Adaptive flammability syndromes in thermo-Mediterranean vegetation, captured by alternative resource-use strategies

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HIGHLIGHTS

- Leaf traits define global resource allocation trade-offs and influence flammability.
- Quest for relations among flammability attributes and links with plant economics.
- Revealed a 2-dimensional flammability spectrum driven by resource-use strategies
- Size controls heat release rate, and leaf economics ignitibility and combustibility.
- Alternative flammability syndromes offer equivalent fitness under recurrent fires.

GRAPHICAL ABSTRACT
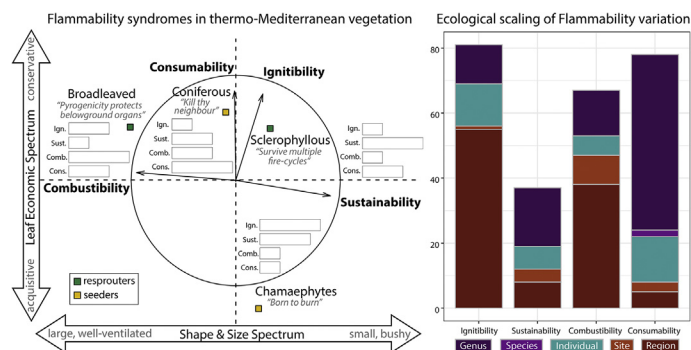
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ABSTRACT

Fire affects and is affected by leaf functional traits indicative of resource allocation trade-offs. Global change drivers constrain both the resource-use strategies and flammability of coexisting species. However, small attention has been given in identifying links among flammability and plant economics. Ambiguity comes from the fact that flammability is a multidimensional trait. Different flammability attributes (i.e. ignitibility, sustainability, combustibility and consumability) have been used to classify species, but no widely-accepted relationships exist between attributes. We hypothesised that flammability is a spectrum (defined by its four attributes) and the alternative flammability syndromes of coexisting species can be captured by their resource-use strategies. Furthermore, we argue that flammability syndromes are adaptive strategies that ensure persistence in the post-fire community. We conducted a large-scale study to estimate all flammability attributes on leaves from nine, dominant, thermo-Mediterranean species with alternative resource-use and fire-response strategies across a wide environmental and geographic gradient. We assessed the interdependence among attributes, and their variation across ecological scales (genus, species, individual, site and region). Furthermore, we collected 10 leaf functional traits, conducted a soil study and extracted long-term climatological data to quantify their effect on flammability attributes. We found that leaf flammability in thermo-Mediterranean vegetation is a continuous two-dimensional spectrum. The first dimension, driven by leaf shape and size, represents heat release rate (combustibility vs. sustainability), while the second, controlled by leaf economics, presents ignition delay and total heat release (i.e. consumability). Alternative flammability syndromes can increase fitness in fire-prone

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communities by offering qualitative differences in survival or reproduction. Trade-offs and constraints that control the distribution of resource-use strategies across environmental gradients appeared to drive leaf flammability syndromes as well. Tying the flammability spectrum with resource allocation trade-offs on a global scale can help us predict future ecosystem properties and fire regimes and illustrate evolutionary constraints on flammability.

1. Introduction

In Mediterranean climate ecosystems wildfires occur naturally at least since the late Quaternary (Carrión et al., 2003) and plants have developed adaptive mechanisms to cope with them (Pausas and Verdú, 2005; Clarke et al., 2013). Fire disturbance has been found to play an important role in determining species' distributions and vegetation dynamics across landscapes (Bond et al., 2005; Bond and Scott, 2010). By acting as a selective force on plants, fire directly eliminates the most vulnerable individuals in a community and alters environmental conditions, thus promoting (or excluding) specific physiological and morphological functional traits. Structural and chemical leaf traits define how plants acquire and use resources and through their interactions they influence ecosystems properties (Reich et al., 1997; Lavorel and Garnier, 2002; Wright et al., 2004; Díaz et al., 2016). At the same time they determine the amount of energy needed to start the fire reaction and the available fuel area that will interact with the atmospheric oxygen. As such they influence plant flammability (i.e. the ease of plant biomass to burn) and through that fire probability and behaviour (Cornwell et al., 2015; Zylstra et al., 2016). Global change drivers (e.g. greenhouse gas concentrations, climate change, habitat fragmentation, biological invasions) have been found to affect the assembly of communities and their flammability throughout geological time (Bond and Scott, 2010; He et al., 2011). Vegetation shifts can alter the flammability of communities and in return result to fire regime changes (i.e. pattern, frequency, and intensity of fire) that can feedback to determine ecosystems' composition and processes (Belcher et al., 2010; Bond and Scott, 2010; Koutsias et al., 2012). Despite the rich bibliography on the origin and evolution of flammability and its role shaping the biota of our planet (e.g. Belcher et al., 2010; Bond and Scott, 2010; Gagnon et al., 2010; He et al., 2011; Pausas et al., 2012) little is known about how it varies along the spectrum of resource-use strategies employed by plant species.

Resource-use strategies define plants' competitive ability and thus their successful establishment in a community (Reich et al., 2003; Grime, 2006). Plant species allocate their available resources between the functions of growth, survival and reproduction (Grime, 2006). Global covariation patterns among specific leaf functional traits (e.g. Specific Leaf Area: SLA, Leaf Dry Matter Content: LDMC, Leaf Area: L_A), measured across spatial and taxonomic scales, define fundamental resource-allocation trade-offs (i.e. economics spectra) that are used to classify species according to their fitness and predict their responses to disturbances and future distributions (Reich et al., 2003; Wright et al., 2004; Grime, 2006; Díaz et al., 2016). There is a perceived dichotomy on how species respond to disturbances and fire research is often restricted into examining differences among them. Resprouters depend on the survival of root crown and other underground organs for their continued presence in the post-fire community, while obligate seeders rely on (soil or canopy-stored) seed banks for the establishment of a future generation (cohort) of individuals (Pausas et al., 2004; Paula and Pausas, 2008; Vallejo et al., 2012). In nature, resource-use and fire-response strategies vary continuously within and between species, and across communities (Hodgkinson, 1998; Casals et al., 2018; Michelaki et al., 2019) depending on disturbance frequency and severity, and site productivity (Bellingham and Sparrow, 2000; Pausas, 2001; Lavorel and Garnier, 2002; Clarke et al., 2013). Evidence of covariation among functional traits indicative of economic resource allocation trade-offs and these two fire-response

strategies have been gathering from around the world (e.g. Scarff and Westoby, 2006; Saura-Mas and Lloret, 2007; Saura-Mas et al., 2010). In general, resprouting species have been found to follow conservative strategies, allocating more resources to storage tissues, thus being longer-lived and slower-maturing (Verdú, 2000; Pausas et al., 2004; Grime, 2006; Saura-Mas and Lloret, 2007). In the Mediterranean Basin, many resprouting species (e.g., *Quercus coccifera*, *Pistacia lentiscus*) are also more drought-tolerant due to later stomata closure and higher carbon assimilation at lower water potentials than drought-avoiding seeding taxa (such as *Pinus* and *Cistus*) (Pausas et al., 2004; Saura-Mas and Lloret, 2007). However, the patterns of covariation in some cases vary among the different Mediterranean climate ecosystems of the world, thus limiting their predictive power on a global scale (Pausas et al., 2004). Resprouters were present from the Tertiary (pre-Pliocene), before the establishment of the typical Mediterranean climate in the Quaternary (post-Pliocene) when most of the seeding taxa evolved (Suc, 1984; Verdú, 2000; Pausas and Verdú, 2005). The different biogeographical origins of coexisting Mediterranean species constrain both their functional role and flammability in a community (Belcher et al., 2010; Bond and Scott, 2010; He et al., 2011; Díaz et al., 2016).

