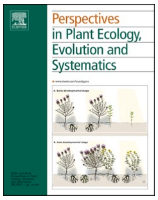
Perspectives in Plant Ecology, Evolution and Systematics 67 (2025) 125867

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees



Are trait responses of tree species across pyroregions indicative of fire-modulated plant functional strategies?

José Maria Costa-Saura [a,*], Gabriele Midolo [b], Carlo Ricotta [c], Mara Baudena [d], Carlo Calfapietra [e], Mario Elia [f], Paolo Fiorucci [g], Simone Mereu [h], Costantino Sirca [a], Donatella Spano [a], Gianna Vivaldo [i], Gianluigi Ottaviani [e]

[a] Department of Agricultural Sciences, University of Sassari, Sassari,Italy; National Biodiversity Future Center (NBFC), Palermo, Italy; Foundation Euro-Mediterranean Center on Climate Change (CMCC), Sassari, Italy
[b] Department of Spatial Sciences, Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Praha-Suchdol, Czech Republic
[c] Department of Environmental Biology, University of Rome 'La Sapienza', Rome, Italy
[d] Institute for Atmospheric Sciences and Climate (ISAC), National Research Council (CNR), Turin, Italy; National Biodiversity Future Center (NBFC), Palermo, Italy
[e] Research Institute on Terrestrial Ecosystems (IRET), National Research Council (CNR), Porano, Italy; National Biodiversity Future Center (NBFC), Palermo, Italy
[f] Department of Soil, Plant and Food Science, University of Bari A. Moro, Bari, Italy
[g] CIMA Research Foundation, 17100 Savona, Italy; National Biodiversity Future Center (NBFC), Palermo, Italy
[h] Institute for bioeconomy (IBE), National Research Council (CNR), Sassari, Italy; National Biodiversity Future Center (NBFC), Palermo, Italy; Foundation Euro-Mediterranean Center on Climate Change (CMCC), Sassari, Italy
[i] Institute of Geosciences and Earth Resources (IGG), National Research Council, Pisa, Italy

ARTICLE INFO

Keywords:
Bark thickness
Fire regime
Functional biogeography
Plant functional traits
Plant height
Pyrogeography
Resprouting
Wood density

ABSTRACT

Fire disturbance is a global eco-evolutionary force affecting plant species persistence and distribution. Pyrogeographic studies so far have identified pyroregions based on their similarity in climate and fire regime parameters. However, which fire-related traits tend to promote or hinder plant species persistence and distribution in different pyroregions remains underexplored. We implement a trait-based approach focusing on 38 tree species in the Mediterranean Basin (Italy), testing whether 1) species distribution across different pyroregions is associated with fire regime, 2) species in different pyroregions exhibit distinct fire-related trait values and, if so, 3) trait differences suggest better abilities to cope with fire and aridity in species distributed in more fire-prone and arid regions (e.g. thicker bark). We ran multivariate analyses (Correspondence Analysis) and linear models (Standardized Major Axis, Ordinary Least Squares) to address our goals. Findings tend to positively answer our questions, emphasizing the importance of including fire-related traits in pyroregionalization studies. Noticeably, the most fire-prone pyroregions collapse into one region from a functional perspective, with species characterized by trait values indicative of adaptations to fire and aridity. A trait-based approach may contribute to refine pyroregionalization exercises while proving useful for management purposes, such as identifying species or life histories whose traits may facilitate their persistence in the face of future, likely exacerbating, fire regimes.

1. Introduction

Fire is an eco-evolutionary force in many regions of the world shaping the distribution of form, function and diversity of plant species (Bond and Keeley, 2005; Keeley et al., 2011; Pausas and Ribeiro, 2017), which in turn affects ecosystem functioning and dynamics (Pausas and Keeley, 2009; Baudena et al., 2020). Pyrogeography, namely the study of the spatial and temporal distribution of fire regimes – and the link to climate, vegetation and human activity (Bowman et al., 2013) – is gaining momentum in recent years because it provides tools to better understand past, current and future ecological patterns as well as potential climate change impacts on ecosystems (Calheiros et al., 2021; Pausas, 2022; Cunningham et al., 2023; Galizia et al., 2023).

Insofar, nearly all studies focused on pyrogeography (e.g. Krawchuk et al., 2009; Pausas, 2022) and the identification of pyroregions (e.g. Galizia et al., 2022, Cunningham et al., 2024) do not consider the role played by plant functional traits in affecting species distribution. Information captured by functional traits may in turn be handy to identify

---

* Corresponding author.
E-mail address: jmcostasaura@uniss.it (J.M. Costa-Saura).

https://doi.org/10.1016/j.ppees.2025.125867
Received 27 September 2024; Received in revised form 6 February 2025; Accepted 24 March 2025
Available online 27 March 2025

pyroregions – as similarly done for other bioregionalization exercises (e.g. Harris et al., 2023) and as proposed by the broader field of functional biogeography (Violle et al., 2014). Indeed, functional traits – *sensu* Violle et al. (2007), namely related to individual growth, survival and reproduction shaping overall plant fitness – can capture how plants modulate their performance to cope with variations in environmental conditions, including disturbances (Lavorel et al., 2002; Westoby and Wright, 2006; Pausas and Bradstock, 2007; Paula et al., 2016) with potential feedback on ecosystem functioning, dynamics and resilience (Lavorel and Garnier, 2002; Grootemaat et al., 2017; Baudena et al., 2020; Magnani et al., 2023). Thus, plant species found in different pyroregions defined by distinct fire regimes should be characterized by distinct fire-related trait patterns – with trait values indicating enhanced abilities to deal with fire in more fire-prone pyroregions. For example, under high-severity fires, species with a thicker bark should better insulate the vascular cambium and protect it from fire damage, while also storing resources to eventually resprout epicormically after fire (He et al., 2012; Pausas, 2015, 2017; Chiminazzo et al., 2023). Therefore, woody species with a thicker bark should be favored in more fire-prone conditions and pyroregions – following predictions of the positive evolutionary association between the fire proneness of an ecosystem or region and fire-related traits (Lamont and He, 2017).

Implementing trait-based approaches to pyroregionalization studies is particularly needed in highly fire-prone biomes, such as in the Mediterranean Basin (Pausas and Verdú 2005; Verdú and Pausas 2007; Paula et al., 2016). This region is characterized by a marked climate seasonality with extended warm and dry summers (Cowling et al., 1996), with fire risk exacerbating in recent years because of rising temperatures and extended drought events (Klausmeyer and Shaw, 2009). In the Mediterranean Basin, plant species are equipped with functional strategies enabling them to cope with aridity and fire (Pausas and Verdú 2005; Jaureguiberry and Diaz 2023; Leys et al., 2024); examples include the dichotomy between resprouters (plants able to recover biomass after disturbance using resources previously stored in stems or roots) and reseeders (plants killed by fire and regeneration occurs from germinating seeds; Bellingham and Sparrow, 2000) or serotiny (plants requiring heat from wildfires to stimulate fruit or cone opening and seed release; Schwilk and Ackerly, 2001; He et al., 2012).

Within the Mediterranean Basin, Italy is one of the most biological diverse areas and covers a large biogeographical gradient of forest ecosystems representative of Mediterranean, Continental and Alpine biomes (e.g. Molina-Venegas et al., 2022). Recently, Italy has been the subject of a pyroregionalization study by Elia et al. (2022) that has detected spatial units defined by similar fire regimes. This study suggests 7 pyroregions that differ among them by their fire density, seasonality and severity, which are also strongly linked to climate (mainly aridity) and human pressure. A step forward to gain insights into the entangled relationships between fire regimes and plant species persistence and distribution is to explore whether and how fire-related traits (bark thickness, plant height, resprouting capacity, wood density; He et al., 2012; Pausas, 2017; Tavşanoğlu and Pausas 2018) differ among pyroregions. Considering the above, by combining data from the Italian Forest Inventory (IFI; assessing species occurrence, abundance and distribution) and fire-related trait values gained at the tree species level, we set out to tackle the following questions: Q1) Are species distribution related to fire regime? Q2) Are different pyroregions distinguished by hosting species having different trait values? If so, Q3) are species distributed in more fire-prone and arid pyroregions characterized by trait values indicative of functional strategies enabling them to cope better with fire and aridity (e.g. thicker bark, higher incidence of resprouters, denser wood)?

