Continental-scale empirical evidence for relationships between fire response strategies and fire frequency

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Materials and Methods	1790
Results	629
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Summary

- Theory suggests that the dominance of resprouting and seeding, two key mechanisms through which plants persist with recurrent fire, both depend on other traits and vary with fire regime. However, these patterns remain largely untested over broad scales.
- We analysed the relationships between average fire frequency, derived from MODIS satellite data, and resprouting and seeding strategies respectively, for approximately 10,000 woody and herbaceous species in Australia. We tested whether leaf economics traits differed among these strategies.
- Probability of resprouting exhibits a monotonic increase with fire frequency for woody plants; for herbaceous plants a hump-shaped relationship is observed. Probability of seeding exhibits a hump shape with fire frequency in woody plants. In herbaceous plants, probability of resprouting was associated with higher leaf mass per area (LMA), and probability of seeding with lower LMA. A broader range of leaf investment strategies occurred in woody plants.
- Our findings provide the largest empirical support to date for theory connecting fire response strategy to fire frequency. Woody seeders appear constrained by immaturity and senescence risk. Herbaceous and woody seeders showed different placements along the leaf economics spectrum, suggesting an important interaction between growth form and growth rate for seeders.

Keywords: fire frequency, fire intensity/severity, resprouting, seeding, life history, leaf traits, Australia

Introduction

Fire is a fundamental ecological process for many ecosystems on Earth (Bond & Keeley, 2005; Andela *et al.*, 2019; McLauchlan *et al.*, 2020), which shapes the evolution of traits that allow organisms to thrive in fire-prone environments (Keeley *et al.*, 2011; He & Lamont, 2018; Pausas & Bond, 2019). A key focus of research has been the mechanisms that enable plants to persist in fire-prone environments. Past research has identified two main strategies adopted by plant species: resprouting from surviving tissues (hereafter 'resprouting') and post-fire germination from seed (hereafter 'post-fire seeding') (Lamont *et al.*, 1991; Whelan, 1995; Bond & van Wilgen, 1996). While some species are capable of one mechanism alone, so-called "obligate" resprouters and seeders, others are capable of both, called "facultative" species. Theoretical and empirical research surrounding these mechanisms suggests that the two strategies exist at opposite ends of a spectrum of resource allocation (Iwasa & Kubo, 1997; D. T. Bell, 2001; Bowen & Pate, 2017), with varying costs and benefits, and depending on the fire regime. It follows that patterns in the relative proportion of these fire response strategies could vary across gradients of fire regime characteristics, such as fire frequency or intensity. Although established in theory (Hilbert, 1987; Bellingham & Sparrow, 2000; Bond & Midgley, 2003; Pausas & Keeley, 2014b), these patterns have remained largely untested on a broad scale, mainly due to the lack of large-scale data on fire regimes and species regeneration mechanisms.

In fire-prone ecosystems, the success of different regeneration mechanisms is dependent on the fire regime, particularly the fire frequency. A fire regime captures the typical event- and frequency-driven characteristics of fires in a given place within an ecological time frame (Gill, 1975), and comprises multiple parameters, including fire frequency, intensity (rate of heat energy release), severity (biological impacts on above- and below-ground vegetation), type (ground, surface, crown, mixed), size and seasonality (McLauchlan *et al.*, 2020). Fire regimes vary markedly between vegetation types, such as in the mesic forests of eastern Australia and boreal forests of North America where fires burn infrequently but often intensely (Gill & Catling, 2002; Keeley & Pausas, 2022), versus the tropical and subtropical savannas in southern Africa and South America which undergo frequent, low-intensity fires (Lehmann *et al.*, 2014). Here, we focus on one major fire regime characteristic, fire frequency, which has been at the core of theory relating to plant trait relationships (e.g., Hilbert, 1987; Bellingham & Sparrow, 2000; Bond & J. J. Midgley, 2003; Pausas *et al.*, 2004). Fire frequency and interval define the length of time between fires in which plants can grow and maintain resprouting organs and/or reach reproductive maturity and produce a sufficient seed bank. Globally, ecosystems range from experiencing frequent fire, that is close to 100 fires per century, to very infrequent, less than one fire per century (Bond et al. 2005).

Theory suggests that the frequency of resprouting and post-fire seeding strategies of woody plants should vary with fire frequency, and interact with growth form and other plant traits. Pausas & Keeley (2014a) likened resprouting and seeding strategies to perennial and annual life history strategies, where fire events are considered equivalent to annual cycles. Resprouters follow a longer-lived, 'perennial' life history as they live and reproduce through many fire intervals (iteroparity) (Pausas & Keeley, 2014a). Conversely, obligate-seeding species follow a shorter-lived, 'annual' life history, with mature individuals typically suffering high mortality after a fire and thus depending on a single reproductive event per generation (semelparity) (Bond & van Wilgen, 1996; Pausas & Keeley, 2014a). Investment in resprouting capacity would be wasted when fires are very rare, but may also be inviable in environments where fire frequency is high, as there is insufficient opportunity for recovery between disturbances (Iwasa & Kubo, 1997; Bellingham & Sparrow, 2000; Pausas & Keeley, 2014a). Bellingham & Sparrow (2000) therefore hypothesised that ability to resprout would increase as disturbance frequency increases, until a threshold where resprouting becomes less viable and so ability to resprout then declines. Similarly, obligate seeders are predicted to be most common at intermediate fire frequencies (Hilbert, 1987; Lamont *et al.*, 1991), as a balance between two competing risks. Obligate seeders suffer an immaturity risk when fire return intervals (FRIs) are too short (Keeley *et al.*, 1999), but can also experience a senescence risk when FRIs are longer than the longevity of the plants and seed bank combined, as these species are reliant on fire to complete their life cycle (Keeley, 1986).

While discussion around plant-fire relationships have predominantly been centred around woody plants, herbaceous plants have been comparatively understudied, despite being an important group that makes up much of the world's most fire-prone ecosystems (Mouillot & Field, 2005; Keeley & Pausas, 2022). We define 'woody' as having a prominent aerial stem that lasts through time and changing environmental conditions (Zanne *et al.*, 2014); in practice, this corresponds to a longer lifespan of the aboveground part of the plant as well as a taller potential height. Recently, Simpson *et al.* (2021) extended the model by Bellingham & Sparrow

(2000) to grasses; however, a small difference in their predictions for grasses was that, although resprouting may decline at very high fire frequencies, it could still be a common strategy, as many grasses can resprout from protected underground buds or insulated leaf bases (Klimešová & Klimeš, 2003; Simpson *et al.*, 2021). Additionally, herbaceous seeders were hypothesised to be less restricted by immaturity risk as their time to maturation is relatively short, supported by findings that the ratio of grass seeders to resprouters was higher at very high frequencies (Simpson *et al.*, 2021).