Leaf flammability is a complex, multidimensional plant trait, difficult to define scientifically, that is described through four attributes: a. ignitibility indicates how fast leaves combust when exposed to a heat source; b. sustainability determines the amount of time the combustion lasts and contributes to the larger fire as a heat source for nearby biomass; c. combustibility demonstrates how well leaves burn and correlates with the rate of fire spread; d. consumability represents the proportion of consumed leaf biomass and correlates with the energy released as heat during burning (Anderson, 1970; Martin et al., 1994). Plant species are known to differ significantly in their flammability attributes even within climatic zones and vegetation types (e.g. Scarff and Westoby, 2006; Simpson et al., 2016). Larger leaves have been found to be more combustible (Scarff and Westoby, 2006; Magalhães and Schwilk, 2012; van Altena et al., 2012; Cornwell et al., 2015) and lower SLA, indicative of conservative resource-use strategies, has been associated with reduced ignitability, but higher consumability (van Altena et al., 2012; Murray et al., 2013; Grootemaat et al., 2015). Seeders have been characterised as fire-prone and associated with fast ignition (Saura-Mas et al., 2010), but leaves from resprouters have been described more combustible and consumable (Scarff and Westoby, 2006). Moreover, non-additive effects have been discovered driven by the most flammable, in terms of sustainability, combustibility and consumability, species in a community regardless of the proportion of biomass that they contribute (Magalhães and Schwilk, 2012; van Altena et al., 2012).

From the above one is left perplexed as to what high leaf flammability is. Many researchers have studied one or some of the flammability attributes in order to classify species according to their leaf flammability (e.g. Scarff and Westoby, 2006; Saura-Mas et al., 2010; Magalhães and Schwilk, 2012; van Altena et al., 2012; Grootemaat et al., 2015; Simpson et al., 2016), but few have attempted to identify relationships between flammability attributes and among flammability attributes and leaf functional traits. If both flammability syndromes and resource-use strategies vary within and between species as a function to environmental pressures, then leaf flammability variation could be predicted from a few key leaf traits indicative of economic trade-offs.

Identifying a global leaf flammability spectrum that coordinates with the global plant trait spectrum of form and function could improve models predicting future fire regimes and ecosystem processes and allow us to elucidate evolutionary constraints on flammability.

In this paper we employ a new approach that incorporates the complex nature of flammability with plant economics. We hypothesised that: (1) at the individual level leaf flammability is a spectrum defined by its four attributes and the alternative flammability syndromes of coexisting species can be better captured by their resource-use strategies, rather than the dichotomy resprouter versus seeder; (2) since in fire-prone ecosystems (where fire-disturbance is frequent enough to act as a selective pressure) flammability syndromes define species' fitness (sensu Bond and Midgley, 1995), they are likely adaptive strategies that ensure persistence in the post-fire community.

This study was designed to tie an individual's leaf flammability to its resource-use strategy and the environmental pressures it is facing. In a previous study we constructed a large, systematic database of 10 leaf functional traits (Table S1) reflecting whole-plant economics (e.g. construction costs, hydraulics, defences, water storage capacity) across a wide environmental and geographic gradient (Michelaki et al., 2019). Here, we further measured all four flammability attributes (i.e. ignitibility, sustainability, combustibility and consumability) on leaves from the same individuals of nine, dominant, lowland, thermo-Mediterranean species with alternative resource-use and fire-response strategies (Table S2). Our sampling design allowed us to identify relationships between leaf flammability syndromes and recourse allocation trade-offs. Such relationships could help us predict future vegetation distributions and ecosystem properties, as well as explain and manage past and future fire regimes. Furthermore we attempted to gain a general ecological understanding of leaf flammability variation by assessing how each flammability attributes' variance is distributed across five, hierarchically structured, taxonomic and spatial scales commonly studied by ecologists: between genera and species (9 species from 6 genera), within-species (810 individuals: on average 90 per species), among sites (65 sites: on average 19 per species), and across regions (10 regions, average of 7 sites per region). Identifying which scales hold the majority of total variance for each attribute could act as blueprint for future research efforts that attempt to demonstrate evolutionary changes in flammability.

2. Materials and methods

2.1. Study location and species

Greece is located in the southeaster part of Europe, stretching from 35°000′ to 42°000′ N and from 19°000′ to 28°300′ E. Mainly bordered by the Mediterranean Sea the country is characterised by Mediterranean-type climate with mild, wet winters and (often extremely) warm and dry summers (di Castri, 1981) during which most fires occur (Tsagari et al., 2011). The lowland vegetation is composed by patches of: open *Pinus halepensis*, *P. brutia* coniferous forests with an evergreen shrub understory (e.g. *Quercus coccifera*, *Phillyrea latifolia*), Mediterranean evergreen forests (e.g. *Pistacia lentiscus*, *Q. coccifera*, *Arbutus unedo*, *A. andrachne*), dense maquis shrublands (e.g. *Q. coccifera*, *Arbutus sp.*, *P. lentiscus*, *P. latifolia*), and open phrygana shrublands populated by cushion-shaped (often aromatic) chamaephytes (e.g. *Cistus sp.*). We selected nine, dominant species following alternative resource-use (Michelaki et al., 2019) and fire-response strategies (Paula et al., 2009) to study their leaf flammability syndromes across their distributions in Greece (Table S2).

2.2. Sampling design

For each species an adequate number of sampling sites was chosen (65 unique sampling sites: on average 19 per species) in order to cover the widest possible natural range of its variability across Greece (for a detailed description of the sampling design please refer to Michelaki et al., 2019). Sampling sites were selected to be satisfactorily uniform (e.g. vegetation composition, aspect, elevation) so that differences among them assimilate environmental heterogeneity (Table S3). An ideal sampling design would be to locate individuals from each species in every sampling site, but such expectations were unrealistic in a large-scale, non-manipulative study where species segregate to some degree along environmental gradients. The topographic characteristics (i.e. latitude, longitude, elevation, aspect, slope, and heat load) of each sampling site were recorded. Within each sampling site, five, sexually mature, healthy, unshaded individuals were randomly selected from as many of the species of interest as possible (810 unique individuals: on average 90 per species).

From each individual approximately 0.5 kg of healthy, sunlit, fully-mature (but not senescing) leaves from around the canopy was collected (as to capture the variability within them) and stored in paper bags. Leaves were sampled at the beginning of the fire-season which coincides with the spring growing-season (i.e. April to July from 2012 to 2015), as to capture the individuals of each species at a similar phenological stage. Leaves, whether alive or dry (retained on branches or in the litter), are the plant organs that ignite first in a fire and the intensity and character of their burn determine fire spread and damage to nearby tissues (Gill and Moore, 1996; Murray et al., 2013; Zhao et al., 2019). As such they largely dictate fire behaviour (Cornwell et al., 2015; Zylstra et al., 2016). While we acknowledge that several other factors affect the fire behaviour of fire-prone communities (e.g. fuel load, continuity, proportions of dead and fine fuel, plant architecture, species composition) the aim here was to compare the flammability attributes (i.e. ignitability, sustainability, combustibility and consumability) of individuals from different species with alternative strategies growing in a variety of conditions along Greece. For that purpose we judged leaf flammability as an adequate surrogate of plant flammability.

