

Multiple ways for enhancing flammability in Mediterranean woody species: a trait-based approach

Nursema Aktepe⁽¹⁻²⁻³⁾,
Çağatay Tavşanoğlu⁽²⁾

Enhanced flammability is a key driver of community assembly and a favored characteristic in fire-dependent ecosystems. In this study, we examined the variability of flammability traits among Mediterranean woody species. We measured eight flammability traits, including leaf traits, branching architecture, and standing biomass traits, across 26 woody species in the understory of pine forests in southwestern Anatolia, Turkey. Given that these species are part of fire-dependent plant communities, where fire provides advantages for persistence, we hypothesized that species would use various ways to increase their flammability. All flammability traits exhibited substantial variation among species. The flammability of the studied species varied depending on the specific trait considered, with no single species consistently exhibiting higher or lower flammability across all traits. Moreover, many species employed distinct strategies to enhance their flammability, such as differences in leaf structure, branching patterns, and biomass characteristics. The interspecific variability in flammability was also evident through a calculated flammability score based on eight traits, providing a valuable framework for ranking species by their flammability. Our findings suggest that the traits driving increased flammability in Mediterranean woody plants are idiosyncratic at the species level. Therefore, multiple traits must be considered to comprehensively study flammability within a plant community. These results have practical implications for the selection of “fire-resistant” plants in land management strategies within the Mediterranean Basin.

Keywords: Among-species Variability, Fire, Flammability, Functional Traits, Mediterranean Basin

Introduction

Many biomes on Earth exhibit flammable vegetation due to climatic seasonality, the accumulation of aboveground biomass, and the presence of ignition sources, either of natural or anthropogenic origin (Keeley 2002, Scarff & Westoby 2006, Marlon et al. 2008, Pausas & Keeley 2009, Michelaki et

al. 2020, Oztürk et al. 2024). In these fire-prone ecosystems – landscapes frequently experience fire, which is a critical factor in shaping vegetation dynamics – several plant traits have been shaped by fire regimes over thousands or even millions of years. Traits such as serotiny (Lamont et al. 2020), resprouting ability (Clarke et al. 2013), thick bark (Pausas 2015), and fire-stimulated germination (Lamont et al. 2019) enable plants to survive or regenerate after fires. Another group of plant traits, known as flammability traits, determines how easily a species ignites, sustains combustion, and contributes to fire intensity, making species more (or less) flammable (Keeley et al. 2011). Flammability traits significantly influence local fire regimes and therefore have significant ecological and socioeconomic consequences (Pérez-Harguindeguy et al. 2013). Enhanced flammability can provide species with an advantage in fire-prone ecosystems, but only if they also possess traits that support post-fire survival or regeneration (Bond & Midgley 1995). Moreover, since flammability traits are under the selection pressure of local or regional fire regimes, among-population variability in flammability traits can also be observed (Pausas et al. 2012, 2017). This is because flammable species often exhibit additional adaptations, such as

post-fire germination or resprouting ability, that enhance their recovery after fire events (Pausas et al. 2012). As a result, fire regimes play a critical role in shaping both flammability traits and associated regeneration strategies in plant species.

Mutch (1970) was the first to propose that the degree of flammability in plants is influenced by the extent to which the plant community is fire-dependent, suggesting that characteristics enhancing flammability are shaped by natural selection. However, Snyder (1984) criticized this hypothesis, arguing that increased flammability may result from the selection of traits serving other functions, such as drought tolerance. Troumbis & Trabaud (1989) questioned the validity of Mutch's hypothesis and outlined specific criteria needed to support the selection of flammability traits, including a genetic basis and underlying mechanisms. Bond & Midgley (1995) later proposed that flammable vegetation arises when flammable species gain a fitness advantage over less flammable neighbors in post-fire environments. A simulation model by Schwilk & Kerr (2002) suggested that increased flammability can evolve as an adaptive strategy, even at the cost of sacrificing parent plants. More recently, empirical evidence suggests that flammability is a variable biological trait subject to natural

□ (1) Institute of Science, Hacettepe University, Beytepe 06800, Ankara (Türkiye); (2) Division of Ecology, Department of Biology, Hacettepe University, Beytepe 06800, Ankara (Türkiye); (3) Department of Biology, Faculty of Sciences and Arts, Kastamonu University, Kastamonu (Türkiye)

@ Çağatay Tavşanoğlu
(ctavsanoglu@gmail.com)

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selection (Saura-Mas et al. 2010, Engber & Varner 2012, Pausas et al. 2012, Moreira et al. 2014). These studies are major steps toward understanding the evolution and ecology of flammability in fire-prone ecosystems (Pausas et al. 2017).

