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Climatic conditions affect shoot flammability by influencing flammability-related functional traits in non-fire-prone habitats

Brief heading: Climatic conditions affect shoot flammability in non-fire-prone habitats.

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Summary

- Plant flammability is an important driver of wildfires, and flammability itself is determined by several plant functional traits. While many plant traits are influenced by climatic conditions, the interaction between climatic conditions and plant flammability has rarely been investigated.
- Here, we explored the relationships among climatic conditions, shoot-level flammability components, and flammability-related functional traits for 186 plant species from fire-prone and non-fire-prone habitats.
- For species originating from non-fire-prone habitats, those from warmer areas tended to have lower shoot moisture content and larger leaves, and had higher shoot flammability with higher ignitibility, combustibility, and sustainability. Plants in wetter areas tended to have lower shoot flammability with lower combustibility and sustainability due to higher shoot moisture contents. In fire-prone habitats, shoot flammability was not significantly related to any climatic factor.
- Our study suggests that for species originating in non-fire-prone habitats, climatic conditions have influenced plant flammability by shifting flammability-related functional traits, including leaf size and shoot moisture content. Climate does not predict shoot flammability in species from fire-prone habitats; here, fire regimes may have an important role in shaping plant flammability. Understanding these nuances in the determinants of plant flammability is important in an increasingly fire-prone world.

Keywords: functional traits, plant flammability, climatic conditions, evolution, wildfire

Introduction

Plant traits reflect the outcome of evolutionary processes of plants interacting with abiotic and biotic resources, conditions, and disturbances (Violle *et al.*, 2007). Many plant traits, both response and effect traits, are related to environmental conditions, although the relations are usually weak at the global scale (Moles *et al.*, 2014; Díaz *et* *al.*, 2016; Wright *et al.*, 2017; Baird *et al.*, 2021). For example, leaf size tends to be smaller at higher latitudes, but larger at wetter or warmer sites (Peppe *et al.*, 2011; Wright *et al.*, 2017). Leaf nitrogen and phosphorus concentrations decrease toward the equator generally as average temperature and growing season length increase (Reich & Oleksyn, 2004). The associations between plant traits and environmental conditions can provide insight into the evolution of plant traits, facilitate an understanding of how plants respond to changing environmental conditions, and predict possible changes in plant distributions under climate change (Schimper, 1904; Wright *et al.*, 2004). However, there is still much to be learned in identifying possible associations between environmental factors and plant traits, especially over large spatial extents, even if the associations between plant traits and environmental conditions have been emphasized by plant ecologists for more than a century (Schimper, 1904; Wright *et al.*, 2004; Šímová *et al.*, 2018).

One trait that has been particularly poorly studied in relation to its interactions with environmental conditions is plant flammability, which describes the capacity of vegetation to ignite and sustain a flame (Pausas *et al.*, 2017). Although many plant traits, such as canopy structure, could affect wildfire behavior, plant flammability is an important driver of wildfires in terrestrial ecosystems, despite its influence may vary with fire intensity (Schwilk & Caprio, 2011; Fernandes & Cruz, 2012; Prior *et al.*, 2017; Cruz *et al.*, 2022). Plant flammability can be decomposed into four components: ignitability (ease of plant ignition), combustibility (the speed or intensity at which a plant burns), sustainability (the length of time a plant continues to burn once ignited) and consumability (proportion of biomass combusted) (Anderson, 1970; Martin *et al.*, 1994). Many functional traits, including chemical, morphological and architectural characteristics, and their interactions combine to affect plant flammability (Schwilk, 2015; Pausas *et al.*, 2017; Alam *et al.*, 2020). A better understanding of plant flammability can inform prediction of wildfire behaviour in each plant community or region and provide useful context for wildfire management. However, plant flammability data are scarce compared to many other plant traits, and flammability studies are often incomparable due to a lack of standard measurement protocols (White & Zipperer, 2010). As a result, the potential drivers of plant flammability, as an inherent plant trait, remain uncertain, and the evolutionary mechanisms associated with plant flammability are still debated (Snyder, 1984; Midgley, 2013; Bowman *et al.*, 2014; Pausas *et al.*, 2017).

There is emerging evidence that fire has played an important role in the evolution of plant flammability (Pausas *et al.*, 2012; Cui *et al.*, 2020b). Under certain fire regimes, selection may drive species to become more or less flammable (He *et al.*, 2011; Pausas *et al.*, 2012; Cui *et al.*, 2020b). However, environmental conditions other than fire have also likely affected plant flammability, probably by influencing flammability-related functional traits (Mason *et al.*, 2016; Krix & Murray, 2018; Cui *et al.*, 2020a). For example, Mason *et al.*(2016) found that variation in traits, such as leaf dry matter content and tannins content, was linked to variation in foliar flammability and suggested that selective pressures other than fire have driven foliar flammability. Cui *et al.*(2020a) showed that shoot flammability across the genus *Dracophyllum* (Ericaceae) was negatively related to leaf size, which may be influenced or selected for by climatic conditions, such as temperature and moisture availability. Thus, plant flammability could be a secondary outcome of selection for other functional traits, which increased individual fitness and coincidentally changed the flammability, especially in non-fire-prone habitats where selection pressure from certain fire regimes was absent (Gould & Vrba, 1982; Snyder, 1984; Midgley, 2013; Resco de Dios, 2020). However, the influence of environmental conditions on plant flammability is poorly understood and has not been investigated across a wide range of taxa and environmental conditions.

Here, we investigated associations among shoot flammability components (ignitibility: ignition frequency, sustainability: burning time, combustibility: maximum temperature, and consumability: burnt biomass), climatic conditions (mean annual temperature (MAT), mean annual precipitation (MAP) and Aridity Index (AI)), and flammability-related functional traits (shoot moisture content (MC) and leaf area (LA)) for 186 species of vascular plants from diverse habitats. We used shoot moisture content and leaf area as traits driving flammability because they may both influence plant flammability (Scarff & Westoby, 2006; de Magalhães & Schwilk, 2012; Van Altena *et al.*, 2012; Zhao *et al.*, 2016; Dehane *et al.*, 2017; Bianchi *et al.*, 2019). Previous research has highlighted the complex relationships between climate, fire, and plant traits (Staver *et al.*, 2011). Archibald *et al.* (2013) identified five 'pyromes', but these were not predicted by climate or biome. Across Australia, Murphy *et al.* (2013) linked a classification of fire activity to climate via latitudinal controls on monsoonal activity. In short, the relationships between trait expression, climate, and fire regime comprise a series of complex feedbacks that are difficult to disentangle (Bowman *et al.*, 2015). Here, we used three key climatic conditions: mean annual precipitation (MAP), mean annual temperature (MAT), and the Aridity Index (AI) to describe the climatic conditions that each species inhabits. We then ask: can we predict species' flammability from the biophysical environment?