To fulfil contrasting life histories, seeders and resprouters may also employ different strategies of resource allocation and growth. Seeders might allocate more resources to rapid aboveground growth and early reproduction, whereas resprouters might allocate more resources to storage organs and protective structures that improve survival and regrowth after fire (Iwasa & Kubo, 1997; D. T. Bell, 2001; Pausas *et al.*, 2004; Bowen & Pate, 2017). These resource allocation strategies could also be manifested in leaf economics traits (Wright *et al.*, 2004), such as leaf mass per area (LMA) and leaf nitrogen (N) content. Fast-growing seeders are expected to have ‘quick-return’ leaves, with low LMA, high leaf nutrients (including N), high leaf turnover and high rates of photosynthesis and respiration, whereas the opposite is expected for slower-growing resprouters (Wright *et al.*, 2004). Past studies investigating leaf traits across fire response strategies have found varying results across climates and ecosystems (Ackerly, 2004; Pausas *et al.*, 2004; Paula & Pausas, 2006; Saura-Mas & Lloret, 2007; Vivian & Cary, 2012), thus raising questions about how generally leaf traits relate to fire strategy. Moreover, the fundamental differences between woody and herbaceous growth forms may also lead to different patterns of leaf traits across fire response strategies (e.g., in grasses; Simpson *et al.*, 2021). Generally, it is known that herbaceous and woody species differ in their leaf traits (Towers *et al.*, 2024), but it remains unclear whether there are further differences within herbaceous species with respect to fire response, and whether such differences are consistent across herbaceous and woody species.

Despite an abundance of theory, the consequences of fire have rarely been evaluated at large biogeographic scales, with data to span hundreds to thousands of species. However, a flourishing of biodiversity resources, such as species distribution, fire occurrence, and trait data, now enables such questions to be addressed. Recently, Simpson *et al.* (2021) tested the effects of fire frequency on the distribution of 734 grass species, globally. While this global analysis of grasses represented a significant advance on our understanding of plant-fire relationships for herbaceous species, the scope of the study was still constrained to just a single plant family with a particular adaptation: having a basal meristem. Here, we use large-scale empirical data to investigate the distribution of fire response strategies at unprecedented scale, by quantifying characteristics for >9,500 species spread across the entire continent of Australia. Specifically, we ask the following questions:

1. What is the distribution of fire frequencies experienced by Australian plant taxa?
2. Do the fractions of plant species that are resprouting and seeding support the hypothesised hump-shaped response with fire frequency, in both woody and herbaceous plants?
3. Within woody and herbaceous species, do leaf traits (LMA and leaf N content) differ between resprouters and non-resprouters, or between post-fire seeders and non-seeders?

Materials and Methods

Study system

Our study area is the continent of Australia, which contains deserts, savanna, tropical and subtropical forests, temperate and Mediterranean woodlands and shrublands, spread across large climatic gradients (Keith, 2017). This range of ecosystems and component species representing different life histories and fire response strategies as well as a large range of fire frequencies (Bradstock, 2010; Murphy *et al.*, 2013), is representative of those observed globally, and thus provides an ideal region to empirically test the theory connecting resprouting and seeding to fire frequency (e.g., Bellingham & Sparrow, 2000; Pausas & Keeley, 2014b).

Fire response and leaf traits

We extracted fire response trait data for Australian plants from AusTraits (v5.0.0), a database which includes data on the fire response strategies of approximately 9578 species (over 40% of all described Australian vascular plants; CHAH, 2023) (Falster *et al.*, 2021). The database harmonises trait data from diverse sources, including field studies, herbaria, and published literature. Our two traits of interest, whether a taxon resprouts and whether it has post-fire seeding, are captured by `resprouting_capacity` and `post_fire_recruitment` (Wenk *et al.*, 2024c). The resprouting trait (`resprouting_capacity`) distinguishes whether individuals in a species or population are killed by fire (<30% resprout), partially resprout (30-70%) or resprout prolifically (>70%). The post-fire seeding trait (`post_fire_recruitment`) specifies whether a plant does or does not display increased germination post-fire. We considered resprouting and post-fire seeding as separate traits given that the traditional resprouter/seeder dichotomy does not capture species that can do both (1672 species or 15% of our dataset was facultative).

Before categorising species as having capacity for post-fire resprouting and post-fire seeding, we filtered out non-native species by only including those that are native in at least one state or territory according to data from the Australian Plant Census (APC) (CHAH, 2023). We excluded hybrid species and species not "accepted" by the APC. We included fire response trait observations at the below-species level (form, variety and subspecies) in addition to the species level, because within-species differences in fire response strategies are also informative. Below-species and species level taxa (terminal taxa) are henceforth collectively referred to as "species". Each species was then categorised as a resprouter or non-resprouter and a (post-fire) seeder or non-seeder. In AusTraits, observations from multiple sources can be recorded for a species in any given trait. Hence, we classified a species as a resprouter if at least 30% of observation recorded resprouting or partial resprouting, and a seeder if at least 30% of observations recorded post-fire recruitment. The absence of seedlings is more difficult to detect than their presence, possibly leading to an inclusion bias towards seeders. Lastly, species were identified as woody or herbaceous using `woodiness_detailed` data from the curated Australian plant growth forms dataset, `Wenk_2022` (Wenk *et al.*, 2024a). We categorised records that were combinations of trait values, e.g., `herbaceous semi_woody`, into groups: woody, herbaceous, semi-woody and ambiguous (Supporting Information Table S1), the last two of which we discarded. This resulted in a dataset of 6387 woody species and 4634 herbaceous species. 10881 species(6276 woody, 4605 herbaceous) had data on resprouting and 3570 species (2661 woody, 909 herbaceous) had data on post-fire seeding.

We also extracted data on two leaf traits, LMA and leaf N content (per unit dry mass), from the AusTraits database, filtering out non-native species. In AusTraits, each observation is on a separate row and values for a numerical trait are standardised to the same units. The value type, e.g., raw value or mean, and number of replicates used to calculate each observation (if a mean) are also recorded in separate columns. To obtain species-level measures of LMA and leaf N, we took the mean of all LMA and leaf N observations respectively for the species. The mean was calculated by dividing by the number of rows (observations), rather than by number of replicates used for each observation, because the majority of observations were raw values (single replicates) and the numbers of replicates used to calculate means were often unreported. 2844 species (2061 woody, 783 herbaceous) had data on LMA and 1637 species (1385 woody, 252 herbaceous) had data on leaf N, in addition to data on at least resprouting or seeding.