Traits that increase plant flammability contribute to the overall flammability of plant communities and vegetation in fire-prone ecosystems, shaping fire dynamics at both community and ecosystem levels. Understanding these traits is crucial for identifying their distribution within plant communities and gaining insights into the ecology and evolution of fire-prone vegetation. Additionally, as flammability traits vary among species, this knowledge can guide forest managers in selecting less flammable species for forest restoration efforts (Neyisçi 1996, Baeza & Santana 2015, Santana et al. 2018). While many studies have examined plant flammability at the species level, our understanding of the variability of flammability traits across species remains limited, especially at broader ecological scales, from plant communities to biomes (Pausas et al. 2012, Cubino et al. 2018, Schertzer & Staver 2018, Stevens et al. 2020).

There are many approaches to studying

flammability in plants. Conceptually, plant flammability can be measured by estimating parameters such as first ignition time, smoke temperature, heat release rate, burning time, maximum temperature, and burnt biomass of plant leaves or shoots when exposed to a heat or ignition source (Murray et al. 2013, Alam et al. 2020, Cui et al. 2020, Murray et al. 2020, Michelaki et al. 2020, Güney et al. 2022). Alternatively, flammability can be assessed by burning a large section of plant material from several species within the same community to evaluate the vegetation-level flammability (Krix & Murray 2018, Alam et al. 2020). Another approach involves estimating fuel loading in plant individuals (Saura-Mas et al. 2010) or examining specific plant traits (Alam et al. 2020, Murray et al. 2020).

Several plant traits are associated with flammability (Popović et al. 2021). Fuel moisture content is a substantial component of plant flammability (Trabaud 1976, Plucinski & Anderson 2008, Ganteaume et al. 2009, Murray et al. 2013) and is the most frequently studied trait (Popović et al. 2021). Leaf traits, such as leaf dry matter content and leaf thickness, are also strongly linked to flammability (Pérez-Harguindeguy et al. 2013, Grootemaat et al. 2015).

Leaf curling is another important flammability parameter, as curled and larger leaves reduce fuel bed bulk density by generating air spaces between fuel particles, which increases flammability (Engber & Varner 2012, Parsons et al. 2015). Branching architecture, particularly branch density, is a key trait associated with flammability (Pérez-Harguindeguy et al. 2013), as dense branching structures increase the exposed surface area, resulting in more flammable canopies (Bond & Midgley 1995). Similarly, plant architecture, including the relative proportions of coarse to fine and dead to live standing fuel biomass, is a critical component of flammability, influencing fire intensity (Schwilk 2003, Saura-Mas et al. 2010, Tavsanoğlu & Pausas 2018). Associations among flammability traits are also notable. For instance, the relationship between fuel moisture content and flammability can depend on leaf dry matter content (Shipley & Vu 2002, Pérez-Harguindeguy et al. 2013). While multiple traits drive the flammability levels of plant individuals and species, most studies focus on only a few traits (Schwilk 2003, Scarff & Westoby 2006, Saura-Mas et al. 2010, Pausas et al. 2012, Murray et al. 2013, Popović et al. 2021), and studies considering several flammability traits simultaneously remain relatively rare (Krix & Murray 2018, Alam et al. 2020, Cui et al. 2020, Michelaki et al. 2020).

Mediterranean Basin ecosystems are characterized by fire-prone vegetation (Keeley et al. 2012) that exhibits diverse fire adaptations, including traits that enhance survival, regeneration, or reproduction following fire events. Examples of these adaptations include the serotinous cones of low-altitude pines, the high resprouting ability of shrubs, post-fire stimulation of flowering in geophytes, thick bark in high-altitude pines, and fire-stimulated germination triggered by heat or smoke in many herbaceous and woody species (Keeley et al. 2012, Tavsanoğlu & Pausas 2018). Flammability is another key fire adaptation associated with Mediterranean plants (Michelaki et al. 2020). In the Mediterranean Basin, various aspects of plant flammability have been extensively studied. Comparative studies have frequently examined the flammability levels of species within plant communities (Neyisçi 1996, Dimitrakopoulos & Papaioannou 2001). Functional hypotheses exploring the relationship between flammability traits and other plant traits have also been tested (Saura-Mas et al. 2010, Baeza & Santana 2015, Pausas et al. 2016, Michelaki et al. 2020). Furthermore, the role of fire regimes in shaping flammability has been acknowledged in Mediterranean ecosystems (Pausas et al. 2012).

Although recent studies have revealed different aspects of plant flammability, gaps remain in understanding the patterns of variability in flammability traits across many ecosystems. In this study, we aimed

Tab. 1 - Plant species studied for flammability traits. GF is growth form, Resp indicates resprouting ability (yes: resprouter; no: non-resprouter), and Code shows the species acronyms used in the tables and graphs throughout the paper.