2. Methods

2.1. Study area and pyroregions

In the Mediterranean Basin, Italy is one of the European countries most affected by wildfires (San-Miguel-Ayanz et al., 2022) so it is important to gain insights into fire-plant relationships (affecting species distribution), and how plants may functionally cope with certain fire regimes at a biogeographic scale. Furthermore, this step is key as increased aridity – caused by ongoing and predicted climate change – can potentially interact with fires in leading to dramatic changes in Mediterranean vegetation (Batllori et al., 2019; Baudena et al., 2020). Italy hosts three biogeographic regions (European Environmental Agency: https://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-3#tab-metadata): the Mediterranean region, covering the southern and coastal areas of the country; the Continental region, which occupies mainly the Po valley in the north and the northern-central section of the Apennines and eastern part of the country; the Alpine region that is mostly located in the northern mountainous regions of the country.

We built upon the pyroregionalization carried out by Elia et al. (2022) based on metrics of fire density (i.e. fire size, number of wildfires, total burn area per year and vegetated area), seasonality (i.e. fire density metrics within and outside of the fire season) and severity (i.e. forest cover loss, see Elia et al., 2022 for details). Briefly, based on the harmonization of Italian wildfire datasets for the period 2007–2017, Elia et al. (2022) clustered Italian administrative provinces according to their similarities in fire characteristics, identifying 7 pyroregions along a putative fire-proneness gradient (Fig. 1): Large summer wildfires (LAS), Extreme, stand-replacing, summer wildfire (EXS), Medium-density summer wildfires (MDS), Alpine high-density wildfires (AHD), Reduced stand-replacing wildfires (RES), Subalpine low-density wildfires (PLD), Alpine High Stand-replacing wildfires (AHS). LAS, EXS and MDS cover the central and southern parts of the country and have the greatest density of wildfires. More specifically, LAS is characterized by having the largest wildfires whereas EXS has the greatest frequency of wildfires with the highest severity. Instead, MDS is characterized by intermediate values of annual burnt area. PLD covers the flat lowlands of northern Italy and is defined by low fire frequency. Finally, AHD, AHS, and RES occupy the Alpine pyroregions with AHD characterized by large wildfires, RES representing the areas with lowest fire frequency and severity, and AHS regions experiencing high-severity fires.

2.2. Species distribution and climate data

We used data from the Italian Forest Inventory (IFI) to estimate tree species abundances (based on diameters at the breast height; DBH) and distribution. The IFI is based on a systematic grid of 1 km^2 with approximately 7500 plots that are distributed to proportionally represent the variety of forest types (Ministero delle Politiche Agrarie e Forestali, 2006). We also checked that the number of IFI plots is proportional to the pyroregions' area (**Fig. S.1**). We focused on the most representative tree species ($N = 38$; see **Table S.1**) discarding plots classified by IFI as plantations and hygrophilous forests. The criterion to select tree species was to sum the DBH of each single species and retain only those representing at least 5 % of total abundance. Then, to account for differences in area across pyroregions in the analyses, we relativized species abundances within each single pyroregion by dividing the sum of diameters of each species by the total sum of diameters in the pyroregion.

To consider the main climatic drivers in region in our analyses, we extracted climate variables, namely mean annual temperature (MAT) and mean annual precipitation (MAP), from CHELSA (Karger et al., 2017; at 30 arc seconds resolution) for each forest inventory plot location, using the function "Chelsa.Clim.download" from *ClimDatDownloadR* R package (Jentsch et al., 2024). Finally, for each species we

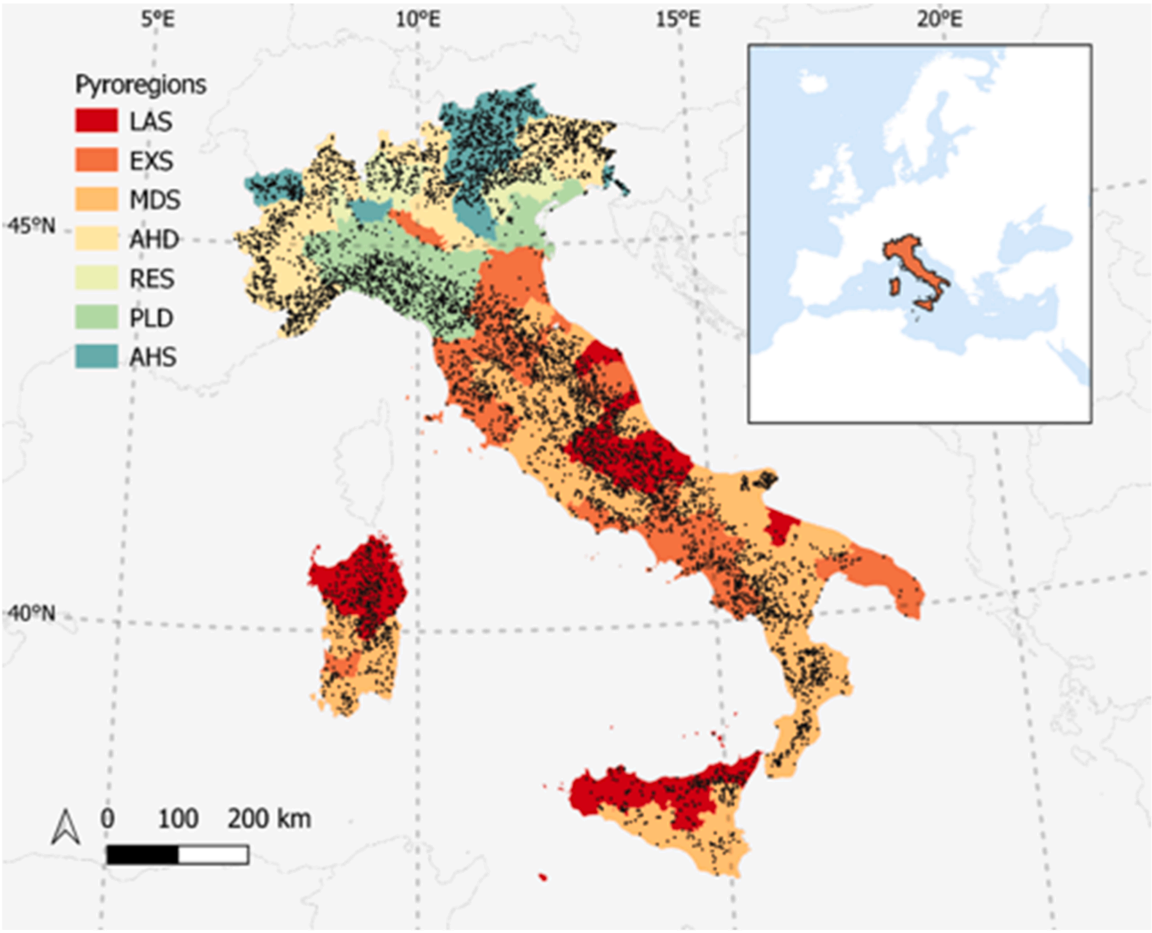


Fig. 1. Italian pyroregions and forest plots. Italian administrative provinces grouped into the pyroregions proposed by Elia et al. (2022) based on fire regime metrics such as annual burnt area, fire frequency, seasonality and severity. Pyroregion colors represent an annual burnt area gradient indicative of fire proneness (red = more fire prone; green = less fire prone). Dots represent the location of study plots from the Italian Forest Inventory (IFI). Large summer wildfires (LAS), Extreme stand-replacing summer wildfire (EXS), Medium-density summer wildfires (MDS), Alpine high-density wildfires (AHD), Reduced stand-replacing wildfires (RES), Subalpine low-density wildfires (PLD), and Alpine High Stand-replacing wildfires (AHS).

calculated the mean value for each climate variable based on their occurrence in each plot to represent species' main climatic preference.

2.3. Plant functional traits

We focused on four functional traits that can inform on how plants can cope with fire and aridity (key environmental drivers of species distribution in the Mediterranean Basin) which could be gathered from scientific literature and databases: bark thickness (BT), maximum height (MH), resprouting capacity (RC) and wood density (WD) – see Table 1.