Species occurrences

We extracted species occurrences from the Global Biodiversity Information Facility (GBIF). On the GBIF web portal, we selected ‘present’ occurrence status records of vascular plants in Australia (GBIF.org [2 June 2023] GBIF Occurrence Download DOI: 10.15468/dl.phfr9u). GBIF records were subsequently cleaned in the R environment (R Core Team, 2021). Occurrence records were filtered to post-1900, georeferenced human observation and living and preserved specimen records only. Coordinates with low precision (less than 2 decimal digits) and high uncertainty (>10 000 m) were excluded, as well as coordinates with longitude or latitude recorded as zero. We removed duplicate records and records flagged with the country coordinate mismatch and recorded date unlikely issues in GBIF. A series of checks were conducted with the {CoordinateCleaner} package (Version 2.0-20; Zizka *et al.*, 2019), including removing non-terrestrial and unlikely or invalid coordinates. Coordinates in the ocean or within 2 km of the country centroid, capital centroid and biological institutions were also removed. 13,605,512 observations remained from 21,141,315 after filtering (36% of observations were removed). Species names from GBIF, which use the World Checklist of Vascular Plants (WCVP) backbone, were aligned with names in AusTraits, which are standardised with the APC. 10871 species were matched between AusTraits and GBIF after aligning and updating GBIF names using the {APCalign} package (Wenk *et al.*, 2024b).

Fire frequency

We aimed to determine the mean fire frequency that each species is exposed to across its distribution. Data on fire events were extracted from the MODIS Global Monthly Burnt Area Data Product (MCD64A1), which contains the spatial extent and dates of fires occurring from November 2000 to October 2022 at 500-m resolution. The MODIS satellite detects burn scars by identifying daily changes in surface reflectance after a fire (e.g., vegetation loss, charcoal deposits), which is supplemented with daily active fire data (Giglio *et al.*, 2018). Although only a *c.* 22-year dataset, MODIS data is the best available fire data for Australia at the continental scale.

First, we extracted the occurrence records of a given species and overlayed this with the MODIS data product (500-m grid cells). In each grid cell where the species occurs, we counted the number of fires that had occurred during the *c.* 22-year period. We removed species with less than ten total cells (465 species). We then fit a generalised linear model with a Poisson distribution and an identity link function to the fire event count data to estimate the mean event rate across the observation period and its 95% confidence interval. Mean event rates were converted to fire frequency per century (Supporting Information Fig. S1). 97% of mean fire frequencies per species had a confidence interval size (upper confidence bound minus lower bound) of less than 5 fires per century, and the maximum confidence interval size was 17. 157 (1.4%) species were unable to be fit with a Poisson model, often those with few cells or entirely unburnt cells. Examples of species' spatial distributions and their fire event count data are displayed in Fig. 1.

The Poisson process assumes a constant rate of fire events occurring through time, which is unlikely true for many systems, because of factors such as increasing fire risk with accumulating fuel loads and decreasing fire risk from negative fire-vegetation feedbacks (Fernandes *et al.*, 2012; Héon *et al.*, 2014). However, the true rate of fire over time is highly debated in fire literature (Moritz, 2003; Moritz *et al.*, 2004; Keeley & Zedler, 2009) and hence we used a constant rate as a compromise between increasing and decreasing rates. Also, assuming a different assumption of increasing or decreasing rate of fire would only change the absolute values of fire frequency estimates and have no effect on the absolute ranking of fire frequencies across species, which was sufficient for our analysis. To check our method was producing reasonable numbers, we also compared the mean fire frequencies estimated using the Poisson distribution with values estimated using a method by Simpson *et al.* (2021), which calculates the median fire return interval from fitting a Weibull distribution to all the inter-fire intervals across the grid cells in which a species occurs (Fig. S1). The distribution of fire frequencies across the two methods were largely similar, with the survival analysis method more skewed towards low fire frequencies (Supporting Information Fig. S2).

Data analysis

We analysed the relationships between fire response strategies and fire frequency for woody and herbaceous species using a generalised linear model with a logit link and binomial response in R (R Core Team, 2021). Two separate models were fit with resprouting and post-fire seeding as the response variables and fire frequency (per century) as the predictor variable. We fit a quadratic polynomial function, based on *a priori* hypotheses formed from the literature (quadratic curves; Bellingham & Sparrow, 2000; Simpson *et al.*, 2021) and inspection of the raw data. Resprouting and post-fire seeding were coded as binomial (i.e. TRUE or FALSE equates to resprouts or does not resprout), while fire frequency was log-transformed to reduce skewness and leverage of low fire frequencies. We included a woody or herbaceous variable and any interactions with fire frequency in the resprouting model. For the post-fire seeding model, however, we only included woody species as there were insufficient data to fit the model for herbs (909 herbaceous species versus 2661 woody species). To determine whether accounting for evolutionary relationships would affect the results, we repeated the analyses with phylogenetic logistic regression (Ives & Garland, 2010) using the `phyloglm` function (method set to '`logistic_MPLE`' or maximised penalised likelihood of the logistic regression) from package `{phylolm}` (Ho & Ané, 2014). We used a dated phylogeny for seed plants by Smith & Brown (2018) which contains 356,305 species and combines genetic data from GenBank and phylogenetic data from the Open Tree of Life project. The tree was subsetted to the species in our study; however, due to differences in taxonomy, many species were unable to be matched.

To determine how leaf traits compare between fire response strategies, we fit four linear regressions with LMA and leaf N as individual response variables (log-transformed) and resprouting or post-fire seeding as explanatory variables (R Core Team, 2021). We included a woody or herb variable and an interaction term as additional explanatory variables in each model. We repeated the analyses with phylogenetic linear regression using the same phylogenetic tree as previously (Smith & Brown, 2018) and the `phylolm` function from package `{phylolm}` (Ho & Ané, 2014). *P*-values of estimated marginal means are adjusted with the Tukey method for standard linear regression and with the Bonferroni method for phylogenetic linear regression.

Results

Fire frequency

The average fire frequencies experienced by species in the dataset, across their known distribution, ranged from 0.01 fires per century to 53.3 per century, while the median fire frequency across all species was 1.6 per century (Fig. 2a). The median fire frequencies of the six most speciose Australian plant families (Fig. 2b, in bold) ranged from 2.1 fires per century for Fabaceae to 1.3 fires per century for Asteraceae. Out of the twenty Australian plant families with the highest resprouting data coverage, median fire frequencies ranged from 0.3 (Chenopodiaceae) to 4.3 (Malvaceae) (Fig. 2b). These encapsulate the diversity of fire frequencies that exist across Australia.

