetation type				
	Semi-closed forest	Open forest	Closed shrubland	Open shrubland	Scrubland
Arbutus andrachne	11.11	83.33	4.17	17.65	0
Arbutus unedo	11.11	41.67	0	0	0
Asparagus aphyllus	50.00	83.33	66.67	70.59	25.00
Asperula brevifolia	0	8.33	0	23.53	0
Calicotome villosa	5.56	33.33	20.83	35.29	33.33
Celtis australis	0	0	4.17	0	0
Ceratonia siliqua	5.56	8.33	4.17	11.76	0
Cistus creticus	72.22	91.67	54.17	70.59	50.00
Cistus parviflorus	0	0	4.17	35.29	0
Cistus salviifolius	72.22	75.00	54.17	52.94	50.00

Cotinus coggygria	11.11	0	4.17	0	0
Crataegus monogyna	5.56	0	0	35.29	25.00
Cupressus sempervirens	0	8.33	0	0	0
Cytisopsis pseudocytisus	16.67	0	16.67	0	0
Daphne gnidioides	22.22	0	16.67	52.94	25.00
Daphne sericea	5.56	8.33	0	0	0
Dittrichia viscosa	0	0	0	5.88	0
Erica manipuliflora	27.78	0	58.33	17.65	0
Euphorbia acanthothamnos	0	41.67	0	29.41	8.33
Genista acanthoclada	44.44	75.00	79.17	70.59	58.33
Hypericum empetrifolium	5.56	100.00	12.50	29.41	0
Juniperus oxycedrus	0	0	4.17	0	0
Laurus nobilis	11.11	8.33	0	5.88	0
Lavandula stoechas	38.89	0	54.17	41.18	50.00
Myrtus communis	5.56	0	12.50	5.88	0
Olea europaea	38.89	91.67	25.00	70.59	33.33
Origanum onites	0	8.33	4.17	29.41	16.67
Osyris alba	0	41.67	4.17	41.18	0
Paliurus spina-christi	5.56	0	12.50	0	0
Phillyrea latifolia	61.11	100.00	70.83	52.94	25.00
Phlomis grandiflora	0	25.00	0	35.29	0
Phlomis lycia	22.22	25.00	4.17	52.94	33.33
Pinus brutia	100.00	50.00	95.83	11.76	0
Pistacia lentiscus	27.78	100.00	25.00	76.47	33.33
Pistacia terebinthus	16.67	41.67	12.50	5.88	0
Populus nigra	5.56	0	0	0	0
Ptilostemon chamaepeuce	0	33.33	12.50	5.88	16.67
Pyrus elaeagnifolia	11.11	0	0	29.41	33.33
Quercus aucheri	16.67	66.67	0	47.06	25.00
Quercus coccifera	61.11	91.67	29.17	82.35	33.33
Quercus infectoria subsp. *veneris*	44.44	8.33	16.67	11.76	0
Quercus ithaburensis	0	0	0	0	8.33
Rhamnus punctata	0	0	20.83	0	25.00
Rubia tenuifolia	0	16.67	0	0	0
Ruscus aculeatus	16.67	83.33	16.67	0	0
Sarcopoterium spinosum	50.00	16.67	33.33	70.59	100.00
Satureja thymbra	0	0	16.67	11.76	0
Smilax aspera	22.22	41.67	41.67	11.76	0
Spartium junceum	0	8.33	0	0	0
Styrax officinalis	27.78	0	4.17	17.65	0
Teucrium chamaedrys subsp. *syspirense*	0	0	0	5.88	0
Teucrium polium	0	0	4.17	17.65	0
Teucrium sandrasicum	0	0	4.17	0	0
Thymbra capitata	5.56	8.33	12.50	52.94	16.67

Supplementary Table 5. The density of each species in each vegetation type. Values are the mean (±SD) number of mature individuals per transect in each vegetation type. The results of generalized linear models (GLM) based on (1) the number of individuals of each species without zero data in each transect (GLM assuming Poisson distribution) and (2) the presence and absence of species in each transect (GLM assuming binomial distribution) are given. *Dev.* is the deviance value obtained from GLM analyses, and deviance values lower than 0.05 were stated as 0.0.

Species	Vegetation type					Poisson GLM		Binomial GLM	
	Semi-closed forest	Open forest	Closed shrubland	Open shrubland	Scrubland	Dev.	P	Dev.	P
Arbutus andrachne	0.17±0.5	0.08±0.4	9.42±8.9	2.24±6.7	0	35.6	< 0.0001	33.8	< 0.0001
Arbutus unedo	0.11±0.3	0	1.42±2.6	0	0	3.7	0.0556	19.2	0.0007
Asparagus aphyllus	3.28±5.4	5.25±7.9	12.33±11.3	3.82±5.8	2.25±6.3	58.8	< 0.0001	11.1	0.0250
Asperula brevifolia	0	0	0.33±1.2	0.88±1.7	0	0.0	0.9093	12.4	0.0149
Calicotome villosa	0.06±0.2	1.58±4.8	2.42±4.6	2.06±5.2	0.42±0.7	30.5	< 0.0001	6.7	0.1498
Celtis australis	0	0.21±1.0	0	0	0	-	-	2.5	0.6425
Ceratonia siliqua	0.11±0.5	0.13±0.6	0.33±1.2	0.24±0.7	0	1.2	0.7635	2.5	0.6358
Cistus creticus	22.17±32.2	22.67±36.9	29.25±21.5	12.35±18.5	29.25±55.5	231.6	< 0.0001	7.6	0.1063
Cistus parviflorus	0	0.54±2.7	0	14.59±30.5	0	23.7	< 0.0001	17.6	0.0015
Cistus salviifolius	51.72±55.5	34.33±58.9	39.42±60.0	61.65±92.2	3.75±6.7	822.1	< 0.0001	3.5	0.4716
Cotinus coggygria	1.44±4.7	0.04±0.2	0	0	0	14.7	0.0001	4.9	0.2935
Crataegus monogyna	0.06±0.2	0	0	0.53±1.0	0.33±0.7	0.2	0.9146	17.8	0.0014
Cupressus sempervirens	0	0	0.50±1.7	0	0	-	-	3.9	0.4140
Cytisopsis pseudocytisus	0.94±2.6	1.54±4.9	0	0	0	2.9	0.0861	10.2	0.0377
Daphne gnidioides	0.33±0.7	0.50±1.7	0	6.53±10.1	1.00±2.1	71.5	< 0.0001	14.0	0.0074
Daphne sericea	0.06±0.2	0	0.33±1.2	0	0	1.9	0.1650	4.2	0.3737
Dittrichia viscosa	0	0	0	0.06±0.2	0	-	-	3.2	0.5218
Erica manipuliflora	20.50±38.2	37.25±55.8	0	4.94±12.9	0	81.6	< 0.0001	26.3	< 0.0001
Euphorbia acanthothamnos	0	0	0.83±1.2	2.24±4.4	0.08±0.3	21.6	< 0.0001	21.2	0.0003

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Genista acanthoclada	11.50± 19.5	36.17 ±46.5	12.83± 11.1	39.82± 42.2	37.75± 57.4	361.1	< 0.0001	6.4	0.1693
Hypericum empetrifolium	0.11±0.5	4.13± 15.3	41.42± 30.1	14.24± 29.3	0	76.8	< 0.0001	47.5	< 0.0001
Juniperus oxycedrus	0	0.04± 0.2	0	0	0	-	-	2.5	0.6425
Laurus nobilis	0.17±0.5	0	0.08±0.3	0.06±0.2	0	0.2	0.9042	5.0	0.2857
Lavandula stoechas	9.72±18.8	5.21±6.9	0	1.53±2.2	2.42±3.9	165.4	< 0.0001	14.7	0.0053
Myrtus communis	0.72±3.1	0.17±0.5	0	0.29±1.2	0	19.9	< 0.0001	4.4	0.3581
Olea europaea	1.11±2.2	0.54±1.2	9.42±7.6	4.18±5.4	1.58±3.1	62.4	< 0.0001	21.1	0.0003
Origanum onites	0	0.21±1.0	0.08±0.3	3.00±7.1	3.17±7.9	29.0	< 0.0001	10.4	0.0347
Osyris alba	0	0.79±3.9	2.58±3.6	4.65±11.1	0	15.9	0.0004	24.4	< 0.0001
Paliurus spina-christi	0.22±0.9	1.13±3.2	0	0	0	2.8	0.0952	6.3	0.1809
Phillyrea latifolia	10.00± 15.9	10.17 ±10.2	33.17± 13.5	3.82±4.9	1.58±3.5	242.3	< 0.0001	19.7	0.0006
Phlomis grandiflora	0	0	1.17±2.5	3.71±9.3	0	8.8	0.0030	21.4	0.0003
Phlomis lycia	2.94±7.0	0.46±2.2	0.33±0.7	13.00± 22.6	4.92±10.8	107.2	< 0.0001	14.2	0.0066
Pinus brutia	12.17± 4.7	8.92±7.2	2.08±2.8	0.12±0.3	0	60.2	< 0.0001	75.1	< 0.0001
Pistacia lentiscus	2.22±4.1	1.17±2.8	7.58±6	5.06±5.4	0.50±0.8	29.2	< 0.0001	32.9	< 0.0001
Pistacia terebinthus	0.61±1.8	0.50±1.5	0.58±0.8	0.06±0.2	0	7.7	0.0521	10.4	0.0345
Populus nigra	0.06±0.2	0	0	0	0	-	-	3.1	0.5410
Ptilostemon chamaepeuce	0	0.25±0.7	1.25±3.4	0.06±0.2	0.75±1.8	4.9	0.1795	9.3	0.0543
Pyrus elaeagnifolia	0.50±1.5	0	0	0.82±1.6	2.58±4.9	11.0	0.0040	16.5	0.0024
Quercus aucheri	1.11±3.6	0	1.83±1.9	4.24±7.1	0.67±1.3	34.6	< 0.0001	27.5	< 0.0001
Quercus coccifera	5.39±6.5	4.17± 10.4	12.42± 14.6	13.35± 14.4	2.08±4.1	45.2	< 0.0001	22.6	0.0002
Quercus infectoria subsp. *veneris*	2.39±4.3	1.71±4.2	1.08±3.8	0.18±0.5	0	25.2	< 0.0001	12.9	0.0119
Quercus ithaburensis	0	0	0	0	0.08±0.3	-	-	3.9	0.4140
Rhamnus punctata	0	0.29±0.7	0	0	0.58±1.1	0.9	0.3418	14.6	0.0057
Rubia tenuifolia	0	0	0.25±0.6	0	0	-	-	8.0	0.0901
Ruscus aculeatus	0.28±0.7	0.46±1.6	4.08±5.1	0	0	8.8	0.0126	35.5	< 0.0001
Sarcopoterium spinosum	7.50±12.6	3.75± 10.3	2.08±4.9	52.18± 90.6	146.25 ±97.5	2083.0	< 0.0001	28.0	< 0.0001

Species									
Satureja thymbra	0	2.33±9.6	0	0.35±1.2	0	19.2	< 0.0001	9.1	0.0577
Smilax aspera	1.06±2.1	1.29±2.8	8.50±1.3	0.12±0.3	0	130.9	< 0.0001	13.6	0.0087
Spartium junceum	0	0	0.08±0.3	0	0	-	-	3.9	0.4140
Styrax officinalis	3.94±9.6	0.08±0.4	0	0.65±1.8	0	32.9	< 0.0001	11.5	0.0211
Teucrium chamaedrys subsp. *syspirense*	0	0	0	0.06±0.2	0	-	-	3.2	0.5218
Teucrium polium	0	0.46±2.2	0	0.35±0.8	0	11.9	0.0006	7.9	0.0951
Teucrium sandrasicum	0	0.08±0.4	0	0	0	-	-	2.5	0.6425
Thymbra capitata	0.11±0.5	6.38±17.7	0.08±0.3	39.59±46.2	11.50±35.9	249.4	< 0.0001	14.4	0.0062

Supplementary Table 6. The coverage of each species in each vegetation type. Values are the mean (±SD) cover of mature individuals per transect in each vegetation type. The results of linear models testing the difference of cover values among vegetation types are given for each species. In some cases, statistical analysis could not be performed due to the lack of a species in several vegetation types. Cover values lower than 0.005 were stated as "0.00", while the "0" value means that the species did not present in the corresponding vegetation type.

Species	Vegetation type					Linear model	
	Semi-closed forest	Open forest	Closed shrubland	Open shrubland	Scrubland	F	P
Arbutus andrachne	0.04±0.1	0.02±0.1	15.41±15.9	3.96±12.0	0	1.1	0.3831
Arbutus unedo	0.20±0.8	0	3.01±7.0	0	0	0.5	0.4938
Asparagus aphyllus	0.15±0.3	0.31±0.5	0.66±0.6	0.22±0.4	0.04±0.1	2.0	0.1123
Asperula brevifolia	0	0	0.05±0.2	0.09±0.2	0	0.7	0.4602
Calicotome villosa	0.00±0.0	1.30±4.4	0.88±1.5	0.81±2.4	0.14±0.3	1.0	0.4612
Celtis australis	0	0.01±0.1	0	0	0	-	-
Ceratonia siliqua	0.17±0.7	0.10±0.5	0.60±2.1	0.38±1.1	0	3.7	0.3613
Cistus creticus	3.19±6.0	6.59±15.0	7.83±7.0	1.71±2.9	4.55±8.7	1.5	0.2073
Cistus parviflorus	0	0.03±0.1	0	2.00±4.5	0	0.6	0.4856
Cistus salviifolius	14.91±18.9	4.82±9.4	7.25±11.4	11.00±15.6	0.50±0.8	3.0	0.0293
Cotinus coggygria	0.81±2.4	0.03±0.2	0	0	0	19.6	0.1413

Crataegus monogyna	0.01±0.0	0	0	1.01±3.7	0.39±1.0	0.1	0.8688
Cupressus sempervirens	0	0	0.66±2.3	0	0	-	-
Cytisopsis pseudocytisus	0.07±0.2	0.22±0.8	0	0	0	0.8	0.4153
Daphne gnidioides	0.08±0.2	0.05±0.2	0	1.09±1.9	0.26±0.7	1.4	0.2779
Daphne sericea	0.01±0.0	0	0.57±2.0	0	0	-	-
Dittrichia viscosa	0	0	0	0.00±0.0	0	-	-
Erica manipuliflora	11.41±20.3	24.12±38.6	0	3.55±8.5	0	0.4	0.6542
Euphorbia acanthothamnos	0	0	0.14±0.2	0.16±0.3	0.00±0.0	1.3	0.3217
Genista acanthoclada	2.94±5.1	9.36±13.1	2.84±2.6	9.72±9.9	10.58±17.8	1.9	0.1252
Hypericum empetrifolium	0.00±0.0	0.32±1.0	3.63±2.9	0.87±1.8	0	0.6	0.6112
Juniperus oxycedrus	0	0.00±0.0	0	0	0	-	-
Laurus nobilis	0.17±0.7	0	0.01±0.0	0.05±0.2	0	0.2	0.8579
Lavandula stoechas	0.79±1.5	0.38±0.6	0	0.11±0.2	0.26±0.3	4.5	0.0106
Myrtus communis	0.66±2.8	0.37±1.2	0	0.50±2.0	0	7.2	0.1213
Olea europaea	0.68±1.5	0.52±1.7	18.34±21.0	2.94±4.3	1.36±2.4	4.2	0.0071
Origanum onites	0	0.02±0.1	0.01±0.0	0.28±0.7	0.52±1.2	3.3	0.1153
Osyris alba	0	0.02±0.1	0.23±0.4	0.10±0.2	0	1.4	0.2899
Paliurus spina-christi	0.51±2.2	1.52±4.3	0	0	0	0.4	0.5919
Phillyrea latifolia	12.22±21.3	7.13±7.3	29.65±16.0	4.80±7.4	0.69±1.6	4.6	0.0032
Phlomis grandiflora	0	0	0.24±0.5	0.33±1.0	0	0.0	0.9634
Phlomis lycia	0.34±0.8	0.06±0.3	0.17±0.5	1.44±2.3	1.06±2.3	0.7	0.6048
Pinus brutia	96.09±30.4	61.61±42.7	18.1±23.0	0.26±1.0	0	7.8	0.0003
Pistacia lentiscus	5.63±10.3	2.42±6.1	8.90±11.4	8.64±8.9	3.22±5.7	1.4	0.2637
Pistacia terebinthus	0.34±0.9	0.52±1.5	0.43±0.6	0.07±0.3	0	5.3	0.0260
Populus nigra	0.12±0.5	0	0	0	0	-	-
Ptilostemon chamaepeuce	0	0.02±0.1	0.28±0.8	0.02±0.1	0.18±0.4	0.5	0.6951
Pyrus elaeagnifolia	0.34±1.1	0	0	1.91±4.6	1.37±2.5	0.4	0.6865
Quercus aucheri	4.01±15.3	0	4.82±5.7	2.53±5.0	0.23±0.4	1.9	0.1603
Quercus coccifera	11.34±18.6	2.83±6.7	13.56±16.2	13.53±12.6	2.01±4.0	0.7	0.5647
Quercus infectoria subsp. *veneris*	2.83±4.2	1.67±4.5	0.21±0.7	0.82±2.3	0	0.9	0.4659
Quercus ithaburensis	0	0	0	0	0.1±0.4	-	-
Rhamnus punctata	0	0.07±0.2	0	0	0.29±0.6	6.4	0.0452

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Rubia tenuifolia	0	0	0.02±0.0	0	0	-	-
Sarcoporium spinosum	1.25±2.6	0.38±0.8	0.22±0.6	6.84±12.7	40.28±24.6	12.0	< 0.0001
Satureja thymbra	0	0.37±1.7	0	0.05±0.2	0	0.4	0.5687
Spartium junceum	0	0	0.02±0.1	0	0	-	-
Styrax officinalis	4.06±10.8	0.07±0.4	0	0.50±1.5	0	0.8	0.4957
Teucrium chamaedrys subsp. *syspirense*	0	0	0	0.00±0.0	0	-	-
Teucrium polium	0	0.01±0.1	0	0.03±0.1	0	0.4	0.5887
Teucrium sandrasicum	0	0.01±0.1	0	0	0	-	-
Thymbra capitata	0.01±0.0	0.99±2.8	0.01±0.0	6.80±8.5	1.45±4.3	1.4	0.2921

Supplementary Table 7. The density (ind./transect) and cover (%) of different growth forms for each vegetation type. Values are the mean (±SD) of transects.

Growth Form	Semi-closed forest	Open forest	Closed shrubland	Open shrubland	Scrubland
Density of mature individuals					
subshrub	17.0±26.8	27.0±28.9	48.9±33.7	114.5±96.3	163.4±123.7
shrub	108.9±66.1	137.6±91.4	87.0±55.1	158.7±93.0	77.8±71.8
lar. shrub	27.6±22.8	20.1±15.7	70.2±31.6	35.1±19.8	5.8±9.2
tree	13.1±5.1	10.0±7.4	12.3±8.5	5.4±5.0	4.2±5.5
liana	3.9±6.4	7.3±9.6	21.1±18.5	3.9±5.9	2.2±6.3
Density of saplings					
subshrub	30.9±48.3	56.0±79.3	29.1±18.2	57.5±50.4	38.8±26.8
shrub	83.5±58.4	141.7±114.1	45.3±35.0	129.4±149.5	40.6±44.3
lar. shrub	85.9±78.2	49.5±62.5	105.6±83.7	49.0±40.4	3.5±6.7
tree	10.9±13.3	15.6±24.0	2.4±3.8	0.8±1.3	1.6±1.4
liana	74.6±150.7	35.4±115.3	21.4±18.1	4.3±6.4	0.8±2.3
Cover of mature individuals					
subshrub	2.0±3.5	3.0±3.6	5.2±3.9	15.2±13.6	42.5±26.1
shrub	34.0±22.7	47.2±34.1	20.1±10.2	31.7±20.6	17.3±19.1
lar. shrub	39.4±39.6	16.4±13.1	76.3±34.7	36.5±23.6	6.8±6.8
tree	91.5±31.3	63.1±45.4	37.7±33.8	5.5±5.3	2.8±3.1

Supplementary Table 8. The density (ind./transect) and cover (%) of different regeneration strategies for each vegetation type. Values are the mean (±SD) of transects.

Regeneration Strategy	Semi-closed forest	Open forest	Closed shrubland	Open shrubland	Scrubland
Density of mature individuals					
R-P+c	11.6±4.8	9.1±7.6	2.6±3.0	0.1±0.3	0
R-P+s	78.3±69.5	67.7±79.6	68.7±48.3	90.1±91.1	35.4±60.3
R+P-	32.8±25.6	33.7±32.9	146.6±36.9	60.8±37.7	12.6±14.6
R+P+	44.3±41.2	80.1±72.3	18.3±14.0	101.7±89.0	184.5±69.0
Density of saplings					
R-P+c	10.1±12.9	15.0±23.7	1.7±2.7	0	0.2±0.4
R-P+s	77.3±63.9	97.5±101.9	36.3±36.0	93.4±140.7	29.3±47.1
R+P-	161.2±218.0	88.9±148.9	156.3±93.3	65.6±59.0	4.6±6.4
R+P+	30.5±32.8	67.1±78.5	3.9±3.9	42.4±32.2	45.5±21.1
Cover of mature individuals					
R-P+c	90.4±31.4	62.4±45.7	18.8±22.6	0.2±1.0	0
R-P+s	17.3±19.1	12.7±17.9	15.1±8.8	14.8±15.3	5.3±9.4
R+P-	40.3±39.6	17.8±13.3	100.7±31.1	41.2±25.1	8.6±7.2
R+P+	18.2±19.9	35.4±38.0	4.1±2.5	21.1±15.0	51.0±11.0

Supplementary Table 9. regeneration strategies for each vegetation type. Values are the mean (±SD) of transects. The mean density (ind./transect) and cover (%) of different resprouting ability groups (yes: resprouter, no: non-resprouter) 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.

Resprouting Ability	Semi-closed forest	Open forest	Closed shrubland	Open shrubland	Scrubland	Poisson GLM Dev.	P
Density of mature individuals							
Yes	79.6a	114.6b	166.4c	175.5c	202.4d	1241.0	<0.0001
No	89.9a	76.7b	71.6b	91.1a	35.4c	426.3	<0.0001
Density of saplings							
Yes	194.7a	161.8b	160.5b	115.6c	52.2d	1435.7	<0.0001
No	87.5a	112.6b	37.9c	93.6a	29.5d	1135.2	<0.0001
						Linear Model	
						F	**P**
Cover of mature individuals							
Yes	58.8a	53.3a	105.2b	63.8a	60.8a	7.0	<0.0001
No	107.7a	75.0b	33.9c	15.2c	5.3c	31.7	<0.0001

Supplementary Table 10. The results of pairwise PERMANOVA analyses comparing vegetation types. Statistical significance was considered as P < 0.01 due to several pairwise comparisons.