2.3. Flammability estimation

Due to the scale of our study (that spanned across years and along Greece) we saw fit to investigate the flammability of dried leaves. Many thermo-Mediterranean species retain dead leaves with low moisture content that ignite first acting as catalyst for the ignition of live fuels (Pausas et al., 2012). In field conditions, as wildfires burn and move through the landscape, heat is transferred through the air via radiation preheating and dehydrating unburned fuels up to their ignition point. By bringing all samples in a baseline moisture level we were able to compare leaf flammability attributes' variability within and between species from a variety of habitats, as well as to identify possible relationships with leaf functional traits and environmental characteristics. To prevent rotting the sampled leaves were oven-dried for 48 h at 60 °C as soon as possible after collection and subsequently stored in a desiccator jar with silica gel until the flammability estimation.

We placed 1 g of oven-dried, but otherwise intact leaves from each individual (as to capture the variability among them) in a pile in a ceramic laboratory bowl. Samples composed of small and flat leaves were more densely packed, while large, curvy and spiny leaves provided better ventilated bowls. This allowed us to incorporate flammability differences due to variation in natural packing density and thus oxygen limitation (Scarff and Westoby, 2006; Cornwell et al., 2015). The bowl was placed at the centre of a cold muffle furnace (type 1400, Barnstead Thermolyne, Dubuque, USA) that was kept in a well-ventilated room away from drafts. Neither the bowl nor the leaves had any contact with the furnace walls, so that ignition could only result from radiant heat. The furnace was switched on while its door was always kept open as to not limit the oxygen supply and allow observation of the burning process. We started counting the time when the furnace reached 60 °C to ensure that samples received equal amount of heat. Since moisture must be evaporated before ignition, by starting the flammability estimation at the point of sample dehydration we were able to

simulate the increasing temperature gradient observed in field conditions. We recorded the time at which the smouldering phase started, the time to ignition (sec) as an indicator of ignitibility, and the total burning time (sec) from when the first embers appeared till the end of pyrolysis (when all the embers were extinguished) as a proxy of sustainability (Anderson, 1970; Gill and Zylstra, 2005). When the sample was cooled down and safe to handle its total mass loss was weighted. Combustibility was estimated as the rate of weight loss from the beginning of the smouldering phase till the end of pyrolysis (g sec^{-1}) (Anderson, 1970; Gill and Zylstra, 2005) and consumability as the proportion of fuel consumed (Martin et al., 1994). Samples were burned in a random order.

2.4. Functional traits

For the same individuals additional records of 10 physiological and morphological leaf functional traits directly or indirectly associated with resource-economics at organ, individual, and ecosystem scale have been collected: SLA, m^2 kg^{-1}; LDMC, mg g^{-1}; LCC, LNC and LPC, mg g^{-1}: leaf carbon, nitrogen and phosphorus concentrations; L_L, cm: leaf length; L_{Th}, mm: leaf thickness; L_A, cm^2; L_W, cm: leaf width; $L_A:B_A$, m^2 m^{-2}: leaf area-basal area ratio (Table S1, for measurement details please refer to Michelaki et al., 2019).

2.5. Soil properties

Furthermore, from each sampling site we collected a composite soil sample (from five locations at 30 cm depth). We measured nine basic soil properties known to affect plant functioning and ecosystem dynamics through their influence upon water availability, nutrient cycling and organic matter dynamics (Yassoglou et al., 2017). Particle size distribution was estimated on air-dried, crushed and 2 mm-sieved samples (Bouyoucos, 1962). Water holding capacity (WHC %) was determined via the European maximum WHC method (Gardner, 1986), organic carbon via the Walkley-Blackwet oxidation method (Nelson and Sommers, 1982), soil nitrogen concentration (SNC, mg g^{-1}) by Kjeldahl wet-oxidation (Bremner and Mulvaney, 1982), and soil phosphorus concentration (SPC, mg g^{-1}) via the colorimetric ascorbic acid method (EPA, 1978). Magnesium (Mg) and potassium (K) were extracted with 1 N ammonium acetate at neutral pH (Thomas, 1982) and their concentrations (SMgC and SKC, both in mg g^{-1}) estimated with Sherwood Scientific Ltd. 410 flame photometer (Cambridge, UK). Soil pH and electrical conductivity (EC µS cm^{-1}) were measured in a 1:1 (soil:water) suspension (Smith and Doran, 1996).

The selected biophysicochemical characteristics are known to show high spatial variability in Mediterranean soils (Ibañez and Alba, 1995). WHC is controlled primarily by soil texture and soil organic matter (SOM %). Texture affects water and nutrients availability as the larger surface area of finer soil fractions binds more moisture and reacts better with nutrients (Weil and Brady, 2016). N, P, Mg and K are among the most functionally important nutrients, and their availability and mobility in a given soil are affected by pH and EC (Quesada et al., 2012). These nutrients along with SOM determine the basic structure and function of ecosystems (Kutsch et al., 2010).

2.6. Climate data

Finally, for each sampling site six bioclimatic variables: mean annual temperature (T_{mean}^{an} °C), mean temperature of the warmest quarter (T_{mean}^{wq} °C), total annual precipitation (Prec^{an} mm), precipitation of the warmest quarter (Prec^{wq} mm), and temperature (T^{season}) and precipitation (Prec^{season}) seasonality were obtained from the WorldClim database (i.e. Bioclim variables 1, 10, 12, 18, 4 and 15, Fick and Hijmans, 2017) at 30 s spatial resolution (i.e. approximately 1 km). Temperature and precipitation and their seasonality influence strongly the fire regime of a region. Low moisture and high temperatures are expected to lead to longer fire seasons in the Mediterranean Basin and favour fire ignition by increasing vegetation dryness (Pausas, 2004; Dimitrakopoulos et al., 2011).

2.7. Statistical analysis

To study the variation within each flammability attribute, first we examined its dispersion in the full-dataset and among the individuals of each species and each fire-response strategy (i.e. resprouter or seeder). Then, we checked for statistically significant differences between the different species, fire-response strategies, and across sampling sites (Kruskal-Wallis one-way analyses of variance and Conover's post hoc test, R Core Team, 2017).

To examine the interdependence among flammability attributes, we searched for significant bivariate relationships with standardized major axis regressions (SMA) for all statistically significant correlated attribute pairs (Spearman's correlation, level of significance 0.05). SMA is a symmetric regression appropriate in our case since we are interested in the slope between each pair, regardless of which variable is assigned to X and Y. Moreover, we applied principal components analysis (PCA, based on the correlation matrix with no rotation procedure, FactoMineR R package, Lê and Husson, 2008) to estimate flammability attributes' covariation in the multidimensional space. The analysis was performed on standardized values with "species", "fire-response strategy" and "site" as supplementary categorical variables and 10 leaf functional traits, measured on the same individuals, as supplementary continuous variables. We retained only principal components (PCs) with eigenvalues higher than one, and calculated the cross-correlation matrix between the active continuous variables (i.e. flammability attributes), the supplementary categorical (i.e. "species", "fire-response strategy" and "site") and continuous (i.e. traits) variables, and the remaining PCs. Since the supplementary variables were not involved in the construction of the PCs, their correlation will reveal the distribution of species, fire-response strategies, and sampling sites on the produced flammability plane, as well as how functional trait syndromes affect flammability syndromes.