Fire response strategies and growth forms

Out of 6387 woody species, 4022 were resprouters and 2254 were non-resprouters. 2092 woody species were documented as post-fire seeders and 569 as non-seeders. 1672 species were capable of both resprouting and seeding, i.e. facultative species. In 4634 total herbaceous species, 3006 were resprouters and 1599 were non-resprouters.

Relationships between fire response strategies and fire frequency

The distributions of woody and herbaceous resprouters are displayed in Fig. 3a. The probability of resprouting tends to increase with fire frequency for both woody and herbaceous species (Fig. 4a; Table 1). However, resprouting probability peaks at intermediate fire frequencies for herbaceous species while resprouting probability continues to increase at high fire frequencies for woody species (Fig. 4a; Table 1). Nonetheless, resprouting is still a viable strategy for herbs at high fire frequencies, as >20% of species still exhibit this strategy (Fig. 4a; Table 1). Resprouting is much less likely for herbs than for woody species at very low fire frequencies (Fig. 4a; Table 1). The median fire frequency per century for woody resprouters was 1.84 (standard deviation [SD] = 7.47), in contrast to 1.63 (SD = 4.84) for woody non-resprouters. For herbaceous species, the median fire frequency per century for resprouters was 1.56 (SD = 5.41) and 1.45 (SD = 8.06) for non-resprouters. These relationships were also reproduced when phylogeny was taken into account, although with a slight decline in resprouting probability for woody plants at the highest fire frequencies (Supporting Information Fig. S3a; Supporting Information Table S2).

In woody species, the probability of post-fire seeding is high at intermediate fire frequencies, decreasing dramatically with more frequent fires and very infrequent fires (Fig. 4b; Table 2). The median fire frequency per century for woody post-fire seeders was 1.65(SD = 5.02) while the median fire frequency for non-seeders was 1.79 (SD = 8.87). This unimodal relationship was also seen when accounting for phylogeny (Supporting Information Fig. S3b; Supporting Information Table S2).

Relationships between fire response strategies and leaf traits

In woody species, there was moderate evidence that LMA (log-transformed) is slightly lower in resprouters than non-resprouters (estimate = -0.041, *df* = 2836, *P* = 0.045). However, according to the phylogenetic regression (Supporting Information Table S3), there was very strong evidence that the opposite is true, that woody resprouters have slightly higher LMA than non-resprouters (estimate = 0.031, *df* = 2370, *P* = <0.001). There was very strong evidence that LMA is higher in seeders than non-seeders (estimate = 0.147, *df* = 1494, *P* = <0.0001) (Fig. 5; Table 2).

In herbaceous species, there was very strong evidence that resprouters have higher LMA than non-resprouters (estimate = 0.201, *df* = 2836, *P* = <0.0001), although there was only little evidence of this from the phylogenetic regression (estimate = 0.102, *df* = 2370, *P* = 0.147). There was very strong evidence that post-fire seeders have lower LMA than non-seeders (estimate = -0.177, *df* = 1494, *P* = <0.0001) (Fig. 5; Table 2). In both woody and herbaceous species, there was no evidence that leaf N content is different between resprouters and non-resprouters or between seeders and non-seeders (Fig. 5; Table 2).

Discussion

Australia captures a broad range of vegetation types and fire frequencies, with species mean fire frequencies ranging from 0.01 to 53.3 fires per century. This range reflects those experienced globally. We found that resprouting probability was highest in areas with intermediate fire frequencies (1 to 5 fires per century; Murphy *et al.*, 2013) for herbaceous plants, while resprouting probability continually increases with fire frequency for woody plants. Post-fire seeding is most dominant at intermediate fire frequencies for woody plants. These findings provide the largest empirical support to date for long-held concepts in the literature, that resprouting is inviable when disturbances are too frequent relative to productivity and that post-fire seeding in woody plants is constrained by immaturity risk and senescence risk (Hilbert, 1987; Bellingham & Sparrow, 2000; Pausas, 2001; Bond & J. J. Midgley, 2003; Klimešová & Klimeš, 2003). Among woody species, we did not find support for the predicted decline in resprouting ability at the highest fire frequencies, but this may be attributed to patterns of fire severity. Relationships were largely preserved when accounting for phylogenetic relationships, suggesting that patterns of fire response strategies and fire frequency are occurring across unrelated species.

The hypothesised hump-shaped relationship between resprouting and fire frequency described by Bellingham & Sparrow (2000) for woody plants was found to adequately describe the relationship for herbaceous plants (Fig. 4a). Resprouting may be less energetically viable at high fire frequencies (Grady & Hoffmann, 2012; Fairman *et al.*, 2019). Frequently burnt systems are typically characterised by moderately high-intensity surface fires, as is often the case in Australia (Archibald *et al.*, 2013), likely reducing the survivorship of herbaceous resprouters and instead favouring the fast-growing seeding strategy. Herbs that do resprout, do so from underground organs or basal meristems in the case of grasses (Mott *et al.*, 1985; Simpson *et al.*, 2021). Correspondingly, Australia's northern savannas have a high richness of annual seeders (Andrew & Mott, 1983). In intermediate fire frequencies, herbaceous resprouters outcompete seeders as they can quickly re-establish post-fire using energy reserves (Zimmermann *et al.*, 2008; Simpson *et al.*, 2021). This is seen in the high proportions of herbaceous resprouters in south-eastern Australia where fires are moderately frequent (Pausas & Bradstock, 2007; Hammill *et al.*, 2016) (Fig. 3). At low fire frequencies, resprouting probability decreases, likely due to the high costs of maintaining buds when fires are rare (Simpson *et al.*, 2021). For example, Asteraceae, a primarily herbaceous family, occurs predominantly in seldom burnt environments (median fire frequency per century = 1.3) and has a relatively low proportion of resprouters (44%) (Fig. 2b). Our resprouting results examine a much wider range of fire frequencies compared to Simpson *et al.* (2021), but in the areas of overlap, our results for all herbaceous species are consistent with those they found for Poaceae.