Vegetation types	Number data		Cover data		Presence data	
	R^2	P	R^2	P	R^2	P
Semi-closed forest vs. Closed shrubland	0.188	0.001	0.383	0.001	0.289	0.001
Semi-closed forest vs. Open forest	0.052	0.041	0.097	0.004	0.200	0.001
Semi-closed forest vs. Open shrubland	0.139	0.001	0.374	0.001	0.319	0.001
Semi-closed forest vs. Scrubland	0.268	0.001	0.528	0.001	0.397	0.001
Closed shrubland vs. Open forest	0.169	0.001	0.263	0.001	0.360	0.001
Closed shrubland vs. Open shrubland	0.210	0.001	0.207	0.001	0.333	0.001
Closed shrubland vs. Scrubland	0.416	0.001	0.437	0.001	0.594	0.001
Open forest vs. Open shrubland	0.118	0.001	0.263	0.001	0.272	0.001
Open forest vs. Scrubland	0.220	0.001	0.374	0.001	0.321	0.001
Open shrubland vs. Scrubland	0.157	0.002	0.209	0.001	0.197	0.001

Supplementary Figure 1. Rarefaction curves for Shannon diversity of mature individuals (A) and saplings (B) in the sampled transects.
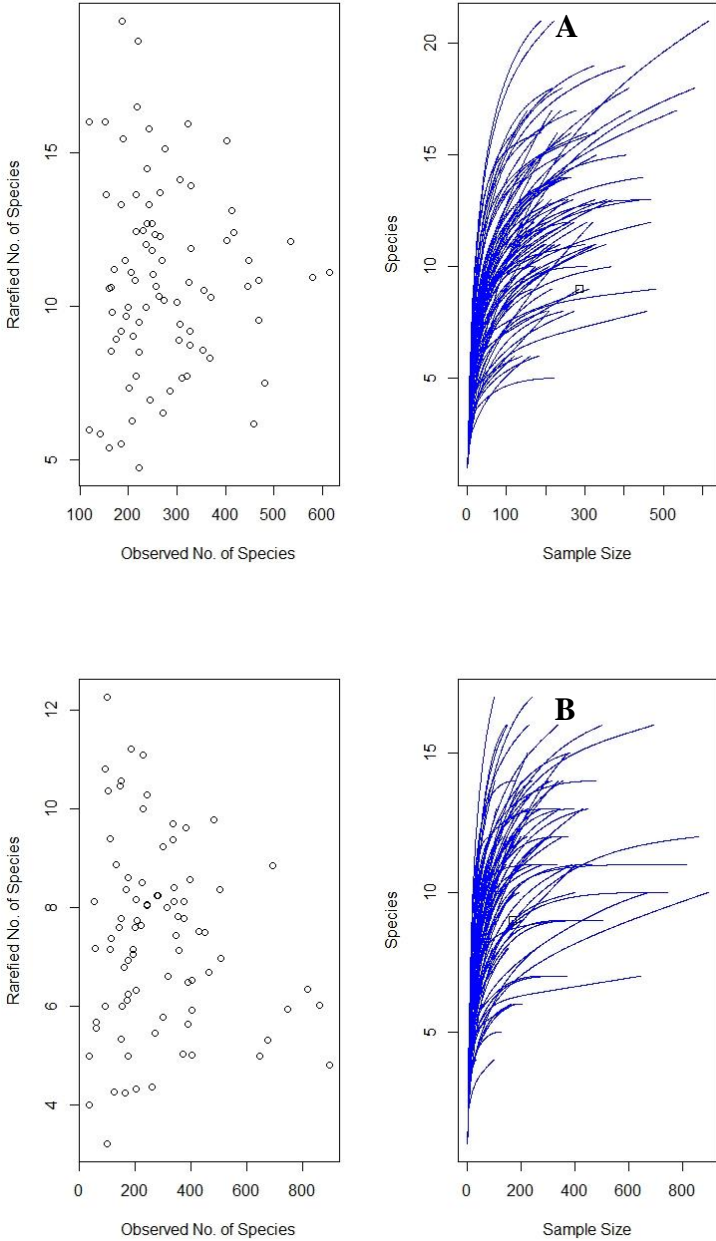
Supplementary Figure 2. Relative total number of mature individuals (A) and saplings (B), and relative total cover mature individuals (C) for two resprouting ability classes (yes: resprouter, no: non-resprouter) in each vegetation type.
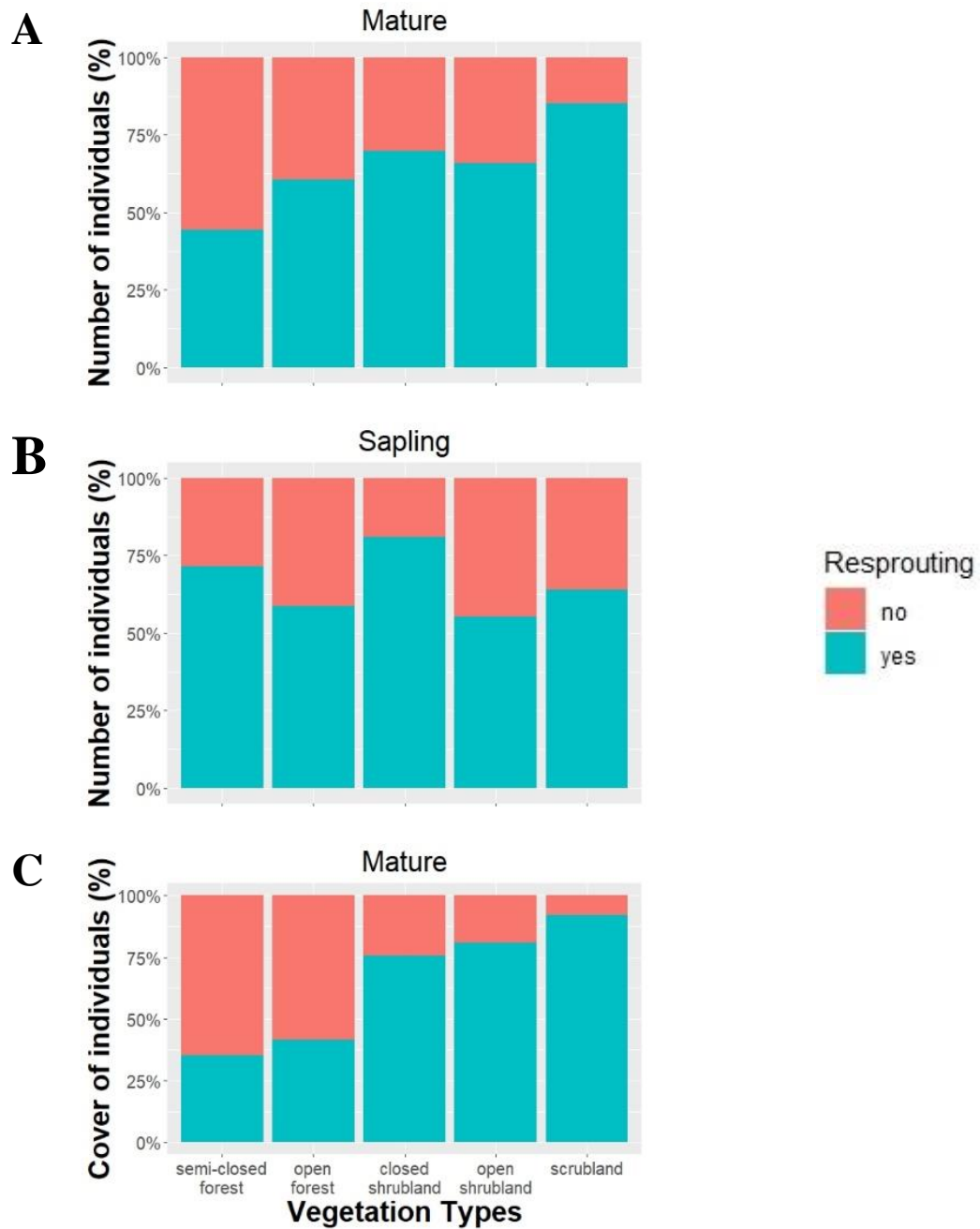
Supplementary Figure 3. Shepard plot for NMDS analyses of the number (a), cover (b), and presence (c) of mature individuals.
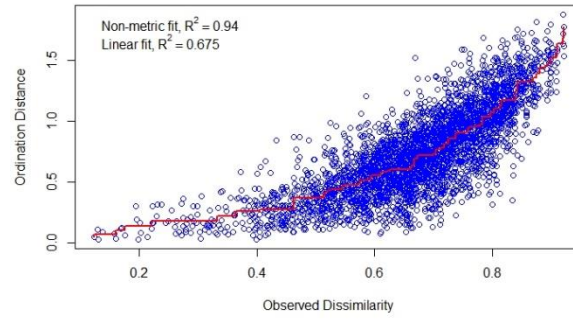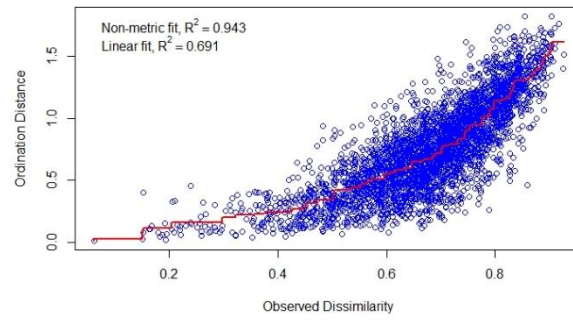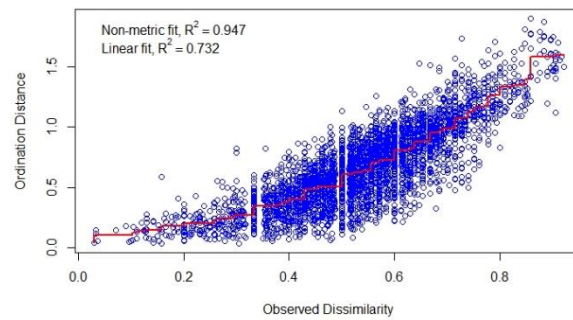
CHAPTER 3: LEAF TRAIT VARIABILITY AT THE SPECIES, FUNCTIONAL GROUP, AND PLANT COMMUNITY LEVELS IN MEDITERRANEAN WOODY VEGETATION*

Abstract

Leaf traits are good indicators of ecosystem functioning and plant adaptations to environmental conditions. We examined the drivers of leaf trait variability in Mediterranean woody vegetation (semi-closed forest, open forest, closed shrubland, open shrubland, and scrubland) in southwestern Anatolia (Turkey). Using linear mixed models, community-weighted trait means, and principal component analysis, we tested how much variability in leaf traits (specific leaf area, leaf thickness, and leaf area) is accounted for species, growth form, resprouting ability, regeneration strategy, and vegetation type. Despite a large amount of leaf trait variability both within- and among-species existed, functional groups still accounted for a significant part of this variability. Resprouters had higher SLA and leaf area and lower leaf thickness than non-resprouters. Although no consistent pattern was observed in three leaf traits in the growth form, we found evidence for the difference in SLA and leaf thickness between shrubs and large shrubs, and subshrubs had smaller leaves than other growth forms. Vegetation type also accounted for a substantial amount of leaf trait variability. Specifically, closed habitats had larger leaf area than open ones, and scrublands had higher SLA, lower leaf thickness, and lower leaf area than other vegetation types. Our results suggest that plant communities in Mediterranean forests and shrublands have higher water use efficiency, more photosynthetic capacity per unit leaf area, and more resistance to drought than scrublands. Our study contributes to a better understanding of the drivers of leaf trait variability at the local scale in Mediterranean plant communities.

Keywords: growth form, plant traits, regeneration strategy, resprouting ability, the Mediterranean Basin.

* This chapter was submitted to an international scientific journal.

3.1. Introduction

Plant functional traits are morphological, physiological, and phenological characteristics of plant species affecting their growth, reproduction, and survival and their response to changing environments (Garnier et al. 2004; Violle et al. 2007; Pérez-Harguindeguy et al. 2013; Garnier et al. 2016; Kühn et al. 2021). Leaf traits are indicators of ecosystem functioning in assessments at the community level (Díaz et al. 2004; de Bello et al. 2010; Stanisci et al. 2020). For instance, specific leaf area (SLA), leaf area, and leaf thickness are leaf traits informing resource use and ecosystem properties (Roche et al. 2004; Paula and Pausas 2006; Li et al. 2022). SLA is often cited as the key plant functional trait (Reich et al. 1992; Wilson et al. 1999; Garnier et al. 2004; Roche et al. 2004), leaf area dramatically affects the energy acquired by a leaf and is related to the water balance (Díaz et al. 2016), and leaf thickness is a proxy of how much physically strong a leaf is (Pérez-Harguindeguy et al. 2013). SLA and leaf thickness are ecologically relevant to resource acquisition and retention (Vile et al. 2005; Frenette-Dussault et al. 2013), while leaf area is related to stress avoidance and light acquisition (Frenette-Dussault et al. 2013). For example, since evergreen species use their leaves as nutrient stores, their leaves are thicker than deciduous species (Witkowski and Lamont 1991; Roche et al. 2004). Species grown in resource-rich environments have higher SLA, and are productive but live shorter (Wilson et al. 1999). On the other hand, higher leaf thickness (Pérez-Harguindeguy et al. 2013), longer leaf longevity (Ackerly et al. 2002), and smaller leaf area (Chirino et al. 2017) are persistent under decreasing precipitation (Kühn et al. 2021), especially species with sclerophyllous leaves with low SLA (Pérez-Harguindeguy et al. 2013; Ayma-Ramay et al. 2021). Many leaf traits have positive or negative associations with each other. For instance, SLA has a negative relationship with leaf thickness (Wilson et al. 1999). Therefore, leaves in sunny conditions have lower SLA (Hodgson et al. 2011) but higher leaf thickness (Pérez-Harguindeguy et al. 2013) than leaves under canopies and *vice versa*. On the other hand, the consistent relationships among leaf economic spectrum traits at the global level (Wright et al. 2004) may not be expressed at the community level and leaf trait dimensions can be locally variable (Messier et al. 2017).

Drivers of leaf trait variability differ across various biomes globally, mainly due to their difference in environmental and disturbance processes (Llerena-Zambrano et al. 2021). Although many leaf traits are phylogenetically conserved (Homeier et al. 2021), among-

and within-species variability also contributes a significant amount to the geographic variation of many leaf traits (Messier et al. 2017; Dong et al. 2020). On the other hand, climatic drivers are among the main drivers of variability in some leaf traits, including leaf area (Geekiyanage et al. 2017; Dong et al. 2020; Llerena-Zambrano et al. 2021), SLA (Wang et al. 2015; Shi et al. 2018; Homeier et al. 2021), and leaf thickness (Geekiyanage et al. 2017; Shi et al. 2018; Homeier et al. 2021). Therefore, studying leaf trait variability at the community level is crucial to understanding the potential of local plant communities to resist prolonged and/or intensified droughts due to climate change. Leaf trait variation among species and communities were studied in several aspects, including along elevational gradients (e.g., Homeier et al. 2021; Llerena-Zambrano et al. 2021) and to compare different environmental conditions (e.g., Geekiyanage et al. 2017, Markesteijn et al. 2007, Wang et al. 2015), functional groups (Jin et al. 2014), and vegetation types (Shi et al. 2018). Considering environmental conditions substantially differ at the regional or local scales, however, more studies are still needed for a better understanding of drivers of leaf trait variability at various scales in different terrestrial biomes.

Mediterranean plant species use strategies to cope with limiting resources related to drought conditions (Mereu et al. 2009; Hernández et al. 2010; Maseyk et al. 2011; Altieri et al. 2015). Leaf traits are especially important for Mediterranean plants in reducing water loss due to drought conditions (Hernàndez et al. 2010; Valencia et al. 2016; Chirino et al. 2017). Woody plant species that dominated the Mediterranean vegetation have small and sclerophyllous leaves with thick epidermal walls and cuticle (Ackerly et al. 2002; Paula and Pausas 2006). These species have been adapted to low water availability (Paula and Pausas 2006; Gillison 2019) and have developed a conservative water use strategy (Kühn et al. 2021). Moreover, drier environments in the Mediterranean Basin include more resource conservative species than wetter ones (Garnier et al. 2019). On the other hand, leaf trait variability in Mediterranean species can be explained by more than climatic factors. As a matter of fact, among-species differences (Husholf and Swenson 2020), local environmental conditions such as light, humidity, or soil nutrients (Domíngez et al. 2012; Campetella et al. 2019), and resprouting ability (Paula and Pausas 2006) can also responsible for leaf trait variation in Mediterranean plant communities.

Mediterranean Basin ecosystems have long experienced several types of natural disturbances, including drought, herbivory, and fire (Lavorel 1999). Since the onset of

the Holocene, human-driven disturbances such as agricultural activities, domestic herbivory, and other kinds of land uses have also significantly contributed to shaping the Mediterranean Basin landscapes (Naveh and Carmel 2004). Therefore, both natural and human-caused disturbances are considered important drivers of the current occurrence and distribution of various vegetation types in the Mediterranean Basin. These vegetation types considerably vary in form, structure, diversity, and human use (Keeley et al. 2012). Mediterranean vegetation has traditionally been classified into three major types: forests, shrublands, and scrublands (Arianoutsou 1998; Blondel and Aronson 1999; Keeley et al. 2012; Kavgacı et al. 2017). However, this primary classification may not encapsulate the remarkable diversity of species, functional groups, and plant communities in the Mediterranean Basin. For example, there are functionally significant differences between open and closed states of forests in several terrestrial biomes on Earth (Bond 2019; Pausas and Bond 2020). Such differences are also likely to occur among different vegetation types of the Mediterranean Basin (Tüfekcioğlu and Tavşanoğlu 2022). Moreover, functional group classifications improve our understanding of ecosystem function and processes (Díaz Barradas et al. 2009) and allow us to follow the patterns of vegetation recovery after disturbances over a long-term period (Kazanis and Arianoutsou 2004; Tavşanoğlu and Gürkan 2014). Although, various Mediterranean vegetation types can be quite complex regarding growth forms and regeneration strategies (Tüfekcioğlu and Tavşanoğlu 2022), different trends can be observed during post-disturbance recovery in different vegetation communities. The resprouting ability plays an essential role in vegetation recovery in the Mediterranean Basin after particular disturbances such as wildfire and drought (Pausas et al. 2016). Moreover, resprouting after disturbance is an important plant trait associated with other plant traits, including several leaf traits (Paula and Pausas 2006).

In this study, we aimed to elucidate the drivers shaping leaf trait variability in Mediterranean woody plant communities. We tested whether leaf traits vary at (1) species, (2) functional group, and (3) plant community levels. We expected to find evidence for the difference in leaf traits among species and different functional groups. We also hypothesized that plant communities in major Mediterranean vegetation types should differ in their leaf trait structure. To test these hypotheses, we measured leaf traits of several species in woody plant communities across various Mediterranean vegetation types (semi-closed forest, open forest, closed shrubland, open shrubland, and scrubland).

Then we examined the variability in leaf traits among species, functional groups (based on the growth form, resprouting ability, and regeneration strategy), and vegetation types.

3.2. Material and Methods

3.2.1. Study Area and Sites

The study area was in southwestern Anatolia (Turkey), which is under a Mediterranean climate characterized by cool, wet winters and hot, dry summers and dominated by Mediterranean vegetation types, including several open and closed vegetation states (Tüfekcioğlu and Tavşanoğlu 2022). We established our study sites in the five most frequent vegetation types of the region: semi-closed Turkish red pine 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). We selected 28 study sites, one ha in size, distributed to different vegetation types by considering their relative area covered in the study area (six for the semi-closed forest, eight for the open forest, four for the closed shrubland, six for the open shrubland, and four for the scrubland. A further detailed explanation of the study sites is given by Tüfekcioğlu and Tavşanoğlu (2022).

3.2.2. Field Sampling and Counts

We collected leaf samples within study sites to measure leaf traits of individual plants in the dry period of the region, i.e., between May and September 2019, and only in September 2020 due to COVID-19 mobility restrictions. We followed the Pérez-Harguindeguy et al. (2013) protocol to select individuals for collecting and storing leaf samples. We selected mature and healthy-looking individuals located in unshaded locations to sample, and we sampled ten leaves from each individual. To not let the leaves dehydrate after collecting, we wrapped leaf samples in moist paper and put them in sealed plastic bags just after we collected the leaves. We blow into the bags before closing them to allow more carbon dioxide inside to minimize the water loss due to transpiration. Finally, bags including leaf samples were stored in a cool box in the field until they were put in a refrigerator at 4°C. We made further processing of leaf samples within 24 h after the collection.

In total, we collected leaf samples from 857 individuals of 38 species, of which 709 individuals of 37 species in 2019 and 148 individuals of 23 species in 2020. Since all plant species were not found in all study sites, the number of individuals sampled varied among study sites and vegetation types. Therefore, we obtained more leaf samples from the most frequent species in comparison to rarer ones (SI Table S1). Moreover, we could not take leaf samples from summer-deciduous species as the time of the leaf fall coincides with the sampling period and from individuals full of unhealthy leaves.

In each study site, we established three belt transects 10×40 m and 10×30 m in size (according to topography) except for a study site including two transects due to topographic limitations. In total, we sampled 83 belt transects. We counted all mature individuals of woody species in each belt transect to obtain abundance data for further use in community weighted mean analyses. Some of those individuals were the same ones on which we made leaf sampling.

3.2.3. Trait Measurements

We measured three leaf traits for each sampled individual: leaf area, leaf thickness, and specific leaf area. We followed the Pérez-Harguindeguy et al. (2013) protocols for measuring leaf traits. We made one measurement on the lamina of each leaf by using a digital micrometer to measure leaf thickness. To measure the leaf area, we scanned the leaves collected from the field and then calculated their one-sided area using the ImageJ program (Rasband 2012). To obtain SLA values for each individual plant, we first weighted leaves using a digital scale after they were dried in the oven at 70°C for 72 h to determine the oven-dry mass of leaves (Pérez-Harguindeguy et al. 2013). After this process, SLA values were calculated by dividing the average leaf area of each individual by the total oven-dry mass value.

3.2.4. Functional Groups

We used three functional grouping systems in this study. First, we classified woody species according to their growth forms as subshrub, shrub, large shrub, tree, and liana. This classification is based on Tavşanoğlu and Pausas (2018) and field observations. We used post-fire resprouting ability as a second, binary classification system: resprouters

and non-resprouters. Finally, we assign species into one of the four regeneration strategy classes reflecting the regeneration properties of species in more detail: (1) non-resprouter propagule persisters with a canopy seed bank (R-P+c), non-resprouter propagule persisters with a soil seed bank (R-P+s), resprouter propagule-non-persisters (R+P-), and resprouter propagule-persisters with a soil seed bank (R+P). This regeneration strategy classification is based on Pausas et al. (2004) with addition of seed bank location for propagule persisters (Pausas 1999; Tavşanoğlu and Gürkan 2014). Resprouting ability and propagule persistence traits used in the latter two classification systems are based on Tavşanoğlu and Pausas (2018) and field observations. Since data for resprouting ability and propagule persistence for some species are missing in the literature and BROT database (Tavşanoğlu and Pausas 2018), and the resprouting ability varies at the population level in some species, we excluded some species from resprouting ability and regeneration strategy analyses. Consequently, although we used data from all 38 species and 857 individuals for growth form analysis, we included 31 species and 784 individuals in resprouting ability analysis and 30 species and 732 individuals in regeneration strategy analysis (SI Table S1).

3.2.5. Data Analysis

First, we revealed among-species variation in the studied leaf traits (i.e., SLA, leaf thickness, and leaf area). We only used species with leaf samples from at least five individuals; thus, the data consisted of 837 individuals belonging to 31 species in this analysis. We made ridgeline plots to visualize within- and among-species variability for each trait. For further investigation of trait variability, we assessed the range (min. and max.) of trait values for each species. Then, we performed a general linear model to reveal differences among species. Moreover, as a proxy for among-species variability in each leaf trait, we calculated the coefficient of variation for each trait based on mean trait data at the species level.

We compared functional group classes for leaf thickness, leaf area, and SLA for each functional grouping system. To analyze the differences among functional group classes, we made violin plots to show the interquartile range and the lower/upper adjacent values and performed linear mixed effects models (LME) for each trait for functional groups. In these models, functional group class and species were considered fixed and random

factors, respectively. Since the number of sampled individuals varied for each functional group class, we performed the LME analysis by weighting data with the number of sampled individuals. We calculated the mean and standard error of leaf traits for each functional group and made multiple comparisons following LME analyses by estimating marginal means for different functional group classes. We also implemented a principal components analysis (PCA) including three leaf traits considered in the study to reveal differences between functional group classes regarding leaf traits.

For the community analysis, we calculated community weighted mean (CWM) by weighting leaf trait values with the abundance of species for each transect (i.e., plant community) (Garnier et al. 2004). In this analysis, we only used trait data of individuals with abundance data sampled within belt transects. For CWM calculation, we used average values for leaf traits for each species. Missing trait data for the species that we could not collect leaf samples in the field were obtained from the BROT database (Tavşanoğlu and Pausas 2018), Hacettepe University Functional Ecology Lab. data (Aktepe 2021; Çoşgun 2022), and the relevant literature (Merchant 1998; Specht et al. 1988; Liakoura et al. 2001; Elmas and Kutbay 2015). Even though there were still some species whose trait data are missing, we concluded that this missing data would not cause any problem for the community analyses since many of these species had low abundance in the field (6, 14, and 8 species for SLA, leaf thickness, and leaf area, respectively).

Following CWM analysis, we performed LME for each trait for vegetation types. In these models, the vegetation type and transect were considered as the fixed and random factors, respectively. We calculated the mean and standard error of leaf traits for each vegetation type and made multiple comparisons following LME analyses by estimating marginal means for different vegetation types. Finally, we implemented a principal components analysis (PCA) including three leaf traits considered in the study to present differences between vegetation types regarding leaf traits.

All the analyses were performed in the R environment (R Core Team 2020). We used *ggridges* package (Wilke 2021) for drawing ridgeline plots, *ggplot2* package (Wickham 2016) for drawing violin and box plots, *lme* function in the *nlme* package (Pinheiro and Bates 2000) for performing LMEs, *emmeans* function in the *emmeans* package (Lenth

2020) for estimating marginal means following LMEs, *prcomp* and *pairwise.adonis* functions in the *vegan* package (Oksanen et al. 2019) for performing PCA.