Species	Family	Code	GF	Resp
<i>Arbutus andrachne</i> L.	Ericaceae	Aan	large shrub	Yes
<i>Arbutus unedo</i> L.	Ericaceae	Aun	large shrub	Yes
<i>Asparagus aphyllus</i> L.	Asparagaceae	Aap	liana	Yes
<i>Astragalus</i> sp.	Fabaceae	Ast	subshrub	Unknown
<i>Cistus creticus</i> L.	Cistaceae	Ccr	shrub	No
<i>Cistus salvifolius</i> L.	Cistaceae	Csa	shrub	No
<i>Crataegus monogyna</i> Jacq.	Rosaceae	Cmo	large shrub	Yes
<i>Daphne gnidioides</i> Jaub. & Spach	Tymelaeaceae	Dgn	shrub	Unknown
<i>Euphorbia characias</i> L.	Euphorbiaceae	Ech	subshrub	Yes
<i>Genista acanthoclada</i> DC.	Fabaceae	Gac	shrub	Yes
<i>Hypericum empetrifolium</i> Willd.	Hypericaceae	Hem	subshrub	Yes
<i>Juniperus oxycedrus</i> L.	Cupressaceae	Jox	large shrub	Yes
<i>Laurus nobilis</i> L.	Lauraceae	Lno	large shrub	Yes
<i>Myrtus communis</i> L.	Myrtaceae	Mco	large shrub	Yes
<i>Olea europaea</i> L.	Oleaceae	Oeu	tree	Yes
<i>Origanum onites</i> L.	Lamiaceae	Oon	subshrub	Yes
<i>Phlomis grandiflora</i> H.S.Thomps.	Lamiaceae	Pgr	shrub	Unknown
<i>Phlomis lycia</i> D. Don	Lamiaceae	Ply	shrub	Yes
<i>Phillyrea latifolia</i> L.	Oleaceae	Pla	large shrub	Yes
<i>Pistacia lentiscus</i> L.	Anacardiaceae	Ple	large shrub	Yes
<i>Pistacia terebinthus</i> L.	Anacardiaceae	Pte	large shrub	Yes
<i>Quercus cerris</i> L.	Fagaceae	Qce	tree	Yes
<i>Quercus coccifera</i> L.	Fagaceae	Qco	large shrub	Yes
<i>Spartium junceum</i> L.	Fabaceae	Sju	large shrub	Yes
<i>Styrax officinalis</i> L.	Styracaceae	Sof	large shrub	Yes
<i>Teucrium divaricatum</i> Sieber ex Heldr.	Lamiaceae	Tdi	subshrub	Yes

to characterize the interspecific variability in flammability traits in Mediterranean woody species, anticipating significant trait variation among species. We employed a trait-based approach to assess the flammability of species, focusing on fuel loading and the characteristics of leaves and branches. Given that the study species are part of fire-dependent plant communities where fire provides advantages for persistence (Tavsanoglu & Pausas 2018), we hypothesized that species adopt different strategies to enhance flammability. Specifically, we expected the traits responsible for increased flammability in Mediterranean plants to be species-specific. To test this hypothesis and clarify variability in flammability traits among Mediterranean species, we examined several leaf traits, branching architecture, and fuel loading properties in 26 woody plant species dominating the understory of Mediterranean pine forests in southwestern Turkey.

Methods

Study area and sampling design

The study was conducted in southwestern Anatolia, a region characterized by Mediterranean vegetation. The area experiences a Mediterranean climate, with dry summers and mild, wet winters, as classified by the Köppen system (Peel et al. 2007). Frequent crown fires, originating from both natural and anthropogenic sources, make this region one of the most fire-prone areas in Turkey (Oztürk et al. 2024). The fire regime in the region is pri-

marily shaped by its climatic conditions, particularly summer drought, and the dominance of highly flammable vegetation types, including pine forests, maquis shrublands, and scrublands. These fires play a critical role in driving vegetation dynamics and influencing the composition and structure of local plant communities.

We selected 24 study sites, each 1 ha in size, within the study area to sample woody species for their flammability traits (Tab. S1 in Supplementary material). Although several burned sites exist across the region, all selected sites were mature Turkish red pine (*Pinus brutia* Ten.) forests that had remained unburned for at least 50 years. The study sites spanned elevations from sea level to over 1000 m and were situated on limestone bedrock.

We selected the five most dominant understory species at each study site to sample for their flammability traits. The dominant pine species (*Pinus brutia*) was excluded due to methodological limitations, as its height and large biomass made it impractical to sample for whole-plant and combustibility traits. For each of the five species at each site, three individuals were randomly selected for sampling. In sites with low woody species richness, we sampled fewer species, as it was not possible to identify five dominant woody species. In total, we measured and collected samples from 363 individuals representing 26 plant species across the study sites (Tab. 1, Tab. S2 in Supplementary material). These species belong to different taxonomic families and growth forms, including trees, shrubs,

and lianas. Most of the sampled species are capable of resprouting after crown fires, while a few lack this ability (Tab. 1). Since not all species were present at every site, the number of individuals sampled per species varied from 3 to 69 (Tab. S2).

Trait measurements

We performed trait measurements on individuals of the selected species both in the field and in the laboratory. To capture multiple components of plant flammability, we measured four leaf traits (leaf dry matter content, leaf moisture content, leaf thickness, and leaf curliness), one whole-plant trait (branching architecture), and three combustibility traits (dead to live fuel ratio, coarse to fine fuel ratio, and dead fine fuel proportion – Tab. 2). We followed published protocols to sample, measure, and estimate traits, drawing on a standardized methodology paper (Pérez-Harguindeguy et al. 2013), plant trait database studies (Tavsanoglu & Pausas 2018, Kattge et al. 2020), and specific research articles (Dimitrakopoulos & Papaioannou 2001, Engber & Varner 2012, Murray et al. 2013, Parsons et al. 2015, Grootemaat et al. 2017) (Tab. 2).