Additionally, we implemented partial least squares regression using the SIMPLS algorithm (PLSR, pls R package, Mevik et al., 2016). This is a relative importance analysis that allowed us to estimate the effect of leaf functional traits, edaphic, climatic, and topographic characteristics on leaf flammability attributes variation and to identify the strongest drivers for each attribute. The predictor variables (i.e. leaf functional traits and environmental characteristics) were mapped into a smaller set of orthogonal latent vectors (LVs) and regressed against each flammability attribute. The PLSR algorithm iteratively aims to choose LVs that maximally explain the response variable. For each flammability attribute only predictors with normalised regression coefficients greater than one were retained via backward selection and the optimum number of LVs was estimated with cross-validation before rebuilding each model. Visual inspection of the residual plots did not reveal any obvious deviations from homoscedasticity or normality in any of the accepted models (Zuur et al., 2010). Sand and clay percentages were cosine and sine transformed prior to the analysis to remove circularity, respectively aspect was transformed into two new variables ("Northness" and "Eastness"). This supervised multivariate technique was favoured since its unaffected by the high multicollinearity among the predictor variables considered in this study.

Lastly, we partitioned leaf flammability variation across five ecological scales with nested random effects models (lme4 R package, Bates et al., 2015). For each flammability attribute a model was fitted in the following syntax: *Flammability attribute ~ (1|Genus/Species/Site) + (1|Region/Site)*, to determine the fraction of the total variance explained by each ecological scale independently. Since our dataset represents only a subset of the edaphic and climatic variability of the Greek terrestrial environment and considers just nine thermo-Mediterranean species all factors were treated as random without interaction term. All variables were Box-Cox transformed and all parameters were estimated

by the restricted maximum likelihood method. We did not detect any visually obvious deviations from homoscedasticity or normality, thus we proceeded with variance components analysis (Zuur et al., 2010). Leaf flammability variation is created in response to a range of ecological and evolutionary drivers. Different drivers of variation act at different ecological scales. Our sampling design allows us to largely ascribe the variance at specific ecological scales to particular drivers of leaf flammability variation. By grouping conspecific individuals from distinct environments into the "*Species*" and "*Genus*" scales we can partition the proportion of the total leaf flammability variance driven by genetic differences arising from adaptive evolution or drift. While by grouping populations of different, coexisting species into communities and biomes (i.e. "*Site*" and "*Region*" scales), we can isolate the fraction of the total leaf flammability variance driven by environmental gradients (i.e. climate, soil, topography). Finally, the proportion of intraspecific leaf flammability variation at the "*Individual*" scale reflects developmental instability, age, sexual genetic mixing, and plastic and filtering responses to micro-environmental gradients.
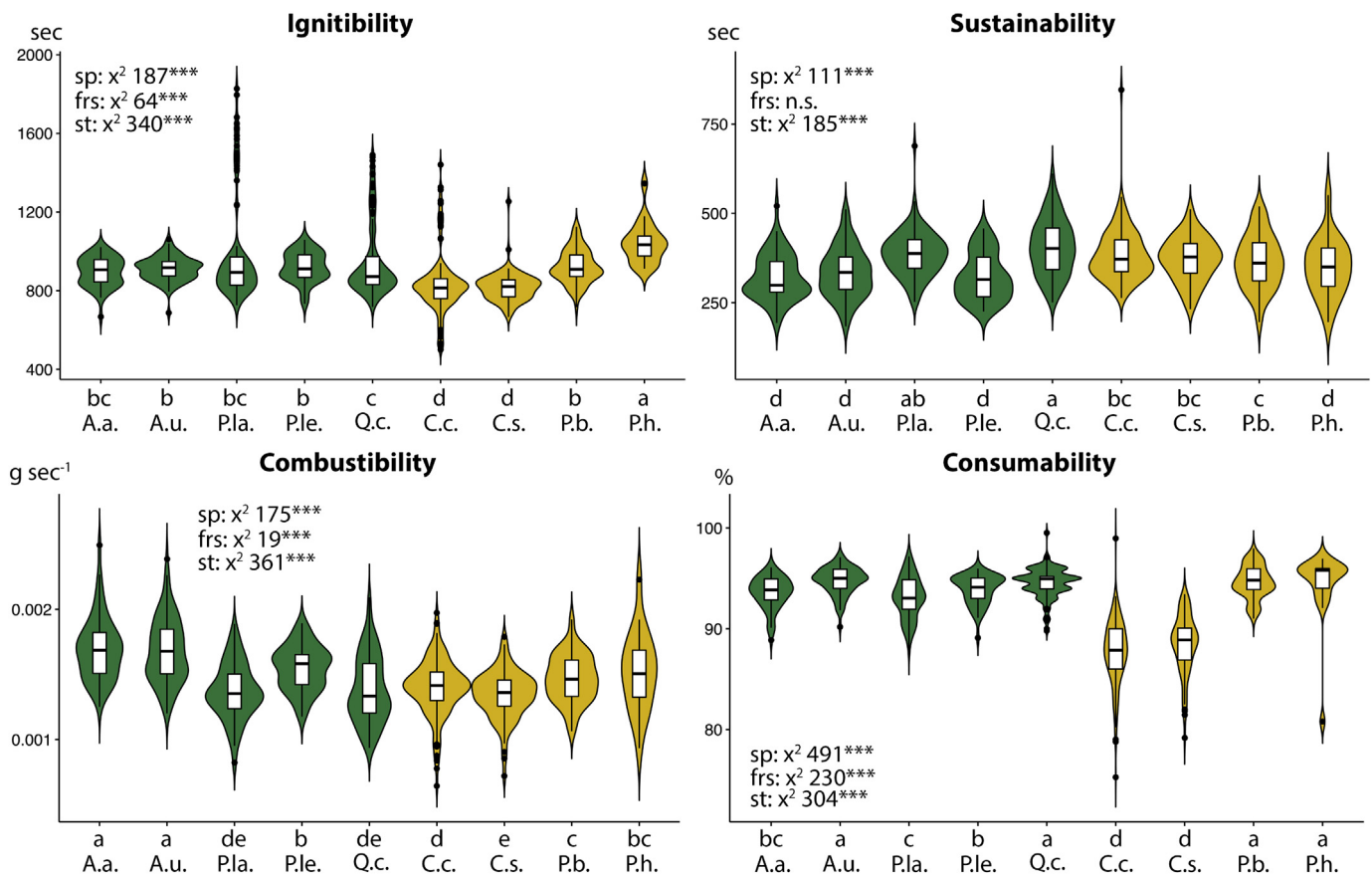
3. Results

### 3.1. Leaf flammability syndromes and resource allocation trade-offs

In this study we estimated the leaf flammability attributes of nine, dominant, thermo-Mediterranean species across Greece (Table S4). Ignition time varied from 8.3 to 30.5 min (mean 15.1 min, C.V.: coefficient of variation 18%) and the burning phase was sustained from 3.1 to 14.1 min (mean 6.2 min, C.V. 22%), during which 75.3 to 99.5% of the

leaves were consumed (mean 92.3%, C.V. 4%), on a rate of $6 \ 10^{-4}$ to $25 \ 10^{-4}$ g sec^{-1} (mean $15 \ 10^{-4}$ g sec^{-1}, C.V. 17%). When we segregated species according to their fire-response strategies we observed that leaves from resprouters ignited over a minute later and were consumed almost completely (94% C.V. 2% over 90% C.V. 5% for seeding species), but small differences were detected in combustibility (resprouters carry slightly more combustible leaves), and no statistically significant differences in sustainability (7 s) among the leaves of seeding and resprouting species (Fig. 1, Kruskal-Wallis one-way analyses of variance and Conover's post hoc test). However, significant variability was observed for all measured flammability attributes among leaves from species that employ the same fire-response strategy but alternative recourse-use strategies and among leaves from individuals growing in different environmental conditions.