Woody species exhibit a similar relationship to herbaceous species, where resprouting probability increases with fire frequency (Fig. 4a); however, unlike herbaceous species, resprouting probability does not decline at very high fire frequencies, or declines only slightly according to the phylogenetic analysis (Supporting Information Fig. S3a). Resprouting probability is highest for woody species in frequently burnt systems, evidenced in the high proportion of woody resprouters across northern Australia, compared to herbaceous resprouters (Fig. 3a). This may seem inconsistent with the decline in resprouting at high disturbance frequencies predicted by Bellingham & Sparrow (2000); however, patterns in fire severity may explain this discrepancy. Resprouting appears to be more common in response to less severe disturbances (Vesk & Westoby, 2004). Fire regimes in the savannas of northern Australia are characterised by frequent low to moderately high-intensity surface fires (Williams *et al.*, 1998; Morgan, 1999; Murphy *et al.*, 2013; Archibald *et al.*, 2013), rather than crown fires, which adults of woody resprouting species, particularly tree species, are more likely to survive than herbaceous species due to low flame heights (Barlow *et al.*, 2003; Lawes *et al.*, 2011a). The majority of adult trees in these savannas resprout epicormically (Clarke *et al.*, 2015), while juvenile trees, which are more likely to be top-killed, predominantly resprout from underground organs (Werner & Franklin, 2010). This could explain the continual increase of resprouting probability even at the highest fire frequencies. Woody species in these savannas that are unable to resprout tend to survive through thick bark (Lawes *et al.*, 2011a,b). We expect to see a similar pattern for woody plants in places other than Australia, because places with frequent fires are fundamentally constrained to have low- to moderate-intensity fire (Archibald *et al.*, 2013). At low fire frequencies, found in both the arid and wet extremes of Australia, resprouting is less likely and may have evolved in response to disturbances other than fire (Pausas & Keeley, 2014b; Pausas *et al.*, 2016). Resprouting in these mesic systems is probably enabled by higher productivity, compared to their arid counterparts (Bellingham & Sparrow, 2000), as seen in slightly higher resprouting proportions in temperate Australia compared to the largely unburnt arid interior (Fig. 3).

Post-fire seeding displayed the characteristic hump-shaped relationship with fire frequency for woody species (Fig. 4b). This affirms that many woody seeders are constrained by 'immaturity risk', where seeders are unable to reach reproductive maturity if fire frequency is too high (Keeley *et al.*, 1999), and 'senescence risk', where seeders are unable to produce a new cohort of seedlings when FRIs are longer than the longevity of the seed bank (Keeley, 1986). Whilst woody seeders are restricted by 'immaturity risk' in environments that burn frequently, herbaceous seeders are generally able to reach reproductive maturity much more rapidly and thus some can persist even in FRIs as short as one year (e.g., grass annual seeders; Mott *et al.*, 1985; Werner & Franklin, 2010; Simpson *et al.*, 2021). Interestingly, there are some woody seeding species that evolve to dramatically reduce their time to maturity and may eventually be considered herbaceous, such as *Androcalva rosea*, which can reproduce and senesce in less than 16 months, despite its sub-shrub growth form (S. A. J. Bell & Copeland, 2004). However, immaturity risk is a species-specific concept, where shortening FRIs are likely detrimental to a species irrespective of whether it is adapted to high, moderate or low fire frequencies. In general, woody obligate seeders have longer maturity ages than herbaceous seeders (Smith & Donoghue, 2008), explaining the decline of woody seeders at high fire frequencies. Although herbaceous seeders are less constrained by high fire frequencies, they are also expected to decline at lower fire frequencies due to high competition and senescence risk (Zimmermann *et al.*, 2008; Pausas & Keeley, 2014b; Simpson *et al.*, 2021), but this remains untested.

In order to avoid immaturity risk, seeders were hypothesised to adopt a fast-growing strategy along the leaf economics spectrum, expressed by a lower investment in each leaf (lower LMA), high nutrient contents (higher leaf N) and high photosynthetic rates (Wright *et al.*, 2004). This was supported by our results for herbaceous species, including strong evidence that herbaceous resprouters have higher LMA than herbaceous non-resprouters and herbaceous seeders have lower LMA than herbaceous non-seeders (Fig. 5). Herbaceous species seem adequately described by the hypothesis that these two fire response strategies have contrasting life histories: one that avoids immaturity risk through a faster growth strategy and another that is slower-growing and prioritises resource retention in between fires (Pausas *et al.*, 2004; Pausas & Keeley, 2014a).

In woody species, there was little evidence that seeders adopt a faster-growing leaf economics strategy than resprouters. Instead, we found very strong evidence that LMA is actually higher in seeders than non-seeders, suggesting that at least for some woody seeders, a resource-retaining strategy (higher LMA, lower leaf nutrients) between fires may be more important than fast growth to reduce immaturity risk. This is especially important where drought is recurrent, a common event across large areas of the Australian continent (Jiang *et al.*, 2017), likely experienced by woody seeders which dominate at intermediate fire frequencies (Fig. 4). Many obligate seeders in Mediterranean climates have been found to be drought tolerant, associated with functional traits including longer leaf life span, high LMA and lower leaf turgor loss point (Ackerly, 2004; Paula & Pausas, 2006; Saura-Mas & Lloret, 2007). This resource-conserving strategy is exhibited in the woody family Proteaceae, which has higher average LMA and lower leaf N than most other Australian plant families (Fig. 2b; Cornwell *et al.*, 2014). Woody species that live in fire-prone environments but do not resprout primarily survive fires via thick bark (Hoffmann *et al.*, 2009; Lawes *et al.*, 2011b; Brando *et al.*, 2012); these fire-resisting species would also likely be resource-conservative rather than fast-growing. Additionally, leaf functional traits may vary throughout an individual's lifespan (Henn & Damschen, 2021). A seeder may prioritise growth at early life stages to establish quickly post-fire, but later shift to a more resource-conservative strategy (Funk *et al.*, 2021). Slow-growing woody seeders may be particularly vulnerable to immaturity risk under increasing fire frequencies (Bradstock & Kenny, 2003; Kraaij *et al.*, 2013).

This analysis was at the species and below-species level, but in response to shifting fire regimes, there may also be intraspecific changes to fire adaptation. Resprouting and seeding are not mutually exclusive fire response strategies; they are coexisting approaches which have shifting proportions along different gradients of fire regime characteristics. The viability of both strategies across much of the fire frequency gradient also explains the high proportion of facultative species (species able to both resprout and seed) in Australia overall (1672 species or

15% of the dataset was facultative), and populations of these species may be under shifting evolutionary pressures throughout their ranges.

