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The effects of fire frequency on leaf and bark flammability strategies in subtropical semi-humid evergreen broadleaved forests in China

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Lack of knowledge of plant flammability has impeded the understanding of ecological feedbacks between fire and vegetation. We measured flammability traits of 263 woody plant species in the subtropical semi-humid regions of China to identify plant flammability strategies and assess the impact of fire frequency on different plant flammability syndromes that were defined as combinations of flammability strategies of leaves and bark. The results indicated that 40.0%, 39.1% and 20.9% of woody plant species had hot-, fast- and low-flammable leaves, respectively, and 28.2%, 35.7% and 36.1% of species had hot-, fast- and low-flammable bark, respectively. Tree species (47.5%) had a higher percentage of flammability strategy separation between leaves and bark than large shrubs (19.7%) and shrub species (18.2%). Community-level evidence showed that species with fast- or hot-flammable leaves and bark may gain a notable advantage with repeated fires. Structural equation models indicated that more frequently burned forests were associated with infertile soil, shrub enrichment and lower species richness, subsequently leading to favour on flammable plant species. Thus, a positive feedback loop would be generated between the dominance of flammable species in the plant communities and fire frequency, fostering the characteristics of fire regimes in the semi-humid evergreen broadleaved forests.

This article is part of the theme issue 'Novel fire regimes under climate changes and human influences: impacts, ecosystem responses and feedbacks'.

1. Introduction

Fire frequency, as one of the fundamental characteristics of a fire regime, is jointly determined by fuel load accumulation, fuel flammability and ignition events, revealing ecological and evolutionary links between the fuel syndrome and fire regime of a fire-prone ecosystem [1–3]. The impact of fire frequency extends to ecological filtering processes that selectively favour specific traits and species [4–6], thus playing a critical role in species coexistence, forest structure and community assembly [5,7–9].

In a generally recognized paradigm, fire occurrence is determined by a scale-related hierarchical framework [10]. Among regions of a similar climate, distinct fire regimes often arise from variations in differentiated community assembly, which is characterized by different dominant species [11,12]. For example, the difference in fire intensity and burned area of boreal forests between northern North America and Eurasia was attributed to different fuel characteristics of their dominant tree species, evergreen *Picea* and *Pinus* versus deciduous *Larix*, respectively [12,13]. Within the region of subtropic semi-humid climate in southwest China, the heterogenic topography also creates a mosaic of different fire regimes, maintaining conifer forests dominated by Yunnan pine (*Pinus yunnanensis*) on the sunny south slopes and ridges with more frequent fires, and evergreen broadleaved forests at the shady slopes and valley bottom, influenced by infrequent and light-severity fires [14,15]. Vegetation plays a crucial role in influencing a fire regime through factors such as fuel load and flammability, which are determined by multiple plant traits [7,8,16]. The feedback between tree species and the local fire regime remains an open question. This prompts investigation into whether tree species are selectively filtered by the local fire regime and post-fire environment, or if, conversely, tree species play an active role in driving the divergence of fire regimes.

Limited knowledge of plant flammability traits and fire-adaptive strategies that indicate the ability of burning and flame spreading has hindered a comprehensive understanding of the extent and underlying mechanisms of ecological feedback between fire and vegetation [16–18]. To address this issue, Pausas *et al*. [17] proposed a conceptual framework that identified three flammability strategies (non-flammable, fast-flammable and hot-flammable), with regard to the likelihood of ignition and differentiated burning behaviours among plant species. Species of three flammability strategies exhibit distinct survival and reproduction behaviours under recurrent fires. Non-flammable plants are rarely burned; fast-flammable plants could survive fires and mostly resprout in post-fire communities; and hot-flammable plants have high mortality rates but exhibit post-fire recruitment through enhanced seeding, including more effective seed regeneration, dispersal and germination [19]. Despite the significance of these findings, there remains a notable gap in demonstrating the association between flammability strategies and the ecological fitness of plant species [17,20].

Given that plant flammability strategies are subject to natural selection at both organ and individual levels, it is suggested that the flammability strategies of species may differ among plant organs [17], influenced by the magnitude and frequency of fire disturbances. Notably, canopy leaves and trunk bark are the main parts of woody plant species burned in canopy and surface fires, respectively [21]. As fire-exposed tissues, their flammability could be considered a fire-response trait that is susceptible to fire disturbances [22]. Therefore, investigating the differences in the flammability strategy of leaves and bark, as well as the combinations of their strategies as plant flammability syndromes (PFSs) should enhance our understanding of plant resilience and adaptation to varying fire disturbances. It is thus worthwhile to explore the distribution of different flammability strategies of leaves and bark and how plants with different PFSs adapt to and change with different fire frequencies, aiming to demonstrate the ecological effects of fire frequency on forest composition and species coexistence with regard to fire adaptation.

Our research is conducted in the subtropic southwest China, which is characterized by the subtropical monsoon climate and widespread distribution of the mixed Yunnan pine–evergreen broadleaved forests [23–26]. This region is identified as a wildfire hotspot due to limited annual precipitation (700–900 mm) with strong seasonality that is regulated by the Indian Ocean Monsoon and intensive human activities that cause most of the fire events [23,24]. In this study, we measured the flammability traits of 263 common woody plant species to identify their flammability strategies. Utilizing the community composition data, we explored the pathways through which fire frequency influences PFSs in this region. Based on our earlier understanding that this vegetation type is a typical fire-prone ecosystem [14,27,28], we hypothesized that common woody plant species in this type of forest communities should exhibit either hot- or fast-flammable strategies in their leaves and bark. Additionally, we assume that more flammable species thrive in habitats with more frequent fires.

2. Material and methods

(a) Study area and wildfire distribution

This study was conducted across the Central Yunnan Plateau (CYP) in Yunnan Province, southwest China (figure 1). This region is near mainland Southeast Asia, which is one of the global hotspots of both biodiversity and wildfire activity [30]. The climate of this region is subtropical semi-humid, and the zonal vegetation type is semi-humid evergreen broadleaved forests (SEBFs), which have been extensively fragmented by wildfires and human disturbances. These forests have largely been replaced by conifer forests dominated by *P. yunnanensis* (Yunnan pine), as well as secondary mixed forests and shrublands [24,31].

To assess the fire frequency of the study area, we used the fire counts of 20 years (2001−2020) from fire points product of moderate resolution imaging spectrometer (MODIS; MOD14A1 and MYD14A1) [32]. The number of fire counts was calculated by the active fire hot spots that occurred within the 1 km grid cells. As a result, some areas such as the northwest and south of CYP region are experiencing more frequent fires in last two decades. Based on the pattern of wildfire frequency in the study area and average fire return interval of about 12 years (average fire frequency = 0.08 times per year) [29], we classified the areas into the following three classes: NOFI (grid cells with no fire incidence in 20 year period, fire counts = 0, fire frequency = 0), HIFI (grid cells with three or more fires in the period, fire counts ≥3, fire frequency ≥ 0.15 times per year) and other areas (grid cells with one or two fires, 0 < fire counts < 3, fire frequency = 0.05–0.10 times per year, which was close to average fire frequency [29]).