3.3. Results

3.3.1. Variation Among Species

Leaf traits showed substantial variation both within- and among-species (Fig. 3.1, SI Table S2). In our dataset, SLA values of the sampled species varied between 5.21 *(Cistus parviflorus)* and 24.47 (*Paliurus spina-christi*) mm^2mg^{-1}, leaf thickness values between 0.180 (*Paliurus spina-christi*) and 0.867 (*Phlomis lycia*) mm, and leaf area values between 8.2 *(Erica manipuliflora)* and 2316.0 *(Laurus nobilis)* mm^2. Leaf area had the highest coefficient of variation value (116.2) in comparison to other traits (44.8 and 39.1 for SLA and leaf thickness, respectively), therefore, it was the most variable trait among species. Differences among species were significant in all leaf traits (for SLA F = 38.4, leaf thickness F = 67.9, and leaf area F = 279.8, P < 0.0001 for all). The variability among species in SLA and leaf area in our study falls into the range for the existing trait measurements in the Mediterranean Basin: 1.55 and 32.36 mm^2mg^{-1} for SLA, and 3.0 and 2610.0 mm^2 for leaf area (except two extreme values up to 11968 mm^2) (in comparison to the ranges in the BROT database; Tavşanoğlu and Pausas 2018).
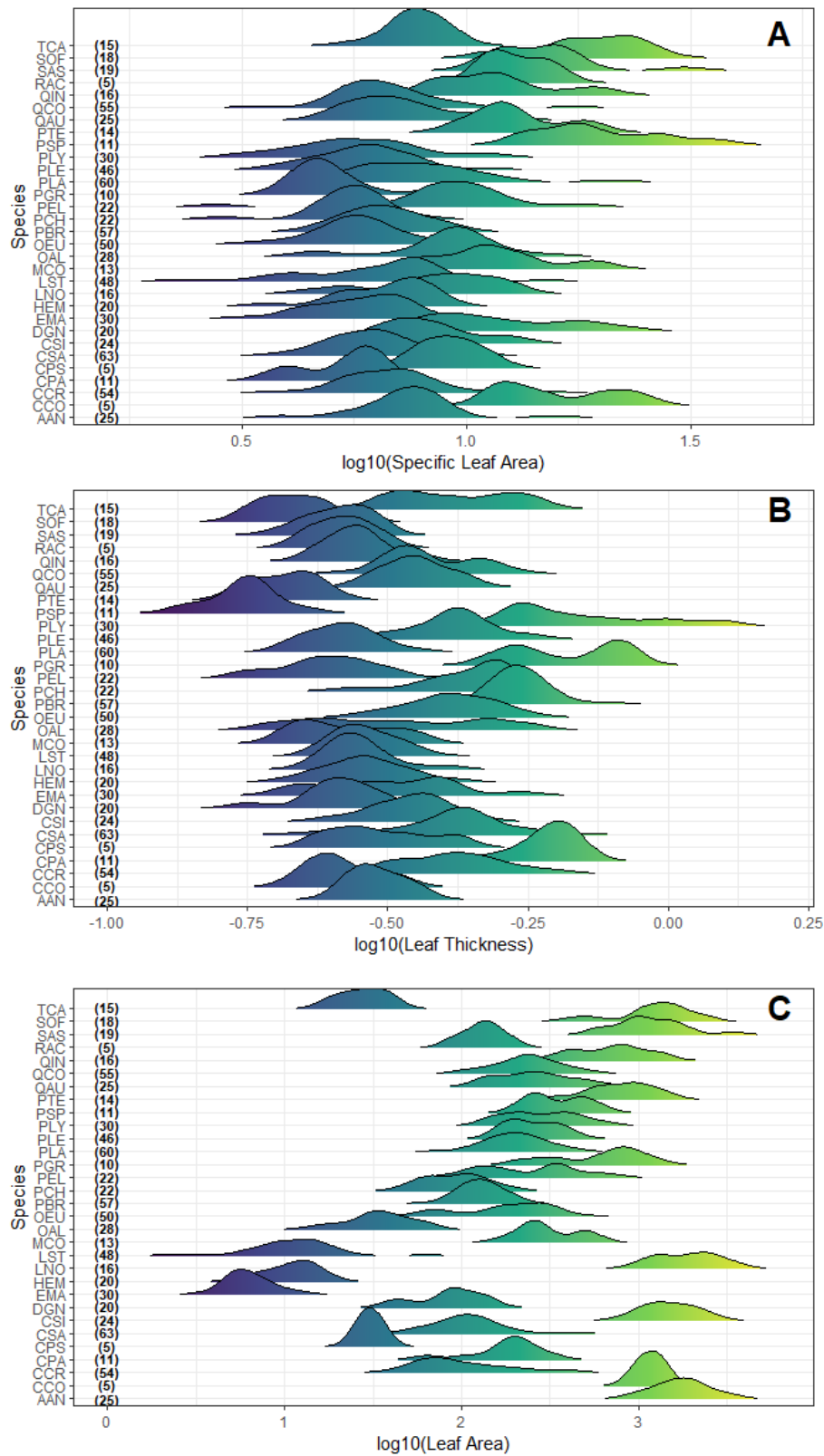
Figure 3.1. Within- and among-species variation in the specific leaf area (A), leaf thickness (B), and leaf area (C). Each graph within the figures indicates within-species variability for the corresponding species (code at the y-axis). Species codes are given in Suppl. Table 1. The numbers in parentheses are the sample size.

3.3.2. Variation at the Functional Group Level

Despite a large amount of variability both within- and among-species for the studied leaf traits existed (Fig. 3.1, SI Table S2), functional groups still accounted for a significant part of this variability. Different functional grouping systems explained trait variability at various degrees (Fig. 3.2, SI Table S3). Accordingly, we also found evidence for differences among functional groups in different classification systems. Specifically, the growth form and regeneration strategy were accounted for ca. 30% of the variability in three leaf traits (PCA analysis, $R^2 = 0.28$ and $R^2 = 0.26$, respectively, both P = 0.001), while the resprouting ability explained only ca. 10% of the total variability in leaf traits ($R^2 = 0.10$, P = 0.001).
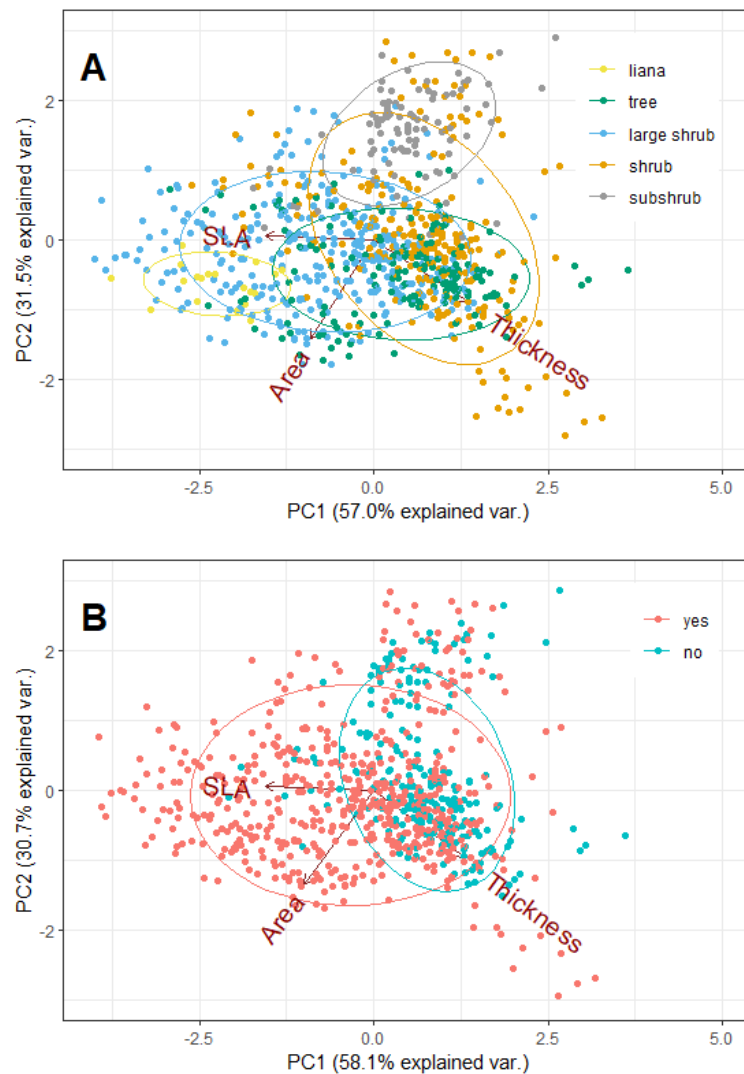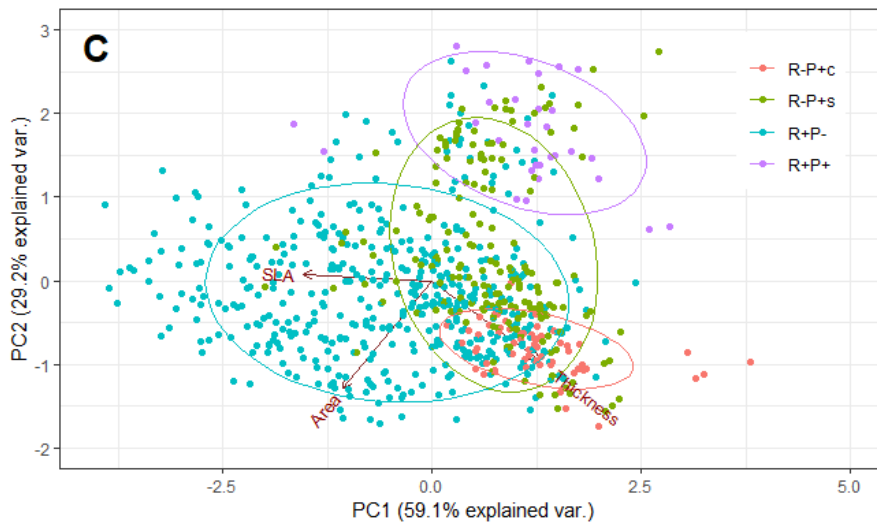
Figure 3.2. Principal component analysis graph for specific leaf area, leaf thickness, and leaf area for different functional group classifications according to (A) growth form, (B) resprouting ability, and (C) regeneration strategy. Different colors represent different functional groups. Each data point is the mean value in the study area of individuals measured, and eclipses indicate the standard deviation of each group.

We observed the lowest SLA values in individuals of some shrubs (*Erica manipuliflora, Phlomis lycia*, and *Ptilostemon chamaepeuce*) and the highest ones in those of some large shrubs (*Cotinus coggygria, Paliurus spina-christi*, and *Styrax officinalis*), while other growth forms exhibited no clear pattern (SI Table S2). Indeed, there was evidence for the difference in SLA between shrubs and large shrubs (Fig. 3.3, SI Table S4). We also observed a difference in leaf thickness values between shrubs and large shrubs (higher and lower values, respectively), but trees also had higher leaf thickness than large shrubs (Fig. 3.3, SI Table S4). Subshrubs had smaller leaves than any other growth form group (Fig. 3.3, SI Table S4), and the species with the largest leaves were all large shrubs (*Arbutus andrachne, Ceratonia silique, Cotinus coggygria,* and *Laurus nobilis,* SI Table S2).
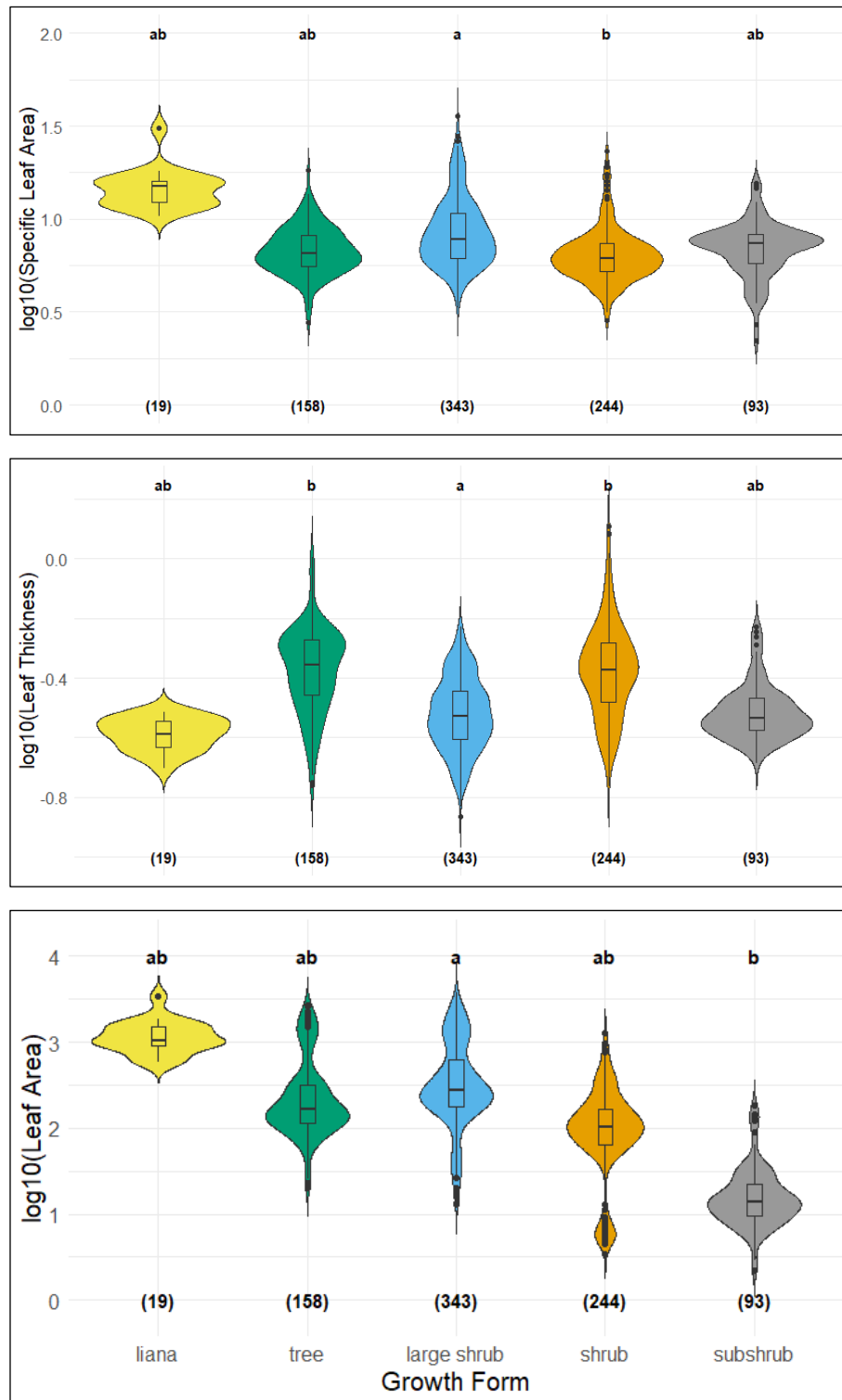
Figure 3.3. Comparison of specific leaf area, leaf thickness, and leaf area for different growth forms. The letters above indicate statistical test results as having different letters mean a significant difference between two groups, and the numbers in parentheses at the bottom represent the sample size (i.e., individuals measured).

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We obtained consistent results using two alternative grouping approaches based on the regeneration mode; resprouting ability and regeneration strategy (Fig. 3.4, SI Table S4). In general, resprouters had higher SLA and leaf area and lower leaf thickness values than non-resprouters at both species (SI Table S2) and functional group levels (Fig. 3.4, SI Table S4). Although we found no evidence of difference in SLA among regeneration strategy groups, a clear distinction was obtained when comparing resprouting ability classes (resprouters vs. non-resprouters) (Fig. 3.4). Moreover, this difference can be attributed to the higher SLA values of species with R+P- strategy but not to those with the R+P+ strategy with similar SLA values with non-resprouters (Fig. 3.4, SI Table S4). In terms of leaf thickness, the leaves of the non-resprouters were thicker than the resprouters, and this difference was mainly due to *Pinus brutia* with the R-P+c strategy. Similar to the pattern we observed in SLA, we found evidence that resprouters had larger leaves than non-resprouters, but this difference was due to solely R+P- strategists but not species with R+P+ strategy (Fig. 3.4, SI Table S4).
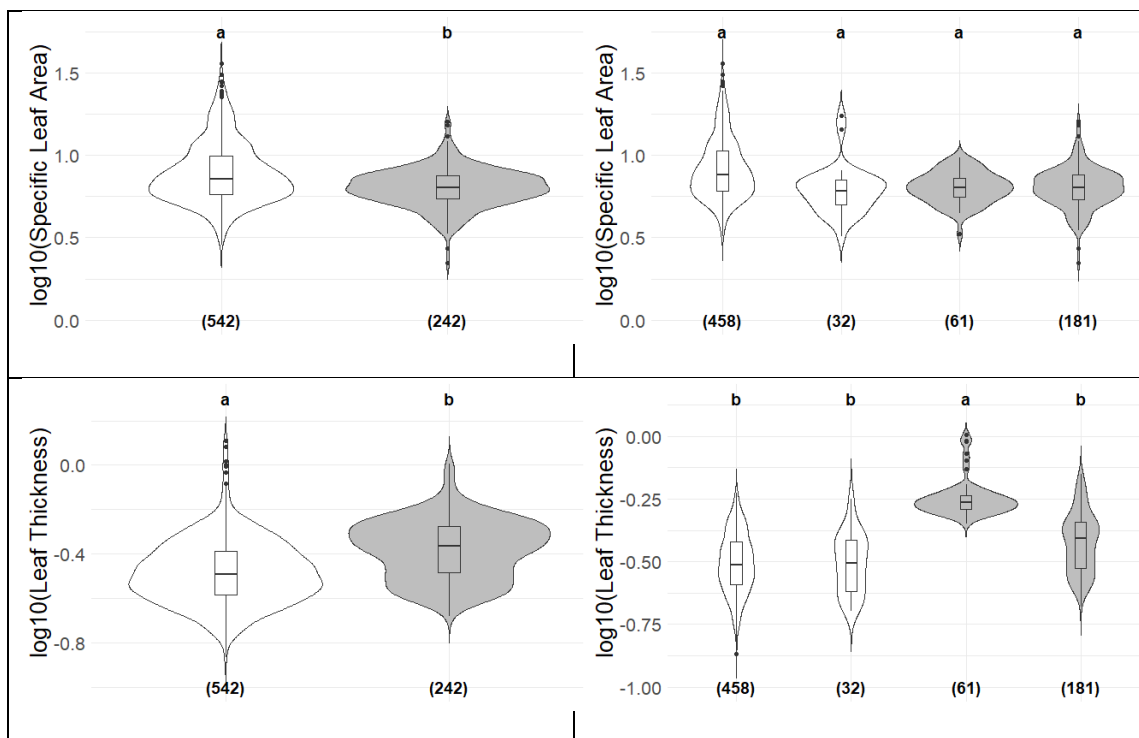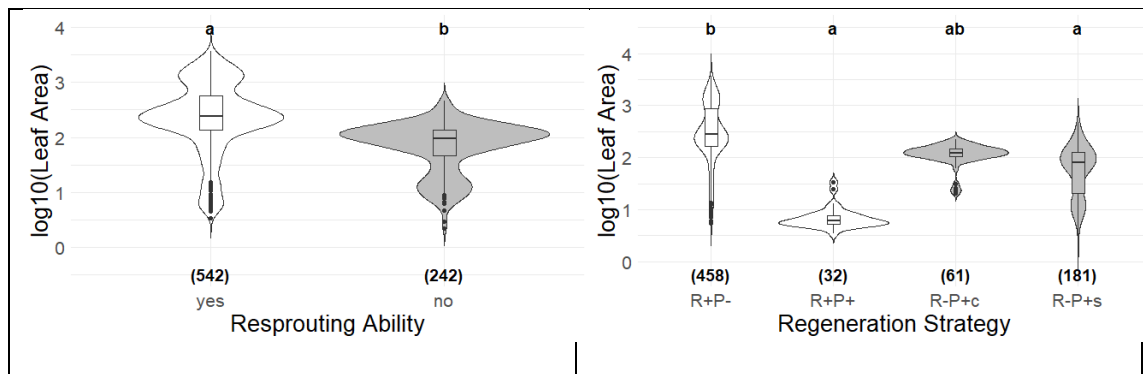
Figure 3.4. Comparison of specific leaf area, leaf thickness, and leaf area for resprouting (yes/no, at the left panel) and regeneration strategies classes (at the right panel). The letters above indicate statistical test results as having different letters mean a significant difference between two groups, and the numbers in parentheses at the bottom represent the sample size (i.e., individuals measured). In all graphs, white and gray plots represent resprouters and non-resprouters, respectively.

3.3.3. Variation at the Community and Vegetation Type Levels

Since the abundance of species varied in plant communities belonging to different vegetation types, the contribution of each species to the community trait mean also differed among vegetation types (SI Table S5). Consequently, PCA analysis showed that the vegetation type explains a considerable variation in leaf traits among local plant communities ($R^2 = 0.29$, $P = 0.001$, Fig. 3.5). Plant communities in semi-closed forest, open forest, closed shrubland, and open shrubland were relatively similar for the studied leaf traits, while scrubland differed from these vegetation types (Fig. 3.5, SI Table S6). Scrubland had higher SLA, lower leaf thickness, and lower leaf area than other vegetation types in many cases (Fig. 3.6, SI Table S7). Although this general trend, we provided no evidence for the difference between scrubland and open forest regarding leaf thickness and leaf area (Fig. 3.6, SI Table S7). Other exceptions we observed were including the similar leaf area values obtained for scrubland and open shrubland, the lower leaf thickness in the open forest than in semi-closed forest and open shrubland, and the higher leaf area in closed shrubland than in open forest and open shrubland (Fig. 3.6, SI Table S7). We revealed that a few species dominated the scrublands with relatively higher SLA, lower leaf thickness, or lower leaf area values (*Cistus creticus*, *Genista acanthoclada*, *Sarcopoterium spinosum*, and *Thymbra capitata*, SI Table S5) were responsible for the

difference in leaf traits between the communities in scrubland and those of other vegetation types.
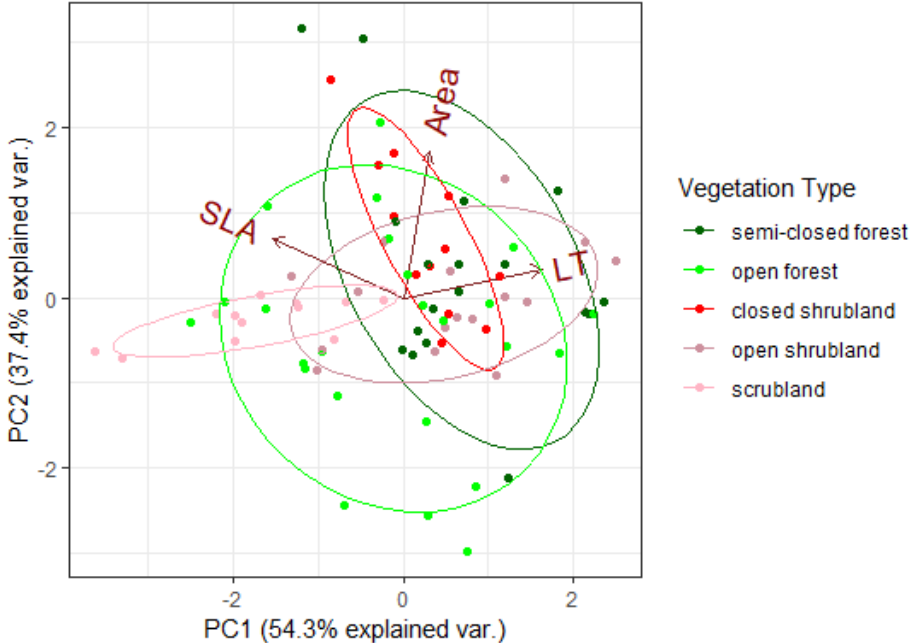
Figure 3.5. Principal component analysis graph of community weighted mean values for specific leaf area, leaf thickness, and leaf area among different vegetation types. Each data point is community-weighted mean value of each transect, and eclipses indicate the standard deviation of each vegetation type.
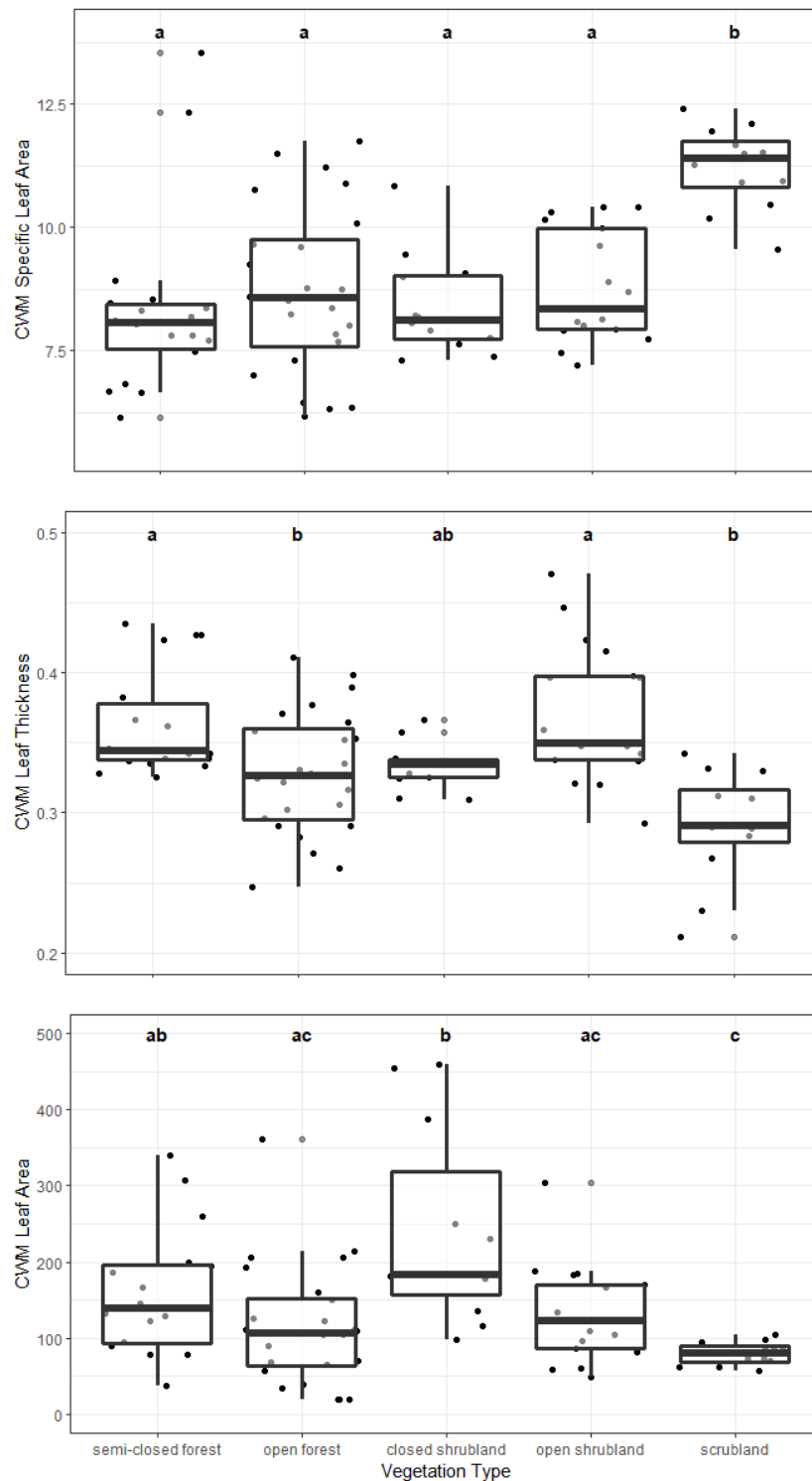
Figure 3.6. Comparison of community weighted mean values for specific leaf area (A), leaf thickness (B), and leaf area (C) among vegetation types. Each data point is community-weighted mean value of each transect. The letters above indicate statistical test results as having different letters mean a significant difference between two groups.