Fire frequencies have never been static through geological time, and humans have changed fire regimes through increased ignitions, and more recently, fire suppression and climate change (Krawchuk *et al.*, 2009; Pausas & Keeley, 2009; Andela *et al.*, 2017; Balch *et al.*, 2017). Moreover, European practices in Australia with regard to fire are fundamentally different to those of the Traditional Owners (Perry *et al.*, 2018). We acknowledge that a key limitation to using data from the MODIS satellite is its short snapshot of 22 years. While fire frequencies in that 22-year period may not reflect preceding periods, the MODIS data has been used (with even shorter periods) to detect large-scale differences in fire regimes (e.g., Bond & G. F. Midgley, 2012). The 22-year period is likely sufficient to distinguish very fire-prone environments from infrequently burnt environments, and for a successful ranking of mean fire frequencies across species. Because mean fire frequency was calculated across each species' range, we expect that a species with more unburnt points than another will effectively rank the species as more fire-sensitive than species with less unburnt points. Additionally, species occurring in mostly or all unburnt cells, often also occurring in few cells overall, were excluded when a valid set of coefficients to fit the model could not be found (157 species). Because of the ubiquity of fire across the Australian continent, only 1.1% of species in our dataset occurred in entirely unburnt cells, after filtering species occurring in less than ten pixels.

Large-scale patterns of fire response strategies are common ecological hypotheses that relate to how plants respond to fire, and disturbance more broadly (e.g., Bellingham & Sparrow, 2000; Bond & J. J. Midgley, 2003; Pausas & Keeley, 2014a). However, sufficient data to empirically test these hypotheses have only become available recently. Our findings are one of the first to provide a broad overview of how fire response strategies sort along a fire frequency gradient, using large-scale, real-world data. Our work is timely, as fire regimes are currently being altered due to climate change and other human-influenced drivers (Hardesty *et al.*, 2005; Pausas & Keeley, 2014b; Andela *et al.*, 2017; Canadell *et al.*, 2021), potentially leading to shifts in the distribution of each fire response strategy and the modification, expansion and contraction of various vegetation communities (Nolan *et al.*, 2021). Slow-growing obligate seeders are particularly vulnerable to increasing fire frequencies when paired with warmer and drier conditions, which limit plant growth and hence diminish the fire interval window required for their persistence (‘interval squeeze’; Enright *et al.*, 2015). Predicting vegetation responses to shifting fire regimes needs to be underpinned by both clear theory and robust empirical analyses; our results add continental-scale empirical data to this effort.

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Author Contribution

SY, WC, MO and DF designed the study. SY extracted and analysed the data, and SY, WC, MO and DF interpreted the data. SY wrote the manuscript with help from all the authors.

Data Availability

Data and R code are available at this GitHub repository: https://github.com/yangsophieee/clean_fire_response_strats.

References

Ackerly D. **2004**. Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs* **74**: 25–44.

Andela N, Morton DC, Giglio L, Chen Y, van der Werf GR, Kasibhatla PS, DeFries RS, Collatz GJ, Hantson S, Kloster S *et al.* 2017. A human-driven decline in global burned area. *Science* **356**: 1356–1362.

Andela N, Morton DC, Giglio L, Paugam R, Chen Y, Hantson S, van der Werf GR, Randerson JT. **2019**. The Global Fire Atlas of individual fire size, duration, speed and direction. *Earth System Science Data* **11**: 529–552.

Andrew MH, Mott JJ. **1983**. Annuals with transient seed banks: the population biology of indigenous *Sorghum* species of tropical north-west Australia. *Australian Journal of Ecology* **8**: 265–276.

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.

Balch JK, Bradley BA, Abatzoglou JT, Nagy RC, Fusco EJ, Mahood AL. **2017**. Human-started wildfires expand the fire niche across the United States. *Proceedings of the National Academy of Sciences* **114**: 2946–2951.

Barlow J, Lagan BO, Peres CA. **2003**. Morphological correlates of fire-induced tree mortality in a central Amazonian forest. *Journal of Tropical Ecology* **19**: 291–299.

Bell DT. **2001**. Ecological response syndromes in the flora of southwestern Western Australia: fire resprouters versus reseeders. *The Botanical Review* **67**: 417–440.

Bell SAJ, Copeland LM. **2004**. *Commersonia rosea* (Malvaceae sl: Lasiopetaleae): a new, rare fire-ephemeral species from the upper Hunter Valley of New South Wales. *Telopea* **10**: 581–587.

Bellingham PJ, Sparrow AD. **2000**. Resprouting as a life history strategy in woody plant communities. *Oikos* **89**: 409–416.

Bond WJ, Keeley JE. **2005**. Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* **20**: 387–394.

Bond WJ, Midgley JJ. **2003**. The evolutionary ecology of sprouting in woody plants. *International Journal of Plant Sciences* **164**: S103–S114.

Bond WJ, Midgley GF. **2012**. Carbon dioxide and the uneasy interactions of trees and savannah grasses. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**: 601–612.

Bond WJ, van Wilgen BW. **1996**. Surviving fires—vegetative and reproductive responses. In: *Fire and plants*. Dordrecht: Springer, 34–51.

Bowen BJ, Pate JS. **2017**. Patterns of storage tissue and starch distribution in the young taproot of obligate seeders and resprouters of Australian Proteaceae (Juss.): possible evidence of homoplastic evolution. *Austral Ecology* **42**: 617–629.

Bradstock RA. **2010**. A biogeographic model of fire regimes in Australia: current and future implications. *Global Ecology and Biogeography* **19**: 145–158.

Bradstock RA, Kenny BJ. **2003**. An application of plant functional types to fire management in a conservation reserve in southeastern Australia. *Journal of Vegetation Science* **14**: 345–354.

Brando PM, Nepstad DC, Balch JK, Bolker B, Christman MC, Coe M, Putz FE. **2012**. Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology* **18**: 630–641.

Canadell JG, Meyer CP, Cook GD, Dowdy A, Briggs PR, Knauer J, Pepler A, Haverd V. **2021**. Multi-decadal increase of forest burned area in Australia is linked to climate change. *Nature Communications* **12**: 6921.

CHAH. **2023**. Australian Plant Census, Centre of Australian National Biodiversity Research.

Clarke PJ, Lawes MJ, Murphy BP, Russell-Smith J, Nano CEM, Bradstock R, Enright NJ, Fontaine JB, Gosper CR, Radford I, *et al.* **2015**. A synthesis of postfire recovery traits of woody plants in Australian ecosystems. *Science of The Total Environment* **534**: 31–42.

Cornwell WK, Westoby M, Falster DS, FitzJohn RG, O'Meara BC, Pennell MW, McGlinn DJ, Eastman JM, Moles AT, Reich PB *et al.* **2014**. Functional distinctiveness of major plant lineages. *Journal of Ecology* **102**: 345–356.