Materials and Methods

Shoot-level flammability data

We used shoot-level flammability data from 186 species (119 indigenous to New Zealand and 67 exotic species introduced from other parts of the world, Table S1) from our previous study (Cui *et al.*, 2020b). Shoot-level flammability components for each species, including ignition frequency (IF), maximum temperature (MT), burning time (BT), and burnt biomass (BB), were measured by burning at least six 70 cm length shoot samples (Cui *et al.*, 2020b). Ignition frequency is the percentage of samples that sustained fire after the blowtorch used to ignite them was turned off and represents ignitibility. Maximum temperature is the maximum temperature of the burning sample recorded on an infrared laser thermometer after the blowtorch was turned off and represents combustibility. Burning time is how long the sample burns after turning off the blowtorch and represents sustainability. Burnt biomass is the percentage of combusted biomass after the flame goes out and represents consumability.

Shoot moisture content

To calculate shoot moisture content, a subsample of twigs and leaves was taken from each shoot sample before burning and weighed to determine their fresh mass (FM). Thus, at least six samples were measured for shoot moisture content for each species. These subsamples were oven-dried at 65°C for 48 h and weighed for dry mass (DM). Moisture content (MC; %) of the subsamples was calculated as:

$$MC = (FM - DM) / DM \times 100\%$$

Leaf area

We did not directly measure leaf area. Instead, we extracted all available data on leaf size for our species from several online resources, including New Zealand Plant Conservation Network (https://www.nzpcn.org.nz/), New Zealand Plants (https://nzflora.landcareresearch.co.nz/), The Gymnosperm database (https://www.conifers.org/), eFlora (http://www.efloras.org/). For each species, leaf area was calculated by multiplying midpoints of the range of leaf length and leaf width. For species with compound leaves, leaflet area was used for analysis.

Habitat conditions

We categorized the 186 species as originating from fire-prone or non-fire-prone habitats depending on the description of habitat type of the biogeographical origin of each species as derived from numerous sources (see methods and supplementary materials from Cui *et al.*, 2020b). Geographical records of each species were extracted from the Global Biodiversity Information Facility (http://www.gbif.org) by using the R package *rgbif* version 3.7.2. Then, we used the R package *CoordinateCleaner* version 2.0-20 (Zizka *et al.*, 2019) to remove erroneous or overly imprecise geographical coordinates for each species, such as those in the ocean areas or in botanical gardens. For each location, mean annual temperature (MAT) and mean annual precipitation (MAP) were obtained from WorldClim version 2.1 (https://www.worldclim.org/) at 0.5-arc minute resolution (Fick & Hijmans, 2017). Aridity Index (AI) for each location (the ratio of mean annual precipitation to mean annual reference evapo-transpiration) was extracted from Global Aridity Index and Potential Evapo-Transpiration (ET0) Climate Database v2 (0.5-arc minute resolution, Zomer *et al.*, 2022). MAT, MAP and AI were analyzed as they are among the most important environmental factors influencing plant traits (Wright *et al.*, 2017; Baird *et al.*, 2021; Harris *et al.*, 2022). Sexton *et al.* (2009) hypothesized that if gene flow occurs among populations of a given species across its native range, then the mean phenotypic trait values of this species will be related to their mean climate variables. In addition, previous studies suggested that the bioclimatic envelope of a species tends to remain unchanged over space and time (Pearman *et al.*, 2008; Wiens *et al.*, 2010; Harris *et al.*, 2022). Therefore, we used the average values of climatic variables from all occurrence locations of each species to represent the bioclimatic envelope of the species.

Data analysis

We focused on interspecific variations and ignored the intraspecific variations in flammability components, flammability-related functional traits and climatic conditions in this study. To evaluate the phylogenetic signal of climatic conditions, flammability components and flammability-related traits, a dated phylogeny with 186 species was obtained from a phylogeny for vascular plants (GBOTB.extended.tre) using R package *V.phylomaker* version 0.1.0 (Jin & Qian, 2019). We quantified the phylogenetic signal using the 'phylosignal' function in the R package *picante* version 1.8.2 (Kembel *et al.*, 2010). As we detected significant phylogenetic signals in flammability components, climatic conditions and flammability-related traits (Table S2), we used phylogenetic generalized least square (PGLS) models, which accounts for phylogenetic autocorrelation in model residuals, to analyse the associations among flammability components, climatic conditions, and flammability-related traits using the R package *Caper* version 1.0.1. (Valverde-Barrantes *et al.*, 2017; Orme *et al.*, 2018; Jardine *et al.*, 2020). Principal component analysis (PCA) was performed to evaluate the relationship of the climatic conditions, flammability components and flammability-related traits for species from non-fire-prone habitats using the 'princomp' function in R. To compare the climatic conditions between fire-prone and non-fire-prone habitats, the non-parametric Mann-Whitney U test was employed using the ‘wilcox.test’ function in R. Plots were drawn using Origin 8.0 software and the R package *ggplot2* version 3.3.6 (Wickham, 2016). All statistical analyses were conducted in R 4.2.0 (R Core Team 2022).

Results

Shoot flammability components were significantly related with shoot moisture content and leaf size

Shoot moisture content of the species ranged from 8.8% (*Ammophila arenaria*) to 381.2% (*Hypochaeris radicata*) (shoot moisture content was measured for 153 species); leaf size varied from 1.13 mm^2 (*Dacrycarpus dacrydioides*) to 170,000 mm^2 (*Phormium tenax*) (leaf area data were collected for 161 species) (Table S1). All shoot-level flammability components were significantly negatively related to shoot moisture content (Table 1), that is, species with higher shoot moisture content were less flammable. Leaf area was significantly negatively related to burnt biomass (r^2 = 0.06, Table 1), indicating larger leaved species were consumed less by fire.