(b) Forest investigation, sampling and flammability measurements

For testing the flammability of plants broadly, we randomly selected 205 sites across the CYP to collect plant leaf and bark samples of a total of 263 woody plant species, with at least three replicates per species at different sites (figure 1). The sampled

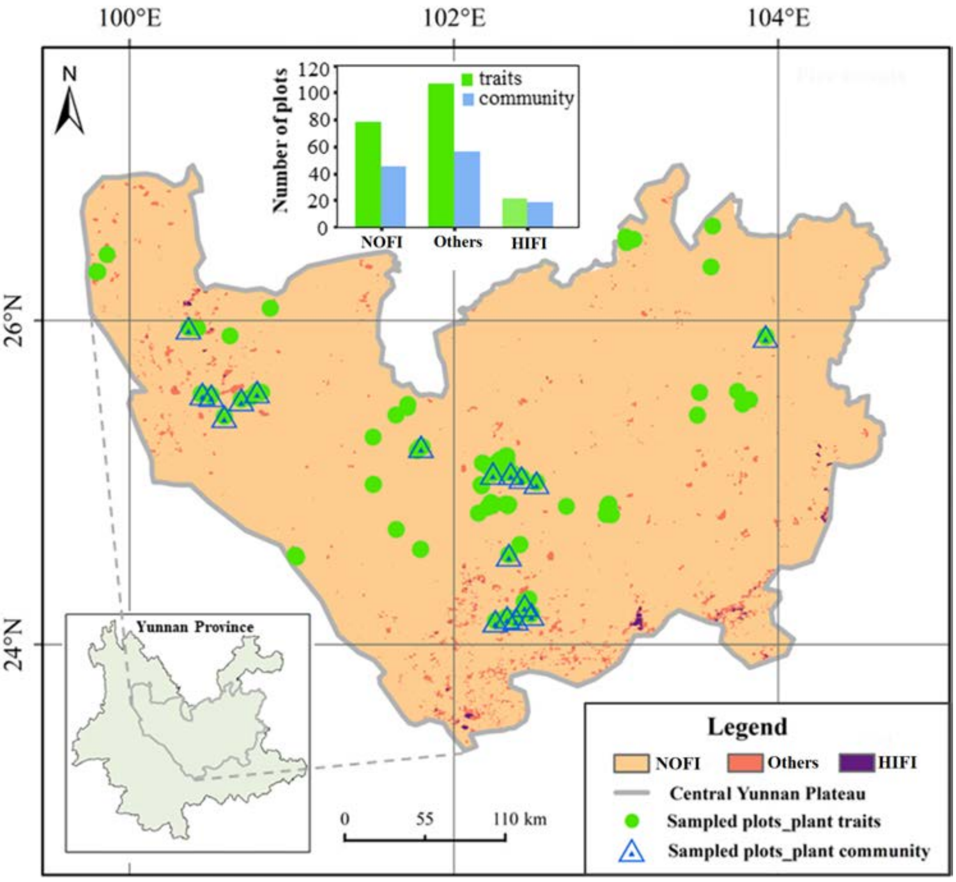

Figure 1. Map of study area and the distribution of fire counts during 2001–2020. Blue triangles, sampling plots of forest communities; green circles, sampling plots for plant traits. Sub-figures: the left bottom was the location of the CYP region in Yunnan Province, and the histogram shows the distribution of sampled plots of plant traits (green) and investigated community (blue) with different fire frequencies. Abbreviations of different fire frequencies: NOFI (no fire incidence in 20 years), HIFI (fire counts ≥ 3). 'Others' indicates 0 < fire counts < 3, which was close to average fire frequency [29].

species were classified into three growth forms including tree, large shrub and shrub based on *Flora of Yunnan* and *Flora of China* [33,34], based on their average height and branching features. Samples were obtained using leaves and bark from healthy and mature plants. We collected canopy leaves per individual from plants growing under relatively optimal conditions to avoid leaves with obvious symptoms of pathogen or herbivore attack. We also collected 100 cm^2 bark samples (over sapwood) at breast height above the soil (trees) or base (not trees) per individual.

Among those traits sampling sites, we selected 19 sites to investigate communities and assess the effects of fire frequency on plant flammability strategies. We applied a stratified random sampling procedure, based on the fire frequency level (i.e. HIFI, NOFI and others), keeping those sites far enough apart from each other (at least 5.66 km in between; figure 1). At each site, we selected typical forest communities on two aspects of the mountains (sunny and shady) and three slope positions (valley, middle slope and upper slope) and sampled a total of 120 forest plots (20 × 20 m area, each further divided into four subplots of 10 × 10 m). We recorded species names in each community to evaluate species richness, measured basal area of each woody plant, and summed by species in each subplot. A total of 163 woody species in the plant trait data were recorded in the community investigation. We also measured topographic features (slope position, aspect and slope angle), following reference [15], collected a surface soil sample of 500 g at the depth of 0–5 cm in each plot, brought the soil samples back to the laboratory and processed them following the standard procedure [35] before analysing pH value, total nitrogen (TN) and organic carbon (OC). For the specific measuring methods, refer to Luo *et al*. [15]. The organic matter component (OMC) represents the primary factor derived from a principal component analysis conducted using OC and TN [36].

Flammability measurements of leaves and bark were performed in the laboratory using the cone calorimeter (CONE, TTech-GBT16172, FTT, England) with the ISO-5660-1 method [37,38]. We measured the flammability of 263 common woody plant species in SEBFs, covering 84.5% of the woody species in the community. The radiation intensity of the cone calorimeter was set to 35 kW m^{-2}, and the temperature of the burner vessel at a distance of 25 mm from the radiation cone was leading to 650°C. The set temperature was chosen to be sure that most samples would ignite and could detect the differences in flammability across species based on our pilot experiments. The oxygen concentration was set to 20.85–20.95% to simulate burning in the air. A fan at the entrance produced a forced airflow through the tunnel with 24 l/s. Before the burning experiment, all leaves and bark samples were air-dried for 72 h at a temperature of 65°C. The flammability traits of different tissue types mostly depend on the quality of the tissues, and the architecture and structure of the samples [39]. Therefore, three replicates of 3 g (±0.5 g) plant samples for each species were laid without crushing in the centre of a 100 × 100 mm burner vessel for preserving natural states. For most species, samples were laid together naturally to resemble well-aerated fuel beds. For species with large leaves or thick bark, 3 g (±0.5 g) samples were cut and burned as sections. All samples ignited successfully at 650°C, and there were no non-flammable materials remained in the burning experiments. The cone calorimeter recorded the time to ignite (TTI) and flaming time duration (FT) during the combustion. The maximum flame height (FH) was recorded during the combustion (the maximum record of FH was 55 cm).

(c) Data analyses

We selected three flammability traits, namely TTI, FT and FH, which represent ignitability, sustainability and ability of flame spread [17]. Then we normalized flammability data and clustered the species into low-flammable, hot-flammable and fast-flammable strategies based on the three dimensions of flammability traits. We used 'fit.pam' function in R package 'cluster' [40] with partition around medoids clustering to eliminate the noise of outliner. Then we plotted the species on scatterplots to show the interspecific variation within different flammability strategies, using R package 'rgl' [41].

We proposed to establish a concept of species-level PFSs, based on combinations of the flammability strategy of leaves and bark of woody plant species (figure 2). These PFSs related to flammability strategies based on nine combinations of leaf and bark flammability strategies (Fast + Fast, Fast + Hot, Fast + Low, Hot + Fast, Hot + Hot, Hot + Low, Low + Fast, Low + Hot and Low + Low), and each represented a species-level flammability strategy (figure 2). The PFSs include plants with flammable (fast- or hot-flammable strategies) leaves and bark (FLFB), plants with flammable leaves and non-flammable (low-flammable strategy) bark (FLNB), plants with non-flammable leaves and flammable bark (NLFB), and plants with non-flammable leaves and non-flammable bark (NLNB). Specifically, both FLNB and NLFB represent the separation of flammability strategies between leaves and bark, indicating the presence of two distinct flammability strategies within a single plant species.