We sampled ten mature, undamaged leaves from each plant for leaf trait measurements. For species with smaller leaves, twigs containing more than ten leaves were collected to retain leaf moisture content until measurements were conducted. We placed these leaves in tea filter bags along with a piece of moistened filter paper. We later placed three filter bags from

Tab. 2 - Flammability traits used in the study, along with their units, definitions, measurement or estimation methods, and related references. References for field or laboratory measurements specifically used in our study are underlined.

Trait	Trait full name	Unit	Definition of trait	Measuring/Estimation	References
LDMC	Leaf dry matter content	mg g ⁻¹	The ratio of the dry mass of the leaf to the corresponding water-saturated fresh mass	LDMC = Leaf dry weight / water-saturated leaf weight	<u>Pérez-Harguindeguy et al. (2013)</u> , Kattge et al. (2020)
LMC	Leaf moisture content	%	Percentage of water in a leaf determined as a ratio of dry weight	LMC = [(fresh weight - dry weight) / dry weight] · 100	De Lillis et al. (2009)
LT	Leaf thickness	mm	The thickness of an individual leaf	Digital slide caliper	Engber & Varner (2012), <u>Pérez-Harguindeguy et al. (2013)</u> , Grootemaat et al. (2017), Kattge et al. (2020)
LC	Leaf curliness	mm	The distance of a leaf on flat ground up to the highest curling point	Millimeter ruler	Engber & Varner (2012), Parsons et al. (2015), Grootemaat et al. (2017)
BR	Branching architecture	cm	The ratio of the length of the lateral branches of the species to the corresponding number of branches	BR = Length of the lateral branches / number of branches	<u>Pérez-Harguindeguy et al. (2013)</u>
DLF	Dead to live fuel ratio	Ratio	Dead to live fuel biomass ratio	DL = (Dead fine fuel biomass [f.b.] + Dead coarse f.b.) / (Live fine f.b. + Live coarse f.b.)	Saura-Mas et al. (2010)
CFF	Coarse to fine fuel ratio	Ratio	Coarse (≥ 6 mm diameter) to fine fuel (< 6 mm diam.) biomass ratio, including live and dead material	CFF = (Live coarse f.b. + Dead coarse f.b.) / (Live fine f.b. + Dead fine f.b.)	Saura-Mas et al. (2010), Tavsanoglu & Pausas (2018)
DFF	Dead fine fuel amount	%	Standing fine (< 6 mm diam.) dead biomass attached to the plant during the dry season expressed in proportion of the total aboveground biomass	DFF = (Dead fine f.b. / Total biomass) · 100	Saura-Mas et al. (2010), Tavsanoglu & Pausas (2018)

individuals of each species at a study site into air-inflated, sealed plastic bags. These were stored in a cooler during fieldwork and then in a refrigerator until measurements were conducted.

Leaf curliness and leaf thickness measurements were performed before measuring leaf fresh mass. Leaf curliness (LC) was determined by measuring the distance from the leaf surface to its highest curling point on a level surface using a millimeter ruler (Engber & Varner 2012, Parsons et al. 2015, Grootemaat et al. 2017 – Tab. 2). Average curliness values of ten leaves from each individual were calculated. Leaf thickness (Lt) was measured with a digital micrometer positioned at the center of the leaf, avoiding leaf veins (Pérez-Harguindeguy et al. 2013 – Tab. 2). We measured fresh weights of leaves using a digital scale within 24 h of sampling. The same leaves were oven-dried at 70 °C for 72 h to determine their dry weights (Pérez-Harguindeguy et al. 2013). Leaf moisture content (LMC) was calculated as the ratio of the difference between fresh and dry weights to the dry weight (Murray et al. 2013), while leaf dry matter content (LDMC) was calculated as the ratio of dry mass to water-saturated fresh mass (Pérez-Harguindeguy et al. 2013).

We examined two main branches per plant in the field to determine branching architecture (BR). For each main branch, we counted the number of lateral branches and measured the main branch length. Then, we calculated branching architecture as the number of lateral branches per unit length of the main branch (Tab. 2).

To reveal the combustibility component of plant flammability, we estimated standing fuel loading by measuring fine and coarse, as well as live and dead, standing plant material for each sampled individual. We collected biomass samples from the

same individuals used for leaf sampling in the field. Immediately after collection, we sorted the living and dead plant material into separate paper bags and stored the samples in a dark, low-humidity box until transport to the laboratory. In the laboratory, we further divided the material into two fuel classes based on diameter: fine (<6 mm) and coarse (>6 mm). All leaf material was classified as fine fuel. This process resulted in data for four standing fuel classes for each individual: fine dead, fine live, coarse dead, and coarse live. The classified plant material was then dried at 80 °C for 48 h in a temperature-controlled oven to determine the dry mass of each fuel class (Pérez-Harguindeguy et al. 2013). Using these data, we calculated three combustibility traits (Saura-Mas et al. 2010, Tavsanoğlu & Pausas 2018): dead to live fuel ratio (DLF), coarse to fine fuel ratio (CFF), and dead fine fuel proportion (DFF – Tab. 2).