Climatic conditions affected shoot flammability in non-fire-prone habitats, but not in fire-prone habitats

Climatic conditions varied greatly across the 186 species. *Citrus limon* (Rutaceae) habitats had the highest MAT (20.31 °C) and *Luzula pumila* (Juncaceae) had the lowest MAT (5.05 °C). The highest MAP was observed in *Dracophyllum densum* (Ericaceae) habitats (3325.61 mm), and the lowest MAP was for *Pinus ponderosa* (Pinaceae) habitats (532.80 mm). The Aridity Index of the 186 species habitats ranged from 0.32 (*Pinus ponderosa*, Pinaceae) to 3.31 (*Dracophyllum densum*, Ericaceae). According to the biome classification based on MAT and MAP (Whittaker, 1970), the habitats of the 186 species include woodland/grassland/shrubland, temperate forest, tropical seasonal forest and temperate rainforest (Fig. 1).

Fifty-nine species were categorized as originating from fire-prone habitats, while 127 species came from non-fire-prone habitats (Table S1). There were significant differences in climate between fire-prone and non-fire-prone habitats, with the latter being warmer, wetter, and humider (Table 2). In non-fire-prone habitats, shoot flammability was significantly correlated with climatic conditions (Fig. 2; Table 3). Ignition frequency ($r^2 = 0.05$), maximum temperature ($r^2 = 0.07$) and burning time ($r^2 = 0.07$) increased with the increase of MAT; the Aridity Index was negatively related to maximum temperature ($r^2 = 0.02$) and burning time ($r^2 = 0.03$). In fire-prone habitats, shoot flammability was not significantly correlated with any climatic condition.

Climatic conditions affect shoot flammability by influencing flammability-related functional traits in non-fire-prone habitats

Across species originating from non-fire-prone habitats, shoot moisture content was negatively related to MAT ($r^2 = 0.06$), while positively related to MAP ($r^2 = 0.06$) and AI ($r^2 = 0.05$). In contrast, leaf area was positively related to MAT ($r^2 = 0.24$), but negatively related to MAP ($r^2 = 0.05$) and AI ($r^2 = 0.07$). Thus, for species from non-fire-prone habitats, plants in warmer areas are likely to have lower shoot moisture content and larger leaves, thus potentially having higher ignition frequency, burning time and maximum temperature (Fig. 3; Table 3). In wetter areas, plants tended to have higher shoot moisture content and smaller leaves, thus, having lower burning time and maximum temperature (Fig. 3; Table 3).

Discussion

Climate conditions are important controls of how plant traits are expressed (Bussotti *et al.*, 2015; Bjorkman *et al.*, 2018; de Oliveira *et al.*, 2020). For example, changes in temperature have multiple effects on leaf nutrient content (Reich & Oleksyn, 2004), specific leaf area (Rosbakh *et al.*, 2015) and wood density (Swenson & Enquist, 2007), thereby affecting plant production capacity and adaptive strategies (Moles *et al.*, 2014). Precipitation influences many plant traits, such as leaf thickness, leaf size, and leaf moisture content (de Oliveira *et al.*, 2020; Baird *et al.*, 2021). The variability of traits with climatic conditions will likely cause variations in plant flammability, as plant flammability is determined by many functional traits (Schwilk, 2015; Pausas *et al.*, 2017; Alam *et al.*, 2020). However, how climatic conditions affect interspecific variations in plant flammability has hardly been reported, especially across wide taxonomic and environmental ranges. We found that the environmental factors that affected shoot flammability varied between fire-prone and non-fire-prone habitats. In non-fire-prone habitats, plants in warmer areas tend to have lower shoot moisture content and larger leaf size, as well as higher shoot flammability with higher ignitibility, combustibility, and sustainability. In wetter areas, plants have higher moisture content and lower shoot flammability with lower combustibility and sustainability. The moisture content of plants is one of the key determinants of flammability and higher moisture content usually results in a decrease in all flammability variables (Popović *et al.*, 2021). Plants occurring in warmer and drier areas of non-fire-prone habitats have higher shoot flammability due to their lower shoot moisture content. Leaf size is negatively related to burnt biomass; that is, the percentage of burnt biomass is less in larger-leaved species. Plants occurring in warmer areas have lower shoot moisture content and larger leaves. As a result, no significant variation in burnt biomass was detected in our study. In summary, plant flammability is predicted by MAT and AI, but only for those species originating in non-fire-prone environments.

For species originating from fire-prone habitats, we found no significant relationship between climatic conditions and shoot flammability. In fire-prone habitats it has been argued that fire regime plays an important role in shaping plant flammability (Gagnon *et al.*, 2010; Calitz *et al.*, 2015). For example, Pausas *et al.* (2012) showed that individuals of the Mediterranean shrub species *Ulex parviflorus* (Fabaceae) from sites with a history of frequent fire were more flammable than those growing in sites without recurrent fire (but see Fernandes & Cruz, 2012). We infer that fire regimes likely shaped shoot flammability in fire-prone habitats and disrupted pre-existing relationships between climatic conditions and plant flammability observed in species from regions where fire is absent or infrequent. We recommend further exploration of this topic via targeted sampling of species across the five pyromes of Archibald *et al.* (2013) to isolate differences associated with fire activity or fire regime, or across biomes, to better elucidate climatic differences (as per Calitz *et al.*, 2015).

The evolution of plant flammability has attracted considerable interest since Mutch (1970) first hypothesized that plant communities in fire-prone habitats may evolve to become more flammable. Despite many studies having been conducted during the last half-century, the evolutionary mechanism underpinning plant flammability remains debated (Snyder, 1984; Midgley, 2013; Bowman *et al.*, 2014; Pausas *et al.*, 2017). Fire may be an important factor that has affected plant flammability in fire-prone habitats (Pausas *et al.*, 2012; Cui *et al.*, 2020b); however, plant flammability could also be an incidental by-product of selection on other functional traits in response to environmental conditions, such as cold and drought, especially in non-fire-prone habitats (Snyder, 1984; Midgley, 2013; Cui *et al.*, 2020a). Our study suggested that the determinants of shoot flammability varied across fire-prone and non-fire-prone habitats. In non-fire-prone habitats, climatic conditions affected shoot flammability via influencing flammability-related traits, such as moisture content; while in fire-prone habitats, climate did not influence shoot flammability; fire regimes may be of greater importance. Our study provides a crucial first step in understanding the determinants of plant flammability, which is important for fire management in a warmer world. Here, we used shoot-level flammability because the shoot scale preserves much of the architecture of the plant and has been strongly correlated with expert opinions based on observation of plant flammability in the field (Wyse *et al.*, 2016; Alam *et al.*, 2020). In this study, we considered a limited set of climatic factors (albeit those known to delimit biomes) and flammability-related functional traits. More environmental factors, such as soil conditions (Gibson *et al.*, 2015) and additional flammability-related functional traits, such as leaf thickness and leaf dry matter content (Alam *et al.*, 2020), should be explored both within (Cui *et al.*, 2022) and between species to identify the determinants of plant flammability.