In our system some general relationships can be observed among the measured flammability attributes: highly combustible leaves did not sustain fire for long and those that ignited after a longer exposure, were also consumed to a greater extent (Figs. 2 and S1). When we partitioned this covariation structure into distinct components two orthogonal axes explained 80% of the total inertia (Fig. 3, Table S5). The first principal component (PC, 44.6%) was negatively driven by combustibility and positively by sustainability, and primarily associated with architectural leaf traits (i.e. L_A, L_L, L_W, L_A:B_A). This axis opposes individuals with larger leaf area per unit of invested biomass (i.e. the broadleaved evergreen arborescent shrubs in our study) whose leaves emerged highly combustible ($16.4 \ 10^{-4}$ g sec^{-1} C.V. 13%) and extinguished fire fast (after 5.4 min C.V. 21%), against less combustible (e.g. the sclerophyllous $13.8 \ 10^{-4}$ g sec^{-1} C.V. 17%, and chamaephytes shrubs


Fig. 1. Kernel distribution density for each leaf flammability attribute measured across Greece, aggregated at the species level, for nine, dominant, thermo-Mediterranean species (see also Table S4). For each flammability attribute the results of the Kruskal-Wallis one-way analysis of variance (***: $p < 0.001$; n.s., not significant) among the different species (sp), fire-response strategies (frs: green for resprouters and yellow for seeders), and sampling sites (st) are given, along with the results of the Conover's post hoc test for each species in a descending order (from highest to lowest mean values; $n = 810$; A.a.: *Arbutus andrachne*; A.u.: *Arbutus unedo*; C.c.: *Cistus creticus*; C.s.: *Cistus salviifolius*; P.b.: *Pinus brutia*; P.h.: *Pinus halepensis*; P.la.: *Phillyrea latifolia*; P.le.: *Pistacia lentiscus*; Q.c.: *Quercus coccifera*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
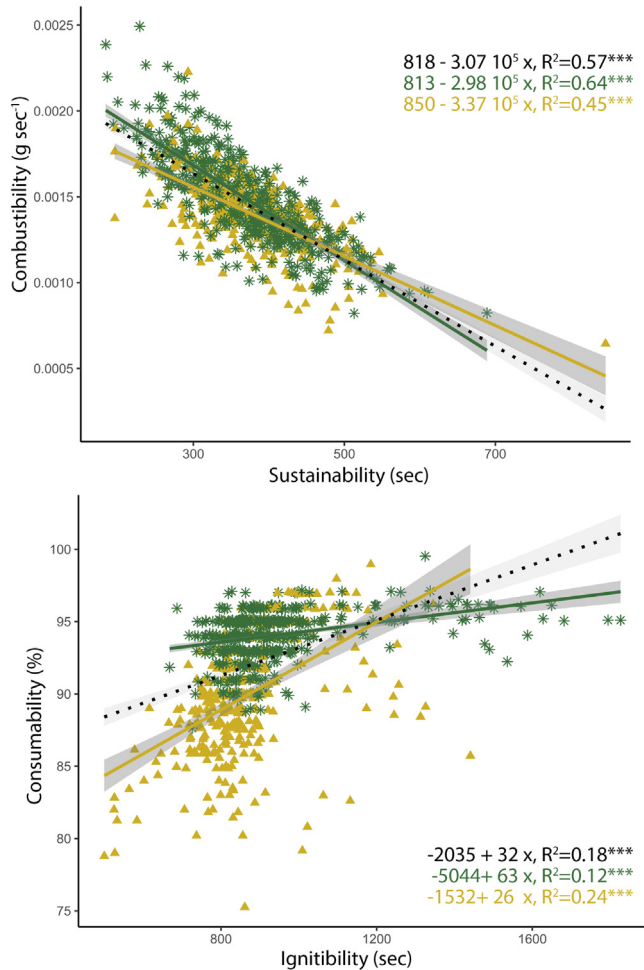
Fig. 2. Bivariate relationships (i.e. standardized major axis regressions, $y = \alpha + \beta x$; ***: $p < 0.001$) among leaf flammability attributes measured in Mediterranean, lowland, thermophilous vegetation along Greece for the full dataset (black dotted lines; $n = 810$) and among alternative fire-response strategies: green for resprouters ($n = 473$) and yellow for seeders ($n = 337$). Grey polygons depict the 95% confidence intervals inferred via bootstrapping (see also Fig. S1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$13.7 \, 10^{-4} \, \mathrm{g \, sec^{-1}}$ C.V. 15%) individuals with bushier canopies composed of smaller leaves that sustained fire longer (over 6 min C.V. 18%). The second PC (35.6%) was driven by consumability and ignitibility, and associated with structural leaf functional traits (i.e. SLA, LDMC, LCC, LNC, LPC). Acquisitive leaves (with high SLA, LNC and LPC, i.e. from the *Cistus* shrubs in our dataset) ignited 2 min faster but were consumed poorly (88% C.V. 3%), contrary to conservative, tough leaves (i.e. high LDMC, LCC, and L_{Th}, e.g. pine needles) that displayed higher fire-resistance (e.g. time to ignition for *P. halepensis* needles over 17 min, C.V. 10%) and consumability (95% C.V. 3%). These two dimensions define a spectrum of alternative, coexisting leaf flammability syndromes in thermo-Mediterranean vegetation, better captured by species resource-use strategies rather than their fire-response strategies.