The studied traits are among the most commonly used to assess plant flammability (Pérez-Harguindeguy et al. 2013 – see also references in Tab. 2) and exhibit variable relationships with it. Specifically, flammability increases with LDMC, LC, DLF, and DFF, while it decreases with LMC, BR, LT, and CFF (Schwilk 2003, Scarff & Westoby 2006, Saura-Mas et al. 2010, Pausas et al. 2012, Murray et al. 2013, Pérez-Harguindeguy et al. 2013).

Data analysis

We used descriptive statistics and box-plots to examine the variability in flammability traits among species. Trait data were tested for normality and homoscedasticity using the Shapiro-Wilk test and histograms. Data were log-transformed prior to all analyses to better approximate normality and ensure homogeneity of variances. We performed all analyses in the R environ-

ment (<https://www.r-project.org/>).

For each trait, we performed a one-way analysis of variance (ANOVA) to identify differences among species, followed by Tukey's HSD test for multiple comparisons. Based on significant differences identified through *post-hoc* tests ($P < 0.05$), we assigned each species to one of the following flammability level groups for each trait: high, moderate-high, moderate, moderate-low, and low. Threshold values for each flammability level group for each trait were determined using this assignment procedure. However, in a few cases where sample sizes were too small to detect significant differences, exceptions to this rule were made during the grouping process. To visualize flammability levels, we used different colors to represent the groups in trait variability graphs. This approach allowed us to identify specific groups of relative flammability levels by considering the relationship of each trait with flammability (i.e., some traits had a positive relationship, while others had a negative one). Additionally, we used one-way ANOVA to analyze among-species differences in the proportion of fuel fractions of standing biomass for each trait. We used a percent stacked bar chart to display the proportion of fuel fractions for each species.

To calculate the “flammability score”, representing the overall flammability of each species, we first assigned species to flammability level groups (low: 1, moderate-low: 2, moderate: 3, moderate-high: 4, and high: 5) for each trait based on thresholds derived from ANOVA and Tukey HSD tests (see Tab. S4 in Supplementary material). These thresholds were determined by dividing the trait ranges into meaningful intervals that reflected observed ecological variation. For highly correlated traits (e.g., DLF and DFF; $r > 0.70$ – Fig. S1), their contributions were averaged to avoid overrepresentation in the flammability score. The flammability level scores across traits were summed to calculate the overall flammability score, with equal weight assigned to each trait. This integrative approach enabled us to compare the relative flammability of species while minimizing biases arising from redundant trait information.

Results

All flammability traits showed substantial variation among the studied species ($P < 0.0001$ – Tab. 3; Figs. S2-S9, Tab. S3 in Supplementary material). The range of leaf trait values varied considerably across species, with a sixfold difference observed for leaf dry matter content and a 31-fold difference for leaf moisture content. Branching architecture was among the most variable traits, exhibiting approximately a 36-fold difference between minimum and maximum values. Fuel loading traits also displayed pronounced variability among species, ranging from zero (i.e., lacking dead, coarse, or dead fine fuels) to 4.2 and 16.0 for DLF and CFF, respectively, and a 60.0%

Tab. 3 - Descriptive statistics of among-species variability in flammability traits. Results of one-way ANOVAs testing differences among species for each trait are also provided. *n* refers to the number of species considered for each trait. Species (codes as listed in Tab. 1) with minimum and maximum values are indicated in parentheses.

Trait	n	Min	Median	Mean	Max	F	P
Leaf dry matter content (mg g ⁻¹)	22	150.8 (ply)	576.7	557.4	934.0 (qco)	52.4	<0.0001
Leaf moisture content (%)	22	9.6 (pte)	100.2	115.3	298.4 (ech)	22.6	<0.0001
Branching (cm)	26	1.080 (ast)	7.345	9.206	38.5 (ech)	39.5	<0.0001
Leaf curliness (mm)	22	0.16 (pla)	0.52	0.60	2.72 (aan)	60.6	<0.0001
Leaf thickness (mm)	22	0.14 (jox)	0.27	0.31	1.02 (ply)	52.4	<0.0001
Dead to live fuel ratio	26	0 (sju)	0.09	0.23	4.23 (aap)	4.6	<0.0001
Coarse to fine fuel ratio	26	0 (aap,ast,tdi)	1.67	2.02	16.0 (dgn)	34.2	<0.0001
Dead fine fuel amount (%)	26	0 (sju)	5.61	9.14	60.0 (oon)	10.1	<0.0001

value for DFF (Tab. 3, Fig. 1).