In conclusion, we infer that climatic conditions affect shoot flammability by influencing flammability-related functional traits in non-fire-prone habitats. This supports the idea that plant flammability could be an emergent property of variation in flammability-related functional traits (Cui *et al.*, 2020a). Our large-scale investigation of the relationship between plant flammability, functional traits, and climatic conditions provided new insights into the determinants of plant flammability, which is important for wildfire management in an increasingly fire-prone world.

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Author contributions

This idea was developed by XC. Flammability data were collected by XC, TJC, JPC, SVW, MAA and DC; climatic data were collected by DD, BW, SL, SZ and LX. Analyses were conducted by DD, CY, XC and SL. XC, DD, TJC, AMP and GLWP led the writing of the manuscript with critical input from HLB, ZX and CH. All authors gave final approval for publication. XC and DD contributed equally to this work.

Data availability

The data that supports the findings of this study are available in the supplementary material of this article.

Competing interests

None declared.

References

Alam MA, Wyse SV, Buckley HL, Perry GLW, Sullivan JJ, Mason NWH, Buxton R, Richardson SJ, Curran TJ. **2020**. Shoot flammability is decoupled from leaf flammability, but controlled by leaf functional traits. *Journal of Ecology* **108**: 641–653.

Anderson HE. **1970**. Forest fuel ignitibility. *Fire Technology* **6**: 312–319.

Archibald S, Lehmann CER, Gómez-Dans JL, Bradstock RA. **2013**. Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences* **110**: 6442–6447.

Baird AS, Taylor SH, Pasquet-Kok J, Vuong C, Zhang Y, Watcharamongkol T, Scoffoni C, Edwards EJ, Christin P-A, Osborne CP, *et al.* **2021**. Developmental and biophysical determinants of grass leaf size worldwide. *Nature* **592**: 242–247.

Bianchi LO, Oddi FJ, Muñoz M, Defossé GE. **2019**. Comparison of Leaf Moisture Content and Ignition Characteristics among Native Species and Exotic Conifers in Northwestern Patagonia, Argentina. *Forest Science* **65**: 375–386.

Bjorkman AD, Myers-Smith IH, Elmendorf SC, Normand S, Rüger N, Beck PSA, Blach-Overgaard A, Blok D, Cornelissen JHC, Forbes BC, *et al.* **2018**. Plant functional trait change across a warming tundra biome. *Nature* **562**: 57–62.

Bowman DMJS, French BJ, Prior LD. **2014**. Have plants evolved to self-immolate? *Frontiers in Plant Science* **5**: 590.

Bowman DMJS, Perry GLW, Marston JB. **2015**. Feedbacks and landscape-level vegetation dynamics. *Trends in Ecology & Evolution* **30**: 255–260.

Bussotti F, Pollastrini M, Holland V, Brüggemann W. **2015**. Functional traits and adaptive capacity of European forests to climate change. *Environmental and Experimental Botany* **111**: 91–113.

Calitz W, Potts AJ, Cowling RM. **2015**. Investigating species-level flammability across five biomes in the Eastern Cape, South Africa. *South African Journal of Botany* **101**: 32–39.

Cruz MG, Alexander ME, Fernandes PM, Cruz MG, Alexander ME, Fernandes PM. **2022**. Evidence for lack of a fuel effect on forest and shrubland fire rates of spread under elevated fire danger conditions: implications for modelling and management. *International Journal of Wildland Fire* **31**: 471–479.

Cui X, Paterson AM, Alam MA, Wyse SV, Marshall K, Perry GLW, Curran TJ. **2020a**. Shoot-level flammability across the *Dracophyllum* (Ericaceae) phylogeny: evidence for flammability being an emergent property in a land with little fire. *New Phytologist* **228**: 95–105.

Cui X, Paterson AM, Perry GLW, Wyse SV, Alam MA, Huang C, Zhou S, Xiao L, Lai C, He F, *et al.* 2022. Intraspecific variation in shoot flammability in *Dracophyllum rosmarinifolium* is not predicted by habitat environmental conditions. *Forest Ecosystems* **9**: 100017.

Cui X, Paterson AM, Wyse SV, Alam MA, Maurin KJL, Pieper R, Padullés Cubino J, O'Connell DM, Donkers D, Bréda J, *et al.* 2020b. Shoot flammability of vascular plants is phylogenetically conserved and related to habitat fire-proneness and growth form. *Nature Plants* **6**: 355–359.

Dehane B, Hernando C, Guijarro M, Madrigal J. **2017**. Flammability of some companion species in cork oak (*Quercus suber* L.) forests. *Annals of Forest Science* **74**: 60.

Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Colin Prentice I, *et al.* 2016. The global spectrum of plant form and function. *Nature* **529**: 167–171.

Fernandes PM, Cruz MG. **2012**. Plant flammability experiments offer limited insight into vegetation–fire dynamics interactions. *New Phytologist* **194**: 606–609.

Fick SE, Hijmans RJ. **2017**. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**: 4302–4315.

Gagnon PR, Passmore HA, Platt WJ, Myers JA, Paine CET, Harms KE. **2010**. Does pyrogenicity protect burning plants? *Ecology* **91**: 3481–3486.

Gibson RK, Bradstock RA, Penman T, Keith DA, Driscoll DA. **2015**. Climatic, vegetation and edaphic influences on the probability of fire across mediterranean woodlands of south-eastern Australia. *Journal of Biogeography* **42**: 1750–1760.

Gould SJ, Vrba ES. **1982**. Exaptation-a missing term in the science of form. *Paleobiology* **8**: 4–15.

Harris C, Brummitt N, Cobbold CA, Reeve R. **2022**. Strong phylogenetic signals in global plant bioclimatic envelopes. *Global Ecology and Biogeography* **31**: 2191–2203.

He T, Lamont BB, Downes KS. **2011**. Banksia born to burn. *New Phytologist* **191**: 184–196.

Jardine EC, Thomas GH, Forrestel EJ, Lehmann CER, Osborne CP. **2020**. The global distribution of grass functional traits within grassy biomes. *Journal of Biogeography* **47**: 553–565.

Jin Y, Qian H. **2019**. V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. *Ecography* **42**: 1353–1359.

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO. **2010**. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**: 1463–1464.