We used the importance value (IV) to measure the significance of a species in a given ecosystem [42]. The IV for tree species were calculated and summed up for relative abundance, relative frequency and relative dominance. These components of the plot-based IV were calculated using data from four subplots within each plot, with the following formula: relative abundance = (abundance of a species/total abundance of all species) × 100; relative frequency = (frequency of a species/total frequency of all species) × 100; and relative dominance = (total basal area of a species/total basal area of all species) × 100. For large shrub and shrub species, IV of a plant species was calculated as (cover of a species/total cover of all species) × 100. Moreover, IV was also used as a proxy for the significance of different PFSs within communities and was assessed by summing IVs of species belonging to the same PFSs. In addition, we calculated the relative IV of different PFSs by plant growth forms using the formula: $(\Sigma(\text{IV of the same PFS})/\Sigma(\text{IV of the same plant growth forms})) \times 100$. This approach provides a better understanding of the distribution of different PFSs across various plant growth forms in post-fire communities. To compare the distribution of PFSs between areas with varying fire frequencies and highlight the effects of fire, we selected to compare only NOFI and HIFI areas to reduce complexity and minimize the influence of other factors. We then employed the non-parametric Duncan test to assess differences in the plot-based IV of various PFS plants between NOFI and HIFI, in order to characterize the distribution of different PFS plants. To unravel the pathway through which fire frequency influences the flammability of forest communities, we used structural equation models (SEM) to deduce direct and indirect effects of fire frequency, along with climate, topography, soil properties and biotic factors, on the IV of all FLFB species within the community. The multiple comparisons of different PFS plants across different fire frequency areas were conducted with Duncan test in R package 'agricolae' [43]. The SEM analyses were conducted with raw data of fire frequency using the R packages 'piecewiseSEM' [44], and the path coefficients of each path (β), indicating the strength of the relationship, were reported. We calculated the R^2 to assess the fit of component models, and p values, along with Akaike information criterion (AIC), were used to evaluate the fitness of the SEM models. All statistical analyses were conducted using R (R Development Core Team, 2022) and its packages as mentioned.

3. Results

(a) Flammability strategies of leaves and bark

According to the conceptual model (figure 3a), the leaves and bark of the 263 woody plant species were classified into three flammability strategies: low-flammable, hot-flammable and fast-flammable strategies (figure 3b,c). Low-flammable strategy is characterized by low ignitability (high TTI) and a slow spread rate (low FH). Leaves with fast- and hot-flammable strategies both exhibit high ignitability and a rapid spread rate, with hot-flammable leaves requiring more time to burn out (high FT). Similar to leaves, bark with fast- and hot-flammable strategies both exhibit high ignitability but differ in spread rate.

The frequency distribution of three flammability strategies in leaves and bark among 263 woody plant species varied across different growth forms (figure 4a,b). The leaves of about 80% of the woody species were either fast- or hot-flammable, irrespective of growth forms, exhibiting both high ignitability (igniting within 10 s) and a rapid spread rate (mostly ≥40 cm; figure 4a; electronic supplementary material, figure S1). The barks of more than half tree species were low-flammable, while 58.0% of shrub species' bark was identified as fast-flammable (figure 4b). Furthermore, bark of tree species showed significantly lower ignitability and spread rate and higher sustainability compared to bark of large shrubs and shrub species (all $p < 0.01$; electronic supplementary material, figure S1).

(b) The plant distribution of plant flammability syndromes and its changes with fire frequencies

Plant species with different PFSs based on the flammability strategy of leaves and bark coexist in the communities, and their frequency distributions differed across growth forms (figure 4c). The percentages of FLFB plants as a combination of flammable

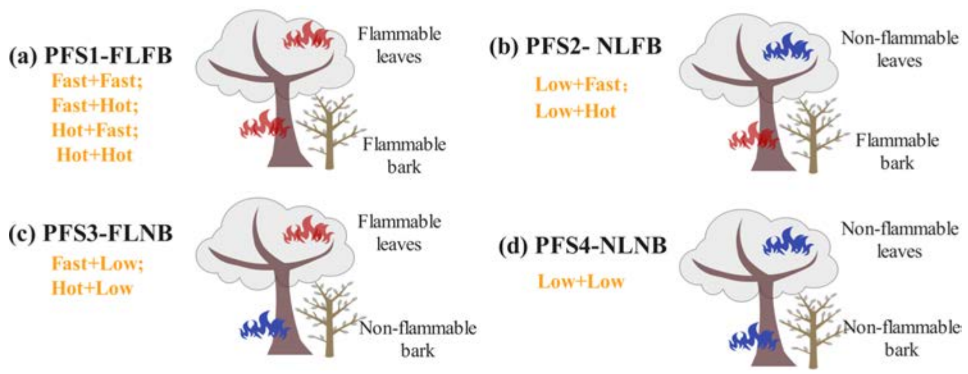

Figure 2. Four main PFSs in the SEBFs, indicated by their leaf and bark flammability strategy combinations (yellow bold words). 'Fast', 'Hot' and 'Low' were short for fast-flammable, hot-flammable and low-flammable strategy, respectively. Specifically, fast- and hot-flammable strategies of leaves and bark implied they were flammable, and low-flammable strategy implied they were non-flammable. Four PFSs are identified according to nine combinations of flammability strategies of leaves and bark.

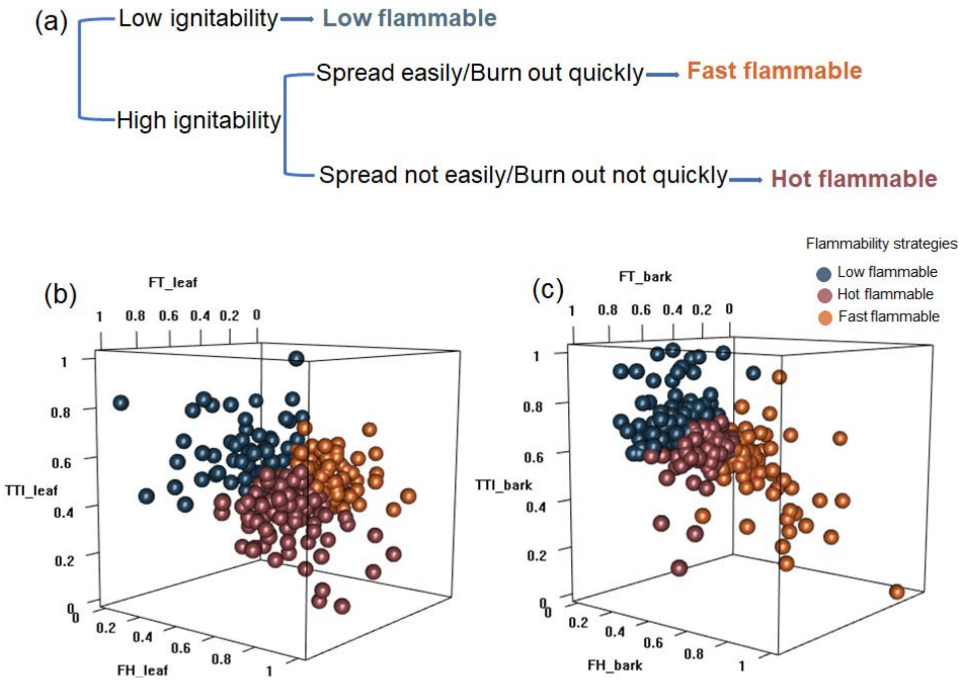

Figure 3. (a) Tree branching diagram: the criteria for classifying plant flammability strategies, adapted from [17]. (b,c) Three-dimensional scatterplots: the classification of the flammability strategies for (b) leaves and (c) bark. The colour of the points on the plots indicates the different flammability strategies. TTI, FT and FH represent time to ignition (ignitability), flame duration (sustainability) and maximum height of flame (ability of flame spread), respectively. TTI, FT and FH were normalized before clustering analysis.