Species exhibited varying levels of flammability across different traits, with no single species consistently showing higher or lower flammability across all traits. Consequently, many species ranked at the low end of the flammability continuum for one trait while appearing at the highly flammable end for another (Fig. 2, Figs. S2-S9 in Supplementary material). For example, *Phillyrea latifolia* exhibited highly flammable characteristics for leaf dry matter content and leaf moisture content (Fig. 2, Figs. S2-S3) but had lower flammability based on its leaf curliness (Fig. 2, Fig. S5). Moreover, in some species, multiple traits contributed significantly to their overall flammability. For instance, *Quercus coccifera* displayed high or moderate-high flammable characteristics in three leaf traits and branching architecture, while *Arbutus andrachne* ranked at the more flammable end of the trait continuum for four leaf traits (Fig. 2, Fig. S2-S6). Similarly, *Asparagus aphyllus* and *Astragalus* sp. demonstrated very high flammability in all four traits measured.

In contrast, some species (*Laurus nobilis*, *Styrax officinalis*, *Spartium junceum*, and *Phlomis* spp.) were at the less flammable end of trait continua for several traits (Figs. S2-S9 in Supplementary material). Even though these species had relatively lower overall flammability scores (Fig. 2), they exhibited flammable characteristics in a few specific traits. For instance, the flammability of *L. nobilis* was higher due to its leaf moisture content, while the leaf thickness and curliness of *S. officinalis* contributed to its flammability. Similarly, both *Phlomis lycia* and *P. grandiflora* exhibited higher flammability when leaf curliness was considered alone. Additionally, a few other traits uniquely contributed to the flammability of each of these species.

These results indicated that all but a few of the studied species exhibited a flammable character for at least one trait included in the study. Since traits contributing to higher flammability were species-specific, the ranking of species by flammability value varied significantly across traits (Figs. S2-S9 in Supplementary material). Consequently, interspecific variation in flammability persisted when considering the overall flammability score (FS) derived from the eight measured flammability traits (Fig. 2). In this sense, species could be ranked by their overall flammability, with *Asparagus aphyllus*, *Astragalus* sp., and *Genista acanthoclada* achieving the highest flammability scores (FS = 5.00, 5.00, and 4.00, respectively), while *Spartium junceum* presented the lowest score (FS = 1.67). Other notable species include *Quercus coccifera* (FS = 3.50) and *Arbutus andrachne* (FS = 3.57), which had relatively high scores, and *Laurus nobilis* (FS = 2.14), which had a lower score. The flammability score of other species ranged from 3.43 to 2.71 (Fig. 2).

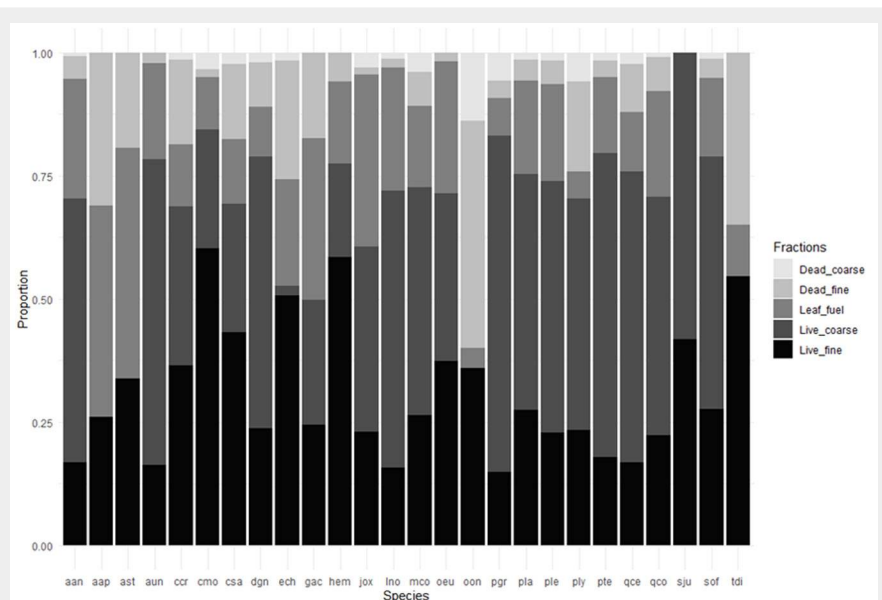


Fig. 1 – The proportion of plant fractions (dead and live, fine and coarse materials, and leaves) based on total dry weight for each species. Species codes are provided in Tab. 1.

Discussion

Our study demonstrated that the traits contributing to increased flammability in Mediterranean woody plants are idiosyncratic at the species level. Traits such as complex branching structure, retention of standing dead material, and curved, dense, or thin leaves, which enhance plant flammability, were found in various combinations across the studied species. These findings confirm our hypothesis that the Mediterranean woody species analyzed in the study area possess diverse traits contributing to higher flammability.