Krix DW, Murray BR. **2018**. Landscape variation in plant leaf flammability is driven by leaf traits responding to environmental gradients. *Ecosphere* **9**: e02093.

de Magalhães RMQ, Schwilk DW. **2012**. Leaf traits and litter flammability: evidence for non-additive mixture effects in a temperate forest. *Journal of Ecology* **100**: 1153–1163.

Martin R, Gordon D, Gutierrez M, Lee D, Molina Terrén D, Schroeder R, Sapsis D, Stephens S. **1994**. Assessing the flammability of domestic and wildland vegetation. In: *Proceedings of the 12th Conference on Fire and Forest Meteorology, SAF Publ. 94-02.* Bethesda, MD, USA: SAF, 130–137.

Mason NWH, Frazao C, Buxton RP, Richardson SJ. **2016**. Fire form and function: evidence for exaptive flammability in the New Zealand flora. *Plant Ecology* **217**: 645–659.

Midgley JJ. **2013**. Flammability is not selected for, it emerges. *Australian Journal of Botany* **61**: 102–106.

Moles AT, Perkins SE, Laffan SW, Flores-Moreno H, Awasthy M, Tindall ML, Sack L, Pitman A, Kattge J, Aarssen LW, *et al.* **2014**. Which is a better predictor of plant traits: temperature or precipitation? *Journal of Vegetation Science* **25**: 1167–1180.

Murphy BP, Bradstock RA, Boer MM, Carter J, Cary GJ, Cochrane MA, Fensham RJ, Russell-Smith J, Williamson GJ, Bowman DMJS. **2013**. Fire regimes of Australia: a pyrogeographic model system. *Journal of Biogeography* **40**: 1048–1058.

Mutch RW. **1970**. Wildland Fires and Ecosystems–A Hypothesis. *Ecology* **51**: 1046–1051.

de Oliveira ACP, Nunes A, Rodrigues RG, Branquinho C. **2020**. The response of plant functional traits to aridity in a tropical dry forest. *Science of The Total Environment* **747**: 141177.

Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. **2018**. Caper: Comparative Analyses of Phylogenetics and Evolution in R. *R package version, 1.0.1*, 1-50.

Pausas JG, Alessio GA, Moreira B, Corcobado G. **2012**. Fires enhance flammability in *Ulex parviflorus*. *New Phytologist* **193**: 18–23.

Pausas JG, Keeley JE, Schwilk DW. **2017**. Flammability as an ecological and evolutionary driver. *Journal of Ecology* **105**: 289–297.

Pearman PB, Guisan A, Broennimann O, Randin CF. **2008**. Niche dynamics in space and time. *Trends in Ecology & Evolution* **23**: 149–158.

Peppe DJ, Royer DL, Cariglino B, Oliver SY, Newman S, Leight E, Enikolopov G, Fernandez-Burgos M, Herrera F, Adams JM, *et al.* 2011. Sensitivity of leaf size and shape to climate: global patterns and paleoclimatic applications. *New Phytologist* **190**: 724–739.

Popović Z, Bojović S, Marković M, Cerdà A. **2021**. Tree species flammability based on plant traits: A synthesis. *Science of The Total Environment* **800**: 149625.

Prior LD, Murphy BP, Williamson GJ, Cochrane MA, Jolly WM, Bowman DMJS. **2017**. Does inherent flammability of grass and litter fuels contribute to continental patterns of landscape fire activity? *Journal of Biogeography* **44**: 1225–1238.

Reich PB, Oleksyn J. **2004**. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences* **101**: 11001–11006.

Resco de Dios V. **2020**. *Plant-Fire Interactions: Applying Ecophysiology to Wildfire Management*. New York, NY, USA: Springer International Publishing.

Rosbakh S, Römermann C, Poschlod P. **2015**. Specific leaf area correlates with temperature: new evidence of trait variation at the population, species and community levels. *Alpine Botany* **125**: 79–86.

Scarff FR, Westoby M. **2006**. Leaf litter flammability in some semi-arid Australian woodlands. *Functional Ecology* **20**: 745–752.

Schimper AFW. **1904**. Plant-Geography upon a Physiological Basis. *Nature* **70**: 573–574.

Schwilk DW. **2015**. Dimensions of plant flammability. *New Phytologist* **206**: 486–488.

Schwilk DW, Caprio AC. **2011**. Scaling from leaf traits to fire behaviour: community composition predicts fire severity in a temperate forest. *Journal of Ecology* **99**: 970–980.

Sexton JP, McIntyre PJ, Angert AL, Rice KJ. **2009**. Evolution and Ecology of Species Range Limits. *Annual Review of Ecology, Evolution, and Systematics* **40**: 415–436.

Šímová I, Violle C, Svenning J, Kattge J, Engemann K, Sandel B, Peet RK, Wiser SK, Blonder B, McGill BJ, *et al.* 2018. Spatial patterns and climate relationships of major plant traits in the New World differ between woody and herbaceous species. *Journal of Biogeography* **45**: 895–916.

Snyder JR. **1984**. The role of fire: Mutch ado about nothing? *Oikos* **43**: 404.

Staver AC, Archibald S, Levin SA. **2011**. The Global Extent and Determinants of Savanna and Forest as Alternative Biome States. *Science* **334**: 230–232.

Swenson NG, Enquist BJ. **2007**. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany* **94**: 451–459.

Valverde-Barrantes OJ, Freschet GT, Roumet C, Blackwood CB. **2017**. A worldview of root traits: the influence of ancestry, growth form, climate and mycorrhizal association on the functional trait variation of fine-root tissues in seed plants. *New Phytologist* **215**: 1562–1573.

Van Altena C, van Logtestijn R, Cornwell W, Cornelissen H. **2012**. Species composition and fire: non-additive mixture effects on ground fuel flammability. *Frontiers in Plant Science* **3**: 63.

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.

White RH, Zipperer WC. **2010**. Testing and classification of individual plants for fire behaviour: plant selection for the wildland–urban interface. *International Journal of Wildland Fire* **19**: 213–227.

Whittaker RH. **1970**. *Communities and Ecosystems*. New York, NY, USA: Macmillan.

Wickham H. **2016**. *ggplot2: Elegant Graphics for Data Analysis*. New York, NY, USA: Springer International Publishing.

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Jonathan Davies T, Grytnes J-A, Harrison SP, *et al.* **2010**. Niche conservatism as an emerging principle in ecology and conservation biology: Niche conservatism, ecology, and conservation. *Ecology Letters* **13**: 1310–1324.