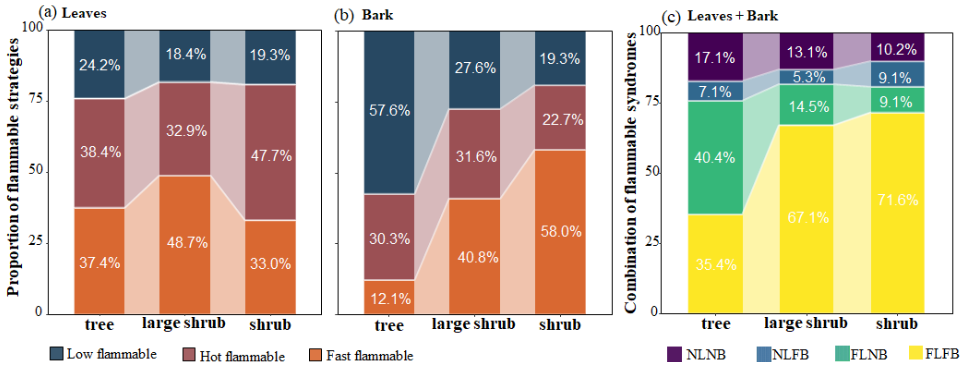

Figure 4. The distribution of different flammability strategies and flammability syndromes across three growth forms of woody plants. (a,b) Percentages of different flammability strategies for (a) leaves and (b) bark. (c) Percentages of different flammability syndromes based on four combinations of flammability strategies for leaves and bark. In addition, 'FLNB' and 'NLFB' represent the separation of flammability strategies across different organs of a single plant. This separation indicates the presence of two distinct flammability strategies in leaves and bark of a single plant species (i.e. FLNB and NLFB).

leaves and bark were higher in both large shrub (67.1%) and shrub (71.6%) species than in tree species (35.4%), while a much higher percentage of FLNB plants comprised tree species than large shrub and shrub species. Plants exhibiting NLFB comprised

Table 1. Relative IVs of different PFS plants within the community and by plant growth forms. Multiple comparisons with Duncan test were conducted between NOFI (unburned) and HIFI (frequently burned) areas (mean ± SE). Different letters indicate significant differences in multiple comparisons. Bold annotations indicate significant differences in important values between NOFI and HIFI areas ($p < 0.05$). 'All' refers to the percentages of different flammability strategies among all woody species (including tree/large shrub/shrub species).

different PFSs	all		tree		large shrub		shrub	
	NOFI	HIFI	NOFI	HIFI	NOFI	HIFI	NOFI	HIFI
FLFB	**83.3 ± 2.3^{b}**	**95.1 ± 1.4^{a}**	61.1 ± 5.6^{a}	76.0 ± 8.0^{a}	98.7 ± 0.6^{a}	98.2 ± 0.9^{a}	99.6 ± 0.2^{a}	98.7 ± 0.2^{a}
FLNB	**15.1 ± 2.3^{a}**	**3.7 ± 1.4^{b}**	**35.8 ± 5.5^{a}**	**12.0 ± 4.2^{b}**	0.6 ± 0.03	—	0.1 ± 0.1	—
NLFB	0.9 ± 0.4^{a}	1.2 ± 0.4^{a}	2.1 ± 0.9^{a}	11.8 ± 8.1^{a}	**$4.96 \times 10^{-16\,b}$**	**1.8 ± 0.9^{a}**	0.3 ± 0.2^{a}	1.3 ± 0.7^{a}
NLNB	0.6 ± 0.3^{a}	0.1 ± 0.3^{a}	1.0 ± 0.5^{a}	0.2 ± 0.2^{a}	0.6 ± 0.3	—	—	—
all	100	100	100	100	100	100	100	100

only 7.1, 5.3 and 9.1% of tree, large shrub and shrub species. Moreover, tree species are predominantly (59.6%) composed of 'Fast + Low', 'Hot + Hot' and 'Hot + Low' combinations (electronic supplementary material, figure S2), represented of the FLFB and FLNB types (figure 4c). In contrast, over 46% of large shrub species exhibit 'Fast + Fast' and 'Fast + Hot' combinations, and 53.4% of shrub species display 'Fast + Fast' and 'Hot + Fast' combinations. In addition, figure 4c (showing the percentages of separation between leaves and bark that indicate the presence of two distinct flammability strategies within a single plant, represented by the sum of percentages of FLNB and NLFB) showed that tree species (47.5%) had a higher percentage of flammability strategy separation between leaves and bark compared to large shrub (19.7%) and shrub species (18.2%; figure 4c).

For three plant growth forms, the composition of different PFSs was found to be quite similar among areas with different fire frequencies (table 1). The majority of woody plant species are characterized by FLNB in both high fire frequency (HIFI) and low fire frequency (NOFI) areas. However, FLFB plants gain more advantage in HIFI areas ($p < 0.05$) for all woody species, while more FLNB species were observed in NOFI areas ($p < 0.05$). Specifically, the IV of woody plant species with the 'Fast + Fast' combination in HIFI areas was significantly higher than in NOFI areas, and 'Fast + Low' plants took more advantages in NOFI areas (electronic supplementary material, table S1). Moreover, there were more plant species with consistent flammability strategy in leaves and bark in HIFI areas (electronic supplementary material, table S2).

(c) Possible pathways of fire frequency effects on flammable plants

The SEMs for the prevalence of flammable plants (IV_FLFB) in the community exhibited good fitness and explained 48% of the variance (figure 5a; SEMs for other PFSs, please see electronic supplementary material, figure S3). The IV of FLFB in the community had a highly positive correlation with the IV of shrub species ($\beta = 0.53$) and was also positively correlated with fire frequency ($\beta = 0.14$) while being negatively correlated with species richness ($\beta = -0.22$). Additionally, fire frequency and soil OMC had an indirect effect on IV of FLFB by increasing the IV of shrubs (figure 5a; electronic supplementary material, figure S2). Taken together, IV of shrubs, species richness, the mean temperature of dry season (MTDQ) and fire frequency dominated the thriving of flammable plants in the community (figure 5b).

The SEMs (figure 5a,b) further illustrated the pathways through which fire frequency influenced subtropical semi-humid forests. Initially, MTDQ directly increased fire frequency ($\beta = 0.29$), indicating that higher temperatures during dry quarter resulted in more frequent fires. Then a causal path from fire frequency to soil properties (OMC and pH) showed that more frequent fires lead to less fertile and more acidic soils ($\beta_{\mathrm{OMC}} = -0.52$; $\beta_{\mathrm{pH}} = -0.24$). Fire frequency had both direct and indirect effects on community structure, with the indirect effects influenced by soil properties. Additionally, fire frequency indirectly exerted negative effects on species richness through its impact on soil properties and shrub enrichment. Ultimately, fire frequency promotes the prevalence of FLFB plants in the community, both directly and indirectly mediated by biotic factors.