WD and MH were obtained from Costa-Saura et al. (2019), where data were sourced from Zanne et al. (2009) and forest inventories of different European countries. Bark thickness was gathered from BROT database (Tavşanoğlu and Pausas 2018). We carried out an additional literature review to fill gaps in species' trait values (data sourced from: Şen et al., 2011; Favillier et al., 2015; Bär and Mayr, 2020; Sousa et al., 2021). RC was obtained from Harrison et al. (2021), which was based on BROT and TRY (Kattge et al., 2020) databases, also complemented by a literature research. We focused on interspecific differences, namely we assigned a single trait value per species – as routinely done in functional biogeographic studies executed at coarse scales (e.g. Harris et al., 2023; Midolo, 2024).

Table 1
List of the four plant functional traits used in this study (with abbreviation, variable type and units in brackets), their functional role, the number of species for which the trait was available, and key references wherein trait description and functional relevance are explained in detail.

Trait name [variable type, units]	Functional meaning	N species	References
Bark thickness (BT) [Continuous, mm]	Resource storage and sharing; Tissue protection and thermal insulation; Response to drought and fire	22	He et al. (2012); Pausas, (2015); Rosell, (2016); Chiminazzo et al. (2023)
Maximum height (MH) [Continuous, m]	Light competition; Persistence under surface fire regimes; Escape from disturbance trap(s)	38	Pausas et al. (2004); Moles et al. (2009); Wakeling et al. (2011)
Resprouting capacity (RC) [Categorical, yes/no]	Recovery from disturbances (e.g. fires); Drought tolerance	35	Bellingham and Sparrow, (2000); He et al. (2012); Pausas (2015); Zeppel et al. (2015)
Wood density (WD) [Continuous, g cm-^{3}]	Mechanical support, Water storage and transport; Resistance to embolism; Disturbance defense (e.g. fires)	36	Burrows, (2002); Chave et al. (2009); Ibanez et al. (2017)

2.4. Statistical analysis

To answer whether species occurrence and distribution are related to fire (Q1), we carried out a Correspondence analysis (CA) to identify which species can better describe each pyroregion, and to detect main axes of variation. CA is a multivariate statistical method suitable to analyze the relationship between categorical variables and detect synthetic dimensions that capture similarities across the data (Pereira et al., 2022; van Dam et al., 2021). Indeed, CA can provide more accurate results than other methods (such as PCA or NMDS) as it better accounts for nonlinear changes in species abundances (Hirst and Jackson, 2007). Given the large percentage of variation explained in our data (see results), we retained species' and pyroregions' positioning along the first dimension (that we linked to a fire-proneness gradient) for the next analytical steps. Then, to unravel putative single main fire-related drivers behind the ordination of the main dimension, we ran a linear regression (ordinary least squares; OLS) correlating the pyroregions position along the first CA axis (response variable) with their respective wildfire metrics (explanatory variable) taken from Elia et al. (2022). Additionally, to examine whether fire regime and climate are independent factors shaping species distribution in the study area, we calculated the Pearson correlation coefficient between species' CA scores (i.e. their position in the fire proneness gradient) and species' mean value for MAT and MAP (see Section 2.2). We used the "CA" function in *FactoMineR* R package for CA analysis (Le et al., 2008) and "lm" function from *stats* R package (R Core Team, 2022) for linear regressions.

For the functional trait analysis, we first ran a Standardized major axis (SMA) linear regression to assess significant relationships between pairs of continuous plant functional traits (BT, MH, WD) to aid interpretations of trait values among pyro-regions, using the "sma" function in the *smatr* R package (Warton et al., 2012) – this method being the most suitable to gain insights into bivariate trait coordination and scaling relationships (Warton et al., 2006). Then, to address whether pyroregions are functionally different (Q2), we tested for significant differences in trait values across pyroregions. To account for differences in species abundance across pyroregions, we consider the number of plots in which the species occur in each pyroregion. We performed a Kruskal-Wallis test followed by a Dunn's Post-Hoc Test with Bonferroni correction (functions "Kruskal.test" and "dunn.test" from R packages *stats* and *dunn.test* (Dinno, 2024), respectively) since these tests are preferable when continuous data are not normally distributed and heteroskedastic. Instead, for categorical traits (i.e. RC), we performed a z-test for equal proportions with Bonferroni correction (function "pairwise.prop.test" from R package *stats*). Finally, to address if trait values in more fire-prone regions are indicative of species having better strategies to cope with fire than in less fire-prone ones (Q3), we ran OLS linear regression (a logistic regression in the case of categorical data such as RC) to detect significant relationships between species position in the fire-proneness gradient axis (set as predictor) and species' functional trait values (set as response variable). The variation explained was reported using the coefficient of determination (R^2) and the deviance explained (D^2) for linear and logistic regressions, respectively ("lm" and "glm" functions from *stats* R package).

3. Results

3.1. *Species occurrence and distribution across pyroregions*

Results from the CA show that the two main axes explain around 85 % of the variation. The first dimension accounts for 65.7 % of the variation, with the Alpine pyroregions (especially AHS) placed on one end of the gradient whereas the Mediterranean ones (LAS, MDS, EXS) on the other end (Fig. 2). Indeed, species typically associated with Mediterranean climate (e.g. *Quercus ilex*, *Pinus halepensis*) are located in this part of the axis whereas species adapted to cold climates (e.g. *Picea abies*, *Pinus cembra*) sit on the other end.

The second axis, instead, explains a much lower level of variation (19.9 %). However, this axis is seemingly dominated by an "arch-effect" which is a statistical artefact (van Dam et al., 2021; Hill, 1974) and thus we discard it.

In terms of fire regime, results show a significant relationship between the position of the pyroregions in the first CA dimension and both the annual burnt area and fire seasonality (slope p-value = 0.024 and 0.029; R^2 0.67 and 0.65, respectively; **Fig. S.2**) – which are however correlated between them (r = -0.9, p-value=0.003). Additionally,

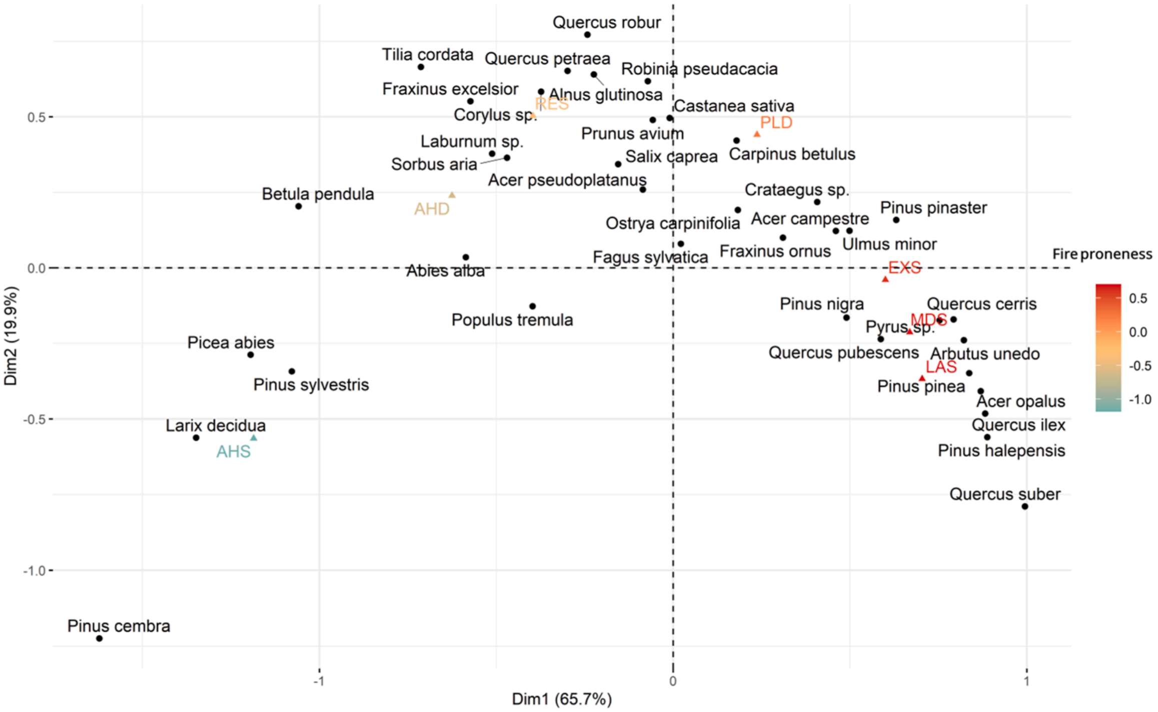


Fig. 2. Location of species and pyroregions along the two main axes ordered by correspondence analysis (see Fig. 1 for pyroregions' acronym definition); the first axis is associated with a putative fire-proneness gradient.

species position in the first CA dimension is also highly correlated with species' climatic preferences in terms of MAT and MAP (r = 0.87 and r = -0.75, respectively; p-values<0.01), with species ordered along a warm-dry *vs* cold-wet gradient (**Fig. S.3**).