Wright IJ, Dong N, Maire V, Prentice IC, Westoby M, Díaz S, Gallagher RV, Jacobs BF, Kooyman R, Law EA, *et al.* **2017**. Global climatic drivers of leaf size. *Science* **357**: 917–921.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, *et al.* **2004**. The worldwide leaf economics spectrum. *Nature* **428**: 821–827.

Wyse SV, Perry GLW, O'Connell DM, Holland PS, Wright MJ, Hosted CL, Whitelock SL, Geary IJ, Maurin KJL, Curran TJ. **2016**. A quantitative assessment of shoot flammability for 60 tree and shrub species supports rankings based on expert opinion. *International Journal of Wildland Fire* **25**: 466.

Zhao W, Cornwell WK, van Pomeren M, van Logtestijn RSP, Cornelissen JHC. **2016**. Species mixture effects on flammability across plant phylogeny: the importance of litter particle size and the special role for non-*Pinus* Pinaceae. *Ecology and Evolution* **6**: 8223–8234.

Zizka A, Silvestro D, Andermann T, Azevedo J, Duarte Ritter C, Edler D, Farooq H, Herdean A, Ariza M, Scharn R, *et al.* **2019**. CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution* **10**: 744–751.

Zomer RJ, Xu J, Trabucco A. 2022. Version 3 of the Global Aridity Index and Potential Evapotranspiration Database. *Scientific Data* **9**: 409.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Table S1 Data and relevant information of the 186 species used in this study.

Table S2 Phylogenetic signals of climatic conditions and functional traits. *P*-values give the significance of Pagel's λ.

Table 1. Pairwise relationships between flammability components and flammability-related functional traits of all species.

	MC[1] (%)		LA[2] (cm^2)	
	Slope	r^2	Slope	r^2
IF (%)	**-0.965*****	0.275	-0.049	0.006
MT (°C)	**-0.372*****	0.348	-0.008	0.001
BT (s)	**-0.963*****	0.306	-0.006	0.000
BB (%)	**-0.849*****	0.265	**-0.152*****	0.062

[1] 153 species have shoot moisture content data.

[2] 161 species have leaf area data.

Slope and r^2 values were taken from the phylogenetic least-squares (PGLS) model. IF, ignition frequency; MT, maximum temperature; BT, burning time; BB, burnt biomass; MC, shoot moisture content; LA, leaf area. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 2. Variation in climatic conditions between fire-prone and non-fire-prone habitats.

Climatic conditions	Fire-prone (n=59)	Non-fire-prone (n=127)	*P* value
Mean annual temperature (°C)	9.96 ± 3.24	11.06 ± 2.97	*
Mean annual precipitation (mm)	1297 ± 667	1770 ± 614	***
Aridity Index	1.23 ± 0.69	1.67 ± 0.65	***

Statistical differences were analyzed using Mann-Whitney U test. Data are presented as the mean values ± standard deviation. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 3 Pairwise relationships between flammability components, climatic conditions, and flammability-related functional traits of species from fire-prone and non-fire-prone habitats.

		IF (%)		MT (°C)		BT (s)		BB (%)		MC (%)		LA (cm^2)	
		Slope	r^2	Slope	r^2	Slope	r^2	Slope	r^2	Slope	r^2	Slope	r^2
Fire-prone	MAT (°C)	0.559	0.002	0.288	0.013	0.814	0.010	0.177	0.002	-0.379	0.019	**1.662***	0.081
	MAP (mm)	0.208	0.005	0.222	0.019	0.714	0.023	0.415	0.004	-0.047	0.001	**-1.422***	0.105
	AI	-0.013	0.000	0.027	0.006	0.097	0.009	0.039	0.002	-0.004	0.000	**-0.447****	0.156
	MC^1 (%)	**-1.137*****	0.382	**-0.459*****	0.429	**-1.077*****	0.254	**-0.973*****	0.319				
	LA^2 (cm^2)	-0.109	0.012	-0.014	0.003	-0.010	0.000	-0.128	0.027				
Non-fire-prone	MAT (°C)	**1.290****	0.051	**0.460****	0.067	**1.195****	0.071	0.133	0.001	**-0.694****	0.062	**3.733*****	0.235
	MAP (mm)	-0.370	0.001	-0.181	0.097	-0.536	0.022	-0.178	0.003	**0.501****	0.057	**-1.341***	0.051
	AI	-0.117	0.006	**-0.055***	0.024	**-0.141***	0.025	-0.036	0.002	**0.114***	0.045	**-0.395****	0.069
	MC^3 (%)	**-0.975*****	0.271	**-0.336*****	0.340	**-0.908*****	0.390	**-0.902*****	0.321				
	LA^4 (cm^2)	-0.057	0.007	0.005	0.001	0.027	0.002	**-0.156****	0.069				

[1] 53 species have shoot moisture content data.

[2] 52 species have leaf area data.

[3] 100 species have shoot moisture content data.

[4] 109 species have leaf area data.