Enright NJ, Fontaine JB, Bowman DM, Bradstock RA, Williams RJ. **2015**. Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment* **13**: 265–272.

Fairman TA, Bennett LT, Nitschke CR. **2019**. Short-interval wildfires increase likelihood of resprouting failure in fire-tolerant trees. *Journal of Environmental Management* **231**: 59–65.

Falster D, Gallagher R, Wenk EH, Wright IJ, Indiarto D, Andrew SC, Baxter C, Lawson J, Allen S, Fuchs A *et al.* **2021**. AusTraits – a curated plant trait database for the Australian flora. *Scientific Data.* doi: 10.1038/s41597-021-01006-6

Fernandes PM, Loureiro C, Magalhães M, Ferreira P, Fernandes M. **2012**. Fuel age, weather and burn probability in Portugal. *International Journal of Wildland Fire* **21**: 380–384.

Foster CN, Barton PS, MacGregor CI, Catford JA, Blanchard W, Lindenmayer DB. **2018**. Effects of fire regime on plant species richness and composition differ among forest, woodland and heath vegetation. *Applied Vegetation Science* **21**: 132–143.

Funk JL, Larson JE, Vose G. **2021**. Leaf traits and performance vary with plant age and water availability in Artemisia californica. *Annals of Botany* **127**: 495–503.

Giglio L, Boschetti L, Roy DP, Humber ML, Justice CO. **2018**. The Collection 6 MODIS burned area mapping algorithm and product. *Remote Sensing of Environment* **217**: 72–85.

Gill AM. **1975**. Fire and the Australian flora: a review. *Australian Forestry* **38**: 4–25.

Gill AM, Catling PC. **2002**. Fire regimes and biodiversity of forested landscapes of southern Australia. In: Bradstock RA, Williams JE, Gill AM, eds. *Flammable Australia: the fire regimes and biodiversity of a continent*. Cambridge, UK: Cambridge University Press, 351–369.

Grady JM, Hoffmann WA. **2012**. Caught in a fire trap: recurring fire creates stable size equilibria in woody resprouters. *Ecology* **93**: 2052–2060.

Hammill K, Penman T, Bradstock R. **2016**. Responses of resilience traits to gradients of temperature, rainfall and fire frequency in fire-prone, Australian forests: potential consequences of climate change. *Plant Ecology* **217**: 725–741.

Hardesty J, Myers R, Fulks W. **2005**. Fire, ecosystems, and people: a preliminary assessment of fire as a global conservation issue. *The George Wright Forum* **22**: 78–87.

He T, Lamont BB. **2018**. Baptism by fire: the pivotal role of ancient conflagrations in evolution of the Earth’s flora. *National Science Review* **5**: 237–254.

Henn JJ, Damschen EI. **2021**. Plant age affects intraspecific variation in functional traits. *Plant Ecology* **222**: 669–680.

Héon J, Arseneault D, Parisien MA. **2014**. Resistance of the boreal forest to high burn rates. *Proceedings of the National Academy of Sciences* **111**: 13888–13893.

Hilbert DW. **1987**. A model of life history strategies of chaparral shrubs in relation to fire frequency. In: Tenhunen JD, Catarino FM, Lange OL, Oechel WC, eds. *Plant response to stress*. Berlin, Heidelberg: Springer, 597–606.

Ho LST, Ané C. **2014**. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Systematic Biology* **63**: 397–408.

Hoffmann WA, Adasme R, Haridasan M, T. de Carvalho M, Geiger EL, Pereira MAB, Gotsch SG, Franco AC. **2009**. Tree topkill, not mortality, governs the dynamics of savanna–forest boundaries under frequent fire in central Brazil. *Ecology* **90**: 1326–1337.

Ives AR, Garland T Jr. **2010**. Phylogenetic logistic regression for binary dependent variables. *Systematic Biology* **59**: 9–26.

Iwasa Y, Kubo T. **1997**. Optimal size of storage for recovery after unpredictable disturbances. *Evolutionary Ecology* **11**: 41–65.

Jiang M, Felzer BS, Nielsen UN, Medlyn BE. **2017**. Biome-specific climatic space defined by temperature and precipitation predictability. *Global Ecology and Biogeography* **26**: 1270–1282.

Keeley JE. **1986**. Resilience of mediterranean shrub communities to fires. In: Dell B, Hopkins AJM, Lamont BB, eds. *Resilience in mediterranean-type ecosystems*. Dordrecht: Springer, 95–112.

Keeley JE, Ne'eman G, Fotheringham CJ. **1999**. Immaturity risk in a fire-dependent pine. *Journal of Mediterranean Ecology* **1**: 41–48.

Keeley JE, Pausas JG. **2022**. Evolutionary ecology of fire. *Annual Review of Ecology, Evolution and Systematics* **53**: 203–225.

Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA. **2011**. Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* **16**: 406–411.

Keeley JE, Zedler PH. **2009**. Large, high-intensity fire events in southern California shrublands: debunking the fine-grain age patch model. *Ecological Applications* **19**: 69–94.

Keith DA. **2017**. *Australian Vegetation*. Cambridge University Press.

Klimešová J, Klimeš L. **2003**. Resprouting of herbs in disturbed habitats: is it adequately described by Bellingham-Sparrow's model? *Oikos* **103**: 225–229.

Kraaij T, Cowling RM, van Wilgen BW, Schutte-Vlok A. **2013**. Proteaceae juvenile periods and post-fire recruitment as indicators of minimum fire return interval in eastern coastal fynbos. *Applied Vegetation Science* **16**: 84–94.

Krawchuk MA, Moritz MA, Parisien MA, Dorn JV, Hayhoe K. **2009**. Global pyrogeography: the current and future distribution of wildfire. *PLoS ONE* **4**: e5102.

Lamont BB, Lemaitre DC, Cowling RM, Enright NJ. **1991**. Canopy seed storage in woody plants. *Botanical Review* **57**: 277–317.

Lawes MJ, Adie H, Russell-Smith J, Murphy B, Midgley JJ. **2011a**. How do small savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark thickness. *Ecosphere* **2**: art42.

Lawes MJ, Richards A, Dathe J, Midgley JJ. **2011b**. Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant Ecology* **212**: 2057–2069.

Lehmann CER, Anderson TM, Sankaran M, Higgins SI, Archibald S, Hoffmann WA, Hanan NP, Williams RJ, Fensham RJ, Felfili J, *et al.* 2014. Savanna vegetation-fire-climate relationships differ among continents. *Science* **343**: 548–552.