4. Discussions

Flammability distinction is believed to play a pivotal role in niche differentiation and community assembly for plant species living in fire-prone ecosystems [17,45,46]. Flammability strategies are defined by distinctions in different dimensions of flammability [17], and the classification of these strategies can be validated across various ecological contexts using the global flammability database [47]. This study reveals that plants with different flammability strategies can coexist in subtropical SEBFs. It is posited that flammable fuel beds serve as the evolutionary cradle for non-flammable woody plant species, facilitating their coexistence [17]. A notable example is the evolutionary adaptation of low-flammable species, such as pines with self-pruning, in response to the presence of highly flammable grasses in tropical biomes [46]. It is crucial to recognize that the flammability strategies of species can vary across different organs, reflecting distinct flammability syndromes that correspond to diverse fire disturbances [17,46]. Yunnan pine (*P. yunnanensis*), a dominant species in the secondary forests in the study region, possesses fast-flammable leaves and low-flammable bark (FLNB), adapting effectively to frequent surface fires through self-pruning mechanisms and thick bark (figure 6c) [48]. A co-occurring species, *Cyclobalanopsis delavayi* (Fagaceae),

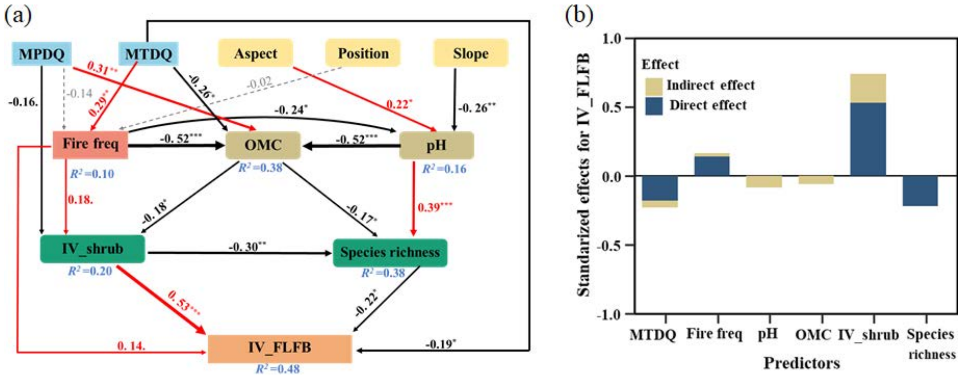

Figure 5. (a) SEM of climate (blue), topography (yellow), soil (brown), biotic factors (green) and fire frequency (red) as predictors for IV of FLFB plants (IV_FLFB) (orange) in the community (Fisher's $C = 30.02$, AIC $= 165.613$, $p = 0.663$). The path coefficients as standardized effect sizes are adjacent to arrows, and arrow width is proportional to the strength of relationship. Solid red and black arrows: significant positive and negative paths ($p < 0.10$), respectively; dotted grey arrows: insignificant paths ($p > 0.10$). R^2: the variance explained by predictors. Significant relationships: . $p < 0.10$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. (b) The direct and indirect effects estimated by SEM. Indirect effect = indirect pathway standardized coefficients × pathway standardized coefficients of direct and indirect factors. Abbreviations as per the text: MTDQ = mean temperature of the driest quarter; MPDQ = mean precipitation of driest quarter; Aspect = aspect of mountain slope; Position = position of mountain slope; Slope = slope angle of mountain slope; Fire freq = fire frequency; OMC = organic matter content; IV_shrub = importance value of shrub species; IV_FLFB = importance value of FLFB species.

also features fast-flammable leaves and low-flammable thick insulating bark (FLNB) [49] (figure 6d). Less flammable species (NLFB and NLNB) are typically found in areas with infrequent fires (figure 6e,f) and might be independent of fire (electronic supplementary material, figure S3c,d). Another type of less flammable species (FLNB) can survive and reproduce after fires due to the low ignitability of their bark, despite living in fire-prone ecosystems [17]. Nonetheless, research on adaptation and plasticity of flammability strategies in different species under varying fire regimes is still rare.

Consistent with findings about the impact of fire frequency on plant communities [4,11,50], this study reveals that areas experiencing more frequent burning had more flammable plants (FLFB) in SEBFs. For example, FLFB plants like *P. yunnanensis* var. *pygmaea* and *Lithocarpus mairei* dominate areas subjected to quite frequent burning, taking advantage from post-fire resprouting (figure 6a) [27,28,51]. The other FLFB species, *Rhododendron delavayi* (Ericaceae), also gains competitive advantage from epicormic resprouting after fires (figure 6b). We found that the FLFB plants have high branching, which makes them susceptible to easy ignition and rapid spread during combustion, while also extending combustion residence time. These characteristics of FLFB species contribute to the generation of fires that eliminate co-occurring species and create open spaces conducive to post-fire recruitment. However, it is necessary to explore the relationship between plant functional traits, architecture and flammability strategies, as well as their interactions in conferring fitness benefits to plants living under recurrent fires.

Nonetheless, fire frequency exerts diverse impacts on vegetation structure in various fire-prone ecosystems across different climates. Studies report that in Mediterranean shrublands and savannas, which are frequently disturbed by intense fires, fire frequency plays a crucial role in maintaining plant diversity and preventing tree encroachment [5,52–54]. Infrequent but intense fires in boreal forests contribute to stand replacement and enable recovery from fire-resistant species [13,55–57]. Increasing fire frequencies driven by intensive human activities and climate warming could have unexpected and significant impacts on the dynamics of subtropical broadleaved forests, which have experienced lower fire frequencies compared to other fire-prone ecosystems [58,59]. The recurrent fires can stimulate evolution of woody species in forests with a multilayered structure [60–63]. Shrubs are likely to be killed or top-killed by fires and thus tend to have a uniform flammability strategy for both leaves and bark [64]. However, for trees to grow up to a distinct, taller growth form, the bark is expected to protect the cambium from injury and persist through fire cycles [65]. Moreover, our data indicated that tree bark is more likely to exhibit a low-flammable strategy, in contrast to that of shrubs and even large shrub species. Overall, these differences in bark and architecture may explain the different fire adaptations in flammability strategy and post-fire mortality of trees and shrubs.

Fire–vegetation feedback has been well described in many regions of the world [12,66,67]. These feedbacks are crucial for understanding the maintenance of flammable and non-flammable plant communities. Frequent burning generally maintains flammable plant communities, while long fire intervals enable shade-tolerant and fire-sensitive species to produce closed forest canopy [67]. The feedback between fire and vegetation arises from community assembly and trait evolution [11]. In our study, the selection of flammable plant species through post-fire ecological filtering was observed. Certain species were notably absent from frequently burned sites, resulting in a simplified vegetation structure. Specifically, some species are filtered by post-fire soil properties and shrub enrichment [14]. Notably, higher flammability of the plant community is typically associated with soils of low fertility, as evidenced by comparisons among six vegetation types with different dominant species in the Cerrado Domain [68]. Therefore, it is necessary to evaluate the strength of fire–vegetation feedback in our study region at different temporal and spatial scales [69,70].