Our results revealed that several species exhibited very high flammability across multiple traits. Most of these species (*Quercus coccifera*, *Arbutus* spp., *Cistus*

salviifolius, *Phillyrea latifolia*, and *Genista acanthoclada*, among others) are characteristic components of Mediterranean shrublands and also occur in the understory of low-altitude pine forests (Tüfekcioglu & Tavsanoğlu 2022). Conversely, many species with relatively lower flammability scores (e.g., *Phlomis grandiflora*, *Phlomis lycia*, *Styrax officinalis*, and *Laurus nobilis*) could be considered more flammable when specific traits are evaluated in isolation. For instance, considering the negative relationship between leaf thickness and flammability (Montgomery & Cheo 1971, Grootemaat et al. 2017, Cubino et al. 2018), *S. officinalis*, *C. monogyna*, and *P. terebinthus* exhibited highly flammable characteristics due to their thinner leaves. Similarly, leaf curliness

Species	LDMC	LMC	BR	LC	LT	CFF	DLF	DFF	FS
aap	-	-	1.5	-	-	0	1.797	28.33	5.00
ast	-	-	3.3	-	-	0	1.434	25.65	5.00
gac	-	-	2.8	-	-	1.44	0.458	17.14	4.00
aan	658.9	98.3	12.8	1.921	0.242	3.28	0.071	4.55	3.57
qco	648.9	86.9	5.8	0.777	0.319	2.40	0.120	6.80	3.50
pla	669.3	77.2	6.9	0.312	0.250	1.95	0.086	4.82	3.43
csa	561.4	108.4	6.0	0.647	0.384	0.64	0.304	14.81	3.36
oeu	654.4	89.2	3.7	0.381	0.317	0.90	0.020	1.41	3.29
qce	341.5	79.3	10.5	1.060	0.230	3.74	0.168	10.05	3.29
ccr	482.9	109.2	5.5	0.525	0.412	0.92	0.226	12.69	3.21
aun	553.4	106.7	8.5	1.646	0.214	3.69	0.027	2.08	3.14
hem	389.5	73.2	10.9	0.216	0.223	0.28	0.071	5.48	3.14
ple	713.8	102.7	10.1	0.374	0.322	2.27	0.106	5.86	3.07
mco	621.3	126.2	8.5	0.403	0.185	2.07	0.108	6.00	3.07
oon	313.8	169.5	17.6	0.213	0.223	0.39	1.619	43.94	3.00
ech	590.4	253.8	27.0	0.474	0.252	0.10	0.632	21.83	3.00
dgn	574.8	109.7	8.9	0.335	0.203	2.78	0.108	7.10	2.93
tdi	393.6	157.9	8.0	0.288	0.335	0	0.788	36.42	2.93
jox	554.1	116.5	4.6	0.230	0.252	1.95	0.110	1.86	2.86
cmo	407.3	125.6	3.7	0.298	0.234	0.46	0.054	1.24	2.86
pte	435.3	103.6	14.3	0.607	0.211	3.84	0.074	3.43	2.79
pgr	659.7	94.7	15.5	0.990	0.776	5.04	0.118	3.60	2.71
ply	211.1	123.9	12.7	1.255	0.945	2.75	0.462	19.40	2.71
sof	216.1	201.2	11.1	0.951	0.208	2.69	0.067	4.24	2.71
lno	533.2	108.5	14.6	0.493	0.434	3.60	0.036	1.55	2.14
sju	-	-	22.9	-	-	1.19	0	0	1.67

Fig. 2 – Mean values of nine flammability traits for each species and their overall flammability scores (FS). The flammability level of each species and trait is represented by different colors: red (high), orange (moderate-high), yellow (moderate), light green (moderate-low), and dark green (low). Species are sorted by their overall flammability scores. Detailed graphs for each trait are provided in Figs. S2-S9. Trait names are listed in Tab. 2, species codes are provided in Tab. 1, and trait units are given in Tab. 3.

contributed to the overall flammability of *P. lycia*, *P. grandiflora*, and *S. officinalis*, even though these species had relatively lower flammability scores. *L. nobilis*, which had the lowest flammability score among species for which all eight traits were measured, could be mistakenly classified as flammable if only leaf moisture content were considered. We observed these inconsistencies across all the species examined, as each species could be considered highly flammable for certain traits but not for others. This finding suggests that Mediterranean plants in fire-dependent communities exhibit species-specific strategies for flammability, supporting the idea of alternative flammability syndromes that provide equivalent fitness under frequent fire regimes (Michelaki et al. 2020). Given the intra- and interspecific variability in flammability traits observed in our study and across different ecosystems (Murray et al. 2013, Santacruz-García et al. 2019, Michelaki et al. 2020), defining such flammability syndromes could improve our understanding of fire-related dynamics at regional or global scales. Jaureguiberry & Díaz (2023) recently proposed that plant flammability may represent the third dimension of plant fire syndromes, alongside classical resprouting and seeding. This hypothesis is based on evidence that plant species in Mediterranean-type ecosystems are more flammable than those in many other ecosystems. Our results partially support this argument, as all species in our study, except *Spartium junceum* and *Laurus nobilis*, exhibited at least one highly flammable trait. Consequently, considering flammability as a component of plant fire syndromes may enhance our understanding of the drivers of trait variation in the plants from fire-prone ecosystems.