To estimate the relative importance of leaf functional traits and environmental characteristics on each flammability attribute we applied PLSR (Fig. 4-lollipop plots, Table S6). Since our aim was to identify significant relationships, rather than to precisely predict each attribute, we were only interested in significant regression coefficients (i.e. mean change) whose interpretation is unaffected by R^2 values. R^2 captures the high variability (around the mean) observed at the individual scale for each of the measured flammability attributes. Resource-conservative and larger leaves (LCC and L_L 2% of the explained variance, LDMC 1%) ignited after longer exposure to heat and smothered fire
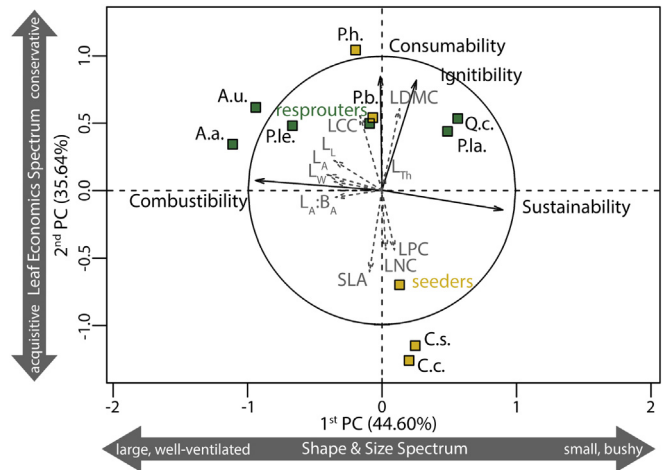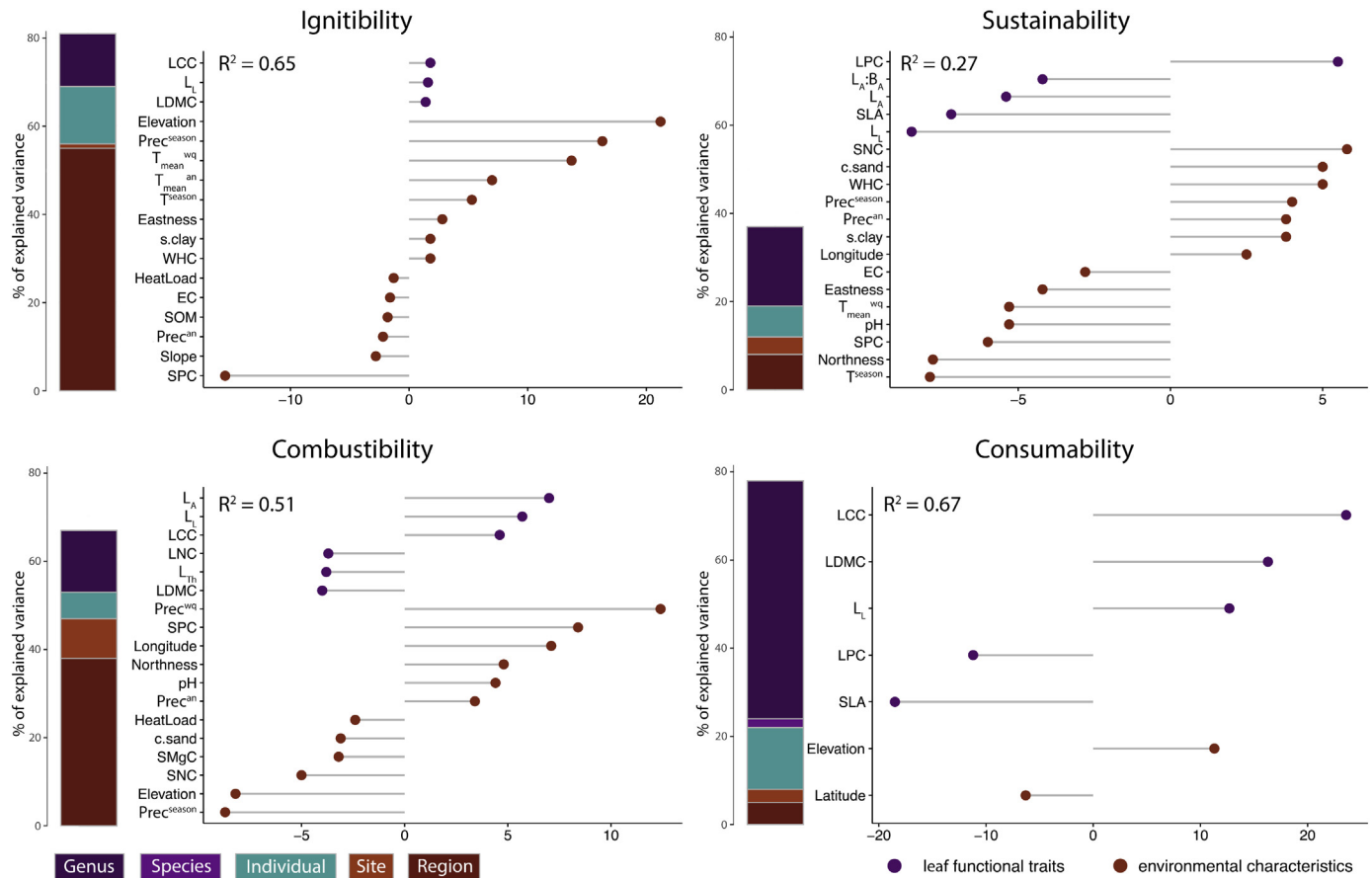

Fig. 3. Principal components analysis performed on leaf flammability attributes (variables in black) measured in Mediterranean, lowland, thermophilous vegetation along Greece, with 10 leaf functional traits measured on the same individuals as supplementary, continuous variables (in grey) and "species" and "fire-response strategy" (green for resprouters and yellow for seeders) as supplementary, categorical variables (see also Table S5) ($n = 810$; PC: principal component; SLA, $\mathrm{m^2 \, kg^{-1}}$: specific leaf area; LDMC, $\mathrm{mg \, g^{-1}}$: leaf dry matter content; L_{Th}, mm: leaf thickness; LNC, LPC & LCC, $\mathrm{mg \, g^{-1}}$: leaf nitrogen, phosphorus & carbon concentrations; L_A, $\mathrm{cm^2}$: leaf area; L_W, cm: leaf width; L_L, cm: leaf length; $L_A{:}B_A$, $\mathrm{m^2 \, m^{-2}}$: leaf area-basal area ratio; A.a.: *Arbutus andrachne*; A.u.: *Arbutus unedo*; C.c.: *Cistus creticus*; C.s.: *Cistus salviifolius*; P.b.: *Pinus brutia*; P.h.: *Pinus halepensis*; P.la.: *Phillyrea latifolia*; P.le.: *Pistacia lentiscus*; Q.c.: *Quercus coccifera*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rapidly (L_L -9%, SLA -7%, L_A -5%, LPC 5%, $L_A{:}B_A$ -4%) while being more combustible (L_A 7%, L_L 6%, LCC 5%, LDMC, L_{Th} and LNC -4%) and consumable (LCC 24%, SLA -18%, LDMC 16%, L_L 13%, LPC -11%). As we move upwards the altitudinal gradient plants carry less combustible (-8%) leaves that took longer to ignite (21%) but once aflame burned hotter (consumability 11%). North- and east-facing slopes in the North hemisphere catch sun mainly in the morning when the temperature is still lower, thus are generally cooler and wetter. Communities established at northeast-facing slopes carried leaves that took longer to ignite (eastness 3%, heat load -1%) but were more combustible (northness 5%, heat load -2%) and smother fire fast (northness -8%, eastness -4%). In nutrient-richer soils plants supported leaves that ignited (SPC -15%, SOM and EC -2%) and exhausted fire fast (sustainability SPC -6%, pH -5%, sand 5%, EC -3%, combustibility SNC -5%, SMgC and sand -3%). Plants acclimated to drier summers carried leaves that resisted ignition for longer ($\mathrm{Prec^{season}}$ 16%), but once aflame were less combustible ($\mathrm{Prec^{wq}}$ 12%, $\mathrm{Prec^{season}}$ -9%, $\mathrm{Prec^{an}}$ 3%) and burned for longer ($\mathrm{Prec^{an}}$ and $\mathrm{Prec^{season}}$ 4%). Finally, leaves from individuals adapted to higher (annual and especially summer) temperatures took longer to ignite ($\mathrm{T^{wq}_{mean}}$ 14%, $\mathrm{T^{an}_{mean}}$ 7%, $\mathrm{T^{season}}$ 5%) and extinguished fire faster ($\mathrm{T^{season}}$ -8%, $\mathrm{T^{wq}_{mean}}$ -5%).

3.2. Leaf flammability variation across ecological scales

The partitioning of leaf flammability variance across five ecological scales revealed unequal distributions among the studied flammability attributes (Fig. 4-bar plots). The majority of total variance in ignitibility (57%) and combustibility (47%) occurs at the "*Region*" and "*Site*" scales mainly driven by large scale environmental variability. While in consumability the majority of total variance is detected at the "*Genus*" scale (54%), primarily constrained by species' evolutionary histories. Great variability was observed in sustainability among the measured individuals (C.V. 21%), but just 37% of the total variation was driven by the mechanisms considered in this study. The "*Species*" scale stands out as it explains none of the total variance in any of the flammability attributes (but consumability, 2%). However, all attributes, (including