Fire frequency affects community assembly and shapes the mosaic landscape of SEBFs and pine forests in the CYP [29]. Studies suggest that the most flammable species in a community may disproportionately influence ecosystem flammability [71,72], and even small changes in the abundance of flammable species can have significant ecological impacts. Given that more frequent fires are being exacerbated by higher temperatures during dry periods at a global scale [73], this trend can also lead

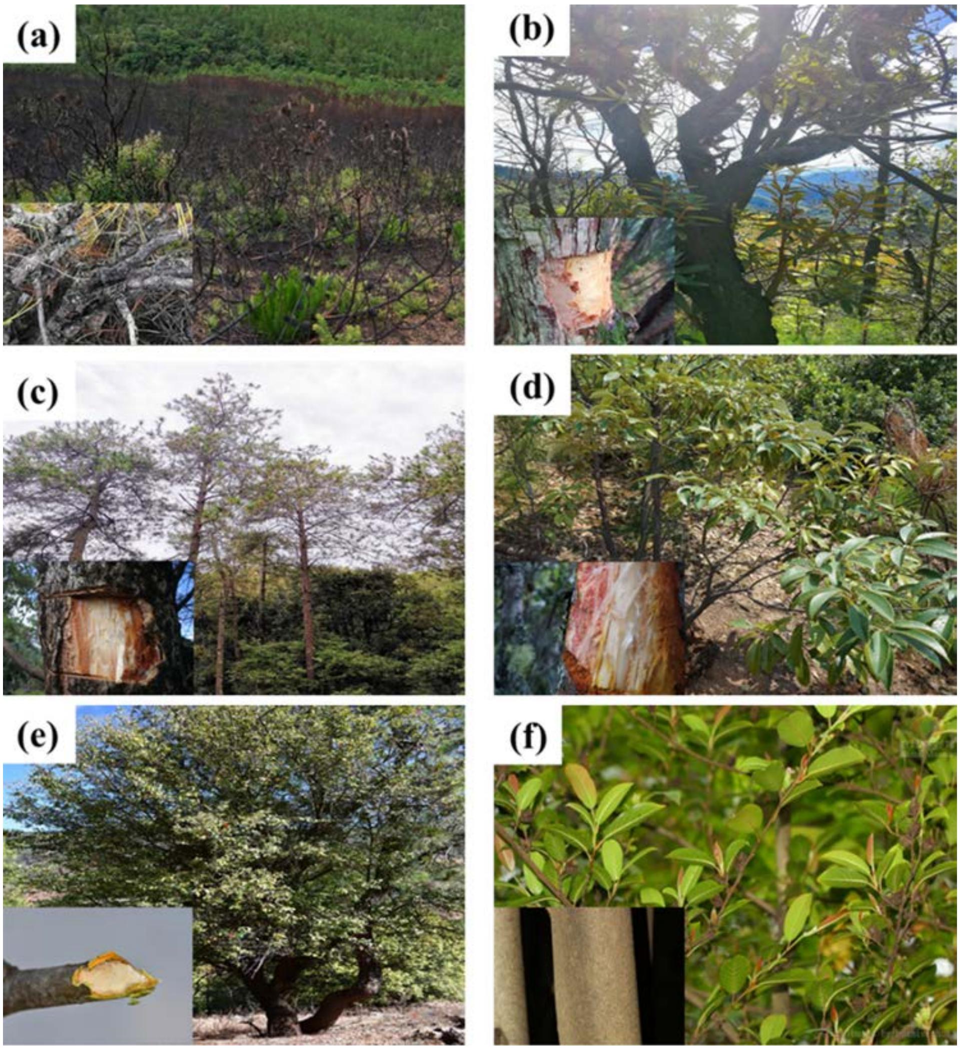

Figure 6. Examples of species with different PFSs in subtropical SEBFs. (a) *Pinus yunnanensis* var. *pygmaea* and (b) *Rhododendron delavayi* are classified as FLFB plants; both resprout after fires. (c) *Pinus yunnanensis* and (d) *Cyclobalanopsis delavayi* are FLNB plants, with thick bark ensuring survival from surface fires. (e) *Docynia delavayi*, an NLFB species with low ignitability of leaves. (f) *Stewartia calcicole* (Theaceae), an NLNB species, common in areas of infrequent fires.

to the change of dominant tree species and an increase of flammable plants within subtropical SEBFs. Local plant communities affect fire regimes through different forest compositions, and the increase of burning probability promotes the presence of more flammable plants. Research on feedback between fire and vegetation is crucial for comprehending ecosystem dynamics, resilience and adaptation to fire in this region, and will provide insights useful for adaptive forest management and post-fire ecosystem restoration.

5. Conclusions

This study reveals that most woody plant species in the subtropical SEBFs in China exhibit high flammability. These flammable plants might play an important role in maintaining fire-prone ecosystems and contribute to the increasing fire frequency in this region. Additionally, some species with low ignitability are able to survive ongoing fires. Consequently, woody plant species with diverse flammability strategies for leaves and bark can coexist under the local fire regime. Moreover, tree species had a higher percentage of flammability strategy separation between leaves and bark than large shrub and shrub species, suggesting their different adaptation to fire disturbances. The study also highlights a self-reinforcing cycle in which local plant communities can alter fire frequency. This cycle involves the promotion of more flammable plants associated with infertile soil and low species richness that result from shrub enrichment. The positive feedback between flammability strategies and the local fire regime contributes to a better understanding of vegetation dynamics and adaption to fire disturbances.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The original data related to this paper are accessible via the link: https://geodata.pku.edu.cn/ and also available on request to the corresponding author.

Supplementary material is available online [74].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. C.L.: data curation, formal analysis, investigation, methodology, writing—original draft, writing—review and editing; Z.S.: conceptualization, funding acquisition, methodology, project administration, resources, supervision, writing—review and editing; X.W.: investigation, writing—review and editing; M.X.: data curation, methodology; Y.X.: data curation, investigation; T.Y.: data curation, investigation; J.P.: conceptualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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References