3.4. Discussion

Our results reveal the significant within- and among-species variability in leaf traits in Mediterranean woody plants. Despite this substantial variability, our study provides evidence that leaf trait variation in Mediterranean woody plants can be partly explained by plant functional groups, including growth form, resprouting ability, and regeneration strategy. Our analyses further showed that vegetation type also accounts for a significant proportion of leaf trait variability at the local community level. Therefore, the results supported our hypotheses and initial expectations.

The distribution of plant trait values among different vegetation types has drawn little research attention globally, but such studies provide notable insights into our understanding of the evolution and ecology of biomes and regional floras (Dantas and Pausas 2020). In the Mediterranean Basin, differences in SLA values have been observed across various vegetation types along with aridity or elevational gradients (de la Riva et al. 2018; Navarro and Hidalgo-Triana 2021) and between early and late successional stages (Garnier et al. 2004; Kazakou et al. 2006). Plant communities in scrublands in our study area considerably differ in leaf traits, as we obtained the highest SLA and the lowest leaf thickness and leaf area values in scrubland vegetation. Although this difference was due to trait values of a few species that dominated scrublands, it has an ecological significance regarding the response of the plant community to environmental conditions. Leaf area also showed a pattern among vegetation types, such that the plant community in closed vegetations (i.e., closed forest and closed shrubland) had larger community-weighted mean leaf size than open ones (open forest, open shrubland, and scrubland). Species with lower SLA, smaller leaves, and higher leaf thickness are well known to be more tolerant to drought conditions in many ecosystems (Ackerly et al. 2002; Costa-Saura et al. 2016; Nunes et al. 2017; Wright et al. 2017; de la Riva et al. 2018; Kühn et al. 2021). Our results on SLA and leaf thickness suggest that plant communities in Mediterranean forests and shrublands (regardless of their openness status) have higher water use efficiency, more photosynthetic capacity per unit leaf area, and are more resistant to drought than those in scrublands. Considering the prolonged drought conditions in the Mediterranean Basin (and specifically in our study area), plant species in scrublands may have to compensate for their high SLA and low leaf thickness with their small leaf area to have some drought resistance. Moreover, since SLA has a positive relationship with

the relative growth rate (Violle et al. 2007), the results also suggest that plant communities in scrublands consisted of species with faster growth rates than other vegetation types. Thus, our results may indicate that scrublands are at different place of the slow-fast continuum of the life history than forests and shrublands at the community level in the Mediterranean Basin. Therefore, the plant community in scrublands can be expected to have better performance under frequent disturbances (such as fire and herbivory) but worse in the case of drought than shrublands and forests, and vice versa.

Due to the prolonged summer drought, specific leaf traits are expected to be filtered by regional climatic conditions in the Mediterranean Basin,. This filtering process may have resulted in assembling plant communities exhibiting adaptations to drought conditions. For instance, sclerophyll leaves are characteristic of woody plant species in Mediterranean-type ecosystems worldwide; even their floras share no or ancient evolutionary origins (Mooney and Dunn 1970). Fire is another selective force for Mediterranean species operating as fire regimes at the local scale. Although variability in regeneration traits can be attributed to fire regimes in the Mediterranean Basin (Moreira et al. 2012), fire-related traits could not be expected to explain much variability in leaf traits. In our study, in contrast, we found that resprouting ability and regeneration strategy account for some variability in leaf traits. Indeed, there is evidence for the difference in soft and hard leaf traits between resprouters and non-resprouters in the Mediterranean Basin (Paula and Pausas 2006; Hernández et al. 2011). Physiological differences between two regeneration syndromes also lead to the coexistence of these two regeneration strategies in Mediterranean vegetation (Vilagrosa et al. 2014). Such differences are attributed to a trade-off between drought resistance and carbon storage (Paula and Pausas 2006) since resprouters have to allocate more resources to their roots and underground organs that allow them to resprout after a fire. Consequently, resprouters are less tolerant to drought than non-resprouters in the Mediterranean Basin as they have higher SLA than non-resprouters. Although resprouter versus non-resprouter distinction explains a significant amount of leaf trait variability in Mediterranean plants (this study, Paula and Pausas 2006), our results revealed that a further functional separation in regeneration strategy by considering the seed bank locality of non-resprouter species (soil or canopy seed bank) provides a better explanation account for leaf trait variability.

Although herbaceous and woody species differ in height and seed mass at the global scale, they do not differ in leaf traits such as SLA and leaf area (Díaz et al. 2016). In our study, the woody growth form also explained a considerable amount of leaf trait variation. A similar result was obtained by Navarro and Hidalgo-Triana (2021) for SLA by considering trees, large shrubs, and shrubs in a series of Mediterranean shrublands. Vegetation type, growth form, and regeneration strategy all contribute to the leaf trait variability in local plant communities of the Mediterranean Basin. The difference in leaf traits among vegetation types considered in our study may also be attributed to the functional distinctness of these five vegetation types (Tüfekcioğlu and Tavşanoğlu 2022). Besides the variability at functional group and vegetation type levels, we also observed a substantial variation in leaf traits in plant communities at the transect scale. A similar result obtained by Shi et al. (2018) suggesting that ignoring the leaf trait variability at the local scale will underestimate the role of microhabitat filters in community assembly and may lead to restoration plans failing . Studying leaf traits in plant communities at the local scale will provide a better understanding of leaf trait variability in the Mediterranean Basin.

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Supplementary Material to the Chapter 3

Table S1: The species whose leaf samples were collected in the study, and their taxonomic status, the number of individuals sampled, and functional groups. Regeneration strategy (*sensu* Pausas 1999; Pausas et al. 2004) includes information on both resprouting ability after the fire (resprouters: *R+* or non-resprouters: *R-*), post-fire persistence ability via any propagule (propagule-persister: *P+* or propagule-non-persister: *P-*), and the seed bank locality in propagule-persisters (canopy seed bank: *c* or soil seed bank: *s*). Growth form, resprouting ability, post-fire persistence via propagules, and seed bank locality information are based on the BROT database (Tavşanoğlu and Pausas 2018) and field observations. Nomenclature follows Davis (1965-1985), but taxon and family names were updated according to The Plant List (2013).

Species	Species Code	Family	No. individuals	Growth Form	Regeneration Strategy	Resprouting Ability
Arbutus andrachne L.	AAN	Ericaceae	25	large shrub	R+P-	yes
Arbutus unedo L.	AUN	Ericaceae	4	large shrub	R+P-	yes
Calicotome villosa (Poir.) Link	CVI	Leguminosae	2	shrub	R+P+	yes
Ceratonia siliqua L.	CSI	Leguminosae	24	tree	R+P-	yes
Cistus creticus L.	CCR	Cistaceae	54	shrub	R-P+s	no
Cistus parviflorus Lam.	CPA	Cistaceae	11	shrub	R-P+s	no
Cistus salviifolius L.	CSA	Cistaceae	63	shrub	R-P+s	no
Cotinus coggygria Scop.	CCO	Anacardiaceae	5	large shrub	R+P-	yes
Cupressus sempervirens L.	CSE	Cupressaceae	4	tree	R-P+c	no
Cytisopsis pseudocytisus (Boiss.) Fertig	CPS	Leguminosae	5	subshrub	R-P+s	no
Daphne gnidioides Jaub. & Spach	DGN	Thymelaeaceae	20	shrub	unknown	unknown
Daphne sericea Vahl	DSE	Thymelaeaceae	2	shrub	unknown	variable
Erica manipuliflora Salisb.	EMA	Ericaceae	30	shrub	R+P+	yes
Hypericum empetrifolium Willd.	HEM	Hypericaceae	20	subshrub	R+P+	unknown
Juniperus oxycedrus L.	JOX	Cupressaceae	3	large shrub	R+P-	yes
Laurus nobilis L.	LNO	Lauraceae	16	large shrub	R+P-	yes
Lavandula stoechas L.	LST	Lamiaceae	48	subshrub	R-P+s	no
Myrtus communis L.	MCO	Myrtaceae	13	large shrub	R+P-	yes

Olea europaea L.	OEU	Oleaceae	50	tree	R+P-	yes
Osyris alba L.	OAL	Santalaceae	28	large shrub	R+P-	yes
Paliurus spina-christi Mill.	PSP	Rhamnaceae	11	large shrub	R+P-	yes
Phillyrea latifolia L.	PLA	Oleaceae	60	large shrub	R+P-	yes
Phlomis grandiflora H. S. Thomps.	PGR	Lamiaceae	10	shrub	unknown	unknown
Phlomis lycia D. Don	PLY	Lamiaceae	30	shrub	unknown	yes
Pinus brutia Ten.	PBR	Pinaceae	57	tree	R-P+c	no
Pistacia lentiscus L.	PLE	Anacardiaceae	46	large shrub	R+P-	yes
Pistacia terebinthus L.	PTE	Anacardiaceae	14	large shrub	R+P-	yes
Ptilostemon chamaepeuce (L.) Less.	PCH	Compositae	22	shrub	unknown	yes
Pyrus elaeagnifolia Pall.	PEL	Rosaceae	22	tree	unknown	unknown
Quercus aucheri Jaub. & Spach	QAU	Fagaceae	25	large shrub	R+P-	yes
Quercus coccifera L.	QCO	Fagaceae	55	large shrub	R+P-	yes
Quercus infectoria subsp. *veneris* (A.Kern.) Meikle	QIN	Fagaceae	16	large shrub	R+P-	yes
Quercus ithaburensis Decne.	QIT	Fagaceae	1	tree	R+P-	yes
Rhamnus punctata Boiss.	RPU	Rhamnaceae	4	large shrub	unknown	unknown
Ruscus aculeatus L.	RAC	Asparagaceae	5	subshrub	R+P-	yes
Smilax aspera L.	SAS	Smilacaceae	19	liana	R+P-	yes
Styrax officinalis L.	SOF	Styracaceae	18	large shrub	R+P-	yes
Thymbra capitata (L.) Cav.	TCA	Lamiaceae	15	subshrub	unknown	variable

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Table S2: Minimum, mean, and maximum value of individuals for each species for each leaf trait included in the study. Only species with at least five sampled individuals are included. Species codes are given in Table S1.

Species code	SLA (mm² mg⁻¹)			Leaf Thickness (mm)			Leaf Area (mm²)		
	min	mean	max	min	mean	max	min	mean	max
AAN	3.86	9.79	15.71	0.26	0.31	0.36	904.00	2066.65	3229.30
CCO	11.62	17.79	23.95	0.22	0.27	0.33	1001.10	1172.75	1344.40
CCR	3.67	9.84	16.00	0.25	0.45	0.65	35.80	243.50	451.20
CPA	3.76	5.21	6.66	0.49	0.59	0.70	63.20	193.95	324.70
CPS	7.67	9.42	11.17	0.24	0.33	0.42	26.90	30.45	34.00
CSA	3.64	7.25	10.85	0.21	0.46	0.70	45.50	257.15	468.80
CSI	6.00	9.56	13.12	0.24	0.36	0.47	765.40	1738.80	2712.20
DGN	7.13	15.20	23.26	0.17	0.25	0.33	39.20	93.30	147.40
EMA	3.21	5.66	8.10	0.20	0.38	0.56	3.40	8.15	12.90
HEM	3.60	6.20	8.80	0.21	0.31	0.42	5.40	11.90	18.40
LNO	4.43	8.62	12.80	0.23	0.32	0.40	920.20	2316.05	3711.90
LST	2.21	8.67	15.13	0.23	0.31	0.39	2.20	32.85	63.50
MCO	7.68	13.75	19.82	0.21	0.28	0.36	164.70	379.65	594.60
OAL	4.31	9.99	15.67	0.18	0.39	0.59	13.50	41.10	68.70
OEU	3.23	6.38	9.53	0.28	0.43	0.59	35.10	281.35	527.60
PBR	4.42	7.03	9.64	0.45	0.62	0.80	61.00	143.05	225.10
PCH	2.84	5.43	8.01	0.26	0.40	0.53	46.20	119.65	193.10
PEL	2.76	10.52	18.28	0.17	0.31	0.44	79.90	422.85	765.80
PGR	3.99	6.28	8.56	0.47	0.67	0.86	213.50	743.00	1272.50
PLA	5.11	13.65	22.18	0.20	0.28	0.36	66.90	270.95	475.00
PLE	3.71	7.51	11.31	0.27	0.43	0.59	150.30	313.70	477.10
PLY	3.14	7.36	11.57	0.45	0.87	1.28	133.10	408.15	683.20
PSP	13.11	24.47	35.82	0.14	0.18	0.22	210.60	415.55	620.50
PTE	9.48	14.27	19.06	0.17	0.21	0.26	339.30	918.10	1496.90
QAU	4.86	8.77	12.68	0.29	0.36	0.44	128.30	409.80	691.30
QCO	3.34	10.39	17.43	0.26	0.41	0.56	91.90	321.20	550.50
QIN	7.89	14.08	20.27	0.24	0.30	0.36	309.30	852.95	1396.60
RAC	11.14	13.32	15.49	0.23	0.27	0.31	90.60	136.70	182.80
SAS	10.38	20.53	30.68	0.20	0.25	0.31	583.40	1985.20	3387.00
SOF	11.16	19.39	27.61	0.17	0.23	0.29	395.60	1398.10	2400.60
TCA	5.63	7.54	9.45	0.30	0.45	0.59	17.10	29.70	42.30

Table S3: The results of pairwise comparisons between functional group classes for growth form, resprouting and regeneration strategies following principal components analysis (PCA) considering three leaf traits.

Growth Form	R^2	P
Large shrub vs. Liana	0.058	0.001
Large shrub vs. Shrub	0.139	0.001
Large shrub vs. Subshrub	0.377	0.001
Large shrub vs. Tree	0.034	0.001
Liana vs. Shrub	0.201	0.001
Liana vs. Subshrub	0.680	0.001
Liana vs. Tree	0.196	0.001
Shrub vs. Subshrub	0.309	0.001
Shrub vs. Tree	0.068	0.001
Subshrub vs. Tree	0.488	0.001
Regeneration Strategy		
R+P- vs. R+P+	0.173	0.001
R+P- vs. R-P+c	0.077	0.001
R+P- vs. R-P+s	0.161	0.001
R+P+ vs. R-P+c	0.801	0.001
R+P+ vs. R-P+s	0.254	0.001
R-P+c vs. R-P+s	0.087	0.001
Resprouting Ability		
Yes vs. No	0.120	0.001

Table S4: Specific leaf area, leaf thickness, and leaf area of species for each functional classification (growth form, resprouting ability, and regeneration strategy). Values are the mean and the standard error (in parenthesis). Data units are mm^2mg^{-1} for specific leaf area, mm for leaf thickness, and mm^2 for leaf area. *n* is the number of species for each functional group considered in analyses. *L. ratio* is the likelihood ratio estimated for the statistical comparison between a null model including the species as the random factor and the model with both the random and the fixed factor (i.e., growth form, regeneration strategy, or resprouting ability).

	Growth Form					Linear model	
Trait	**Liana**	**Tree**	**Large shrub**	**Shrub**	**Subshrub**	**L.Ratio**	**P**
Specific leaf area	15.0 (1.0)	7.0 (0.2)	9.4 (0.3)	6.8 (0.2)	7.3 (2.2)	11.5	0.0214
Leaf thickness	0.26 (0.01)	0.44 (0.01)	0.31 (0.00)	0.45 (0.01)	0.31 (0.01)	14.3	0.0065
Leaf area	1255.9 (146.8)	399.2 (44.2)	568.4 (36.3)	152.5 (10.9)	22.6 (3.1)	16.4	0.0025
n	1	6	16	10	5		

Trait	Regeneration Strategy					Linear model	
	R+P-	R+P+	R-P+c	R-P+s		L.Ratio	P
Specific leaf area	9.1 (0.2)	6.5 (0.5)	6.5 (0.2)	6.6 (0.1)		8.1	0.0449
Leaf thickness	0.32 (0.00)	0.32 (0.02)	0.57 (0.01)	0.39 (0.01)		21.9	0.0001
Leaf area	586.6 (32.1)	7.9 (1.1)	125.3 (5.5)	93.5 (6.3)		14.2	0.0027
n	21	2	2	5			

Trait	Resprouting Ability		Linear model	
	Yes	No	L.Ratio	P
Specific leaf area	8.6 (0.2)	6.6 (0.1)	5.9	0.015
Leaf thickness	0.35 (0.01)	0.44 (0.01)	9.0	0.0026
Leaf area	517.3 (28.1)	101.5 (5.0)	5.0	0.0252
n	25	7		

Table S5: Recorded number of individuals for each species for each vegetation type and their average leaf trait values used for calculating community-weighted means. Some trait values for some species were obtained from other sources: the BROT database (Tavşanoğlu and Pausas 2018; shown with Φ), Hacettepe University Functional Ecology Lab. data (Aktepe 2021; Coşgun 2022; shown with Ψ) and scientific papers (Merchant 1998; Specht et al. 1988; Liakoura et al. 2001, Elmas and Kutbay 2015) (shown with Ω). Data units are mm²mg⁻¹ for specific leaf area (*SLA*), mm for leaf thickness (*Lt*), and mm^2 for leaf area (*LA*).

Species	Vegetation Type					SLA	Lt	LA
	Semi-closed forest	Open forest	Closed shrubland	Open shrubland	Scrubland			
Arbutus andrachne	3	2	113	38	0	7.61	0.312	1752.45
Arbutus unedo	2	0	17	0	0	9.12	0.253	1754.52
Asparagus aphyllus	59	126	148	65	27	-	-	-
Asperula brevifolia	0	0	4	15	0	-	-	-

Calicotome villosa	1	38	29	35	5	15.84	0.231	29.31
Celtis australis	0	5	0	0	0	17.60Φ	-	100.00
Ceratonia siliqua	2	3	4	4	0	7.54	0.375	1242.80
Cistus creticus	399	544	351	210	351	7.42	0.400	129.56
Cistus parviflorus	0	13	0	248	0	6.12	0.620	146.40
Cistus salviifolius	931	824	473	1048	45	6.36	0.413	112.80
Cotinus coggygria	26	1	0	0	0	16.97	0.260	1170.35
Crataegus monogyna	1	0	0	9	4	14.23Ψ	-	117.80Ψ
Cupressus sempervirens	0	0	6	0	0	2.45Ψ	0.963Ψ	290.40Ψ
Cytisopsis pseudocytisus	17	37	0	0	0	10.18	0.381	32.09
Daphne gnidioides	6	12	0	111	12	14.14	0.278	86.29
Daphne sericea	1	0	4	0	0	5.46	0.316	340.72
Dittrichia viscosa	0	0	0	1	0	9.82Φ	-	53.36Φ
Erica manipuliflora	369	894	0	84	0	5.99	0.315	6.42
Euphorbia acanthothamnos	0	0	10	38	1	-	-	-
Genista acanthoclada	207	868	154	677	453	13.65Ψ	0.156	21.10Ψ
Hypericum empetrifolium	2	99	497	242	0	6.76	0.296	11.67
Juniperus oxycedrus	0	1	0	0	0	6.52Ψ	0.540Φ	19.70Ψ
Laurus nobilis	3	0	1	1	0	10.39	0.251	1984.72
Lavandula stoechas	175	125	0	26	29	6.57	0.280	12.43
Myrtus communis	13	4	0	5	0	13.60	0.280	301.64
Olea europaea	20	13	113	71	19	5.88	0.416	204.13
Origanum onites	0	5	1	51	38	8.50Ψ	-	9.50Ψ
Osyris alba	0	19	31	79	0	8.80	0.399	35.17
Paliurus spina-christi	4	27	0	0	0	23.39	0.185	515.51
Phillyrea latifolia	180	244	398	65	19	8.32	0.262	211.86
Phlomis grandiflora	0	0	14	63	0	5.22	0.647	657.14
Phlomis lycia	53	11	4	221	59	6.25	0.620	229.17
Pinus brutia	219	214	25	2	0	6.45	0.551	139.43
Pistacia lentiscus	40	28	91	86	6	5.81	0.428	240.36
Pistacia terebinthus	11	12	7	1	0	13.43	0.202	687.58
Populus nigra	1	0	0	0	0	10.60Φ	-	100.00
Ptilostemon chamaepeuce	0	6	15	1	9	5.95	0.442	99.01
Pyrus elaeagnifolia	9	0	0	14	31	11.98	0.274	384.41
Quercus aucheri	20	0	22	72	8	6.74	0.365	269.79
Quercus coccifera	97	100	149	227	25	6.64	0.374	249.50
Quercus infectoria subsp. *veneris*	43	41	13	3	0	13.01	0.281	805.01
Quercus ithaburensis	0	0	0	0	1	10.78	0.366	1459.93
Rhamnus punctata	0	7	0	0	7	10.41	0.247	83.27
Rubia tenuifolia	0	0	3	0	0	-	-	-
Ruscus aculeatus	5	11	49	0	0	12.97	0.264	134.70
Sarcopoterium spinosum	135	90	25	887	1755	11.91Ω	0.288Ω	72.50Ω

Satureja thymbra	0	56	0	6	0	2.95Ψ	0.354Ψ	61.09Ψ
Smilax aspera	19	31	102	2	0	19.92	0.244	1269.30
Spartium junceum	0	0	1	0	0	18.80	-	684.25 Ω
Styrax officinalis	71	2	0	11	0	19.08	0.235	1619.04
Teucrium chamaedrys subsp. *syspirense*	0	0	0	1	0	10.32Φ	-	30.54Φ
Teucrium polium	0	11	0	6	0	9.84Φ	0.310Φ	13.20Φ
Teucrium sandrasicum	0	2	0	0	0	-	-	-
Thymbra capitata	2	153	1	673	138	7.80	0.427	28.69

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Table S6: The results of pairwise comparisons between vegetation types following principal components analysis (PCA) considering three leaf traits.

Vegetation Type	R²	P
Open shrubland vs. Scrubland	0.234	0.001
Open shrubland vs. Closed shrubland	0.242	0.002
Open shrubland vs. Open forest	0.046	0.144
Open shrubland vs. Semi-closed forest	0.078	0.068
Scrubland vs. Closed shrubland	0.557	0.001
Scrubland vs. Open forest	0.091	0.042
Scrubland vs. Semi-closed forest	0.287	0.002
Closed shrubland vs. Open forest	0.209	0.003
Closed shrubland vs. Semi-closed forest	0.057	0.170
Open forest vs. Semi-closed forest	0.088	0.022

Table S7: Mean community weighted mean values for specific leaf area, leaf thickness, and leaf area of species for each vegetation type. Values in parentheses are the standard error of the mean. Data units are mm^2mg^{-1} for specific leaf area, mm for leaf thickness, and mm^2 for leaf area. *L.ratio* is the likelihood ratio estimated for the statistical comparison between a null model including the transect as the random factor and the model with both the random and the fixed factor (i.e., vegetation types).