Fig. 4. Lollipop plots Normalised Partial Least Squares Regressions' coefficients presenting the relative importance of leaf functional traits and environmental characteristics on leaf flammability attributes (see also Table S6). Predictors are ranked based upon how strongly each influences the response variable. **Bar plots** Variance partitioning for each leaf flammability attribute measured in Mediterranean, lowland, thermophilous vegetation along Greece, across five ecological scales: between genera and species, within-species, among sites, and across regions. All axes show % of the explained variance ($n = 810$; SLA, $m^2 \, kg^{-1}$: specific leaf area; LDMC, $mg \, g^{-1}$: leaf dry matter content; L_{Th}, mm: leaf thickness; LNC, LPC & LCC, $mg \, g^{-1}$: leaf nitrogen, phosphorus & carbon concentrations; L_A, cm^2: leaf area; L_L, cm: leaf length; $L_A:B_A$, $m^2 \, m^{-2}$: leaf area-basal area ratio; aspect was cosine and sine transformed into two new variables: Northness and Eastness; HL: Heat Load; T^{an}_{mean}, °C: mean annual temperature; T^{wq}_{mean}, °C: mean temperature of the warmest quarter; T^{season}, standard deviation*100: temperature seasonality; $Prec^{an}$, mm: total annual precipitation; $Prec^{wq}$, mm: precipitation of the warmest quarter; $Prec^{season}$, coefficient of variation: precipitation seasonality; WHC, %: water holding capacity; SOM, %: soil organic matter; sand and clay % were cosine and sine transformed to remove circularity; SNC, SPC, SMgC, $mg \, g^{-1}$: soil nitrogen, phosphorus and magnesium contents; EC, $\mu S \, cm^{-1}$: electrical conductivity).

sustainability, 7%) and especially consumability (14%) and ignitibility (13%), displayed considerable within-species variation driven by genetic, developmental and micro-environmental differences among the individuals of each species.

4. Discussion

4.1. Flammability is a continuous spectrum defined by its attributes

By studding all four flammability attributes (i.e. ignitibility, sustainability, combustibility, and consumability) on species with alternative resource-use and fire-response strategies across their distributions in Greece (Fig. 1, Table S4) we were able to detect some fundamental relationships that define leaf flammability in thermo-Mediterranean vegetation (Figs. 2, 3, Table S5). Leaves that took longer to ignite were also consumed thoroughly, while less combustible ones sustained fire for longer. Our results demonstrate that leaf flammability variation can be captured by a two dimensional plane produced by its four attributes. The first dimension is associated with combustion rate and sustainability driven by leaf shape and size, and the second with ignitibility and consumability controlled by leaf economics. Previous studies have consistently demonstrated that leaf flammability has two major dimensions: one related with heat release rate (i.e. combustibility) and controlled by size through its effect on natural packing (Magalhães and Schwilk, 2012; Schwilk, 2015; Cornwell et al., 2015), and a second

associated with total heat release (i.e. consumability in this study) used to predict soil heating and damage to well-protected tissues (Schwilk, 2015). This second dimension in the past has been represent by sustainability and has been found to be negatively correlated to the first (Magalhães and Schwilk, 2012; Grootemaat et al., 2015). Ignitibility has been reported as orthogonal to both sustainability and combustibility (Grootemaat et al., 2015; Simpson et al., 2016).

We propose that a non-hierarchical scheme for the classification of species according to their leaf flammability, such as the one presented here, may be more useful in describing general patterns of fire-related vegetation dynamics. Knowledge of species leaf flammability syndromes (mean and standard deviation) can inform fire-regime management, plant-lists for landscaping in the Wildland–Urban Interface, conservation of rare species and restoration efforts.

4.2. Resource-use strategies reflect alternative leaf flammability syndromes

The identified leaf flammability spectrum cannot be adequately explained by the dichotomy between seeders and resprouters, but it can be captured by species' leaf trait syndromes. Relationships among the measured leaf traits reveal a spectrum of alternative, coexisting resource-use strategies in our system: from fast-growing, acquisitive tissues with higher nutrient concentrations, to thick and sturdy leaves and stems that provide hydraulic efficiency (Michelaki et al., 2019). We observe that these investment trade-offs also reflect alternative

flammability syndromes that confer fitness in fire-prone ecosystems (Fig. 3, Table S5). Leaves from shrubs that employ resource-acquisitive strategies (i.e. high SLA and nutrient concentrations, low LCC and LDMC, e.g. *Cistus* species) ignited faster and sustained fire for longer, making them "dangerous" neighbours. However, these leaves did not burn well, promoting moderate intensity fires that would stimulate germination of their soil-stored seeds, but protect seed viability from high temperatures (Scarff and Westoby, 2006; Paula and Pausas, 2008). These chamaephytes often colonise old fields and highly degraded ecosystems, thus benefit from being flammable (in this case ignite fast and sustain fire), because fire opens gaps that enhance establishment opportunities for a future generation of individuals.

At the opposite end of the flammability spectrum we found individuals carrying conservative leaves, among them pines that form thick and sturdy needles (with high LDMC and LCC) with increased hydraulic efficiency. Pine needles displayed the slowest ignitibility, but highest residence time. This flammability syndrome delays ignition, but once aflame needles burn hot and for a long time, spreading fire to make space for a future generation of trees. These species have been described as fire prone due to needle architecture and structure (i.e. resins, oils and volatile products) and retention of dead fuel in the canopy (Bond and Midgley, 1995; Schwilk and Ackerly, 2001). Regeneration capacity depends on the accumulation of sufficient seed bank of serotinous cones banked in the canopy between fire intervals (i.e. 15–30 years depending on environmental conditions and site quality) (Thanos and Daskalakou, 2000). Extended drought periods have steadily increased fire occurrence and as a result many of the early pine woodlands are being taken over by shrublands (Baeza et al., 2007; Koutsias et al., 2012).

All studied evergreen arborescent shrubs are located towards the conservative extreme of the resource-allocation spectrum (Michelaki et al., 2019) and (like pines) carry leaves that resisted fire for longer but once aflame were consumed to a greater extent releasing more heat. Sclerophyllous evergreen arborescent shrubs (e.g. *Q. coccifera*, *P. latifolia*) produce small, tough, fibrous leaves characterised by efficient resource conservation (i.e. the sclerophylly syndrome: high LDMC, L_{Th} and LCC, low SLA, LNC, LPC, L_A, L_L and L_W) (Michelaki et al., 2019). These leaves that minimize nutrient loss and increase competitive ability in dry and unproductive habitats (Wright et al., 2004; Grime, 2006; Pérez-Ramos et al., 2012) displayed belated ignitibility and low combustibility, but increased consumability and the highest sustainability. This leaf flammability syndrome in combination with their well-protected tissues and high resprouting capacity confers survival during multiple fire cycles and allows coexistence with highly flammable species (in this case species that ignite fast, or are more combustible) unable to survive prolonged extreme temperatures (Vesk and Westoby, 2004; Pausas and Keeley, 2014). Contrary to conservative individuals that can afford greater photosynthetic area per unit of invested biomass with higher leaf water content (high SLA and L_A, low L_{Th} and LCC, e.g. *Arbutus* species, *P. lentiscus*), whose leaves ignited a minute earlier and were consumed fast and hot spreading fire to others (i.e. displayed the highest combustibility). Water in plant tissue acts as heat sink, increasing the amount of energy required for fuels to ignite and sustain combustion. This pyrogenic flammability syndrome decreases fire-residence time and soil heating, thus protecting below-ground organs that implement resprouting (Vesk and Westoby, 2004; Scarff and Westoby, 2006; Gagnon et al., 2010). These species produce seeds with little or no dormancy and benefit from shorter and low-intensity fires that do not obliterate parent plants (Paula and Pausas, 2008).