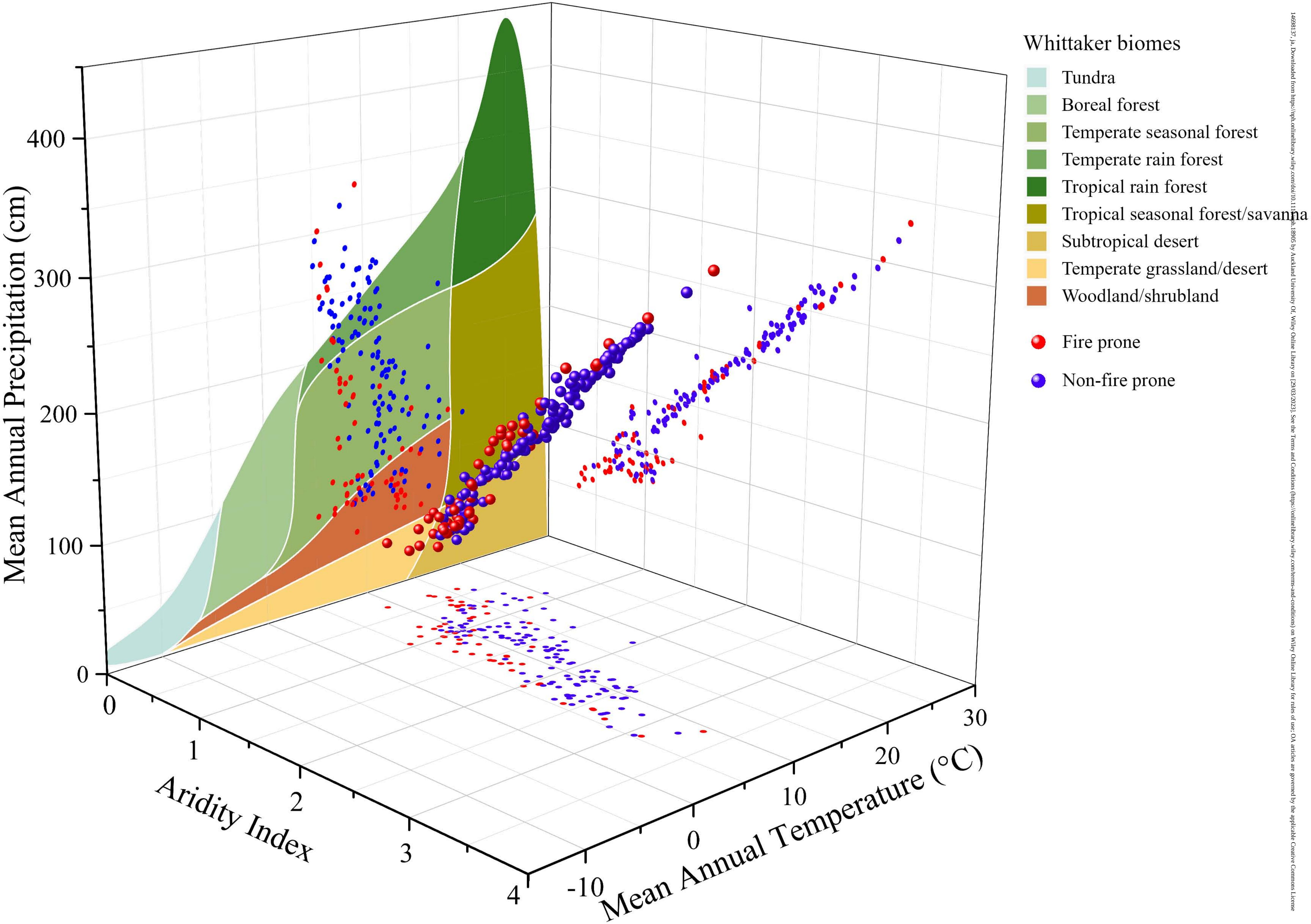
Slope and r^2 values were taken from the phylogenetic least-squares (PGLS) model. IF, ignition frequency; MT, maximum temperature; BT, burning time; BB, burnt biomass; MC, shoot moisture content; LA, leaf area; MAT, mean annual temperature; MAP, mean annual precipitation; AI, Aridity Index. **P* < 0.05, ***P* < 0.01, ****P* < 0.001.