Trait	Semi-closed forest	Open forest	Closed shrubland	Open shrubland	Scrubland	Linear model	
						L.Ratio	P
Specific leaf area	8.3 (0.4)	8.7 (0.3)	8.4 (0.3)	8.7 (0.3)	11.2 (0.2)	30.7	<0.0001
Leaf thickness	0.36 (0.01)	0.33 (0.04)	0.33 (0.00)	0.37 (0.01)	0.29 (0.01)	31.0	<0.0001
Leaf area	235.3 (67.1)	115.2 (16.3)	283.4 (44.1)	130.8 (18.5)	79.7 (3.8)	20.4	<0.0001

CHAPTER 4: RESISTANCE AND RESILIENCE TO FIRE AND CLIMATE CHANGE BASED ON FUNCTIONAL STRUCTURE OF WOODY PLANT COMMUNITIES IN MEDITERRANEAN VEGETATION*

Abstract

The Mediterranean Basin is one of the most threatened ecosystems by global change drivers such as major drought and frequent fires. It is very important to know the resilience and resistance responses of the communities to disturbances, and plant traits approach have been used frequently in such studies. We conducted fieldworks in 83 belt transects of 28 study sites for five vegetation types (semi-closed forest, open forest, closed shrubland, open shrubland and scrubland). We counted all mature individuals of woody species, measured cover and plant height of every individual, and collected leaf samples from 857 individuals of 38 species to calculate leaf area, leaf thickness and specific leaf area. As our aim was to reveal differences between resilience and resistance capacity levels of woody plant communities in Mediterranean vegetation, we selected related in total 17 plant traits for each capacity separately. For the absent trait values, we compiled from other databases and literature research. We performed community weighted mean (CMW) and principal component analysis (PCA) for abundance and cover data of individuals to analyze woody plant communities considering the positive or negative relationships of the selected plant traits to the resilience and resistance capacities. We found that open states are more resilient than closed states to fire and climate change both with abundance and cover data, however, there are no significant differences regarding to resistance capacities. On the other hand, according to cover data, the climate change resistance capacities are progressing from the highest to the lowest as forest-shrubland-scrubland, respectively. Our findings clearly shows for a trade-off between resilience and resistance capacities to fire and climate change. As a matter of fact, scrubland has the highest resilience, but the lowest resistance capacity to fire and climate change. We highlight our method as a robust novel approach to integrate resilience and resistance capacities of ecosystems in conservation and restoration planning considering disturbances such as fire and climate change.

Keywords: climate change, fire, functional traits, plant community, resilience, resistance, open and closed vegetation states, the Mediterranean Basin

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4.1. Introduction

Global change drivers are biotic and abiotic disturbances in the ecosystems as a result of human activities (Avolio et al., 2015). It is very important to know the factors that cause changes in plant species composition (Komatsu et al., 2019). Vegetation types alter over time as a result of anthropogenic global change drivers such as land-use, disturbance regime and climate changes (Franklin et al., 2016). Extreme climate conditions such as severe drought and anomalous temperatures affect plant compositions by triggering ecosystem disturbances (Breshears et al., 2005; Lloret & Granzow-de la Cerda, 2013; de la Riva et al., 2017). Global change drivers can also cause fire regime change. In fact, the effect of the fire regime altered by humans on vegetation dynamics overshadows even the effects of climate change (Avolio et al., 2015). Fire includes many biotic and socioeconomic drivers (Pausas & Keeley, 2014), is both an ecological force that shapes plant communities around the world (Bond & Keeley, 2005; Vilà-Cabrera et al., 2008) and has been instrumental in improving the specific adaptations in many plant species (Bond & Keeley, 2005). Mediterranean-type ecosystems have been under the influence of both anthropogenic and natural disturbances for centuries (Lavorel, 1999), and are the most risky type of the world due to the effects of climate change (Giorgi & Lionello, 2008; Enright et al., 2014). As a result of climate change, it has been recorded that especially major droughts (Cubash et al., 1996) and frequent fires (Lavorel, 1999) decrease the community stability and resilience capacities of plant composition structure in Mediterranean type ecosystems (Prieto et al., 2009; Doblas-Miranda et al., 2015; Liu et al., 2017).

Resilience and resistance are two main keys engaged how the ecosystem responses to disturbance events (Westman, 1978; de la Riva et al., 2017). Resilience is the capacity of an ecosystem, community, or species to return to the pre-disturbed situation (Potts et al., 2006; Bernhardt-Römermann et al., 2011; de la Riva et al., 2017). Resistance, on the other hand, is the capacity to remain unchanged despite the disturbance (Bernhardt-Römermann et al., 2011; Angeler & Allen, 2016). These processes cause changes in the community from time to time (Lloret et al., 2012) and help us to understand the damage severity and recovery capacities after disturbances (Paz et al., 2018). Understanding the changes in resilience (de Frutos et al., 2015) and resistance capacities in communities will guide us about the vulnerability of those communities after a disturbance event.

In recent years, functional trait approach has been used to predict the effects of global change on the plant communities (Lavorel & Garnier, 2022). Plant traits are successful in assessing the plant communities under environmental changes, as they represent characteristics such as resource use, habitat demands, and growth rates of plant species (Lavorel et al., 1997; Cornelissen et al., 2003; de Bello et al., 2013; Schellenberger Costa et al., 2017). Therefore, trait-based approach has been acknowledged as a powerful tool in community ecology (Wright et al., 2004; Wright et al., 2005; Kattge et al., 2011). It has even been reported that community ecology should be reconstructed through plant functional traits (McGill et al., 2006). Community weighted mean method, used recently on community ecology, reveals dominant trait values within the community (Garnier et al., 2004) helps us to understand the functional structure of the communities (de Bello et al., 2013) and plays an important role in trait-based ecology (Miller et al., 2018). Studies conducted on the community-weighted mean method in recent years indicate that weighting the average trait value of a species by taking account of its abundance in the community more clearly presents the ecosystem function when compared to functional diversity (Roscher et al., 2012; Cohen et al., 2014).

The effects of fire and climate change on the functional structure of communities has not been fully understood (de la Riva et al., 2017). The following studies have been conducted using different approaches; Pausas et al. (2004) used the resprouting ability and seed bank traits to examine crown-fire ecosystems against fire regime change, while Enright et al. (2014) expanded this assessment by adding the effects of climate change. In the study of de la Riva et al. (2017), community resistance and resilience to extreme climatic events were evaluated by taking account of some leaf, stem, root, seed and whole-plant traits. On the other hand, Bernhardt-Römermann et al. (2011) separated traits related to resilience (leaf dry matter content, specific leaf area and leaf anatomy) and resistance (leaf size and leaf distribution along the stem). Many studies evaluated the resistance and resilience capacity of plant communities to fire and climate change are based on approaches using only a few critical traits (Lavorel, 1999; Enright et al., 2014; Rodman et al., 2020). But, including more traits for such analyses would be a more robust approach to understand the potential response of plant communities to climate change and fire.

In this study, we aimed to examine the drivers of resilience and resistance capacities to fire and climate change in fire-prone Mediterranean woody vegetation. We ask the following specific question: Do woody plant communities in Mediterranean vegetation differ from each other at (1) climate change resilience, (2) climate change resistance, (3) fire resilience and (4) fire resistance capacity levels? Considering the functional differences among these vegetation types (Tüfekcioğlu & Tavşanoğlu, 2022a), we hypothesized that woody plant communities across fire-prone Mediterranean vegetation types (semi-closed forest, open forest, closed shrubland, open shrubland, and scrubland) should differ in resilience and resistance capacities to fire and climate change. We tested this hypothesis using a trait-based approach by measuring or compiling 17 plant traits related to resistance and resilience to fire and climate change. In this way, we compared the resilience and resistance capacities to fire and climate change in different fire-prone Mediterranean woody plant communities.

4.2. Material and Methods

4.2.1. Overview

In this study, we developed a new approach to reveal and compare resilience and resistance capacities to fire and climate change among different vegetation types (Figure 4.1). First, we selected 17 plant traits providing information regarding the resilience and resistance to fire and climate change (Table S1). On the one hand, we did assignment for selected plant traits to their effect (positive "1", neutral "0" and negative "-1") on resilience and resistance to fire and climate change with literature research, on the other hand, we collected and classified plant trait data of the species by conducting field studies in the Mediterranean vegetation, laboratory measurements and database research. We reclassified each species regarding to the positive or negative plant traits assignments and gathered trait average scores of each species for resilience and resistance to fire and climate change. As a result, we achieved to compare for each vegetation type by using community weighted mean (CWM) analysis.
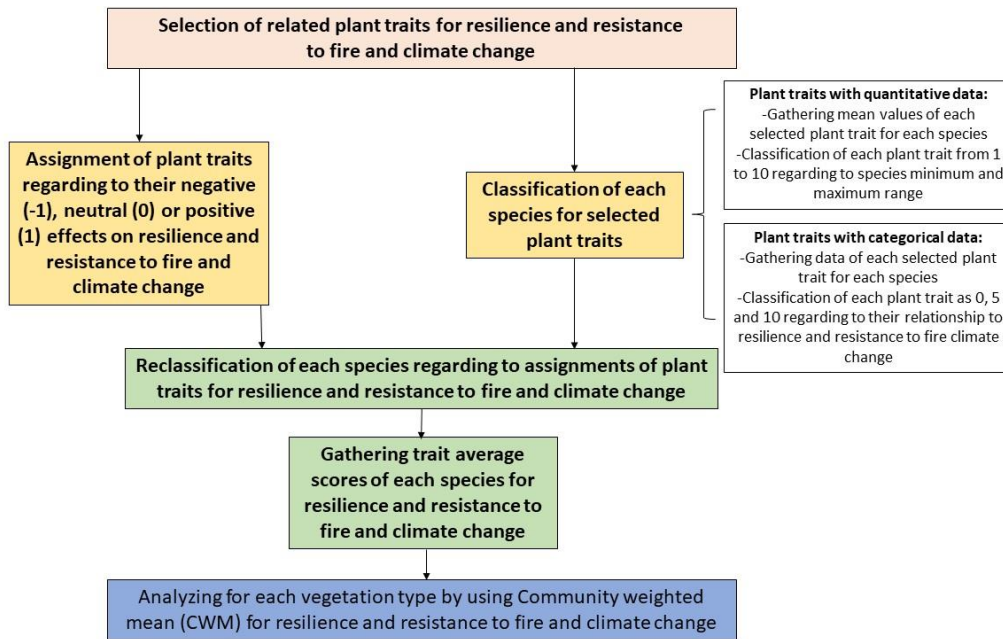
Figure 4.1. The method schema for the assessment of woody plant communities regarding to resilience and resistance capacities to fire and climate change.

4.2.2. Study Area and Sites

The study area was located in southwestern Anatolia (Turkey) eastern Mediterranean Basin (36.686° N, 27.362° E at the westernmost point and 36.835° N, 28.640° E at the easternmost point). The Mediterranean Basin is one of the biodiversity hotspots with a mosaic landscape structure due to the frequent occurrence of wildfires and various human activities (Myers et al., 2000). Moreover, southwestern Anatolia is of additional importance for biodiversity as it served as refugium for biodiversity during the Pleistocene glacial periods (Médail & Quézel, 1997). Dominating vegetation of the study area was maquis shrublands and Turkish red pine (*Pinus brutia* Ten.) forests. These woody-dominated vegetations were found at different openness states, both as open (open forests, open shrublands, and scrublands) and closed habitats (semi-closed forests and closed shrublands) (Tüfekcioğlu & Tavşanoğlu, 2022a).

We focused on five vegetation types dominating the study area: semi-closed forest, open forest, closed shrubland, open shrubland, and scrubland. We used digitalized forest management plans and maps obtained from the General Directorate of Forestry of Turkey. We also considered the accessibility, past forestry activities and wildfire history of the study sites, as we wanted to stabilize conditions of the study sites with each other.

As a result of this information and interviews with local foresters, we selected 28 study sites one ha in size. As the coverage of the target vegetation types in the study area varied, we selected different number of study sites for each vegetation type according to their relative coverage in the study area. Accordingly, we performed field studies in 6 semi-closed forests, 8 open forests, 4 closed shrublands, 6 open shrublands, and 4 scrublands.

4.2.3. Field Measurements and Counts

We conducted field measurements and counts in the dry period of the region, i.e. between May and September of 2019, and only in September of 2020 due to COVID-19 mobility restrictions. In each study site, we conducted our research within three belt transects 10 × 40 m (400 m²) in size. Because of topography, one transect in a study area was missing and 13 belt transects were established at the size of 10 × 30 m (300 m²). In such cases, we calculated studied variables by considering the size of the transect. In total, we sampled 83 belt transects. In each belt transect, we counted all mature individuals of woody species. We also calculated their canopy cover (hereafter, cover) by measuring two perpendicular diameter lengths and using the average value as the diameter of each individual. When possible, we identified plant species in the field, but in some cases we took samples to identify them in the herbarium (Hacettepe University herbarium, HUB). In the study, the nomenclature follows the Turkish flora book (Davis, 1965-1985) and The Plant List (2013) for the updated taxonomy for some taxa.

We collected data for four plant traits in the field: Maximum plant height (hereafter, height), specific leaf area (hereafter, SLA), one-sided projected surface area of a leaf (hereafter, leaf area), and leaf thickness. We measured height of every individual we observed in transects using a tape measure, but for the database, we considered the maximum value we obtained for each plant species in the study area. For SLA, leaf area, and leaf thickness, we collected leaf samples from 857 individuals of 38 species in the field (709 individuals of 37 species in 2019 and 148 individuals of 23 species in 2020). We collected ten healthy-looking leaves from plant individuals in good conditions and wrapped them immediately in moist papers. Then we put the sample in a plastic bag and blow into it to prevent the leaves from getting dehydrated and minimize the water loss. We stored plastic bags including leaf samples in a cool box, and completed leaf area and thickness measurements within 24 h (Pérez-Harguindeguy et al., 2013).

4.2.4. Laboratory Measurements

We scanned leaves from each individual to digitalize leaf samples for further analyses. Next, we measured their leaf thickness by using a digital micrometer. Finally, we dried the leaf samples of each individual in separate metal sample containers in a temperature-controlled oven at 70°C for 72 h (Pérez-Harguindeguy et al., 2013). We weighted oven-dried leaves using a digital scale to obtain dry weight of leaves for each individual. We calculated the leaf area from the scanned leaf images using ImageJ program (Rasband, 2012). At last, we calculated the SLA value by dividing the average leaf area value by the total dry weight for each individual.

4.2.5. Classification of Each Species for Selected Plant Traits

In addition to trait data on four plant traits we obtained from our field and laboratory works (see previous sections above), we compiled other plant trait data from the BROT database (Paula et al., 2009; Tavşanoğlu & Pausas, 2018), Hacettepe University Functional Ecology Laboratory databases (Aktepe, 2021; Çoşgun, 2022), and relevant published materials (Specht et al. 1988; Merchant, 1998; Liakoura et al., 2001; Elmas & Kutbay, 2015).

We averaged the value of traits with quantitative data, thus we only used one plant trait value for each species, i.e., only one SLA value for a species. Following that, we categorized mean value in several classes from 1 to 10 according to the minimum and maximum range of the average trait values of each species (Table S1). We made this process for traits with continuous data structure, namely SLA, leaf area, leaf thickness, height, mass-based leaf nitrogen content (hereafter: LNCm), seed mass, wood density, leaf dry matter content (hereafter: LDMC), leaf lifespan, coarse:fine fuel ratio (hereafter: CCF), and dead:fine fuel proportion (hereafter: DFF). Since the difference between minimum and maximum values in height and seed mass traits is very high, we used logarithmic values with base 10 for the classification (Table S2).

We classified traits with semi-quantitative or categorical data into two (0 or 10) or three classes (0, 5, or 10). We made this process for bark thickness, seed bank, leaf phenology,

leaf shape, resprouting ability, and post-fire seedling emergence (Table S3). In the bark thickness trait, we classified the species with a thin bark with 0, but those with moderate and thick ones were classified as five and ten, respectively. In the leaf phenology classification, winter deciduous, evergreen, and winter semi-deciduous species were graded by 0, but 10 were assigned to drought semi-deciduous species. For leaf shape, species with broad and linear leaves were classified with 0 and 5, respectively, while species with scale-like or needle-like leaves with 10 (Table S3).

Dissimilar to other categorical traits, we evaluated resprouting ability, seed bank, and post-fire seedling emergence as combined traits consisting of several traits. By combining several traits with the same function for our main questions (climate change and fire) into one trait, we decrease the number of missing cells for species in these traits. Specifically, by following the relevant traits in the BROT database (Tavşanoğlu and Pausas, 2018), we combined three traits regarding resprouting capacity (after fire, after disturbances, and after clipping) into a new trait named "Resprouting ability", and two traits regarding seed bank presence (canopy and soil seed bank) into the trait "Seed bank". The former trait was used both for a proxy of climate change and fire resilience, while the latter was only used for climate change resilience to prevent redundancy with the "post-fire seedling emergence" trait that also includes seed bank trait data (see below for further explanation).

In the case of "post-fire seedling emergence" trait in our study, we combined several traits regarding seed bank presence and the germination and seedling emergence after fires in the BROT database (Tavşanoğlu and Pausas, 2018). These traits were "chemical germination cues" (i.e. smoke- or nitrate-stimulated germination), "heat-stimulated germination", "canopy seed bank", "soil seed bank", and "post-fire seedling emergence". We considered the new "post-fire seedling emergence" trait only for fire resilience, but not for climate change resilience to prevent redundant data use (see above). In order to balance the weight of these three traits in resilience calculations for the plant community, we classified 7 for obligate seeders (non-resprouters, only seeders) and 10 for obligate resprouters (non-seeders, only resprouters). This difference in classes between resprouters and seeders was because the presence of higher risks of establishment of seedlings than resprouts due to stochastic events preventing successful germination and seedling survival such as seed predation, weather conditions, and herbivory effects (Parra

and Moreno, 2017). Accordingly, for facultative resprouters (both resprouter and seeder), we classified 7 for each trait, therefore the total score of these species became 14. Finally, species with variable post-fire seedling emergence, we gave them 3.5 (half of seven) (Table S3).

4.2.6. Assignment of Plant Traits Regarding Their Effects to Resilience and Resistance to Fire and Climate Change

In this study, we defined resilience as the recovery capacity of species after a disturbance (Potts et al., 2006; Bernhardt-Römermann et al., 2011; de la Riva et al., 2017), and resistance as the withstand capacity of species both to fire and climate change (Bernhardt-Römermann et al., 2011; Angeler & Allen, 2016). Based on the evidence regarding the effects of each plant trait to resistance and resilience to fire and climate change (Table S1), we selected five traits for the climate change resilience, 11 for the climate change resistance, five for the fire resilience, and seven for the fire resistance. We assigned plus or minus signs (or zero) to each trait to indicate its negative, neutral, or positive effect on the resilience and resistance capacity in relation to fire and climate change (Table S1). For example; since the lower SLA value is known to allow more resistance to drought conditions (Kühn et al., 2021), we considered that the climate change resistance capacity has a negative correlation with SLA. Similarly, as species with resprouting ability has an advantageous in post-fire recovery (Tavşanoğlu & Gürkan, 2014), the fire resilience capacity considered positively related with resprouting ability trait.

4.2.7. Reclassification and Gathering Trait Average Score of Each Species Regarding to Assignments of Plant Traits

To prepare four main datasets (resilience and resistance to fire and climate change), we reclassified species regarding to positive or negative assignments of plant traits for resilience and resistance to fire and climate change. As example, for resistance to climate change assessment, since SLA has a negative relationship with it, we classified species in reverse way (from 10 to 1), which means the species with lower SLA values had higher class for climate change resistance. On the other hand, for resilience to fire assessment, since resprouting ability has a positive relationship with it, we left the classification as before (from 1 to 10).

Finally, within each dataset, we averaged the trait classes of each species. Thus, we obtained the average score for each species for that dataset (Table S4). However, we followed a different weighting calculation of the fire resilience capacity of species, as we considered that some of the traits have more contribution to the resilience to fire. Thus, the species' scores for LNCm, seed mass, and LDMC traits were multiplied by 0.5, but those of the resprouting ability and seedling emergence trait values considered as they were when calculating the overall fire resilience score of the species.

4.2.8. Data Analysis

We calculated community weighted mean (CWM) by weighting values of resilience and resistance capacities to fire and climate change with the abundance and cover of species for each transect (i.e., plant community) (Garnier et al., 2004). In this analysis, we used the average scores of species four main datasets (mentioned above) with their abundance and cover data sampled within the belt transects. We implemented linear mixed effects models (LME) for each resilience and resistance capacities to fire and climate change (i.e., resilience to climate change, resilience to fire, resistance to climate change, and resistance to fire) for vegetation types. In these models, the vegetation type and transect were considered as the fixed and random factors, respectively. Following LME analysis, we made multiple comparisons by estimating marginal mean for different vegetation types and calculated the mean and standard error of resilience and resistance capacities to fire and climate change for each vegetation type's abundance and cover community weighted mean values.

We also performed principal components analysis (PCA) including resilience and resistance capacities to fire and climate change in the study to present differences between vegetation types regarding resilience and resistance capacities to fire and climate change. In order to better understand the resilience and resistance capacity differences of open and closed habitats to fire and climate change, we calculated the coefficient of variation on community weighted mean (CWM) data at open and closed habitat level. Finally, we compared resilience and resistance capacities of climate change and fire separately for each vegetation type. We used community weighted mean values of resilience to climate change, resilience to fire, resistance to climate change, and resistance to fire for

abundance and cover data. We performed linear regression and added straight line to scatter plot of fire and climate change.

All the analyses were conducted in the R environment (R Core Team, 2021). We used *dplyr* package (Wickham, 2014) in the community weighted mean analysis, *nlme* package (Pinheiro & Bates, 2000) for *lme* function in linear mixed model analysis, *vegan* package (Oksanen et al., 2019) for *prcomp* and *pairwise.adonis* functions in the PCA and pairwise multilevel comparison analyses, and *emmeans* package (Lenth, 2020) for *emmeans* functions in statistical comparison.