3.2. Species trait values across pyroregions

The SMA shows a negative relationship between WD and MH (model slope = −1.33 [-1.79—0.98]; R^2= 0.33; p-value < 0.001) whereas BT is not related to either WD (p-value = 0.90) or MH (p-value = 0.56) (**Fig. S.4**). Plant functional trait values vary across pyroregions (Fig. 3) with some identifiable patterns; species in the most fire-prone pyroregions (LAS, EXS, MDS) are generally characterized by similar plant functional traits (BT, MH, WD), which however largely differ from trait values in the other four less fire-prone pyroregions (AHD, AHS, PLD, RES). These four pyroregions instead tend to differ among them in their functional trait values. Regarding the proportion of resprouters (RC), values are high across all pyroregions, except for AHS.

3.3. Trait patterns along the fire-proneness gradient

BT and WD significantly increase along the fire-proneness gradient, whereas MH decreases (Fig. 4). Conversely, RC shows no relationships (p-value = 0.4).

4. Discussion

We illustrated the usefulness of implementing trait-based approaches to gain insights into which plant functional strategies tend to be advantageous – hence possibly promoting species' local persistence, adaptation and geographic distribution (Pausas and Lamont, 2018) – in different Italian pyroregions. Tree species distributed in more fire-prone pyroregions are characterized by trait values indicative of enhanced abilities to cope with fire (and aridity).

4.1. Species occurrence and distribution are related to fire regime

We positively answered Q1. Results support the idea linked to the presence of a fire-proneness gradient associated with species occurrence

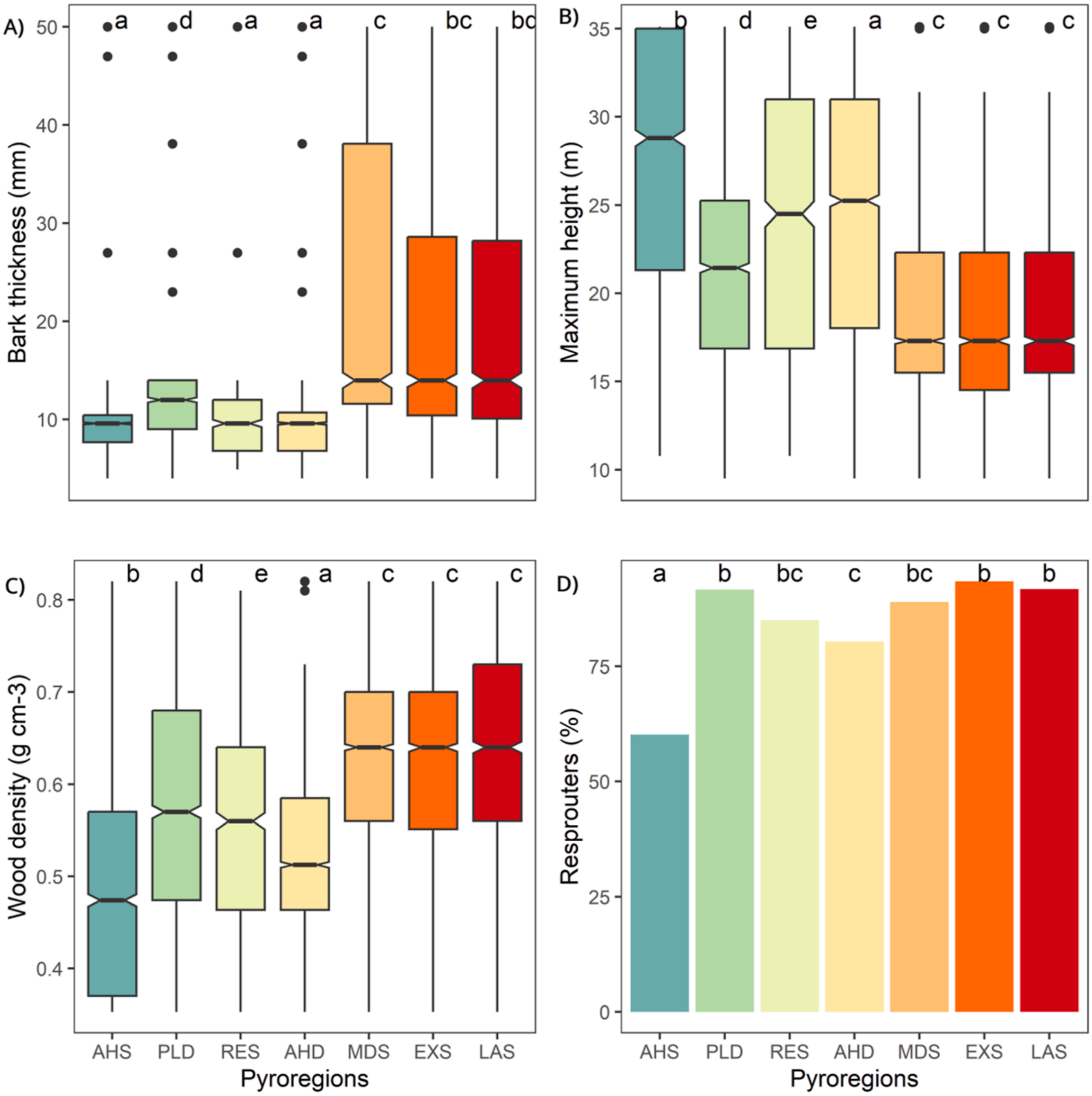


Fig. 3. Boxplots showing the distribution of plant functional traits across pyroregions ordered along a fire-proneness gradient increasing from left to right: a) Bark thickness; b) Maximum height; c) Wood density; d) Resprouting capacity. Different letters identify significant differences (p-value ≤ 0.05).

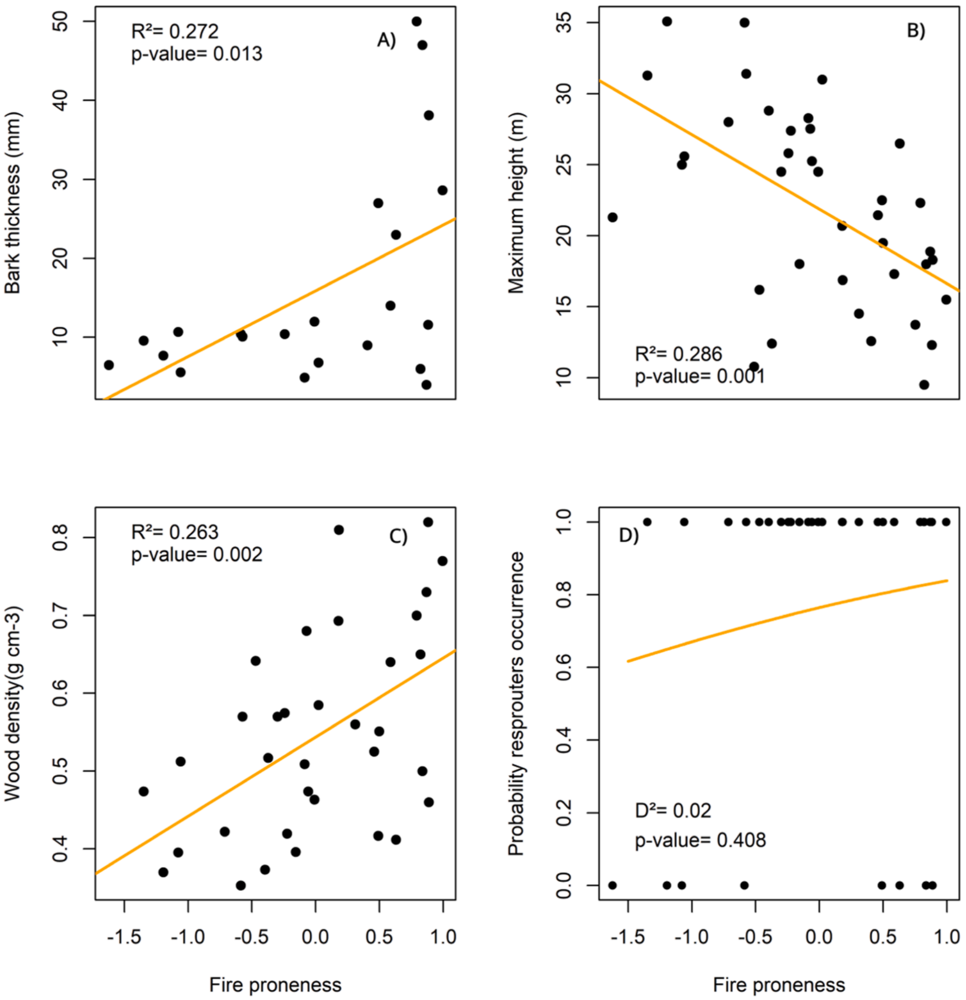


Fig. 4. Patterns of tree species' plant functional traits along the fire-proneness gradient: a) Bark thickness; b) Maximum height; c) Wood density; d) Resprouting capacity. P-value, coefficient of determination (R^2, for OLS linear models) or explained deviance (D^2, for logistic regression) are reported.