1. Rodrigues CA, Zirondi HL, Fidelis A. 2021 Fire frequency affects fire behavior in open savannas of the Cerrado. *For. Ecol. Manage.* **482**, 118850. (doi:10.1016/j.foreco.2020.118850)
2. 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? *J. Biogeogr*. **44**, 1225–1238. (doi:10.1111/jbi.12889)
3. Bajocco S, Ferrara C, Guglietta D, Ricotta C. 2019 Fifteen years of changes in fire ignition frequency in Sardinia (Italy): a rich-get-richer process. *Ecol. Indic*. **104**, 543–548. (doi:10.1016/j.ecolind.2019.05.030)
4. Hannon DR, Moorman CE, Schultz AD, Gray JM, DePerno CS. 2020 Predictors of fire-tolerant oak and fire-sensitive hardwood distribution in a fire-maintained longleaf pine ecosystem. *For. Ecol. Manage.* **477**, 118468. (doi:10.1016/j.foreco.2020.118468)
5. Vilà-Cabrera A, Saura-Mas S, Lloret F. 2008 Effects of fire frequency on species composition in a Mediterranean shrubland. *Écoscience* **15**, 519–528. (doi:10.2980/15-4-3164)
6. Semenova-Nelsen TA, Platt WJ, Patterson TR, Huffman J, Sikes BA. 2019 Frequent fire reorganizes fungal communities and slows decomposition across a heterogeneous pine savanna landscape. *New Phytol*. **224**, 916–927. (doi:10.1111/nph.16096)
7. Emery RK, Hart JL. 2020 Flammability characteristics of surface fuels in a longleaf pine (*Pinus palustris* Mill.) woodland. *Fire* **3**, 39. (doi:10.3390/fire3030039)
8. Pausas JG, Bond WJ. 2020 Alternative biome states in terrestrial ecosystems. *Trends Plant Sci*. **25**, 250–263. (doi:10.1016/j.tplants.2019.11.003)
9. Peterson DW, Reich PB. 2001 Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecol. Appl.* **11**, 914. (doi:10.2307/3061125)
10. Moritz MA, Morais ME, Summerell LA, Carlson JM, Doyle J. 2005 Wildfires, complexity, and highly optimized tolerance. *Proc. Natl Acad. Sci. USA* **102**, 17912–17917. (doi:10.1073/pnas.0508985102)
11. Archibald S *et al*. 2018 Biological and geophysical feedbacks with fire in the earth system. *Environ. Res. Lett*. **13**, 033003. (doi:10.1088/1748-9326/aa9ead)
12. Rogers BM, Soja AJ, Goulden ML, Randerson JT. 2015 Influence of tree species on continental differences in boreal fires and climate feedbacks. *Nat. Geosci*. **8**, 228–234. (doi:10.1038/ngeo2352)
13. de Groot WJ, Cantin AS, Flannigan MD, Soja AJ, Gowman LM, Newbery A. 2013 A comparison of Canadian and Russian boreal forest fire regimes. *For. Ecol. Manag*. **294**, 23–34.
14. Han J, Shen Z, Li Y, Luo C, Xu Q, Yang K, Zhang Z. 2018 Beta diversity patterns of post-fire forests in central yunnan plateau, Southwest China: disturbances intensify the priority effect in the community assembly. *Front. Plant Sci*. **9**, 1000. (doi:10.3389/fpls.2018.01000)
15. Luo C, Shen Z, Li Y, Han J, Pausas JG, Xu Q, Zhang Z, Jiang Y. 2021 Determinants of post–fire regeneration demography in a subtropical monsoon–climate forest in Southwest China. *Sci. Total Environ*. **766**, 142605. (doi:10.1016/j.scitotenv.2020.142605)
16. Stevens JT, Kling MM, Schwilk DW, Varner JM, Kane JM. 2020 Biogeography of fire regimes in western US conifer forests: a trait-based approach. *Glob. Ecol. Biogeogr*. **29**, 944–955. (doi:10.1111/geb.13079)
17. Pausas JG, Keeley JE, Schwilk DW. 2017 Flammability as an ecological and evolutionary driver. *J. Ecol*. (ed M Rees), **105**, 289–297. (doi:10.1111/1365-2745.12691)
18. Cui X *et al*. 2020 Shoot flammability of vascular plants is phylogenetically conserved and related to habitat fire-proneness and growth form. *Nat. Plants* **6**, 355–359. (doi:10.1038/s41477-020-0635-1)
19. Romero B, Ganteaume A. 2021 Effect of fire frequency on the flammability of two mediterranean pines: link with needle terpene content. *Plants* **10**, 2164. (doi:10.3390/plants10102164)
20. Lamounier Moura A, Negreiros D, Fernandes GW. 2023 Effects of fire frequency regimes on flammability and leaf economics of non-graminoid vegetation. *Fire* **6**, 265. (doi:10.3390/fire6070265)
21. Popović Z, Bojović S, Marković M, Cerdà A. 2021 Tree species flammability based on plant traits: a synthesis. *Sci. Total Environ*. **800**, 149625. (doi:10.1016/j.scitotenv.2021.149625)
22. Frejaville T, Curt T, Carcaillet C. 2013 Bark flammability as a fire-response trait for subalpine trees. *Front. Plant Sci*. **4**, 466. (doi:10.3389/fpls.2013.00466)
23. Tang CQ, Zhao M, Li X, Ohsawa M, Ou X. 2010 Secondary succession of plant communities in a subtropical mountainous region of SW China. *Ecol. Res*. **25**, 149–161. (doi:10.1007/s11284-009-0644-z)
24. Han J, Shen ZH, Ying LX, Li GX, Chen AP. 2015 Early post-fire regeneration of a fire-prone subtropical mixed Yunnan pine forest in Southwest China: Effects of pre-fire vegetation, fire severity and topographic factors. *For. Ecol. Manag*. **356**, 31–40.
25. Ying LX, Han J, Du YS, Shen ZH. 2018 Forest fire characteristics in China: Spatial patterns and determinants with thresholds. *For. Ecol. Manag*. **424**, 345–354.
26. Ying L, Shen Z, Yang M, Piao S. 2019 Wildfire detection probability of MODIS fire products under the constraint of environmental factors: a study based on confirmed ground wildfire records. *Remote Sens*. **11**, 3031. (doi:10.3390/rs11243031)
27. Pausas JG, Su W, Luo C, Shen Z. 2021 A shrubby resprouting pine with serotinous cones endemic to southwest China. *Ecology* **102**, 1–4. (doi:10.1002/ecy.3282)
28. Su WH, Shi Z, Zhou R, Zhao YJ, Zhang GF. 2015 The role of fire in the Central Yunnan Plateau ecosystem, southwestern China. *For. Ecol. Manage.* **356**, 22–30. (doi:10.1016/j.foreco.2015.05.015)
29. Si HM, Su WH, Lin ST, Li ZH, Wang QH, Zhang GF, Yang HZ, Yang GM. 2023 Persistence of a pine tree with mixed fire-adapted life history strategy in subtropical spring fire-prone habitats. *For. Ecol. Manage.* **549**, 121495. (doi:10.1016/j.foreco.2023.121495)
30. de Bruyn M *et al*. 2014 Borneo and indochina are major evolutionary hotspots for Southeast Asian biodiversity. *Syst. Biol*. **63**, 879–901. (doi:10.1093/sysbio/syu047)
31. Guo L, Wang Q, Zhou H, Yang B. 1999 Main forest types in central Yunnan Plateau and transmulation tendency. *Yunnan For. Sci. Technol*. **1**, 25–38.
32. Giglio L, Schroeder W, Justice CO. 2016 The collection 6 MODIS active fire detection algorithm and fire products. *Remote Sens. Environ*. **178**, 31–41. (doi:10.1016/j.rse.2016.02.054)