4.3. Results

As a result of the CWM analysis among vegetation types, scrubland was one of the most prominent classes. On one hand, scrubland was the most resilient vegetation type to fire and climate change, on the other hand, the least resistant one (according to both abundance and cover analysis) (Figure 4.2, Figure 4.3, Table S5). As stated Tüfekcioğlu and Tavşanoğlu (2022a), *Sarcopoterium spinosum* dominated the scrubland, and the resilience score of this species (its climate change score was 6 and the min-max values were 0 and 7.3, its fire score was 5.8 and the min-max values were 0 and 10) was above the average, while its resistance score (its climate change score was 5 and the min-max values were 0 and 10, its fire score was 2.3 and the min-max values were 0 and 8.2) was below the average (Table S4). Besides that, semi-closed forest was the most resistant and closed shrubland was the least resilient vegetation type to both fire and climate change (Figure 4.2, Figure 4.3, Table S5).
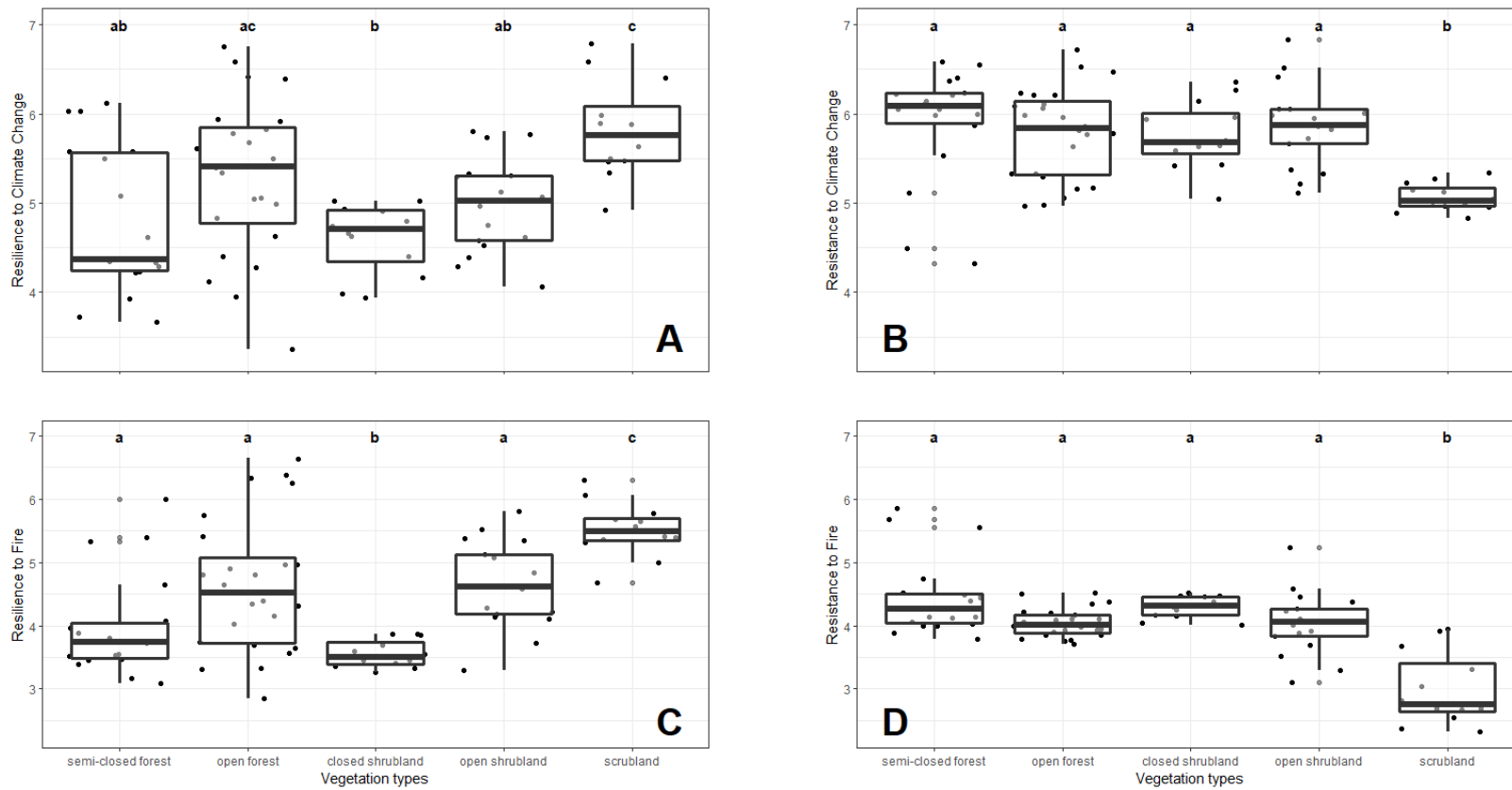
Figure 4.2. Resilience (a) and resistance (b) capacity to climate change and resilience (c) and resistance (d) capacity to fire by using community weighted mean calculation analysis on individual abundance data of each belt transect. Letters above indicate statistical test results as having different letters means significant difference between two groups (P > 0.05).
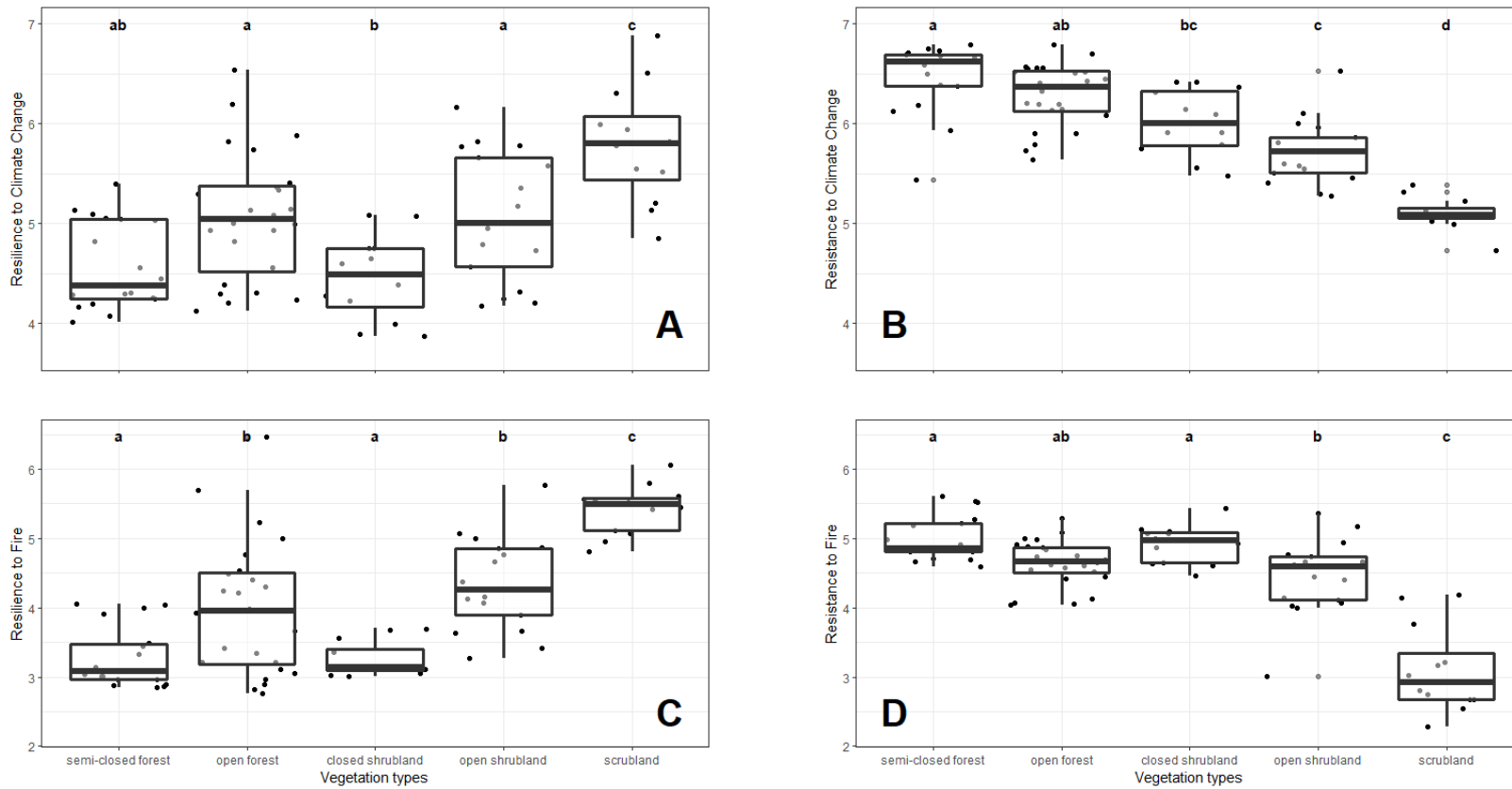
Figure 4.3. Resilience (a) and resistance (b) capacity to climate change and resilience (c) and resistance (d) capacity to fire by using community weighted mean calculation analysis on individual cover data of each belt transect. Letters above indicate statistical test results as having different letters means significant difference between two groups (P > 0.05).

Open habitats (open forest and open shrubland) were relatively close to each other according to result of the abundance data. Compared to the scrubland, they were less resilient and more resistant to fire and climate change (Figure 4.2, Table S5). Considering of the cover data, open habitats were much more resilient to fire and climate change than closed habitats (semi-closed forest and closed shrubland). The highest difference was in fire resilience capacity: 11.4 closed habitats and 21.1 open habitats (Table S8). On the other hand, resistance capacity to climate change started from the highest and went in the order of semi-closed forest, open forest, closed shrubland and open shrubland. This order in fire resistance capacity did not seem so sharp (Figure 4.3).

PCA results (Figure 4.4, R^2=0.29 and R^2=0.53, respectively, both P = 0.001) showed that 82.6% (abundance data) and 86.9% (cover data) of the total variation were represented with the first (PC1) and second (PC2) principal components. However, The PC1 values of both corresponded to the greater variability; 57.4% for abundance and 73.1% for cover data. In both analyzes, resilience capacities to fire and climate change were positively related to PC1, while resistance capacities were negatively contributed. The biggest difference of vegetation types was between scrubland and other types (Table S7). On the other hand, open forest was close to semi-closed forest and closed shrubland, but there was still a difference between semi-closed forest and closed shrubland (Table S7).

There was a negatively relationship between resilience and resistance capacities of fire and climate change; vegetation types with high resilience capacities demonstrate low resistance, where those with high resistance capacities showed low resilient character (Figure 4.5, Figure S2, Table S9). Besides that, this analysis once again revealed that capacities of semi-closed forest and scrubland types were completely opposite; the semi-closed forest class had low resilience but high resistance capacity, on the other hand while scrubland's resilience capacity was high, its resistance capacity was low.
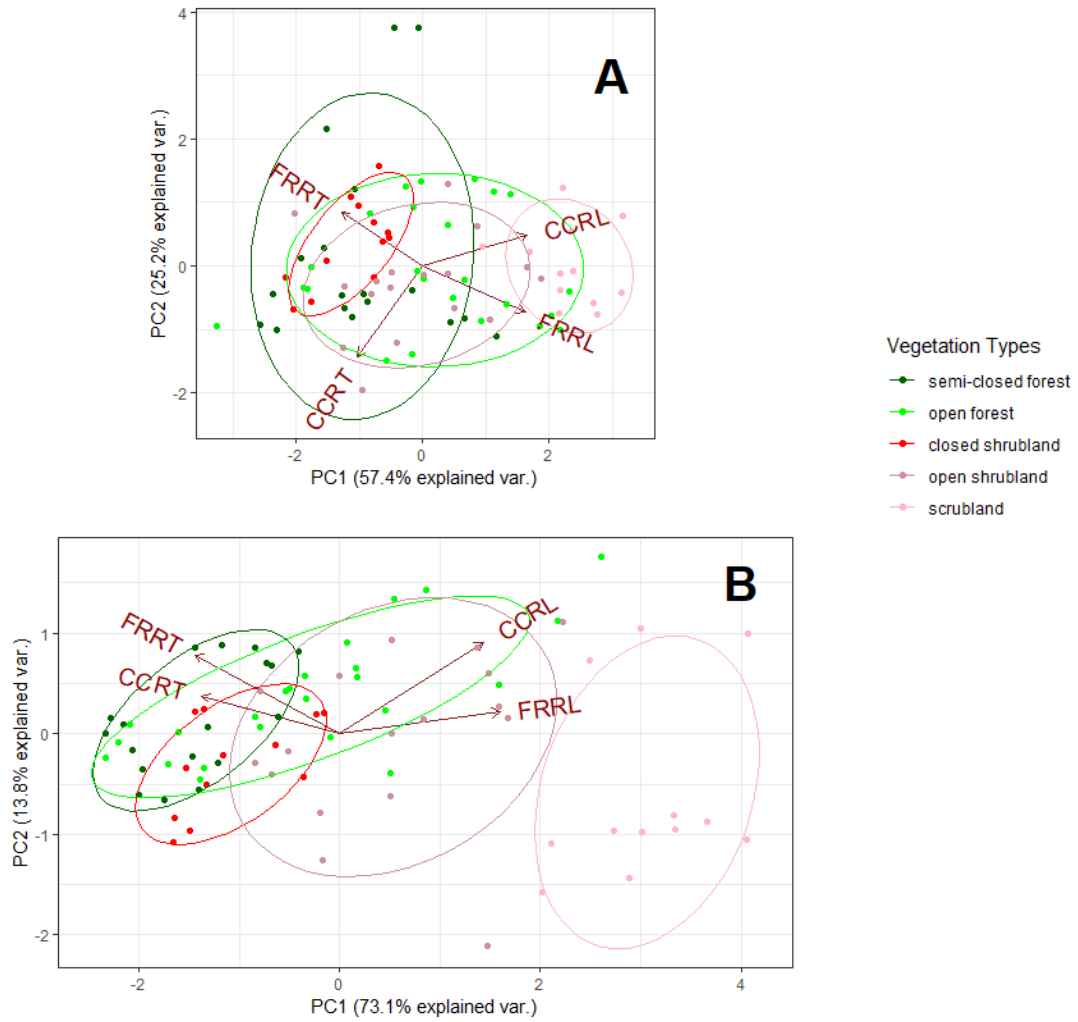
Figure 4.4. PCA analysis for resilience and resistance capacity to fire and climate change by using community weighted mean calculation analysis on individual abundance (a) and cover (b) data of each belt transect (CCRL: Climate Change Resilience, CCRT: Climate Change Resistance, FRRL: Fire Resilience, FRRT: Fire Resistance).
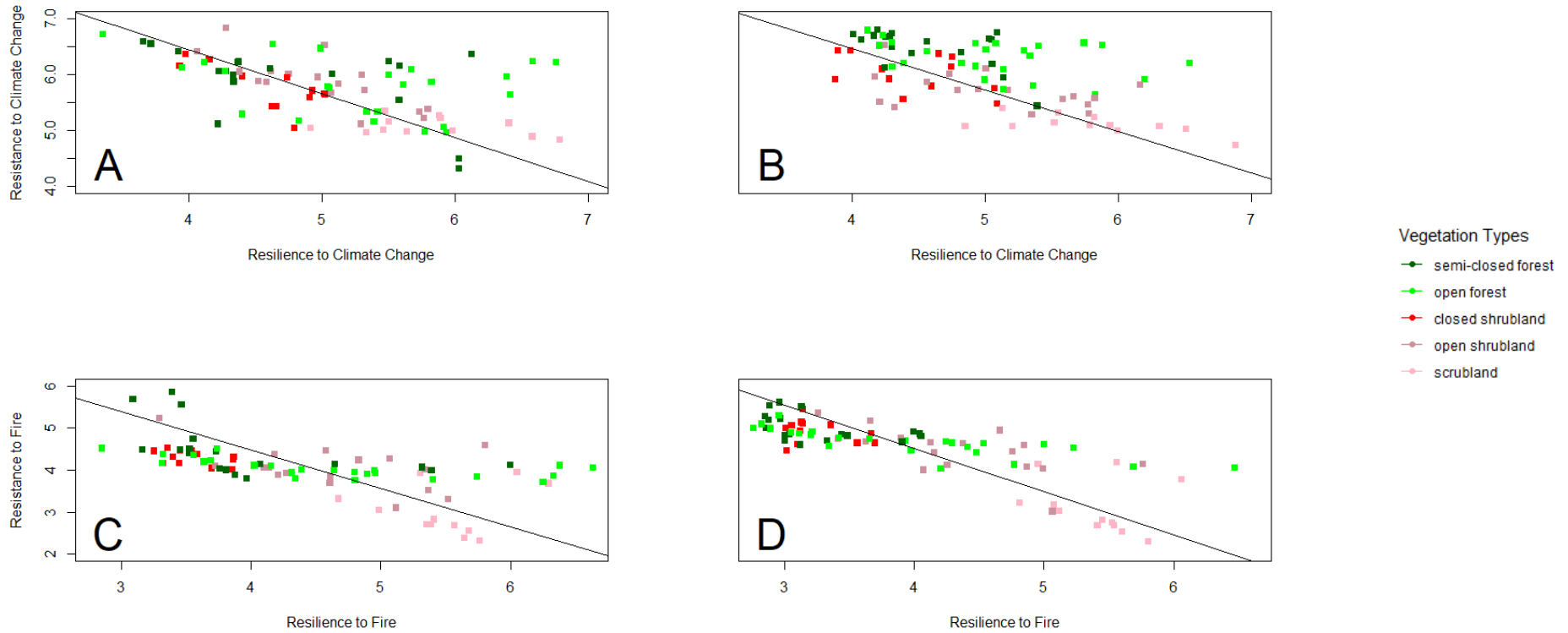
Figure 4.5. The association between resilience and resistance capacity of plant communities to climate change (A, B) and fire (C, D). Values are community weighted means, and different colors refer to different vegetation types. Fitted lines represent the models encapsulating all data. Graphs A and C made using abundance data, while B and D using cover data.

4.4. Discussion

Our results provide new insights that open habitats (open forest and open shrubland) are more resilient than closed habitats (semi-closed forest and closed shrubland) to fire and climate change. PCA analysis results shows that open habitats are positively correlated with PC1 and in line with resilience (CCRL and FRRL) loadings. Besides that, variations in open habitats are more common in resilience analyzes, indicating that heterogeneity is also higher in open habitats. Heterogeneity is an important feature for the resilience capacity of the dynamic structures of complex systems, and silvicultural activities implemented in recent years have been developed to increase heterogeneity (Filotas et al., 2014). As stated by Tüfekcioğlu and Tavşanoğlu (2022a), since open habitats are clearly separated from closed habitats, they should be treated as separate habitat type. Increasing heat waves and wildfires as a result of global change, afforestation implementations and pressure to convert open habitats to forests are also intensified globally (Pausas & Bond, 2020). This management type is realized by transforming open habitats into Turkish red pine (*Pinus brutia*) forests in Mediterranean forestry (Saatçioğlu, 1952). Both the heterogeneity structure and resilience capacity of open habitats with high recovery capacity to fire and climate change are endamaged. Therefore, the ecological importance of open habitats should be highlighted and an integrated approach should be followed on development and implementation strategies in forest management plans.

There is no significant difference on the resistance capacity to fire and climate change between open and closed habitats. Each Mediterranean species has its own flammability character and strategy (Aktepe & Tavşanoğlu, under evaluation), however, the diversity of the resistance scores of species to fire eliminates the difference between plant communities. On the other hand, according to the analysis of the resistance capacity to climate change with the cover data, the forest-shrubland-scrubland ranking from the highest to the lowest stands out. The most important factor determining this result is *Pinus brutia* coverage. As a matter of fact, *P. brutia*'s resistance score to climate change is 7 out of 10 and is one of the resistant species in Mediterranean type ecosystems, because of its thick bark, needle-like leaf shape and high LDMC value (Table S4). Therefore, implementations that will affect the *P. brutia* coverage should be avoided by considering these results in ecosystems where resistance to climate change will be managed.

Our results clearly indicate to a trade-off between resilience and resistance capacities to fire and climate change. Consequently, among the vegetation types we have evaluated, there is no type that stands out with its feature of being both resilient and resistant. Scrubland is the best example supporting this view, as this vegetation type has, by far, the highest resilience but the lowest resistance capacity. Scrubland differs from the forest and shrubland vegetation types in many aspects (Tüfekcioğlu & Tavşanoğlu, 2022a; Tüfekcioğlu & Tavşanoğlu, 2022b) and our results add new evidence to this theory. In Mediterranean-type ecosystems, where the effects of global changes will be most severe, the scrubland which is resilient against severe droughts and fires, is more advantageous than other types regarding to recovery. Scrubland, which is generally transformed into agricultural land and used for grazing activities, should be considered as an important vegetation type considering its resilience capacity for disturbances.

Knowing the resilience and resistance capacities of different vegetation types to fire and climate change is an increasingly important question. Only a few functional traits have been used in studies on this subject, and generally, traits such as resprouting and seed bank have been evaluated (Pausas et al., 2004; Enright et al., 2014). Although resilience and resistance are two closely related definitions that reveal the response of the ecosystem to disturbances, the resistance capacity describes during the disturbance and the resilience capacity after the disturbance. Indeed, Bernhardt-Römermann et al. (2011) uses separate traits for resilience and resistance evaluations, however, it has not been discussed as comprehensively as it was done in this study so far. As Mediterranean ecosystems are under threat of disturbances such as climate change (Enright et al., 2014), major droughts (Cubash et al., 1996) and frequent fires (Lavorel, 1999), determining which traits are important in terms of global change has an important role in planning of protection and restoration implementations (Kühn et al., 2021). Therefore, we highlight that this study produces a robust and novel approach by using several traits for each situation, i.e. resilience to climate change, resistance to climate change, resilience to fire and resistance to fire (Figure 1). Besides that, we argue that this method can also be used to test the responses of other ecosystems to global changes. Indeed, consistency over the space and time of some traits such as SLA (Garnier et al., 2001) is a great advantage to integrate trait assignments into future scenarios on climate, fire, drought or land use change. Using this method will be enlightening to consider the resilient and resistant capacities of vegetation types worldwide.

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Supplementary Material to the Chapter 4

Table S1. Assignments of each plant trait to its negative, neutral, or positive effect on the resilience (RL) and resistance (RT) capacity to fire and climate change. Information on units, definitions and categories of traits are obtained from the study of Pérez-Harguindeguy et al. (2013), and Tavşanoğlu and Pausas (2018).

Trait	Units	Definition	Categories	Climate Change		Fire		References
				RL	RT	RL	RT	
Bark thickness	-	Average bark thickness of the main stem of woody species, for trees at the breast height level	●thin (< =2 mm) ●moderate (2-15 mm) ●thick (>15 mm)	0	1	0	1	Cornelissen et al., 2003 Pérez-Harguindeguy et al., 2013 Schubert et al., 2016
Basic leaf shape	-	Shape of a leaf	●broad ●linear ●scale-like ●needle-like	0	1	0	0	Williams, 2014
Dead:fine fuel proportion (DFF)	%	Proportion of fine dead biomass on the plant	-	0	0	0	-1	Aktepe, 2021
Coarse:fine fuel ratio (CCF)	ratio	Coarse ratio for fine fuel biomass ratio, including live and dead material	-	0	0	0	1	Aktepe, 2021
Leaf area	mm²	Average leaf area of its one-sided projected surface	-	0	-1	0	1	Cornelissen et al., 2003 Frenette-Dussault et al., 2013 Gaüzère et al., 2020 Ingrisch et al., 2018 Kenzo et al., 2015 Pérez-Harguindeguy et al., 2013 Ribeiro et al., 2022
Leaf dry matter content (LDMC)	mg·g⁻¹	The ratio of the oven-dry mass of a leaf to its water saturated fresh mass	-	-1	1	-1	-1	Aktepe, 2021 Bernhardt-Römermann et al., 2011 Blumenthal et al., 2020 Cornelissen et al., 2003 de la Riva et al., 2017

								Frenette-Dussault et al., 2013 Gaüzère et al., 2020 Gillison, 2019 Pérez-Harguindeguy et al., 2013 Saura-Mass et al., 2009 Wilson et al., 1999
Leaf lifespan	months	Average maximum time period of a leaf is alive and active	-	0	1	0	0	Cornelissen et al., 2003 Pérez-Harguindeguy et al., 2013 Reich, 2014
Leaf phenology	-	Only for woody species, phenology of a leaf (*Valid only for drought semi-deciduous species.*)	●winter deciduous ●evergreen ●winter semi-deciduous ●drought semi-deciduous	0	1*	0	0	Cornelissen et al., 2003 Oliveira et al., 2021 Reich, 2014 Ribeiro et al., 2022
Leaf thickness	mm	Thickness of the lamina of a leaf	-	0	1	0	1	Aktepe, 2021 Blumenthal et al., 2020 Pérez-Harguindeguy et al., 2013 Ribeiro et al., 2022
Mass-based leaf nitrogen content (LNCm)	mg·g⁻¹	The ratio of the nitrogen content of a leaf to its dry mass	-	1	-1	1	0	Frenette-Dussault et al., 2013 Gillison, 2019 Kenzo et al., 2015 Ma et al., 2020 Pérez-Harguindeguy et al., 2013 Reich, 2014 Saura-Mass et al., 2009
Maximum height	cm	The maximum height of a plant except extreme conditions	-	0	-1	0	0	Cornelissen et al., 2003 Frenette-Dussault et al., 2013 Kenzo et al., 2015 Kühn et al., 2021 Ma et al., 2020 Pérez-Harguindeguy et al., 2013
Post-fire seedling emergence	-	The following three factors were evaluated together: ●Presence of the stored seeds whether in canopy or soil	●yes ●variable ●no	0	0	1	0	David et al., 2018 del Cacho & Lloret, 2011 Figueroa et al., 2004

		●Average density of seedlings and proportion of seedlings surviving during the first year after fire ●Chemical and heat-stimulated germination						
Resprouting ability	-	Resprouting ability after fire	●yes ●variable ●no	1	0	1	0	Cornelissen et al., 2003 Kühn et al., 2021 Williams, 2014
Seed bank	-	Presence of the stored seeds whether in canopy or soil	●yes ●variable ●no	1	0	0	0	David et al., 2018 del Cacho & Lloret, 2011 Figueroa et al., 2004
Seed dry mass	mg	Average mass of a dry seed	-	1	0	-1	0	Cornelissen et al., 2003 de la Riva et al., 2017 Frenette-Dussault et al., 2013 Pérez-Harguindeguy et al., 2013 Tavşanoğlu & Çatav, 2012 Williams, 2014
Specific Leaf Area (SLA)	mm²·mg⁻¹	The ratio of the one-sided area of a fresh leaf to its oven-dry mass	-	0	-1	0	-1	Aktepe, 2021 Blumenthal et al., 2020 Cornelissen et al., 2003 de la Riva et al., 2017 Gaüzère et al., 2020 Gillison, 2019 Kühn et al., 2021 Frenette-Dussault et al., 2013 Ma et al., 2020 Pérez-Harguindeguy et al., 2013 Reich, 2014 Ribeiro et al., 2022 Saura-Mass et al., 2009 Wilson et al., 1999
Wood density	g·cm⁻³	The ratio of the oven-dry mass of a wood to its water mass of its green volume	-	0	1	0	0	Frenette-Dussault et al., 2013 Gillison, 2019 Kühn et al., 2021 Reich, 2014 Ribeiro et al., 2022

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Table S2. Mean values (m) and classes (c) of each plant species for plant traits with quantitative data. Since the difference between minimum and maximum values in height and seed mass traits is very high, we used logarithmic values with base 10 for the classification, however mean values of them are shown in the table. Plant traits without any data are left blank. The scientific names of species are given in the Supplementary Table 4.