Climatic changes and land-use shifts have been altering the landscape mosaic and fire regime of the Mediterranean region for over 10 millennia. Since the middle of the 20th century decreased precipitation and increased average temperatures and heat wave frequency (Founda et al., 2019) accompanied by major socioeconomic changes in many southern European countries have led to densification of shrublands and transitional woodlands, afforestation, biomass (i.e. fuel)

accumulation, and higher exposure to man induced fires (Moreira et al., 2011; Pausas and Fernández-Muñoz, 2012; Pausas and Millán, 2019). Wildfire risk is predicted to increase significantly worldwide, and especially in southern Europe, during the 21st century (Fyllas and Troumbis, 2009; Liu et al., 2010; Moreno et al., 2014; Turco et al., 2018). As fire occurrence increases becomes in itself an additional factor of change, both by altering carbon budgets (Page et al., 2002; Mouillot and Field, 2005) and by turning forested areas into more flammable shrublands thus perpetuating fire hazard (Moreira et al., 2011; Pausas and Fernández-Muñoz, 2012). In fire-prone ecosystems, changes in the fire regime may be more important than the direct changes in climatic conditions with respect to species' distribution, migration, substitution, and extinction (Flannigan et al., 2000). Fire regimes changes can promote, reduce, or even remove species with particular resource-use strategies and flammability syndromes (Bond and Midgley, 1995; Bond et al., 2005; van Altena et al., 2012). Frequent wildfires have been identified as one of the main causes of forest degradation, especially in the Mediterranean region (Bond et al., 2005; Vallejo et al., 2012). Different vegetation types are expected to vary in their contribution to fuel continuity and total fuel load. Vegetation shifts will lead to leaf trait and flammability changes within communities that will influence future ecosystem properties and fire regimes (Lavorel and Garnier, 2002; Scarff and Westoby, 2006; Magalhães and Schwilk, 2012; van Altena et al., 2012; Zylstra et al., 2016). Evidence of covariation between leaf flammability attributes and functional traits indicative of alternative resource-use strategies are beginning to accumulate from a variety of systems (Scarff and Westoby, 2006; Magalhães and Schwilk, 2012; Murray et al., 2013; Grootemaat et al., 2015). Identifying relationships between resource allocation trade-offs and the leaf flammability spectrum across biomes would improve the predictive value of vegetation dynamic models (e.g. Fyllas and Troumbis, 2009; Zylstra et al., 2016) and help us describe past and future fire regimes under changing environmental and socioeconomic conditions.

4.3. Ecological and evolutionary drivers of leaf flammability variation

Flammability attributes' variance emerged unevenly distributed across scales, revealing that different ecological and evolutionary processes drive each leaf flammability component's values (Fig. 4-bar plots). These results indicate in which flammability attributes future research efforts should focus, depending on the questions they seek to answer and the ecological scale they study. The "*Region*" and "*Site*" scales account for the majority of the explained variance in ignitibility and combustibility, suggesting that these flammability attributes show greater sensitivity to large scale environmental gradients (i.e. climate, soil, topography). Plants acclimated to hotter, drier and nutrient-limited conditions carried more conservative leaves that resisted ignition for longer (Fig. 4-lollipop plots, Table S6). At nutrient-poor, but wetter sites plants could support larger leaves that were more combustible. At lower elevations individuals carried combustible leaves that ignited faster since less energy is required for water evaporation. However, only a small fraction of this environmental variability was observed at the "*Site*" scale. The small amount of variability between neighbouring sites implies that strong filtering processes operate on the overall distribution of leaf flammability components' values within a region. Environmental filtering creates soft constraints at the individual to community scales that can change over short temporal and spatial gradients as the environment changes (Pausas et al., 2012; Pausas and Keeley, 2014). Local changes in moisture and/or nutrient availability may trigger vegetation (and functional traits) shifts that could limit the range of successful flammability syndromes in a community.

Nonetheless, a number of species can pass the filtering process by displaying alternative flammability syndromes (with qualitative differences in survival or reproduction) that offer equivalent fitness. Interspecific variation manifested mainly at the "*Genus*" scale accounts for the majority of the explained variance in consumability (70%) and

sustainability (49%, 21% for combustibility and 15% for ignitibility). Many thermo-Mediterranean species carry conservative leaves with greater proportion of dry matter in relation to saturated weight that display slower production of biomass, longer lifespan and more efficient conservation of water and nutrients (Wright et al., 2004; Grime, 2006), and not all of them are reprouters. These leaves ignited slower, but they were consumed to a greater extent releasing more heat. Leaf shape and size vary greatly among the measured species and were found to determined fire sustainability and spread rate. Larger leaves exhaust fire faster due to better ventilation (Scarff and Westoby, 2006; Cornwell et al., 2015). Aeration between leaves increases oxygen availability and allows thermal radiation to extent further.

One possible limitation of previous flammability studies is that they were performed on few individuals, omitting biologically relevant intra-specific variability. While conspecific plants are systematically treated as identical in terms of their flammability, species-mean values may underestimate a species ability to respond (i.e. survive, grow, and reproduce) to community and fire regime changes (Pausas et al., 2012). Indeed significant amount of the explained variance for all flammability attributes (10–20%) was detected at the "*Individual*" scale, driven by plastic differences among conspecific individuals within sampling sites established along environmental gradients. High levels of plasticity can potentially blur interspecific differences, thus owe to be accounted for in studies comparing leaf flammability among species. We propose that the full ecological and evolutionary significance of flammability can only be understood in the context of its components' variance.

Criticism about the evolution of flammability stem from the term itself, which should not be treated as a single trait but rather as a spectrum, as well as from the disbelief that plants can be driven by mechanisms unrelated to resource capture. Our results show that trade-offs and constraints that define resource-allocation strategies across environmental gradients appeared to drive leaf flammability syndromes as well. Of course many traits that promote (or inhibit) alternative flammability syndromes can be exaptations, i.e. adaptations to other pressures (e.g. water and/or nutrient limitation, high solar radiation, herbivory) (Troumbis and Trabaud, 1989; Keeley et al., 2011; Bowman et al., 2014), but if the benefits a species enjoys from damaging its competitors outweigh the harm its individuals' suffer, then higher flammability, or rather alternative flammability syndromes can increase fitness (Mutch, 1970; Bond and Midgley, 1995; Zedler, 1995; Schwilk and Ackerly, 2001).

5. Conclusions

We report that leaf flammability in thermo-Mediterranean vegetation is a continuous two-dimensional spectrum defined by its four attributes and driven by resource allocation trade-offs. Smaller leaves sustained combustion for longer, while larger leaves were more combustible and extinguished fire faster. Acquisitive leaves ignited faster, but conservative leaves were consumed to a greater extent releasing more heat. Species with distinct resource-use strategies growing along environmental gradients displayed alternative leaf flammability syndromes with different ecological impacts that increase their survival or reproduction under frequent fires. These syndromes can be captured by plants' resource-allocation trade-offs in response to environmental pressures. We discovered that different ecological and evolutionary mechanisms operate independently on each flammability attribute, creating considerable leaf flammability variation. Strong environmental filtering limits the successful leaf flammability syndromes that can persist in a community. However, inter- and intra-specific differences in flammability attributes among individuals with alternative resource-use strategies can promote fire-vegetation feedbacks that will favour particular flammability syndromes, influence ecosystem properties, and affect future fire regimes. Linking plant resource economics with the leaf flammability spectrum on a global scale could open new research avenues in a world facing fast vegetation and socioeconomic changes.

CRediT authorship contribution statement

Chrysanthi Michelaki: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration. **Nikolaos M. Fyllas:** Conceptualization, Methodology, Validation, Investigation, Writing - review & editing, Supervision. **Alexandros Galanidis:** Investigation, Writing - review & editing. **Maria Aloupi:** Validation, Investigation, Resources, Writing - review & editing. **Eleftherios Evangelou:** Investigation, Resources, Writing - review & editing. **Margarita Arianoutsou:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision. **Panayiotis G. Dimitrakopoulos:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.137437.

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