The species-specific nature of flammability traits makes species selection a critical stage in studies addressing flammability-related questions, especially when the number of species included is limited. In such cases, biased estimation of overall flammability can lead to erroneous interpretations of community-level patterns in flammability traits and vegetation flammability. Comparing and sorting plant species by flammability can be effectively achieved by incorporating multiple components of plant flammability (Stevens et al. 2020, Güney et al. 2022). The interspecific variability in flammability was evident in our study through the calculated flammability scores based on eight traits. Our findings on the flammability of woody species in southwestern Anatolia, derived from plant functional traits, do align with a recent study in a nearby region that grouped species based on leaf flammability using laboratory burnings (Güney et al. 2022). Specifically, for species common to both Güney et al. (2022) and our study, *Arbutus andrachne*, *Phillyrea latifolia*, and *Quercus coccifera* were more flammable than *Cistus creticus*, *Myrtus communis*, and *Pistacia terebinthus*.

In this context, our species sorting based on flammability scores, from most to least flammable, is robust, as it integrates multiple leaf traits, a branching trait, and three combustibility traits. Our results suggest that incorporating several components of flammability into studies involving a limited number of species can mitigate potential bias in estimating community flammability (Murray et al. 2020). This approach is also relevant for fire-protection or risk-reducing strategies in wildland-urban interfaces or firebreaks, where planting woody species with low flammability is a key objective. However, our study highlights the challenges of identifying fire-resistant (i.e., hard-to-burn) species in Mediterranean Basin fire-prone ecosystems. Consequently, the effort to plant “less flammable” species may be ineffective, primarily when species selection relies on studies comparing a few species and traits. Searching for less flammable species to construct fire-resistant vegetation belts near human settlements or to create less flammable forest patches is increasingly critical as climate change drives larger and more intense fires. For effective forest management, multiple traits should be considered when selecting less flammable species rather than relying on a single characteristic. For example, based on flammability scores in our study, *Spartium junceum*, *Laurus nobilis*, *Styrax officinalis*, and *Phlomis* spp. are suitable candidates for constructing a less-flammable green belt in forested areas. An integrative approach, such as calculating flammability scores based on multiple flammability traits as in our study, offers a robust framework for making these selections.

Our results are derived from a single region of the Mediterranean Basin and should, therefore, be interpreted cautiously by forest managers who are applying risk-reducing treatments with relatively less flammable species. While our selection of eight traits that capture different aspects of plant flammability likely reduced potential bias in the calculated flammability scores, we acknowledge that a different set of traits could have resulted in different species rankings based on flammability. Notably, there is no scientific consensus on which traits contribute most significantly to plant flammability, highlighting the need for further research to determine the relative importance of specific traits across various ecosystems. Additionally, although plant flammability can be predicted using functional traits, other dimensions of flammability exist at both the plant level (e.g., plant chemicals, litter flammability) and the vegetation level (e.g., meteorological conditions). More comprehensive studies that include a greater diversity of species and traits are urgently needed to identify low-flammability species for management purposes in wildland-urban interfaces and forested landscapes. Investigating interspecific variability in flammability traits within

plant communities may also enhance our understanding of community assembly dynamics in fire-prone ecosystems. In this context, our study contributes to the understanding of the variability in flammability traits among Mediterranean Basin plants, particularly those from the studied region. It offers insights into why Mediterranean vegetation as a whole is highly flammable.

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Data availability statement

The raw data used and analyzed in this study are available in table and graph formats in the Supplementary material.

Conflicts of interest statement

The authors declare no conflicts of interest.

Authors' contribution

Nursema Aktepe: Conceptualization (supporting); data curation (lead); formal analysis (equal); investigation (lead); methodology (equal); resources (equal); software (equal); validation (equal); visualization (equal); writing - original draft (equal); writing - review and editing (equal). Çagatay Tavsanoğlu: Conceptualization (lead); data curation (supporting); formal analysis (equal); funding acquisition (lead); investigation (supporting); methodology (equal); project administration (lead); resources (equal); software (equal); supervision (lead); validation (equal); visualization (equal); writing - original draft (equal); writing - review and editing (equal).

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Supplementary Material

Fig. S1 - Correlation among the studied traits at the species level.

Fig. S2 - Variation in leaf dry matter content across species.

Fig. S3 - Variation in leaf moisture content across species.

Fig. S4 - Variation in branching architecture across species.

Fig. S5 - Variation in leaf curliness across species.

Fig. S6 - Variation in leaf thickness across species.

Fig. S7 - Variation in coarse to fine fuel ratio across species.

Fig. S8 - Variation in dead to live fuel ratio across species.

Fig. S9 - Variation in dead fine fuel amount across species.

Tab. S1 - Species sampled for flammability traits in each study site.

Tab. S2 - The number of individuals sampled and sampling sites for each species included in the study.

Tab. S3 - Value ranges of flammability level groups in each trait.

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