in different pyroregions, namely the 38 studied tree species are ordered along an increasing degree of putative fire-proneness at the pyroregional scale (Fig. 2). This gradient is indeed positively related to a few key fire regime metrics, such as annual burn area and fire seasonality, corroborating the identification of a disturbance-driven gradient. At the same time, our results are consistent with previous findings stressing the inherent collinearity between fire and climate variables – aridity most prominently (Turco et al., 2017; Pausas, 2022). This adds to the fact that the identification of these pyroregions is also associated with differences in drought exposure, anthropogenic pressures and the availability of flammable fuels (Elia et al., 2022).

At the species level, our analysis segregates trees across Italian pyroregions, following biogeographic expectations. Mediterranean species (e.g. *Quercus suber, Quercus ilex, Pinus halepensis, Pinus pinea*) are more common in warmer, drier and more fire-prone pyroregions primarily occurring in southern Italy (LAS, MDS, EXS). Pyroregions associated with mountainous areas located in northern Italy, such as AHS, are instead mostly dominated by Alpine species (e.g. *Pinus cembra, Larix decidua, Picea abies*). Additionally, species preferring a more temperate climate (e.g. *Quercus robur, Carpinus betulus, Fraxinus excelsior, Castanea sativa*) are assigned to AHD, RES and PLD pyroregions – which experience an intermediate degree of fire proneness associated with the Continental biome. Therefore, our results align with previous research, noticing how the effect of fire regime is conflated with that exerted by biogeographic factors and aridity in shaping species' occurrence and distribution within and across pyroregions (Galizia et al., 2022; Pausas, 2022).

4.2. *Species in more fire-prone pyroregions exhibit trait values indicative of better abilities to cope with fire and aridity*

We positively answered Q2 and Q3 as our results show that tree species occurring in more fire-prone and arid pyroregions tend to have different trait values than species in less fire-prone and mesic ones (Fig. 3). In more fire-prone pyroregions, tree species are characterized by having trait values indicative of better abilities to cope with fire and aridity (Fig. 4). These differences mainly involve bark thickness (Pausas et al., 2004; Pausas, 2017) and, to a lesser extent, wood density and plant height. In fact, species preferentially occurring in more fire-prone pyroregions located in central-southern Italy are characterized by having a thicker bark (and a wider range of trait values) than those found in less fire-prone pyroregions situated in the north. This result is also relevant for bark functional ecology (Rosell et al., 2014, 2015; Rosell, 2016; Pausas, 2015, 2017) because: 1) highly variable bark thickness across species in more fire-prone pyroregions may indicate that fire and climate regimes may not have selected for a reduced set of fine-tuned values to cope with putatively constraining environmental conditions, but the opposite; 2) bark thickness is uncorrelated to wood density and plant height in our study, hence allometric relationships between the studied traits are not accountable for the observed patterns of bark thickness. Given this decoupling between bark thickness and the other traits, our inference of fire-modulated strategies (related to tree species being better protected from fire damages by a thicker bark through enhanced cambium thermal insulation) seems to be supported (He et al., 2012; Pausas, 2015; Chiminazzo et al., 2023). Aridity as well may have played a role in affecting the pattern of bark thickness across pyroregions (also in consideration of the fire-climate collinearity), as thicker barks can store more resources, and may eventually contribute to boost epicormic resprouting after damages produced by heatwaves or fires (Richardson et al., 2015; Rosell et al., 2016; Ottaviani et al., 2018).

Results for wood density and plant height are instead less straightforward to interpret. As expected, wood density also increases towards more fire-prone pyroregions; a denser wood may limit fire-cued tree mortality by enhancing cambium thermal insulation and may reduce plant flammability (Brando et al., 2012; Frejaville et al., 2013). At the same time, this trait pattern may be largely affected by the strongly negative allometric relationship with plant height – the slope of the highly significant scaling relationship between these traits being −1.33. Consequently, it is challenging to infer which biotic or abiotic factors exert the main effect shaping patterns of these two traits. For example, competition for, and availability of resources (e.g. nutrients, water) may limit height gain and promote plants with denser woods (Ibanez et al., 2017). Wood density is indeed also associated with other functions, such as resistance to embolism (Chave et al., 2009; Ibanez et al., 2017) as a denser wood may prevent aridity-related mortality (Zuleta et al., 2017) – making it difficult to disentangle and estimate the effect of fire from other drivers on the expression of wood density and plant height.

Unexpectedly, we did not reveal a clear pattern for resprouting capacity. Results suggest a slight increase in the incidence of species with resprouting capacity towards more fire-prone and arid regions (similarly to what found by Harrison et al., 2021). This weak response may be explained by resprouting being advantageous not only in relation to fire shaping vegetation dynamics and functional patterns of mediterranean-type ecosystems (Ojeda, 1998), but also to other types of disturbances, such as damages provoked by frost, snow, lightning or grazing that can frequently occur in less fire prone and mesic Alpine and Continental regions (Adie and Lawes 2023). Also, most of our studied tree species are deciduous and evergreen angiosperms with the potential ability to resprout from above- and/or belowground organs (Tavşanoğlu and Pausas, 2018). Additionally, in this study we classified resprouting as a binary trait (i.e. either a species is able or not to resprout); however, this approach can be too simplistic as resprouting can be examined through a more quantitative and continuous lens, i.e. forming a gradient of vigor (Pausas et al., 2016; Ottaviani et al., 2017). Finally, reseeding (plants killed by fire and regeneration occurs from germinating seeds; Bellingham and Sparrow, 2000) constitutes an alternative yet effective strategy to cope with fire (Ojeda, 1998; Pausas and Keeley 2014) – as, in our case, for a few Mediterranean *Pinus* species (Fig. 2).

4.3. Implications for pyroregionalization studies and management

Our study is based on a previous pyroregionalization based on fire-regime metrics (Elia et al., 2022); we found that, from a functional standpoint, tree species in the three more fire-prone and arid regions have highly similar values of bark thickness, plant height, wood density and, to a lesser extent, resprouting capacity among them. This indicates that while these three pyroregions may differ among them when considering other biotic (e.g. species composition, diversity) and abiotic (e.g. fire regime, climate, land use) parameters, they are not so when incorporating fire-related traits into the picture, namely they tend to form one functional pyroregion (Fig. 4). This suggests that fire regime differences in the three more fire-prone pyroregions may not be marked enough to functionally separate tree species, at least in the short-term (ecological timescale) considered in the background pyroregionalization. Additionally, including other traits not examined in this study (e.g. fire-cued seed germination, flammability, serotiny) may capture more comprehensively plant functional responses to differences in fire regimes (Lamont and He, 2017; Wigley et al., 2020).

A trait-based approach can also help assess the challenge of detecting recent shifts in fire regime (McLauchlan et al., 2020) and complement pyroregionalization studies aimed at wildfire risk management (Elia et al., 2022; Galizia et al., 2022). At the same time, such approach may highlight conflicting areas as well as identify options to reconcile different priorities, associated with biodiversity conservation, ecological restoration and overall mitigation of fire risks.

5. Concluding remarks and outlook

Our study showcases the usefulness of incorporating plant functional traits into biogeographical studies (Violle et al., 2014). Future pyroregionalization exercises may explicitly include fire-related traits in the identification of pyroregions. For example, a possible method may involve the use of hierarchical clustering of species traits' hypervolumes indicative of distinct ecological strategies; these could then be mapped based on species distribution to propose (pyro)regions sharing similar (fire-related) trait values and combinations – as similarly done for bioregions of Africa (Harris et al., 2023). Additionally, comparing the spatial congruence between different pyroregionalizations, also including enhanced fire metrics' estimations at finer scales, would emphasize areas where different methods align, as well as identify high-discrepancy areas wherein further research is required to bridge the gap by including additional variables.