Species / Plant Traits	Dead: fine fuel proportion (DFF)		Coarse: fine fuel ratio (CCF)		Leaf area		Leaf dry matter content (LDMC)		Leaf lifespan		Leaf thickness		Mass-based leaf nitrogen content (LNCm)		Max. Height		Seed dry mass		Specific leaf area (SLA)		Wood density	
	m	c	m	c	m	c	m	c	m	c	m	c	m	c	m	c	m	c	m	c	m	c
AAN	4.6	3.3	7	4.6	1752.5	9	669.7	10	2.6	1	0.3	2			300	6	1.6	4	7.6	3	0.6	7
AAP	28.3	0	1	28.3											75	4	19.3	6				
ABR															64	3						
AUN	2.1	3.7	8	2.1	1754.5	9	422.2	5	13.3	4	0.3	2	13.7	2	306	6	2.7	4	9.1	4	0.7	7
CAU									7.5	2			27.0	10	82	3	125.0	8	17.6	8	0.7	7
CCO					1170.6	6					0.3	2			229	6			17.0	7	0.5	5
CCR	12.7	0.9	2	12.7	129.6	1	363.4	4	6.3	2	0.4	4			75	6	0.6	3	7.4	3		
CMO	1.2	0.5	1	1.2	117.8	1	327.7	3	5.4	1			17.3	4	355	7	71.1	7	14.2	6	0.7	8
CPA					146.4	1					0.6	6			59	3	0.6	3	6.1	2	0.8	10
CPS					32.1	1					0.4	3			59	2			10.2	4		
CSA	14.8	0.6	2	14.8	112.8	1	562.2	8			0.4	4	13.4	2	77	7	1.0	3	6.4	2	0.7	8
CSE					290.4	2	470.8	6			1.0	10			332	7			2.5	1	0.6	5
CSI					1242.8	7			23.3	7	0.4	3			243	5	175. 6	8	7.5	3	0.6	6
CVI					29.3	1	393.7	5			0.2	1			188	6	6.0	5	15.8	7	0.6	6
DGN	7.1	2.8	6	7.1	86.3	1	538.7	8			0.3	2			97	4	16. 7	6	14.1	6		
DSE					340.7	2					0.3	2			314	5			5.5	2		
DVI					53.4	1	235.1	1							94	2	0.3	2	9.8	4		
EAC															85	4						
EMA					6.4	1					0.3	2			133	6			6.0	2		
GAC	17.1	1.4	3	17.1	21.1	1	318.2	3			0.2	1			83	5			13.7	6		
HEM	5.5	0.3	1	5.5	11.7	1	389.6	5			0.3	2			86	4	0.1	1	6.8	3		
JOX	1.9	2.0	4	1.9	19.7	1	498.4	7	21.2	7			11.7	1	115	3	25.5	6	6.5	2	0.6	7

LNO	1.6	3.6	8	1.6	1984.7	10	533.2	8			0.3	2			168	5	586.2	9	10.4	4	0.5	3
LST	22.4	0.1	1	22.4	12.4	1					0.3	2			72	4	0.7	3	6.6	2	0.7	7
MCO	6.0	2.1	5	6.0	301.6	2	621.3	9	20.1	6	0.3	2			146	4	5.6	5	13.6	6	0.6	6
OAL	15.1	0.1	1	15.1	35.2	1	374.2	4			0.4	4	16.4	4	53	4	99.0	7	8.8	4		
OEU	1.4	0.9	2	1.4	204.1	1	464.8	6	26.6	8	0.4	4	15.7	3	268	8	232.0	8	5.9	2	0.8	9
OON	43.9	0.4	1	43.9	9.5	1	313.9	3							71	3	0.1	1	8.5	3		
PBR		1.6	4		139.4	1	561.6	8			0.6	5			1232	10	49.3	7	6.4	2	0.5	3
PCH					99.0	1					0.4	4			108	4	12.1	6	6.0	2	0.7	8
PEL					384.4	2					0.3	2			203	6			12.0	5		
PGR	3.6	5.0	10	3.6	657.1	4	277.7	2			0.7	7			78	3	5.8	5	5.2	2		
PLA	4.8	2.0	4	4.8	211.9	2	669.4	10	33.3	10	0.3	2	12.5	1	220	7	37.9	7	8.3	3	0.7	8
PLE	5.9	2.3	5	5.9	240.4	2	446.4	6	20.9	6	0.4	4	14.0	2	182	6	15.7	6	5.8	2	0.8	10
PLY	19.4	2.8	6	19.4	229.2	2					0.6	6			76	6			6.3	2		
PNI									7.4	2			22.8	8	485	6			10.6	4	0.4	2
PSP					515.5	3					0.2	1			344	8	21.4	6	23.4	10		
PTE	3.4	3.8	8	3.4	687.6	4	467.8	6	5.9	2	0.2	1	19.8	6	228	5	29.9	6	13.4	6	0.8	10
QAU					269.8	2	534.1	8			0.4	3			278	8			6.7	3		
QCO	6.8	2.4	5	6.8	249.5	2	278.5	2	15.1	5	0.4	3	14.9	3	220	7	2334.4	10	6.6	3		
QIN					805.0	5	487.7	7			0.3	2			223	6			13.0	6		
QIT					1459.9	8	502.3	7			0.4	3			240	4			10.8	4		
RAC					134.7	1					0.3	2			56	3	200.1	8	13.0	6	0.7	7
RPU					83.3	1					0.3	2			143	4	13.5	6	10.4	4		
RTE															109	3					0.4	1
SAS					1269.3	7	349.6	4			0.2	2	16.8	4			32.4	6	19.9	9		
SJU	0	1.2	3	0											172	4	11.5	5			0.6	6
SOF	4.2	2.7	6	4.2	1619.0	9	198.6	1			0.2	1			229	6	465.0	9	19.1	8	0.6	6
SSP					72.5	1					0.3	2			46	4	3.9	4	11.9	5	0.6	5
STH					61.1	1	276.6	2			0.4	3			75	3	0.5	2	3.0	1	0.7	8
TCA					28.7	1					0.4	4			48	6	0.2	2	7.8	3	0.6	5
TCH					30.5	1	449.1	6	6.3	2					67	1	11.9	5	10.3	4		
TPO	28.5	0.1	1	28.5	13.2	1	431.1	5					15.1	3	32	1	0.9	3	9.8	4		

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Table S3. Categories (ct) and classes (c) of each plant species for plant traits with categorical data. Plant traits without any data are left blank. The scientific names of species are given in the Supplementary Table 3.

Species / Plant Traits	Bark thickness		Seed bank		Leaf phenology		Leaf shape		Resprouting		Post-fire seedling emergence	
	ct	c	ct	c	ct	c	ct	c	ct	c	ct	c
AAN			no	0	evergreen	0	broad	0	yes	10	no	0
AAP			no	0					yes	10	no	0
ABR			no	0					no	0		
AUN	thin	0	no	0	evergreen	0	broad	0	yes	10	no	0
CAU			no	0	winter deciduous	0	broad	0	yes	10		
CCO			no	0	winter deciduous	0			yes	10	no	0
CCR	thin	0	yes	7	drought semi-deciduous	10	broad	0	no	0	yes	7
CMO	moderate	5	no	0	winter deciduous	0	broad	0	yes	10	no	0
CPA			yes	7	drought semi-deciduous	10	broad	0	no	0	yes	7
CPS			no	0					no	0	yes	7
CSA			yes	7	drought semi-deciduous	10	broad	0	no	0	yes	7
CSE			yes	7					no	0	yes	7
CSI			no	0	evergreen	0	broad	0	yes	10	no	0
CVI	thin	0	variable	7	drought semi-deciduous	10	broad	0	yes	7	yes	7
DGN			no	0					unknown			
DSE			no	0	evergreen	0			variable	5		
DVI			variable	5			linear	5	yes	7	yes	7
EAC	thin	0	variable	7	drought semi-deciduous	10	scale-like	10	yes	7	yes	7
EMA			variable	7	evergreen	0	linear	5	yes	7	yes	7
GAC	thin	0	variable	7	drought semi-deciduous	10	broad	0	yes	7	yes	7
HEM	thin	0	variable	7	evergreen	0	needle-like	10	unknown		variable	3.5
JOX			no	0	evergreen	0	needle-like	10	yes	10	no	0
LNO			no	0	evergreen	0			yes	10	no	0
LST			variable	7	drought semi-deciduous	10			no	0	yes	7
MCO			no	0	evergreen	0	broad	0	yes	10	no	0
OAL	thin	0	no	0	evergreen	0	linear	5	yes	10	no	0
OEU			no	0	evergreen	0	broad	0	yes	10	no	0
OON			no	0					yes	10	no	0

Code												
PBR	thick	10	variable	7	evergreen	0	needle-like	10	no	0	yes	7
PCH			no	0					yes	10		
PEL			no	0					unknown			
PGR			no	0					unknown		no	0
PLA			no	0	evergreen	0	broad	0	yes	10	no	0
PLE	moderate	5	no	0	evergreen	0	broad	0	yes	10	no	0
PLY			no	0					yes	10		
PNI			no	0					yes	10	no	0
PSP			no	0	winter deciduous	0			yes	10	no	0
PTE			no	0	winter deciduous	0	broad	0	yes	10	no	0
QAU			no	0					yes	10		
QCO	moderate	5	no	0	evergreen	0	broad	0	yes	10	no	0
QIN			no	0					yes	10		
QIT			no	0	winter semi-deciduous	0			yes	10	no	0
RAC			no	0	evergreen	0			yes	10	no	0
RPU			no	0					unknown			
RTE			no	0	evergreen	0			yes	10	no	0
SAS	thin	0	no	0	evergreen	0	broad	0	yes	10	no	0
SJU			variable	7	winter deciduous	0			yes	7	yes	7
SOF			no	0	winter deciduous	0	broad	0	yes	10	no	0
SSP	thin	0	variable	7	drought semi-deciduous	10	broad	0	yes	7	yes	7
STH			variable	7	drought semi-deciduous	10	broad	0	variable	5	yes	7
TCA	thin	0	variable	7	drought semi-deciduous	10	linear	5	variable	5	yes	7
TCH			variable	7	evergreen	0	broad	0	yes	7	variable	3.5
TPO	thin	0	no	0	evergreen	0	broad	0	yes	10	no	0
TSA			no	0					unknown			

Table S4. Average scores of species (zero to ten) on the resilience (RL) and resistance (RT) capacity to fire and climate change. Species without any data are left blank.

Species	Species Codes	Climate Change		Fire	
		RL	RT	RL	RT
Arbutus andrachne L.	AAN	3.8	4.4	3.5	6.0
Arbutus unedo L.	AUN	4.4	4.1	3.5	6.0
Asparagus aphyllus L.	AAP	5.3	7.0	4.2	2.5
Asperula brevifolia Vent.	ABR	0	8.0	0	
Calicotome villosa (Poir.) Link	CVI	6.3	4.6	5.0	2.4
Celtis australis L.	CAU	7.0	3.5	5.5	3.0
Ceratonia siliqua L.	CSI	6.0	4.9	3.8	6.0
Cistus creticus L.	CCR	4.3	4.8	3.6	4.3
Cistus parviflorus Lam.	CPA	3.3	7.6	3.7	5.3
Cistus salviifolius L.	CSA	3.0	6.9	2.7	4.3
Cotinus coggygria Scop.	CCO	5.0	4.2	5.0	4.0
Crataegus monogyna Jacq.	CMO	5.8	4.8	3.6	5.0
Cupressus sempervirens L.	CSE	4.0	7.3	3.2	6.8
Cytisopsis pseudocytisus (Boiss.) Fertig	CPS	0	7.3	3.5	3.7
Daphne gnidioides Jaub. & Spach	DGN	3.0	6.4	2.0	4.3
Daphne sericea Vahl	DSE	2.5	6.5	5.0	4.3
Dittrichia viscosa (L.) Greuter	DVI	6.0	6.4	5.9	6.0
Erica manipuliflora Salisb.	EMA	7.0	6.2	7.0	4.0
Euphorbia acanthothamnos Heldr. & Sart. ex Boiss.	EAC	7.0	6.8	7.0	0
Genista acanthoclada DC.	GAC	7.3	4.4	6.0	3.6
Hypericum empetrifolium Willd.	HEM	4.7	6.0	3.8	3.9
Juniperus oxycedrus L.	JOX	4.2	8.5	3.0	5.6
Laurus nobilis L.	LNO	5.5	4.5	3.1	6.7
Lavandula stoechas L.	LST	3.3	7.5	3.7	3.6
Myrtus communis L.	MCO	4.3	5.5	3.5	4.2
Olea europaea L.	OEU	5.2	6.3	3.1	5.2
Origanum onites L.	OON	4.8	7.3	4.8	3.8
Osyris alba L.	OAL	5.6	5.5	3.5	3.9
Paliurus spina-christi Mill.	PSP	5.3	3.3	4.2	1.7
Phillyrea latifolia L.	PLA	3.8	6.8	2.6	4.3
Phlomis grandiflora H. S. Thomps.	PGR	4.7	6.6	2.5	8.2
Phlomis lycia D. Don	PLY	5.0	7.3	10.0	5.8
Pinus brutia Ten.	PBR	4.3	7.0	2.6	5.3
Pistacia lentiscus L.	PLE	4.6	6.3	3.2	5.6
Pistacia terebinthus L.	PTE	5.4	4.7	3.6	5.5
Populus nigra L.	PNI	6.0	3.8	4.7	7.0
Ptilostemon chamaepeuce (L.) Less.	PCH	5.3	7.6	6.3	4.7
Pyrus elaeagnifolia Pall.	PEL	0	5.5		3.3
Quercus aucheri Jaub. & Spach	QAU	4.3	6.2	5.8	4.0
Quercus coccifera L.	QCO	6.4	4.9	3.3	5.9
Quercus infectoria subsp. *veneris* (A.Kern.) Meikle	QIN	4.7	5.0	6.0	4.0
Quercus ithaburensis Decne.	QIT	4.7	5.4	4.0	5.5
Rhamnus punctata Boiss.	RPU	3.0	6.5	2.5	3.3
Rubia tenuifolia d´Urv.	RTE	5.0	4.5	5.0	

Ruscus aculeatus L.	RAC	6.0	6.4	3.8	2.7
Sarcopoterium spinosum (L.) Spach	SSP	6.0	5.0	5.8	2.3
Satureja thymbra L.	STH	5.8	6.4	5.3	5.8
Smilax aspera L.	SAS	5.4	2.7	3.6	3.6
Spartium junceum L.	SJU	6.3	6.5	5.7	6.5
Styrax officinalis L.	SOF	7.3	2.6	4.0	6.5
Teucrium chamaedrys subsp. *syspirense* (C. Koch) Rech. f.	TCH	6.0	5.8	4.0	4.3
Teucrium polium L.	TPO	4.4	5.7	3.7	3.2
Teucrium sandrasicum O. Schwarz	TSA	0	10.0		
Thymbra capitata (L.) Cav.	TCA	4.7	5.9	5.5	3.3

Table S5. Mean community weighted mean values for resilience and resistance capacities to fire and climate change for each vegetation type. Values in parentheses are the standard error of the mean. *L.ratio* is the likelihood ratio estimated for the statistical comparison between a null model including the transect as the random factor and the model with both the random and the fixed factor (i.e., vegetation types).

Abundance	Semi-closed forest	Open forest	Closed shrubland	Open shrubland	Scrubland	Linear model	
						L.Ratio	P
CC Resilience	4.70 (0.2)	5.30 (0.2)	4.60 (0.1)	4.98 (0.1)	5.82 (0.2)	23.1	<0.0001
CC Resistance	5.90 (0.2)	5.78 (0.1)	5.76 (0.1)	5.87 (0.1)	5.07 (0.0)	24.0	<0.0001
FR Resilience	3.99 (0.2)	4.63 (0.2)	3.55 (0.1)	4.63 (0.2)	5.51 (0.1)	38.9	<0.0001
FR Resistance	4.46 (0.1)	4.04 (0.0)	4.29 (0.0)	4.04 (0.1)	3.00 (0.2)	60.2	<0.0001
Cover							
CC Resilience	4.58 (0.1)	5.07 (0.1)	4.46 (0.1)	5.08 (0.2)	5.79 (0.2)	37.0	<0.0001
CC Resistance	6.47 (0.1)	6.28 (0.1)	6.01 (0.1)	5.71 (0.1)	5.10 (0.0)	97.8	<0.0001
FR Resilience	3.28 (0.1)	3.99 (0.2)	3.25 (0.1)	4.34 (0.2)	5.41 (0.1)	66.1	<0.0001
FR Resistance	4.99 (0.1)	4.64 (0.1)	4.91 (0.1)	4.45 (0.1)	3.10 (0.2)	95.2	<0.0001

Table S6. The PC1 and PC2 results of principal component analysis (PCA) for both abundance and cover value of community weighted mean analysis. "CC" is for climate change and "FR" for fire.

Abundance	PC1	PC2
CC Resilience	0.5807	0.2531
CC Resistance	-0.3630	-0.7644
FR Resilience	0.5714	-0.3881
FR Resistance	-0.4523	0.4483
Cover		
CC Resilience	0.4900	0.7114
CC Resistance	-0.4695	0.2957
FR Resilience	0.5474	0.1671
FR Resistance	-0.4897	0.6152

Table S7. The results of pairwise comparisons between vegetation types following principal components analysis (PCA) considering resilience and resistance capacities to fire and climate change by using abundance and cover values of community weighted mean.

Vegetation Types	Abundance		Cover	
	R^2	P	R^2	P
Open shrubland vs. Scrubland	0.625	0.001	0.627	0.001
Open shrubland vs. Closed shrubland	0.575	0.001	0.626	0.001
Open shrubland vs. Open forest	0.448	0.001	0.566	0.001
Open shrubland vs. Semi-closed forest	0.657	0.001	0.834	0.001
Scrubland vs. Closed shrubland	0.901	0.001	0.920	0.001
Scrubland vs. Open forest	0.610	0.001	0.769	0.001
Scrubland vs. Semi-closed forest	0.801	0.001	0.936	0.001
Closed shrubland vs. Open forest	0.379	0.001	0.414	0.001
Closed shrubland vs. Semi-closed forest	0.514	0.001	0.713	0.001
Open forest vs. Semi-closed forest	0.317	0.001	0.442	0.001

Table S8. The results of sample coefficient of variation (CV) for individual abundance and cover data to fire and climate change resilience capacities. Closed habitats mean semi-closed forest and closed shrubland, and open habitats mean open forest and open shrubland vegetation types.

	Abundance		Cover	
	Open habitats	**Closed habitats**	**Open habitats**	**Closed habitats**
CC Resilience	14.68	14.49	12.65	9.50
CC Resistance	8.40	9.45	6.99	6.46
FR Resilience	19.72	17.75	21.09	11.38
FR Resistance	8.95	11.27	9.55	6.07

Table S9. The results of linear regression analyses of the association between resilience and resistance capacity to fire and climate change based on community-weighted means of abundance and cover data.

Vegetation Types	Climate Change		Fire	
	Abundance (R^2)	**Cover (R^2)**	**Abundance (R^2)**	**Cover (R^2)**
Semi-closed forest	0.245	0.290	0.221	0.172
Open forest	0.046	0.115	0.430	0.660
Closed shrubland	0.479	0.106	0.154	-0.016
Open shrubland	0.556	0.133	0.153	0.355
Scrubland	0.032	0.353	-0.085	-0.058
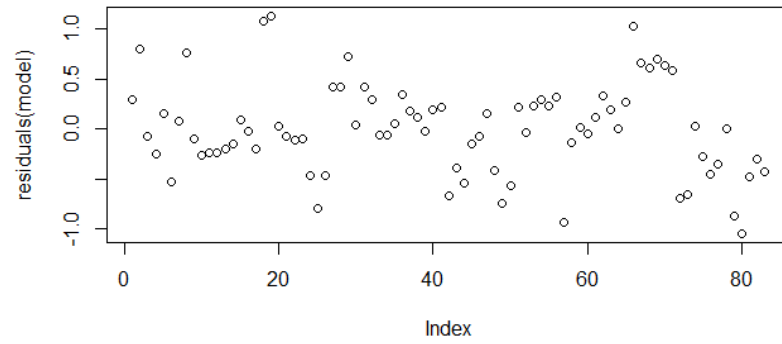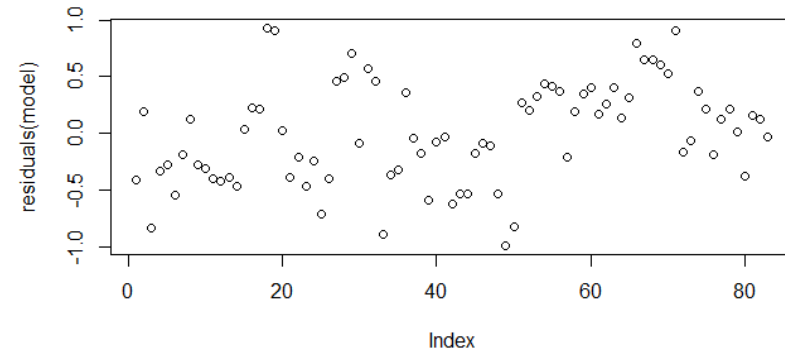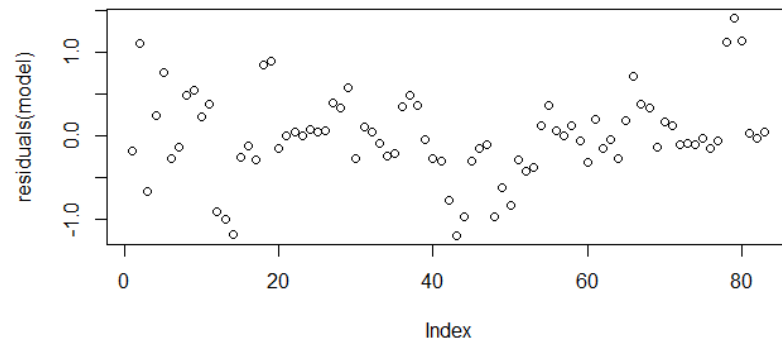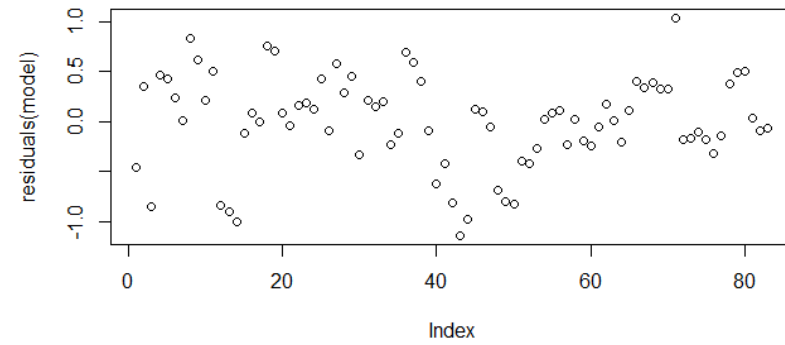
Figure S1. Residuals plots of the vegetation type's comparison in terms of resilience and resistance capacity to climate change [(A) for abundance and (B) for cover data] and fire [(C) for abundance data and (D) for cover data].

CHAPTER 5: MAQUIS VEGETATION IN MEDITERRANEAN TURKEY AND RECOMMENDATIONS FOR FORESTRY PRACTICES*

Abstract

Maquis ecosystems are one of the most uncertain and controversial vegetation type in Turkey. Since the description and classification of maquis differ according to many studies, even the distribution of maquis vegetation in Turkey has not been fully clarified. Besides that, its legal status has been changed many times over the years. While maquis were considered as a forests in the first years of the Republic of Turkey, in line with the constitutional amendments in recent years, maquis areas can be converted into agricultural land if it is beneficial, and it is even encouraged to crop within the scope of firefighting. This study presents new findings emphasizing an approach over alternative states, i.e. open and closed. According to this approach, maquis ecosystems divide into 5 main vegetation types: semi-closed forest, open forest, closed shrubland, open shrubland and scrubland. These vegetation types clearly differ from each other regarding to species diversity and richness, functional group classification (growth form, regeneration strategies and resprouting ability), leaf traits variation (specific leaf area, leaf thickness and leaf area), resilience and resistance capacities to fire and climate change. Based on this classification, it has been revealed that shrub and subshrub are dominant enough to shape plant community features, scrublands are the most resilient vegetation type however the least resistance, and open habitats are more resilient to fire and climate change compared to closed habitats. In Turkey, forestry implementations in the form of transforming maquis into red pine forests should be re-planned regarding to these findings.

Keywords: open and closed habitats, shrubland, scrubland, resilience and resistance, fire and climate change.

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5.1. Definitions of Maquis Vegetation

Mediterranean type ecosystems are located in five regions of the world: the Mediterranean Basin, California, Western and South Australia, Chile and the Cape Region of South Africa (between the 30th and 40th north and south latitudes) (Tavşanoğlu & Gürkan, 2004). They share the same climatic regime with long arid periods and mild rainy winters. The typical vegetation structure of Mediterranean type ecosystems is called "maquis" in the Mediterranean Basin, "chaparral" in California, "kwongan" or "heather" in southwestern Australia, "matorral" in Chile and "fynbos" in South Africa (Rundel et al., 1998). The Mediterranean Region hosts 73% of this ecosystem type globally. The distribution of land areas in California and Southwest Australia follow with 10% each. The rest are Chile with 4% and South Africa with 3% (Cowling et al., 1996).