33. Kunming Institute of Botany. 1977 *Flora of Yunnan*. Beijing, China: Science Press.
34. Wu ZY, Raven PH, Hong DY (eds). 1959–2004 Flora of China. Beijing, China: Science Press.
35. Forster JC. 1995 Soil sampling, handling, storage and analysis. In *Methods in applied soil microbiology and biochemistry* (eds K Alef, P Nannipieri), pp. 49–121. Oxford, UK: Elsevier. (doi:10.1016/b978-012513840-6/50018-5)
36. Delgado-Baquerizo M *et al*. 2013 Decoupling of soil nutrient cycles as a function of aridity in global drylands. *Nature* **502**, 672–676. (doi:10.1038/nature12670)
37. Morandini F, Santoni PA, Tramoni JB, Mell WE. 2019 Experimental investigation of flammability and numerical study of combustion of shrub of rockrose under severe drought conditions. *Fire Saf. J* **108**, 102836. (doi:10.1016/j.firesaf.2019.102836)
38. Liu MH, Yi LT, Yu SQ, Zhou GM, Jiang H, Li XP. 2013 Combustibility of fresh leaves of 26 forest species in China. *J. Trop. For. Sci* **25**, 528–536.
39. Pérez-Harguindeguy N *et al*. 2016 New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot* **64**, 715–716. (doi:10.1071/bt12225_co)
40. Maechler M, Rousseeuw P, Struyf A, Hubert M, Hornik K. 2022 cluster: cluster analysis basics and extensions. R package version 2.1.4. See https://lirias.kuleuven.be/3999459?limo=0.
41. Murdoch D, Adler D. 2022 rgl: 3D visualization using OpenGL. R package version 0.109.8. See https://dmurdoch.github.io/rgl/.
42. Song YC. 2017 *Vegetation ecology*. Beijing, China: Higher Education Press.
43. De Mendiburu F. 2019 Agricolae: statistical procedures for agricultural research. (doi:10.32614/CRAN.package.agricolae)
44. Lefcheck JS. 2016 piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods Ecol. Evol*. **7**, 573–579. (doi:10.1111/2041-210x.12512)
45. Schwilk DW. 2015 Dimensions of plant flammability. *New Phytol*. **206**, 486–488. (doi:10.1111/nph.13372)
46. Poulos H, Barton A, Slingsby J, Bowman D. 2018 Do mixed fire regimes shape plant flammability and post-fire recovery strategies? *Fire* **1**, 39. (doi:10.3390/fire1030039)
47. Ocampo-Zuleta K, Pausas JG, Paula S. 2024 FLAMITS: a global database of plant flammability traits. *Glob. Ecol. Biogeogr*. **33**, 412–425. (doi:10.1111/geb.13799)
48. SUW, Si H, Zhang H, Guo Z. 2023 Fire-adapted traits of four pine trees in the southwestern China. *Acta Ecol. Sin*. **43**, 1064–1072. (doi:10.5846/stxb202101250256)
49. Li S, Li X, Li S, Jin G, Zhou Q, Hu X, Wang Q. 2007 Flame retardancy of wood bark from *Keteleeria evelyniana*, *Pinus yunnanensis* and *Pinus armandii* in Yunnan Province. *J. Zhejiang For. Coll*. **24**, 192–197.
50. Platt WJ, Ellair DP, Huffman JM, Potts SE, Beckage B. 2016 Pyrogenic fuels produced by savanna trees can engineer humid savannas. *Ecol. Monogr*. **86**, 352–372. (doi:10.1002/ecm.1224)
51. Wang, R., He, S. 1992 Lithocarpus mairei community in Kunming area. J. Southwest For. Univ. **12**, 116-125.
52. Tester JR. 1996 Effects of fire frequency on plant species in oak savanna in east-central Minnesota. *B Torrey Bot Club* **123**, 304–308. (doi:10.2307/2996779)
53. Nieuwenhuis A. 1987 The effect of fire frequency on the sclerophyll vegetation of the West Head, New South Wales. *Aust. J. Ecol*. **12**, 373–385. (doi:10.1111/j.1442-9993.1987.tb00957.x)
54. Case MF, Staver AC. 2017 Fire prevents woody encroachment only at higher-than-historical frequencies in a South African savanna. *J. Appl. Ecol*. **54**, 955–962. (doi:10.1111/1365-2664.12805)
55. Bergeron Y, Richard PJH, Carcaillet C, Gauthier S, Flannigan M, Prairie YT. 1998 Variability in fire frequency and forest composition in Canada's Southeastern Boreal Forest: a challenge for sustainable forest management. *Conserv. Ecol*. **2**. (doi:10.5751/es-00049-020206)
56. Kelly R, Chipman ML, Higuera PE, Stefanova I, Brubaker LB, Hu FS. 2013 Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. *Proc. Natl Acad. Sci. USA* **110**, 13055–13060. (doi:10.1073/pnas.1305069110)
57. Stocks BJ, Wotton BM, Flannigan MD, Fosberg MA, Cahoon DR, Goldammer JG. 2001 Boreal forest fire regimes and climate change. In *Remote sensing and climate modeling: synergies and limitations* (eds M Beniston, MM Verstraete), pp. 233–246. Berlin, Germany: Springer. (doi:10.1007/0-306-48149-9_10)
58. Kowaljow E, Morales MS, Whitworth-Hulse JI, Zeballos SR, CatónMGiorgis MA, Rodríguez Catón M, Gurvich DE. 2019 A 55-year-old natural experiment gives evidence of the effects of changes in fire frequency on ecosystem properties in a seasonal subtropical dry forest. *Land Degrad. Dev*. **30**, 266–277. (doi:10.1002/ldr.3219)
59. Wei P *et al*. 2024 Vegetation-fire feedbacks increase subtropical wildfire risk in scrubland and reduce it in forests. *J. Environ. Manag*. **351**, 119726. (doi:10.1016/j.jenvman.2023.119726)
60. He T, Pausas JG, Belcher CM, Schwilk DW, Lamont BB. 2012 Fire-adapted traits of *Pinus* arose in the fiery Cretaceous. *New Phytol*. **194**, 751–759. (doi:10.1111/j.1469-8137.2012.04079.x)
61. Pellegrini AFA *et al*. 2021 Decadal changes in fire frequencies shift tree communities and functional traits. *Nat. Ecol. Evol*. **5**, 504–512. (doi:10.1038/s41559-021-01401-7)
62. Lamont BB. 2022 Historical links between climate and fire on species dispersion and trait evolution. *Plant Ecol*. **223**, 711–732. (doi:10.1007/s11258-022-01232-x)
63. Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA. 2011 Fire as an evolutionary pressure shaping plant traits. *Trends Plant Sci*. **16**, 406–411. (doi:10.1016/j.tplants.2011.04.002)
64. Pellegrini AFA, Anderegg WRL, Paine CET, Hoffmann WA, Kartzinel T, Rabin SS, Sheil D, Franco AC, Pacala SW. 2017 Convergence of bark investment according to fire and climate structures ecosystem vulnerability to future change. *Ecol. Lett*. **20**, 307–316. (doi:10.1111/ele.12725)
65. Schafer JL, Breslow BP, Hohmann MG, Hoffmann WA. 2015 Relative bark thickness is correlated with tree species distributions along a fire frequency gradient. *Fire Ecol*. **11**, 74–87. (doi:10.4996/fireecology.1101074)
66. McLauchlan KK *et al*. 2020 Fire as a fundamental ecological process: research advances and frontiers. *J. Ecol*. **108**, 2047–2069. (doi:10.1111/1365-2745.13403)
67. Pausas JG, Bond WJ. 2022 Feedbacks in ecology and evolution. *Trends Ecol. Evol*. **37**, 637–644. (doi:10.1016/j.tree.2022.03.008)
68. Bueno ML, Dexter KG, Pennington RT, Pontara V, Neves DM, Ratter JA, de Oliveira-Filho AT. 2018 The environmental triangle of the cerrado domain: ecological factors driving shifts in tree species composition between forests and savannas. *J. Ecol*. **106**, 2109–2120. (doi:10.1111/1365-2745.12969)
69. Tepley AJ, Thomann E, Veblen TT, Perry GLW, Holz A, Paritsis J, Kitzberger T, Anderson-Teixeira KJ. 2018 Influences of fire–vegetation feedbacks and post-fire recovery rates on forest landscape vulnerability to altered fire regimes. *J. Ecol*. **106**, 1925–1940. (doi:10.1111/1365-2745.12950)
70. Pausas JG, Dantas V d. L. 2017 Scale matters: fire–vegetation feedbacks are needed to explain tropical tree cover at the local scale. *Glob. Ecol. Biogeogr*. **26**, 395–399.
71. Blauw LG, Wensink N, Bakker L, van Logtestijn RSP, Aerts R, Soudzilovskaia NA, Cornelissen JHC. 2015 Fuel moisture content enhances nonadditive effects of plant mixtures on flammability and fire behavior. *Ecol. Evol*. **5**, 3830–3841. (doi:10.1002/ece3.1628)
72. Varner JM, Kuljian HG, Kreye JK. 2017 Fires without tanoak: the effects of a non-native disease on future community flammability. *Biol. Invasions* **19**, 2307–2317. (doi:10.1007/s10530-017-1443-z)
73. Jones MW *et al*. 2022 Global and regional trends and drivers of fire under climate change. *Rev. Geophys*. **60**. (doi:10.1029/2020rg000726)

74. Luo C, Shen Z, Wang X, Xiahou M, Xie Y, Yang T *et al*. 2025 Supplementary material from: The effects of fire frequency on leaf and bark flammability strategies in subtropical semi-humid evergreen broadleaved forests in China. Figshare. (doi:10.6084/m9.figshare.c.7736314)