The identification of trait patterns across fire-proneness gradients may contribute to assessing interconnected climate change impacts on species distribution and vegetation dynamics. A trait-based functional approach may indeed assist the detection of which plant trait values (average, variability) and combinations (Andrew et al., 2022) may result advantageous, disadvantageous or neutral to cope with changes in fire regimes (e.g. fire frequency and intensity), and how these may interact with ongoing climate changes – as traits can predict how plants may cope with variation in the environment and to estimate feedbacks on ecosystem functioning (Lavorel and Garnier, 2002; Grootemaat et al., 2017). Improving such predictions could be beneficial to the development of fire-risk adaptive management in relation to exacerbating climate events (i.e. extended drought spells, high temperatures) associated with anthropogenic global warming.

To further test the generality and applicability of our findings, the functional approach devised here could be replicated and implemented in other regions characterized by a mediterranean-type climate (which accounts for most Italian pyroregions, especially the more fire-prone and arid ones). This may also help tackling the issue related to the collinearity between fire and climate variables; by replicating to different regions, consistent as well as discrepant lines of evidence may emerge in fire-related trait patterns, reinforcing either the generality or context-dependency of our findings. We also encourage future research to consider more species and ideally other growth forms than trees, such as shrubs and herbs. Moreover, examining trait differences between a set of focal species belonging to contrasting biogeographic elements (*sensu* Molina-Venegas et al., 2022; e.g. widespread across *vs* restricted within pyroregions), ideally including intraspecific variability, may provide further insights into how plants may or may not adjust functionally to persist and distribute within- and across-pyroregions.

CRediT authorship contribution statement

Calfapietra Carlo: Writing – review & editing, Funding acquisition. **Baudena Mara:** Writing – review & editing. **Fiorucci Paolo:** Writing – review & editing. **Elia Mario:** Writing – review & editing. **Sirca Costantino:** Writing – review & editing. **Mereu Simone:** Writing – review & editing. **Vivaldo Gianna:** Writing – review & editing. **Spano Donatella:** Writing – review & editing, Funding acquisition. **Midolo Gabriele:** Writing – review & editing, Methodology, Conceptualization. **Ottaviani Gianluigi:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Conceptualization. **Costa Saura**

Jose Maria: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ricotta Carlo:** Writing – review & editing, Methodology, Conceptualization.

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.

Acknowledgements

This research was funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 - Call for tender no. 3138 of 16 December 2021, rectified by Decree no. 3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union– NextGenerationEU; Award Number: Project code CN_00000033, Concession Decree no. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP J83C22000870007, Project title “National Biodiversity Future Center - NBFC”.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2025.125867.

Data availability

Data will be made available on request.

References

Adie, H., Lawes, M.J., 2023. Solutions to fire and shade: resprouting, growing tall and the origin of Eurasian temperate broadleaved forest. Biol. Rev. 98, 643–661. https://doi.org/10.1111/brv.12923.

Andrew, S.C., Gallagher, R.V., Wright, I.J., Mokany, K., 2022. Assessing the vulnerability of plant functional trait strategies to climate change. Glob. Ecol. Biogeogr. 31, 1194–1206. https://doi.org/10.1111/geb.13501.

Bär, A., Mayr, S., 2020. Bark insulation: ten central Alpine tree species compared. For. Ecol. Manag. 474. https://doi.org/10.1016/j.foreco.2020.118361.

Batllori, E., De Cáceres, M., Brotons, L., Ackerly, D.D., Moritz, M.A., Lloret, F., 2019. Compound fire-drought regimes promote ecosystem transitions in Mediterranean ecosystems. J. Ecol. 107, 1187–1198. https://doi.org/10.1111/1365-2745.13115.

Baudena, M., Santana, V.M., Baeza, M.J., Bautista, S., Eppinga, M.B., Hemerik, L., Garcia Mayor, A., Rodriguez, F., Valdecantos, A., Vallejo, V.R., Vasques, A., Rietkerk, M., 2020. Increased aridity drives post-fire recovery of Mediterranean forests towards open shrublands. N. Phytol. 225, 1500–1515. https://doi.org/10.1111/nph.16252.

Bellingham, P.J., Sparrow, A.D., 2000. Resprouting as a life history strategy in woody plant communities. Oikos 89, 409–416. https://doi.org/10.1034/j.1600-0706.2000.890224.x.

Bond, W.J., Keeley, J.E., 2005. Fire as a global “herbivore”: the ecology and evolution of flammable ecosystems. Trends Ecol. Evol. 20, 387–394. https://doi.org/10.1016/j.tree.2005.04.025.

Bowman, D.M.J.S., O’Brien, J.A., Goldammer, J.G., 2013. Pyrogeography and the global quest for sustainable fire management. Annu. Rev. Environ. Resour. 38, 57–80. https://doi.org/10.1146/annurev-environ-082212-134049.

Brando, P.M., Nepstad, D.C., Balch, J.K., Bolker, B., Christman, M.C., Coe, M., Putz, F.E., 2012. Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. Glob. Change Biol. 18, 630–641. https://doi.org/10.1111/j.1365-2486.2011.02533.x.

Burrows, G.E., 2002. Epicormic strand structure in Angophora, Eucalyptus and Lophostemon (Myrtaceae) - implications for fire resistance and recovery. N. Phytol. 153, 111–131. https://doi.org/10.1046/j.0028-646X.2001.00299.x.

Calheiros, T., Pereira, M.G., Nunes, J.P., 2021. Assessing impacts of future climate change on extreme fire weather and pyro-regions in Iberian Peninsula. Sci. Total Environ. 754. https://doi.org/10.1016/j.scitotenv.2020.142233.

Chave, J., Coomes, D., Jansen, S., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x.

Chiminazzo, M.A., Bombo, A.B., Charles-Dominique, T., Fidelis, A., 2023. To protect or to hide: why not both? An investigation of fire-related strategies in Cerrado woody species. Flora.: Morphol., Distrib., Funct. Ecol. Plants 306. https://doi.org/10.1016/j.flora.2023.152350.

Costa-Saura, J.M., Trabucco, A., Spano, D., Mereu, S., 2019. A height-wood-seed axis which is preserved across climatic regions explains tree dominance in European forest communities. Plant Ecol. 220, 467–480. https://doi.org/10.1007/s11258-019-00928-x.

Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K., Arianoutsou, M., 1996. Plant diversity in mediterranean-climate regions. Trends Ecol. Evol. 11, 362–366. https://doi.org/10.1016/0169-5347(96)10044-6.

Cunningham, C.X., Williamson, G.J., Nolan, R.H., Teckentrup, L., Boer, M.M., Bowman, D.M.J.S., 2024. Pyrogeography in flux: reorganization of Australian fire regimes in a hotter world. Glob. Change Biol. 30 (1). https://doi.org/10.1111/gcb.17130.

van Dam, A., Dekker, M., Morales-Castilla, I., Rodríguez, M., Wichmann, D., Baudena, M., 2021. Correspondence analysis, spectral clustering and graph embedding: applications to ecology and economic complexity. Sci. Rep. 11, 8926. https://doi.org/10.1038/s41598-021-87971-9.

Dinno, A. (2024). dunn.test: Dunn’s Test of Multiple Comparisons Using Rank Sums. https://doi.org/10.32614/CRAN.package.dunn.test.

Elia, M., Giannico, V., Ascoli, D., Argañaraz, J.P., D’Este, M., Spano, G., Lafortezza, R., Sanesi, G., 2022. Uncovering current pyroregions in Italy using wildfire metrics. Ecol. Process. 11. https://doi.org/10.1186/s13717-022-00360-6.

Favillier, A., Lopez-Saez, J., Corona, C., Trappmann, D., Toe, D., Stoffel, M., Rovéra, G., Berger, F., 2015. Potential of two submontane broadleaved species (Acer opalus, Quercus pubescens) to reveal spatiotemporal patterns of rockfall activity. Geomorphology 246, 35–47. https://doi.org/10.1016/j.geomorph.2015.06.010.