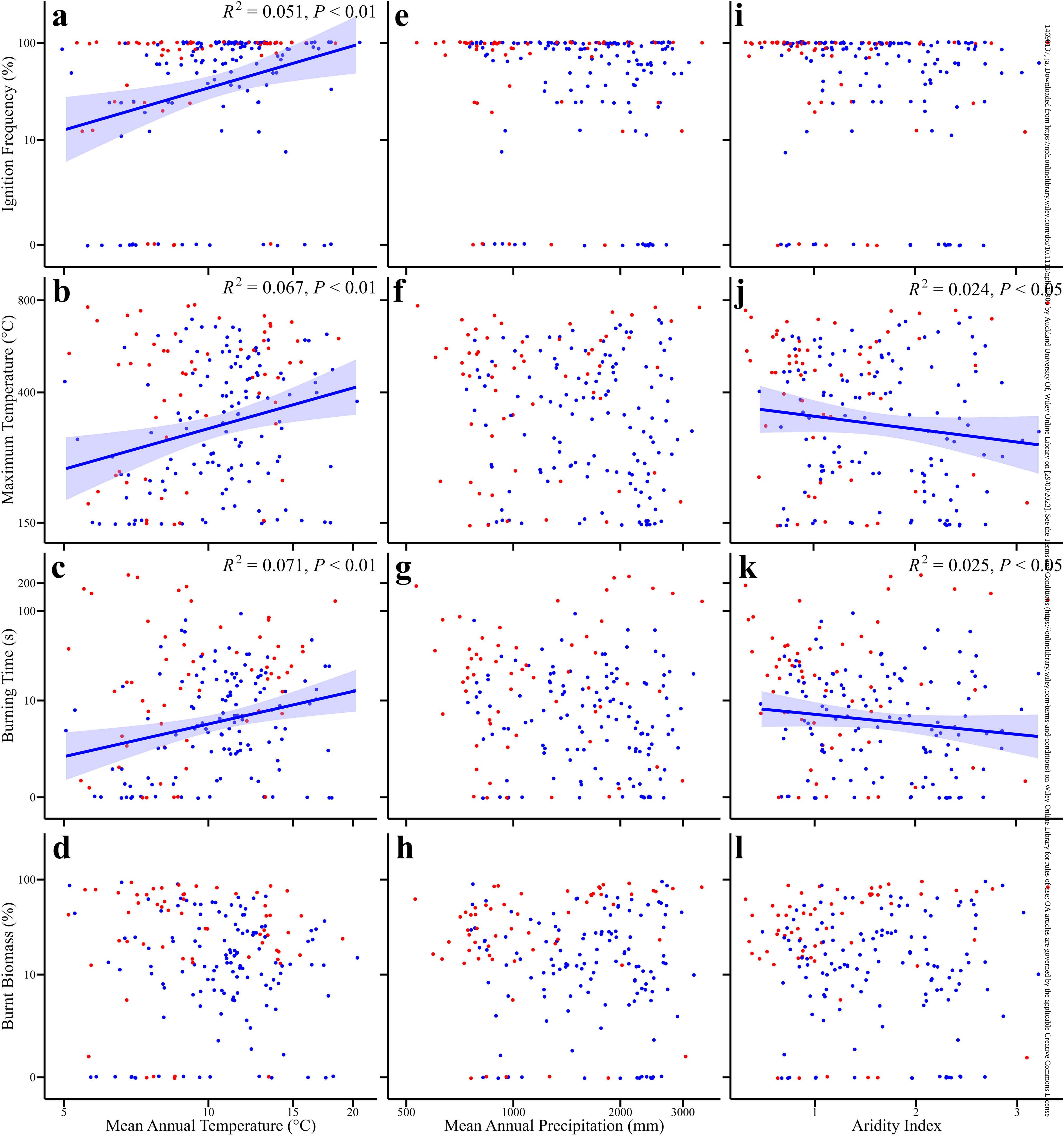
Figure captions

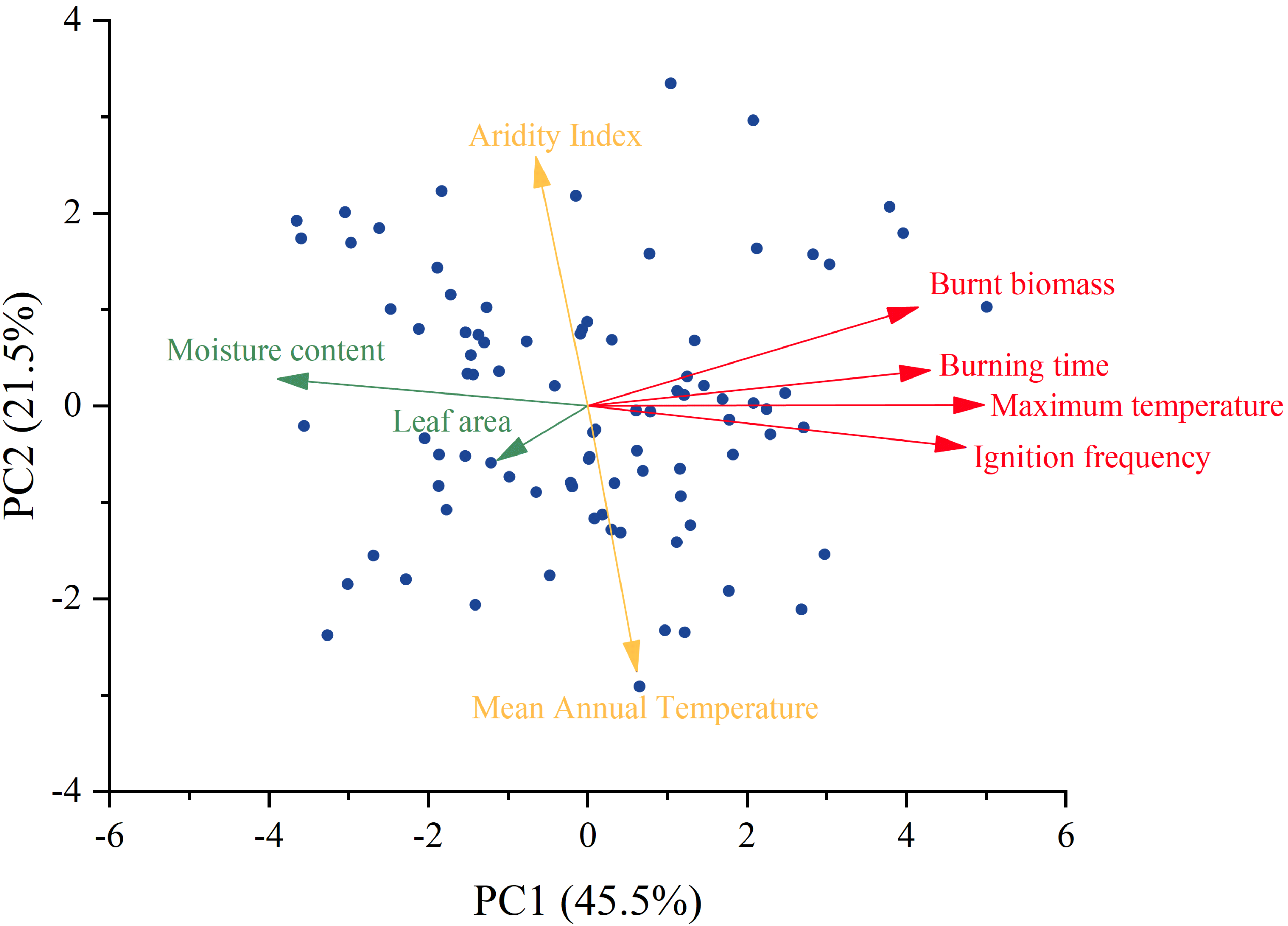
Figure 1 The climatic conditions (MAT, MAP and AI) of the 186 species. Biomes were classified by using MAT and MAP following Whittaker (1970). Higher values in AI represent more humid conditions. Red sphere/point indicates species from fire prone habitats, and blue sphere/point indicates species from non-fire-prone habitats.

Figure 2 The relationships between flammability components and climatic conditions. Blue points indicate species from non-fire-prone habitats, red points indicate species from fire-prone habitats. Blue lines indicate the line of best fit for species from non-fire-prone habitats, red lines indicate the line of best fit for species from fire-prone habitats, the shaded area indicate the range of the 95% confidence intervals, r^2 and *P*-values were calculated by the phylogenetic least-squares (PGLS) model. Higher values in AI represent more humid conditions.

Figure 3 Principal components analysis (PCA) of flammability components, climatic conditions and flammability-related traits across species from non-fire-prone habitats. Red vectors indicate flammability components: ignition frequency, maximum temperature, burning time and burnt biomass; yellow vectors indicate habitat climatic conditions; green vectors indicate flammability-related traits. Higher value in AI represents more humid conditions.


Mean Annual Precipitation (cm)
0
100
200
300
400
Aridity Index
0
1
2
3
4
Mean Annual Temperature (°C)
-10
0
10
20
30
Whittaker biomes
Tundra
Boreal forest
Temperate seasonal forest
Temperate rain forest
Tropical rain forest
Tropical seasonal forest/savanna
Subtropical desert
Temperate grassland/desert
Woodland/shrubland
Fire prone
Non-fire prone


a
$R^2 = 0.051, P < 0.01$
b
$R^2 = 0.067, P < 0.01$
c
$R^2 = 0.071, P < 0.01$
d
e
f
g
h
i
j
$R^2 = 0.024, P < 0.05$
k
$R^2 = 0.025, P < 0.05$
l
Ignition Frequency (%)
100
10
0
Maximum Temperature (°C)
800
400
150
Burning Time (s)
200
100
10
0
Burnt Biomass (%)
100
10
0
5
10
15
20
Mean Annual Temperature (°C)
500
1000
2000
3000
Mean Annual Precipitation (mm)
1
2
3
Aridity Index


4
2
0
-2
-4
-6
-4
-2
0
2
4
6
PC2 (21.5%)
PC1 (45.5%)
Aridity Index
Mean Annual Temperature
Moisture content
Leaf area
Burnt biomass
Burning time
Maximum temperature
Ignition frequency