The definition of maquis differs slightly in the scientific world. The general definition of maquis is a type of Mediterranean vegetation dominated by shrubs, small trees and trees that are characteristically evergreen, hard and small-leaved, xeric and 2-5 m high (Mayer & Aksoy, 1998; Özalp, 2000; Papanastasis, 2000; Aksoy, 2006). In addition, it has been stated that maquis vegetation has a cramped dense structure (Semple, 1919) and can form vegetation in karstic areas even if they are destroyed by fire or other anthropogenic effects since their roots progress along the cracks of limestone in such areas (Atalay et al., 2014). In accordance with some views (Knapp, 1965; Schmidt, 1969; Yaltırık, 1975), garrigue and phrygana formations were formed as a result of the destruction of maquis over time. While these two formations are included in the same vegetation type according to some sources (Yaltırık, 1975; Aksoy, 2006), there are also some opposite views that consider them as separate vegetation types due to species differences (Kavgacı et al., 2021). Ultimately, all of them originally meant *"uncultivated land"* (Rübel, 1914).

Another discussion of maquis concerns their historical formation. The Mediterranean belt consists of sclerophyllous forest-maquis species such as *Arbutus* spp., *Pistacia lentiscus* and *Cistus* spp. and, sclerophyllous forest trees such as *Quercus* spp. and *Olea europea* (Warming, 1909; Mayer & Aksoy, 1998), mainly *Quercus coccifera* (Zohary, 1973). It has also been pointed out that maquis vegetation emerged due to the degradation of these forests over time (Tansley, 1913; Semple, 1919; Polunin-Huxley, 1990; Öztürk, 1995), especially with the use of coppice (Özalp, 2000). However, if the degradation had caused

the destruction of trees and shrubs under them, the forests would not have turned into maquis but directly into garrigue vegetation (Tomaselli, 1977). Another theory is that the reason for the transition from bare soil to forest may not always be "degradation". As a matter of fact, without any disturbances, there is a possibility that garrigue and maquis are a part of progressive evolution (Harshberger, 1926; Rikli, 1943; Tomaselli, 1977). Two examples are the maquis on the undisturbed cliffs of the Mediterranean Sea (Harshberger, 1926; Tomaselli, 1977) and garrigue in the uncultivated areas of southern France (Harshberger, 1926). Akkemik (2021) also stressed that maquis should be called "Mediterranean sclerophyllous forest" so as not to remove them from the forest status, especially for those that have lost their forest structure due to fire damage.

The definition of maquis has expanded legally over time in Turkey. The first official definition was made in law No. 5653 in 1950 as "all kinds of small tree" and species. *Phillyrea latifolia*, *Erica* spp., *Cistus* spp., *Laurus nobilis*, *Arbutus* spp. and *Quercus coccifera* were given as examples. In the following years, according to the Forest Law numbered 6841 in 1956, this definition was expanded to state that maquis consisted of xerophytic, evergreen, hard-leaved small trees with a height of up to 3 m. Species such as *Olea europea*, *Pistacia lentiscus*, *Ceratonia siliqua* and *Juniperus oxycedrus* were also added to the previous species list. Finally, in the Forest Law No. 6831 Forest Cadastre and 2/B Implementation Regulation in 1986, species such as *Asparagus aphyllus*, *Nerium oleander* and *Pyrus elaeagrifolia* were added to the maquis definition. According to the communique "Procedures and Principles for the Implementation of Forest Management Plans", which was put into effect in 2014, maquis vegetation consists of trees, small trees and shrubs that can reach at least two meters in length, and *Arbutus* spp., *Laurus nobilis*, *Myrtus communis*, *Olea europea*, *Pistacia lentiscus* and *Quercus* spp are specified as maquis species. Almost all of these definitions include only small trees in the concept of maquis and almost never consist of shrub and subshrub species less than two meters high.

5.2. The Ecological Importance of Maquis Vegetation

Although maquis are characterized as inefficient in terms of wood yield, they are actually forest areas that are very rich in terms of biological diversity (Adıgüzel et al., 2019). Their dense structure provides a safe environment for many mammal species to hide, shelter, breed and roam (Ambarlı et al., 2019; Kankılıç et al., 2019). Moreover, the fruits of

different maquis species ripening in different seasons constitute an important food source for mammals throughout the year. In particular, its mixture with *Pinus brutia* is defined as a rich vegetation type in terms of tree species composition (Zeydanlı et al., 2019) and is considered to be valuable as an important biodiversity element (Lise et al., 2019). Finally, maquis have other functions such as soil protection and erosion prevention due to their strong root systems (İnal, 1969; Uslu, 1982; Taşdemir et al., 2018) and contributes to the ecosystem function (Aktepe & Tüfekcioğlu, 2021).

5.3. Distribution of Maquis Vegetation in Turkey

The size of the area covered by maquis in Turkey may vary as stated by the old sources: 216,660 hectares (Yiğitoğlu, 1941), 2.5-3 million hectares (İnal, 1969) and 3 million hectares including garrigue (Tomaselli, 1977). Moreover, as stated by Öztürk (1995), about 2 million hectares of maquis are located only as understorey in *Pinus brutia* forests. According to studies conducted in recent years, maquis vegetation covers about 7.5 million hectares of land in the Marmara, Aegean and Mediterranean regions of Turkey (Kaya et al., 2009). This coverage corresponds to approximately 32.7% of Turkey's forests and is more than the *Pinus brutia* forests (22.7%) and *Quercus* spp. forests (29.4%) (Orman Genel Müdürlüğü, 2021).

5.4. Legal Status of Maquis Vegetation and Forestry Practices in Turkey

The first known public statements about maquis in Turkey belong to years 1772 and 1796, when it was suggested that shrubland branches and oaks could be used in the construction of ships (Öztürk, 1995). In 1858, it was stated that shrubs (without mentioning the word maquis) and degraded forests could be used for agricultural activities (Öztürk, 1995). However, in the first years of the Republic of Turkey, in a reference to Forest Law No. 3116 in 1937, maquis were considered within the forest category, whereas heathland was excluded from this definition. In accordance with Law No. 5653 enacted in 1950 and the "Official Instruction Regarding the Determination of Forest Boundaries at the Confluence of Maquis and Forest Fields", maquis that do not produce any kind of non-wood forest output regularly were excluded from the definition of forest. Within this process 490,000 hectares of 780,000 hectares of maquis were removed from the forest classification (Kul, 1996).

According to Forest Law No. 6831, which entered into force in 1956, maquis are considered as forests if they can protect the soil or reduce the risk of erosion. Those that do not meet these conditions are defined as non-forest (Ayanoğlu, 1996). However, until the "Regulation on the Determination of Heathland and Shrubland" published in 1959, implementations continued in line with the old instruction, and during this process, approximately 94,000 hectares of maquis area were removed from the forest category (Kul, 1996). Fortunately, as the restriction of forest boundaries was prohibited in accordance with the 1961 Constitution, the distinction of maquis areas was suspended for a while (Ayanoğlu, 1996). Until the constitutional amendment made in 1970, 5,188 hectares of the 5,263 hectares were taken out of the forest boundary (Kul, 1996). In other words, about 590,000 hectares of maquis area were excluded from the definition of forest between 1950 and 1970.

According to the changes made in Forest Law No. 6831 in 1973, it was decided to remove the maquis areas which had lost their forest quality from the forest category. Following this, within the scope of the constitutional amendment made in 1982, it was decided that the heathland and maquis areas which would be beneficial if converted into agricultural lands should not be considered as forests anymore. As a result of these changes, a total of 410,000 hectares of land lost forest status between 1974 and 1996, and it is thought that most of these areas are maquis (Kul, 1996). In 2000, a new article was added to the Forest Management Regulation as a precaution against not considering maquis as non-forest areas; therefore, maquis were classified as "other deciduous" ("*diğer yapraklı*" in Turkish) stand type (Özalp, 2000; Taşdemir et al., 2018). In 2008, as a result of the amendment made in the technical prospectus, these areas were given the status of productive forest (Güzenge, 2011).

Within the scope of the instruction published by the General Directorate of Forestry in 2012, the maquis areas that were determined as maquis according to Regulation of 1959 were again classified as non-forest areas in the forest management plans, and the other maquis areas determined as maquis by the Forest Cadastre began to be classified as forest areas in the plans. The biggest difference is that implementation activities can be carried out in the maquis, which are considered as forest areas in the plans (Interviews 2022). It was also highlighted that maquis should be converted into *Pinus brutia* forests by conducting afforestation or rehabilitation implementations, since it was thought that a

large portion of the maquis was part of *Pinus brutia* forests in the past. As a matter of fact, in accordance with the communiqués on the "Procedures and Principles of the Implementation of Forest Management Plans" published in 2017, regardless of the percentage of cover, all maquis areas are subject to rehabilitation in order to protect the so-called integrity of the ecosystem.

In the article prepared by the General Directorate of Forestry for the implementations to be applied in maquis areas in 2022, detailed information is given regarding the rehabilitation plans for firefighting and benefiting from non-wood forest products. Accordingly, maquis will be cropped in areas considered as maquis by the Forest Cadastre and in *Pinus brutia* forests with dense maquis as understorey to facilitate firefighting, not exceeding 10 hectares. However, since any cutting implementations on maquis species will cause the individuals to resprout more, these practices will pave the way for coppice forests rather than preventing fire (Türkiye Ormancılar Derneği, 2022).

Other vegetation types, in which maquis species are also located, are open *Pinus brutia* stands with 11-40% coverage ("*1 kapalı Çz*" in Turkish) and *Pinus brutia* stands with 1-10% coverage ("*BÇz" in Turkish*) (Tüfekcioğlu & Tavşanoğlu, 2022a; Orman Genel Müdürlüğü, 2022) and forest soil without any trees (*"OT" in Turkish*) (Tüfekcioğlu & Tavşanoğlu, 2022a). According to Communiques "No. 298 Technical Principles of Silvicultural Practices" and "No. 295 Procedures and Principles for the Implementation of Forest Management Plans", published in 2014 and 2020 respectively, these type of stands are subject to rehabilitation implementations and it was also recommended to use local plant species and increase biological diversity.

5.4. Maquis Vegetation Types in Mediterranean Turkey

Maquis vegetation has a very dynamic structure (Aktepe & Tüfekcioğlu, 2021). The fact that maquis species are entwined and therefore do not have clear boundaries causes the maquis vegetation to be classified clearly from others. Thus, there are different opinions on this issue; Mayer and Aksoy (1998), Polunin-Huxley (1990) and Aksoy (2006) classify maquis based on the dominant species such as *Quercus coccifera* maquis, *Olea europea* maquis, *Arbutus andrachne* maquis or the average height of individuals such as high maquis, low maquis and garrigue (Kavgacı, 2017a). In the study by Harshberger (1926),

as the main factor for classification is the presence of trees, there are four natural vegetation units: garrigue without any trees, garrigue with some tree species such as oak or pine, maquis without any trees, and maquis with some tree species. On the other hand, Keeley et al. (2012) and Kavgacı et al. (2017b) directly divide the eastern Mediterranean vegetation into three main classes as forests, shrubs and phrygana. The alternative biome state, as a prominent approach in recent years, classifies Mediterranean ecosystems as open and closed vegetation types and asserts that open states are continuous and permanent like close states (Pausas & Bond, 2020). Based on this approach, Tüfekcioğlu and Tavşanoğlu (2022a) classified Mediterranean vegetation of Turkey into five main vegetation types (Table 5.1, Figure 5.1).

Table 5.1. Mediterranean vegetation types used in Tüfekcioğlu and Tavşanoğlu (2022a), their corresponding classes in forest management plans (Turkish abbreviations in parentheses) and scientific articles (Keeley et al., 2012; Kavgacı et al., 2017).

| Vegetation Types		
In Tüfekcioğlu and Tavşanoğlu (2022a)	In forest management plans	In scientific articles
Semi-closed forest	Turkish red pine forest with total coverage between 11% and 40% (*"1 kapalı Çz"* in Turkish)	Mediterranean woodlands and forests
Open forest	Turkish red pine forests with total coverage < 10% (*"BÇz" in Turkish*)	-
Closed shrubland	Maquis with total coverage between 11% and 100% (*"Mak3" in Turkish*)	Maquis
Open shrubland	Maquis with total coverage < 10% (*"BMak" in Turkish*)	Phrygana and/or Garrigue
Scrubland	Forest soil without any trees (*"OT" in Turkish*)	Phrygana and/or Garrigue

CLOSED SHRUBLAND

C

Legend
Species
— Arbutus andrachne
— Arbutus unedo
— Asparagus aphyllus
— Calicotome villosa
— Cistus creticus
— Euphorbia acanthothamnos
— Genista acanthoclada
— Hypericum empetrifolium
— Olea europaea
— Osyris alba
— Phillyrea latifolia
— Phlomis grandiflora
— Pistacia lentiscus
— Pistacia terebinthus
— Quercus aucheri
— Quercus coccifera
— Ruscus aculeatus

3.5   1.75   0   3.5 m

OPEN SHRUBLAND

D

Legend
Species
— Arbutus andrachne
— Arbutus unedo
— Asparagus aphyllus
— Calicotome villosa
— Cistus creticus
— Euphorbia acanthothamnos
— Genista acanthoclada
— Hypericum empetrifolium
— Olea europaea
— Osyris alba
— Phillyrea latifolia
— Phlomis grandiflora
— Pistacia lentiscus
— Pistacia terebinthus
— Quercus aucheri
— Quercus coccifera
— Ruscus aculeatus

4.5   2.25   0   4.5 m

Figure 5.1. Top view of transects representing the structure of different vegetation types: (A) Semi-closed forest ("*1 kapalı Çz*" in Turkish), (B) Open forest ("*BÇz" in Turkish*), (C) Closed shrubland ("*Mak3" in Turkish*), (D) Open shrubland ("*BMak" in Turkish*), (E) Scrubland (*"OT" in Turkish*).

5.5. Comparison of Maquis Vegetation Types

5.5.1. Diversity and Species Composition

In a comparison of vegetation types, there are differences between forest-shrubland-scrubland and open and close states of forests and shrublands. Shrublands have the highest value for species richness and diversity, followed by forests and scrublands. A comparison of woody species density and cover percentage in vegetation types using non-metric multidimensional analysis shows that semi-closed and open forest are closely related; however, closed shrubland, open shrubland and scrubland have completely different values from each other. On the other hand, an analysis of the presence of woody species reveals species compositions directly, placing the closed shrubland close to the semi-closed forest and open forest types. Finally, indicator species analysis distinguishes between open and closed shrubland (Tüfekcioğlu & Tavşanoğlu, 2022a).

5.5.2. Functional Structure (Growth Form and Regeneration Strategies)

An evaluation of woody species density and cover percentage in vegetation types indicates that *Pinus brutia* has the highest overlap in semi-closed forest and open forest vegetation types, and these vegetation types are also very rich in density of shrub species. Closed shrublands are dominated by large shrubs, followed by shrubs. In open shrubland vegetation, there are shrub and subshrub species, and *Sarcopoterium spinosum,* as a subshrub species, dominates the scrubland vegetation type (Tüfekcioğlu & Tavşanoğlu, 2022a).

With regards to regeneration strategies, R-P+c (non-resprouter and propagule persister species with a canopy seed bank) strategy is dominant in forest vegetation types because of the *Pinus brutia*. R-P+s (non-resprouter and propagule persister species with a soil seed bank) species are mainly found in all vegetation types except closed shrubland, while R+P- (resprouter and propagule-non-persister species) species are mostly in closed shrubland as most of them have large shrub forms. Finally, R+P+ (resprouter and propagule-persister) species are by far mostly recorded in scrubland, followed by open shrubland and open forest (Tüfekcioğlu & Tavşanoğlu, 2022a).

5.5.3. Leaf Traits Variations

Generally, Mediterranean woody plant species have a low specific leaf area (hereafter: SLA) value, small leaf area and thick leaves to cope with drought. Indeed, *Cistus parviflorus* with its lowest SLA value, *Phlomis lycia* with its highest leaf thickness value, and *Erica manipuliflora* with smallest leaf area value answered to this description. From the view of growth form classification, the most suitable species are in shrub and subshrub forms. Finally, forests and shrublands were relatively similar to each other, whereas scrubland clearly distincted from them (Tüfekcioğlu & Tavşanoğlu, 2022b).

5.5.4. Resilience and Resistance Capacities to Fire and Climate Change

In the study of Tüfekcioğlu and Tavşanoğlu (2022c), resilience and resistance capacities were evaluated according to the number of species and cover of individuals in different vegetation types. While scrubland had the highest resilience capacity to fire and climate change, it was followed by open states (open forest and open shrubland) and closed states

(semi-closed forest and closed shrubland). On the other hand, the resistance capacity to fire and climate change emerged as the lowest type scrubland and even took its place as a separate vegetation class in the principal component analysis. Finally, the climate change resistance capacities of other vegetation types are progressed as semi-closed forest, open forest, closed shrubland and open shrubland respectively, however, their resistance capacities to fire change are close to each other.

5.6. Conclusions and Recommendations for Forestry Practices

5.6.1. Definitions and Classification of Maquis Vegetation Types

Definitions for maquis mostly include tree and large shrub species. However, the fact that subshrub and shrub species are dominant enough to direct the features of plant communities should also be taken into consideration. The best example for this situation is that since shrubs are resistant to drought, areas where these species are most common (semi-closed forest, open forest and open shrubland) are also drought resistant. Therefore, maquis should be defined as a vegetation type consisting of subshrub, shrub, large shrub, tree and liana growth forms in a multi-layered structure. Thus, it can be pointed out that maquis vegetation is an important biodiversity element both in terms of plant species diversity and species composition.

As stated by Tüfekcioğlu and Tavşanoğlu (2022a), although the most obvious difference in Mediterranean vegetation types is between forest-shrubland-scrubland, it is also necessary to consider open and closed states of forests and shrublands as separate vegetation types. All these results show the importance of structural features of vegetation types in the evaluation of Mediterranean Basin plant communities. Therefore, each of these five different vegetation types should be considered separately in the decisions being made for the protection and management practices to be followed in the Mediterranean vegetation. In addition, as semi-closed forest ("*1 kapalı Çz*" in Turkish), open forest ("*BÇz" in Turkish*) and scrubland (*"OT" in Turkish*) also contain maquis species, they should be evaluated as part of the maquis vegetation types in forest management plans. Considering all these factors, the distribution of maquis areas in Turkey should be recalculated and the necessary updates should be made.

5.6.2. Recommendations for Forestry Implementations

The main tendency today is to convert semi-closed forests, open forests and some open shrublands (especially those where some *Pinus brutia* vegetation exists) into *Pinus brutia* forests. On this matter, there are two different theories on the replacement of *Pinus brutia* and maquis. On one hand, *Pinus brutia* forests are generally introduced by human activities and grow rapidly on garrigue vegetation and replace the climax as maquis. As this continues to be supported by human interventions, *Pinus brutia* forests become a stable state (paraclimax); when not supported, they revert to a sclerophyllous forest – that is, the climax state (Tomaselli, 1977; Kavgacı et al., 2016). On the other hand, it is stated that the maquis species fill the open spaces in the *Pinus brutia* forests; therefore, *Pinus brutia* seeds cannot reach the soil and perform natural regeneration. As a result, such areas turn from *Pinus brutia* forests into maquis vegetation (Öztürk, 1995). For this reason, it is recommended that such areas be turned into *Pinus brutia* forests through afforestation (Saatçioğlu, 1952).

As a matter of fact, the instruction published by the General Directorate of Forestry in 2014 and the communiqués "Technical Principles of Silvicultural Practices" and "Procedures and Principles for the Implementation of Forest Management Plans" confirmed the second theory and directed the rehabilitation of maquis and their conversion into *Pinus brutia* forests. However, the destruction of vegetation for any reason, such as the conversion of open shrublands to *Pinus brutia* forests (Kaya et al., 2016), cutting or turning of maquis into coppice forests (Işık et al., 1997; Özalp, 2000) and cleaning all the understorey (Güzenge, 2011) will damage the species' richness and the maquis diversity (Özkan & Özdemir, 2016). Moreover, in areas with a land slope of more than 15%, the removal of maquis from the area will adversely affect the area's ability to protect the soil against erosion (Saatçioğlu, 1952).

For any implementation to be planned for maquis areas, the vegetation type must first be determined. As a matter of fact, it is known that forests and shrublands are more resistant to drought (Tüfekcioğlu and Tavşanoğlu, 2022b) and fire (Tüfekcioğlu and Tavşanoğlu, 2022c) compared to scrublands. For forestry implementations to be planned for these vegetation types, their advantageous resistance capacities should be taken into account. In the future, when the effects of climate change will be seen more, plant communities

with these structures must be protected. On the other hand, even if rehabilitation studies are to be carried out, it should be done with drought-resistant species such as subshrubs and shrubs.

As stated by Tüfekcioğlu and Tavşanoğlu (2022c), scrubland is not resistant to fire and climate change. However, it is the most resilient vegetation type against both fire and climate change compared to other types. In other words, the recovery capacity of the plant composition in scrublands is higher than in other vegetation types in the event of damage due to an increase in temperature, drought or frequent and wild fires. Since scrubland is classified as forest soil without any trees (*"OT" in Turkish*) in forest management plans in Turkey, those that are not subject to rehabilitation are generally opened for grazing. However, the roles of scrublands in the ecosystem must be taken into account when making management decisions regarding promoting ecosystem resilience to fire (Valdecantos et al., 2009).

5.6.3. Conservation strategies for maquis vegetation

Today, according to the Forestry Law, maquis areas that do not have any forest characteristics or soil protection capabilities and would benefit from being converted into agricultural areas are not considered as forests. This has led to the removal of more than one million hectares of maquis area from the forest category in the past. Thus, land use of many maquis areas have been repurposed as agriculture and grazing areas. On the other hand, maquis (considered as forest area) are being transformed into *Pinus brutia* or being cut down for their f non-wood forest products. The majority of the maquis areas which have not undergone any intervention are located either on steep cliffs and slopes or far from settlements. Due to such sanctions, studies for the protection of important ecosystems such as maquis have been very incomplete.

For the protection of maquis, both legal steps and practical applications should come to the fore (Tomaselli, 1977). It is obvious that there is a need for new regulations in the Forestry Law, especially concerning the conversion of maquis into agricultural areas, which affects both their diversity and richness in terms of species, as well as their resilience and resistance capacities. Certain implementations should be avoided as maquis are important and valuable ecosystems, especially considering how resistant they are to

drought. Recovery of damaged maquis is relatively easy and can be achieved in a short time. In order to turn this situation into an advantage, maquis should be left in their natural state as much as possible and should be supported with plant species included in their plant composition if necessary.

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CHAPTER 6: CONCLUSIONS

Mediterranean type ecosystems are one of the most negatively affected ecosystems by global change drivers (i.e. fire, climate change, and drought). Recently, trait based approaches have been used in the studies on disturbance effects of global change drivers at species and community level. The aim of this study was to reveal resilience and resistance capacities of the low altitude Mediterranean woody vegetation types to fire and climate change by using plant traits.

As a result of the thesis, five main woody vegetation types in low altitude Mediterranean woody ecosystems, namely semi-closed *Pinus brutia* forest, open *P. brutia* forest, closed maquis shrubland, open maquis shrubland and scrubland, varied from species diversity and richness, functional group classification and plant community structure. As a matter of fact, although our findings revealed forest-shrubland-scrubland distinction regarding to species diversity and richness, open habitats (open forests and open shrublands) and closed habitats (semi-closed forests and closed shrublands) also differed from each other according to functional group classification. Besides that, our field and laboratory measurements showed a substantially leaf trait variation within- and among-species, functional group classification and woody plant communities of five main vegetation types. Considering leaf characteristics of Mediterranean type plant species (low SLA value, high leaf thickness value and small leaf area), forests and shrublands were more resistant to drought than the scrublands, however, scrublands were also more successful to disturbances such as fire and herbivory. Finally, findings on the resilience and resistance to fire and climate change analysis at the species and plant community level by using several plant traits, open habitats are more resilient to both fire and climate change than closed habitats. Besides that, communities with the most *P. brutia* coverage (forest-shrubland-scrubland, respectively) are more resistant to climate change. On the other hand, scrublands emerged as having the highest resilience but the lowest resistance capacity comparing to other types.

Understanding how the diversity and trait structure of plant communities of the Mediterranean Basin are and how their resilience and resistance ability to fire and climate change will provide a great advantage for enhance implementation of forest management and conservation strategies.

APPENDIX

Appendix 1. Photos From Fieldwork

Appendix 2. Photos From Laboratory Measurements

Appendix 2.1. Measurements of Leaf Thickness

Appendix 2.2. Measurements of Oven-Dry Mass of Leaves

Appendix 2.3. Measurements of Leaf Area