Frejaville, T., Curt, T., Carcaillet, C., 2013. Bark flammability as a fire-response trait for subalpine trees. Front. Plant Sci. 4. https://doi.org/10.3389/fpls.2013.00466.

Galizia, L.F., Barbero, R., Rodrigues, M., Ruffault, J., Pimont, F., Curt, T., 2023. Global warming reshapes European pyroregions. Earth’S. Future 11. https://doi.org/10.1029/2022EF003182.

Galizia, L.F., Curt, T., Barbero, R., Rodrigues, M., 2022. Understanding fire regimes in Europe. Int. J. Wildland Fire 31, 56–66. https://doi.org/10.1071/WF21081.

Grootemaat, S., Wright, I.J., Van Bodegom, P.M., Cornelissen, J.H.C., Shaw, V., 2017. Bark traits, decomposition and flammability of Australian forest trees. Aust. J. Bot. 65, 327–338. https://doi.org/10.1071/BT16258.

Harris, T., Ottaviani, G., Mulligan, M., Brummitt, N., 2023. Trait hypervolumes based on natural history collections can detect ecological strategies that are distinct to biogeographic regions. J. Ecol. 111, 314–326. https://doi.org/10.1111/1365-2745.14005.

Harrison, S.P., Prentice, I.C., Bloomfield, K.J., Dong, N., Forkel, M., Forrest, M., Ningthoujam, R.K., Pellegrini, A., Shen, Y., Baudena, M., Cardoso, A.W., Huss, J.C., Joshi, J., Oliveras, I., Pausas, J.G., Simpson, K.J., 2021. Understanding and modelling wildfire regimes: an ecological perspective. Environ. Res. Lett. 16. https://doi.org/10.1088/1748-9326/ac39be.

He, T., Pausas, J.G., Belcher, C.M., Schwilk, D.W., Lamont, B.B., 2012. Fire-adapted traits of pinus arose in the fiery cretaceous. N. Phytol. 194, 751–759. https://doi.org/10.1111/j.1469-8137.2012.04079.x.

Hill, M.O., 1974. Correspondence analysis: a neglected multivariate method. J. R. Stat. Soc. 23, 340–354. https://doi.org/10.2307/2347127.

Hirst, C.N., Jackson, D.A., 2007. Reconstructing community relationships: the impact of sampling error, ordination approach, and gradient length. Divers. Distrib. 13, 361–371. https://doi.org/10.1111/j.1472-4642.2007.00307.x.

Ibanez, T., Chave, J., Barrabé, L., Elodie, B., Boutreux, T., Trueba, S., Vandrot, H., Birnbaum, P., 2017. Community variation in wood density along a bioclimatic gradient on a hyper-diverse tropical island. J. Veg. Sci. 28, 19–33. https://doi.org/10.1111/jvs.12456.

Jaureguiberry, P., Díaz, S., 2023. A three-dimensional approach to general plant fire syndromes. Funct. Ecol. 37, 2143–2158. https://doi.org/10.1111/1365-2435.14272.

Jentsch, H., Bobrowski, M., & Weidinger, J. (2024). ClimDatDownloadR: Downloads Climate Data from Chelsa and WorldClim. https://doi.org/10.5281/zenodo.7924343.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the earth’s land surface areas. Sci. Data 4. https://doi.org/10.1038/sdata.2017.122.

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Tautenhahn, S., Werner, G.D.A., Aakala, T., Abedi, M., Acosta, A.T.R., Adamidis, G.C., Adamson, K., Aiba, M., Albert, C.H., Alcántara, J.M., Alcázar C, C., Aleixo, I., Ali, H., Wirth, C., 2020. TRY plant trait database – enhanced coverage and open access. Glob. Change Biol. 26 (1), 119–188. https://doi.org/10.1111/gcb.14904.

Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J., Bradstock, R.A., 2011. Fire as an evolutionary pressure shaping plant traits. Trends Plant Sci. 16, 406–411. 〈https://www.sciencedirect.com/science/article/abs/pii/S1360138511000835〉.

Klausmeyer, K.R., Shaw, M.R., 2009. Climate change, habitat loss, protected areas and the climate adaptation potential of species in mediterranean ecosystems worldwide. PLoS ONE 4. https://doi.org/10.1371/journal.pone.0006392.

Krawchuk, M.A., Moritz, M.A., Parisien, M.A., Van Dorn, J., Hayhoe, K., 2009. Global pyrogeography: the current and future distribution of wildfire. PLoS ONE 4. https://doi.org/10.1371/journal.pone.0005102.

Lamont, B.B., He, T., 2017. Fire-proneness as a prerequisite for the evolution of fire-adapted traits. Trends Plant Sci. 22, 278–288. https://doi.org/10.1016/j.tplants.2016.11.004.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct. Ecol. 16, 545–556. 〈http://onlinelibrary.wiley.com/doi/10.1046/j.1365-2435.2002.00664.x/full〉.

Le, S., Josse, J., Husson, F., 2008. FactoMineR: an R package for multivariate analysis. J. Stat. Softw. 25, 1–18. https://doi.org/10.18637/jss.v025.i01.

Leys, B.A., Leydet, M., Meineri, E., Saatkamp, A., Violle, C., 2024. Functional responses of Mediterranean flora to fire: a community-scale perspective. J. Ecol. 113, 433–444. https://doi.org/10.1111/1365-2745.14465.

McLauchlan, K.K., Higuera, P.E., Miesel, J., Rogers, B.M., Schweitzer, J., Shuman, J.K., Tepley, A.J., Varner, J.M., Veblen, T.T., Adalsteinsson, S.A., Balch, J.K., Baker, P., Batllori, E., Bigio, E., Brando, P., Cattau, M., Chipman, M.L., Coen, J., Crandall, R., Watts, A.C., 2020. Fire as a fundamental ecological process: Research advances and frontiers. Journal of Ecology, 8. Blackwell Publishing Ltd., pp. 2047–2069. https://doi.org/10.1111/1365-2745.13403, 5.

Magnani, M., Díaz-Sierra, R., Sweeney, L., Provenzale, A., Baudena, M., 2023. Fire responses shape plant communities in a minimal model for fire ecosystems across the World. Am. Nat. 202, E83–E103. https://doi.org/10.1086/725391.

Midolo, G., 2024. Plant functional traits couple with range size and shape in European trees. Glob. Ecol. Biogeogr. 33. https://doi.org/10.1111/geb.13838.

Ministero delle Politiche Agrarie e Forestali. (2006). Inventario nazionale delle foreste e dei serbatoi forestali di carbonio. Procedure di posizionamento e di rilievo degli attributi di terza fase.

Moles, A.T., Warton, D.I., Warman, L., Swenson, N.G., Laffan, S.W., Zanne, A.E., Pitman, A., Hemmings, F.A., Leishman, M.R., 2009. Global patterns in plant height. J. Ecol. 97, 923–932. https://doi.org/10.1111/j.1365-2745.2009.01526.x.

Molina-Venegas, R., Ottaviani, G., Campetella, G., Canullo, R., Chelli, S., 2022. Biogeographic deconstruction of phylogenetic and functional diversity provides insights into the formation of regional assemblages. Ecography 2022. https://doi.org/10.1111/ecog.06140.

Ojeda, F., 1998. Biogeography of seeder and resprouter Erica species in the Cape Floristic Region-Where are the resprouters? Biol. J. Linn. Soc. 63, 331–347. https://doi.org/10.1111/j.1095-8312.1998.tb01521.x.

Ottaviani, G., Martinkova, J., Herben, T., Pausas, J., Klimesova, J., 2017. On plant modularity traits: functions and challenges. Trends Plant Sci. 22, 648–651. https://doi.org/10.1016/j.tplants.2017.05.010.

Ottaviani, G., Tsakalos, J.L., Keppel, G., Mucina, L., 2018. Quantifying the effects of ecological constraints on trait expression using novel trait-gradient analysis parameters. Ecol. Evol. 8, 435–440. https://doi.org/10.1002/ece3.3541.

Paula, S., Naulin, P.I., Arce, C., Galaz, C., Pausas, J.G., 2016. Lignotubers in Mediterranean basin plants. Plant Ecol. 217, 661–676. https://doi.org/10.1007/s11258-015-0538-9.

Pausas, J.G., 2015. Bark thickness and fire regime. Funct. Ecol. 29, 315–327. https://doi.org/10.1111/1365-2435.12372.

Pausas, J.G., 2017. Bark thickness and fire regime: another twist. N. Phytol. 213, 13–15. https://doi.org/10.1111/nph.14277.

Pausas, J.G., 2022. Pyrogeography across the western Palaearctic: a diversity of fire regimes. Glob. Ecol. Biogeogr. 31, 1923–1932. https://doi.org/10.1111/geb.13569.

Pausas, J.G., Bradstock, R.A., 2007. Fire persistence traits of plants along a productivity and disturbance gradient in mediterranean shrublands of south-east Australia. Glob. Ecol. Biogeogr. 16, 330–340. https://doi.org/10.1111/j.1466-8238.2006.00283.x.

Pausas, J.G., Bradstock, R.A., Keith, D.A., Keeley, J.E., Hoffman, W., Kenny, B., Lloret, F., Trabaud, L., 2004. Plant functional traits in relation to fire in crown-fire ecosystems. Ecology 85, 1085–1100. https://doi.org/10.1890/02-4094.

Pausas, J.G., Keeley, J.E., 2009. A burning story: the role of fire in the history of life. BioScience 59, 593–601. https://doi.org/10.1525/bio.2009.59.7.10.

Pausas, J.G., Lamont, B.B., 2018. Ecology and biogeography in 3D: the case of the Australian Proteaceae. J. Biogeogr. 45, 1469–1477. https://doi.org/10.1111/jbi.13348.

Pausas, J.G., Pratt, R.B., Keeley, J.E., Jacobsen, A.L., Ramirez, A.R., Vilagrosa, A., Paula, S., Kaneakua-Pia, I.N., Davis, S.D., 2016. Towards understanding resprouting at the global scale. N. Phytol. 209, 945–954. https://doi.org/10.1111/nph.13644.

Pausas, J.G., Ribeiro, E., 2017. Fire and plant diversity at the global scale. Glob. Ecol. Biogeogr. 26, 889–897. https://doi.org/10.1111/geb.12596.

Pausas, J.G., Verdú, M., 2005. Plant persistence traits in fire-prone ecosystems of the Mediterranean basin: a phylogenetic approach. Oikos 109, 196–202. https://doi.org/10.1111/j.0030-1299.2005.13596.x.

Pereira, J.M.C., Oom, D., Silva, P.C., Benali, A., 2022. Wild, tamed, and domesticated: three fire macroregimes for global pyrogeography in the Anthropocene. Ecol. Appl. 32. https://doi.org/10.1002/eap.2588.

R Core Team. (2022). R: A language and environment for statistical computing. ⟨https://www.R-project.org/⟩.

Richardson, S.J., Laughlin, D.C., Lawes, M.J., Holdaway, R.J., Wilmshurst, J.M., Wright, M., Curran, T.J., Bellingham, P.J., McGlone, M.S., 2015. Functional and environmental determinants of bark thickness in fire-free temperate rain forest communities. Am. J. Bot. 102, 1590–1598. https://doi.org/10.3732/ajb.1500157.

Rosell, J.A., 2016. Bark thickness across the angiosperms: more than just fire. N. Phytol. 211, 90–102. https://doi.org/10.1111/nph.13889.

Rosell, J.A., Castorena, M., Laws, C.A., Westoby, M., 2015. Bark ecology of twigs vs. main stems: functional traits across eighty-five species of angiosperms. Oecologia 178, 1033–1043. https://doi.org/10.1007/s00442-015-3307-5.

Rosell, J.A., Gleason, S., Méndez-Alonzo, R., Chang, Y., Westoby, M., 2014. Bark functional ecology: evidence for tradeoffs, functional coordination, and environment producing bark diversity. N. Phytol. 201, 486–497. https://doi.org/10.1111/nph.12541.

San-Miguel-Ayanz, J., Durrant, T., Boca, R., Maianti, P., Libertá, G., Artés-Vivancos, T., Oom, D., Branco, A., de Rigo, D., Ferrari, D., Pfeiffer, H., Grecchi, R., Onida, M., Löffler, P. (2022). Forest Fires in Europe, Middle East and North Africa 2021, Publications Office of the European Union, Luxembourg, 2022, https:// doi: 10.2760/34094, JRC130846.

Schwilk, D.W., Ackerly, D.D., 2001. Flammability and serotiny as strategies: correlated evolution in pines. Oikos 94, 326–336. https://doi.org/10.1034/j.1600-0706.2001.940213.x.

Şen, A., Quilhó, T., Pereira, H., 2011. Türkiye'deki Quercus cerris L. var. cerris'in kabuk anatomisi. Turk. J. Bot. 35, 45–55. https://doi.org/10.3906/bot-1002-33.

Sousa, V., Ferreira, J.P.A., Miranda, I., Quilhó, T., Pereira, H., 2021. Quercus rotundifolia bark as a source of polar extracts: structural and chemical characterization. Forests 12. https://doi.org/10.3390/f12091160.

Tavşanoğlu, Ç ., Pausas, J.G., 2018. Data descriptor: a functional trait database for Mediterranean Basin plants. Sci. Data 5. https://doi.org/10.1038/sdata.2018.135.

Turco, M., Von Hardenberg, J., AghaKouchak, A., Llasat, M.C., Provenzale, A., Trigo, R. M., 2017. On the key role of droughts in the dynamics of summer fires in Mediterranean Europe. Sci. Rep. 7, 1–10. https://doi.org/10.1038/s41598-017-00116-9.

Verdú, M., Pausas, J.G., 2007. Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities. J. Ecol. 95, 1316–1323. https://doi.org/10.1111/j.1365-2745.2007.01300.x.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892. https://doi.org/10.1111/j.2007.0030-1299.15559.x.

Violle, C., Reich, P.B., Pacala, S.W., Enquist, B.J., Kattge, J., 2014. The emergence and promise of functional biogeography. Proc. Natl. Acad. Sci. 111, 13690–13696. https://doi.org/10.1073/pnas.1415442111.

Wakeling, J.L., Staver, A.C., Bond, W.J., 2011. Simply the best: the transition of savanna saplings to trees. Oikos 120, 1448–1451. https://doi.org/10.1111/j.1600-0706.2011.19957.x.

Warton, D.I., Duursma, R.A., Falster, D.S., Taskinen, S., 2012. smatr 3- an R package for estimation and inference about allometric lines. Methods Ecol. Evol. 3, 257–259. https://doi.org/10.1111/j.2041-210X.2011.00153.x.

Warton, D.I., Wright, I.J., Falster, D.S., Westoby, M., 2006. Bivariate line-fitting methods for allometry. Biol. Rev. Camb. Philos. Soc. 81, 259–291. https://doi.org/10.1017/S1464793106007007.

Westoby, M., Wright, I.J., 2006. Land-plant ecology on the basis of functional traits. Trends Ecol. Evol. 21, 261–268. https://doi.org/10.1016/j.tree.2006.02.004.

Wigley, B.J., Charles-Dominique, T., Hempson, G.P., Stevens, N., Tebeest, M., Archibald, S., Bond, W.J., Bunney, K., Coetsee, C., Donaldson, J., Fidelis, A., Gao, X., Gignoux, J., Lehmann, C., Massad, T.J., Midgley, J.J., Millan, M., Schwilk, D., Siebert, F., Kruger, L.M., 2020. A handbook for the standardised sampling of plant functional traits in disturbance-prone ecosystems, with a focus on open ecosystems. Aust. J. Bot. 68, 473–531. https://doi.org/10.1071/BT20048.

Zanne, A., Lopez-Gonzalez, G., Coomes, D., Ilic, H., Jansen, S., Lewis, S., Miller, R.B., Swenson, N.G., Wieman, M.C., Chave, J., 2009. Data from: towards a worldwide wood economics spectrum [Dataset]. Dryad. https://doi.org/10.5061/dryad.234.

Zeppel, M.J.B., Harrison, S.P., Adams, H.D., Kelley, D.I., Li, G., Tissue, D.T., Dawson, T. E., Fensham, R., Medlyn, B.E., Palmer, A., West, A.G., Mcdowell, N.G., 2015. Drought and resprouting plants. N. Phytol. 206, 583–589. https://doi.org/10.1111/nph.13205.

Zuleta, D., Duque, A., Cardenas, D., Muller-Landau, H.C., Davies, S.J., 2017. Drought-induced mortality patterns and rapid biomass recovery in a terra firme forest in the Colombian Amazon. Ecology 98, 2538–2546. https://doi.org/10.1002/ECY.1950.