McLauchlan KK, Higuera PE, Miesel J, Rogers BM, Schweitzer J, Shuman JK, Tepley AJ, Varner JM, Veblen TT, Adalsteinsson SA *et al.* 2020. Fire as a fundamental ecological process: research advances and frontiers. *Journal of Ecology* **108**: 2047–2069.

Morgan JW. **1999**. Defining grassland fire events and the response of perennial plants to annual fire in temperate grasslands of south-eastern Australia. *Plant Ecology* **144**: 127–144.

Moritz MA. **2003**. Spatiotemporal analysis of controls on shrubland fire regimes: age dependency and fire hazard. *Ecology* **84**: 351–361.

Moritz MA, Keeley JE, Johnson EA, Schaffner AA. **2004**. Testing a basic assumption of shrubland fire management: how important is fuel age? *Frontiers in Ecology and the Environment* **2**: 67–72.

Mott JJ, Williams J, Andrew MH, Gillison AN. **1985**. Australian savanna ecosystems. *Ecology and Management of the World's Savannas*: 56–82.

Mouillot F, Field CB. **2005**. Fire history and the global carbon budget: a 1° × 1° fire history reconstruction for the 20th century. *Global Change Biology* **11**: 398–420.

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.

Nolan RH, Collins L, Leigh A, Ooi MKJ, Curran TJ, Fairman TA, Resco de Dios V, Bradstock R. **2021**. Limits to post-fire vegetation recovery under climate change. *Plant, Cell & Environment* **44**: 3471–3489.

Paula S, Pausas JG. **2006**. Leaf traits and resprouting ability in the Mediterranean basin. *Functional Ecology* **20**: 941–947.

Pausas JG. **2001**. Resprouting vs seeding – a Mediterranean perspective. *Oikos* **94**: 193–194.

Pausas JG, Bond WJ. **2019**. Humboldt and the reinvention of nature. *Journal of Ecology* **107**: 1031–1037.

Pausas JG, Bradstock RA. **2007**. Fire persistence traits of plants along a productivity and disturbance gradient in mediterranean shrublands of south-east Australia. *Global Ecology and Biogeography* **16**: 330–340.

Pausas JG, Bradstock RA, Keith DA, Keeley JE. **2004**. Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* **85**: 1085–1100.

Pausas JG, Keeley JE. **2009**. A burning story: the role of fire in the history of life. *BioScience* **59**: 593–601.

Pausas JG, Keeley JE. **2014a**. Evolutionary ecology of resprouting and seeding in fire‐prone ecosystems. *New Phytologist* **204**: 55–65.

Pausas JG, Keeley JE. **2014b**. Abrupt climate-independent fire regime changes. *Ecosystems* **17**: 1109–1120.

Pausas JG, Pratt RB, Keeley JE, Jacobsen AL, Ramirez AR, Vilagrosa A, Paula S, Kaneakua-Pia IN, Davis SD. **2016**. Towards understanding resprouting at the global scale. *New Phytologist* **209**: 945–954.

Perry JJ, Sinclair M, Wikmunea H, Wolmby S, Martin D, Martin B. **2018**. The divergence of traditional Aboriginal and contemporary fire management practices on Wik traditional lands, Cape York Peninsula, Northern Australia. *Ecological Management & Restoration* **19**: 24–31.

R Core Team. **2021**. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. [WWW document] URL https://www.R-project.org/.

Saura-Mas S, Lloret F. **2007**. Leaf and shoot water content and leaf dry matter content of Mediterranean woody species with different post-fire regenerative strategies. *Annals of Botany* **99**: 545–554.

Simpson KJ, Jardine EC, Archibald S, Forrestel EJ, Lehmann CER, Thomas GH, Osborne CP. **2021**. Resprouting grasses are associated with less frequent fire than seeders. *New Phytologist* **230**: 832–844.

Smith SA, Brown JW. **2018**. Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany* **105**: 302–314.

Smith SA, Donoghue MJ. **2008**. Rates of molecular evolution are linked to life history in flowering plants. *Science* **322**: 86–89.

Towers IR, Vesk PA, Wenk EH, Gallagher RV, Windecker SM, Wright IJ, Falster DS. **2024**. Revisiting the role of mean annual precipitation in shaping functional trait distributions at a continental scale. *New Phytologist* **241**: 1900–1909.

Vesk PA, Westoby M. **2004**. Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology* **92**: 310–320.

Vivian LM, Cary GJ. **2012**. Relationship between leaf traits and fire-response strategies in shrub species of a mountainous region of south-eastern Australia. *Annals of Botany* **109**: 197–208.

Wenk EH, Coleman D, Gallagher RV, Falster DS. **2024a**. A near-complete dataset of plant growth form, life history, and woodiness for all Australian plants. *Australian Journal of Botany* **72**.

Wenk EH, Cornwell WK, Fuchs A, Kar F, Monro AM, Sauquet H, Stephens RE, Falster DS. **2024b**. APCalign: an R package workflow and app for aligning and updating flora names to the Australian Plant Census. *Australian Journal of Botany* **72**.

Wenk EH, Sauquet H, Gallagher RV, Brownlee R, Boettiger C, Coleman D, Yang S, Auld T, Barrett R, Brodribb T, *et al.* 2024c. The AusTraits plant dictionary. *Scientific Data* **11**: 537.

Werner PA, Franklin DC. **2010**. Resprouting and mortality of juvenile eucalypts in an Australian savanna: impacts of fire season and annual sorghum. *Australian Journal of Botany* **58**: 619–628.

Whelan RJ. **1995**. *The ecology of fire*. Cambridge, UK: Cambridge University Press.

Williams RJ, Gill AM, Moore PHR. **1998**. Seasonal changes in fire behaviour in a tropical savanna in northern Australia. *International Journal of Wildland Fire* **8**: 227–239.

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.

Zanne AE, Tank DC, Cornwell WK, Eastman JM, Smith SA, FitzJohn RG, McGlinn DJ, O'Meara BC, Moles AT, Reich PB *et al.* 2014. Three keys to the radiation of angiosperms into freezing environments. *Nature* **506**: 89–92.

Zimmermann J, Higgins SI, Grimm V, Hoffmann J, Münkemüller T, Linstädter A. **2008**. Recruitment filters in a perennial grassland: the interactive roles of fire, competitors, moisture and seed availability. *Journal of Ecology* **96**: 1033–1044.

Zizka A, Silvestro D, Andermann T, Azevedo J, Ritter CD, 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.

Figures and Tables

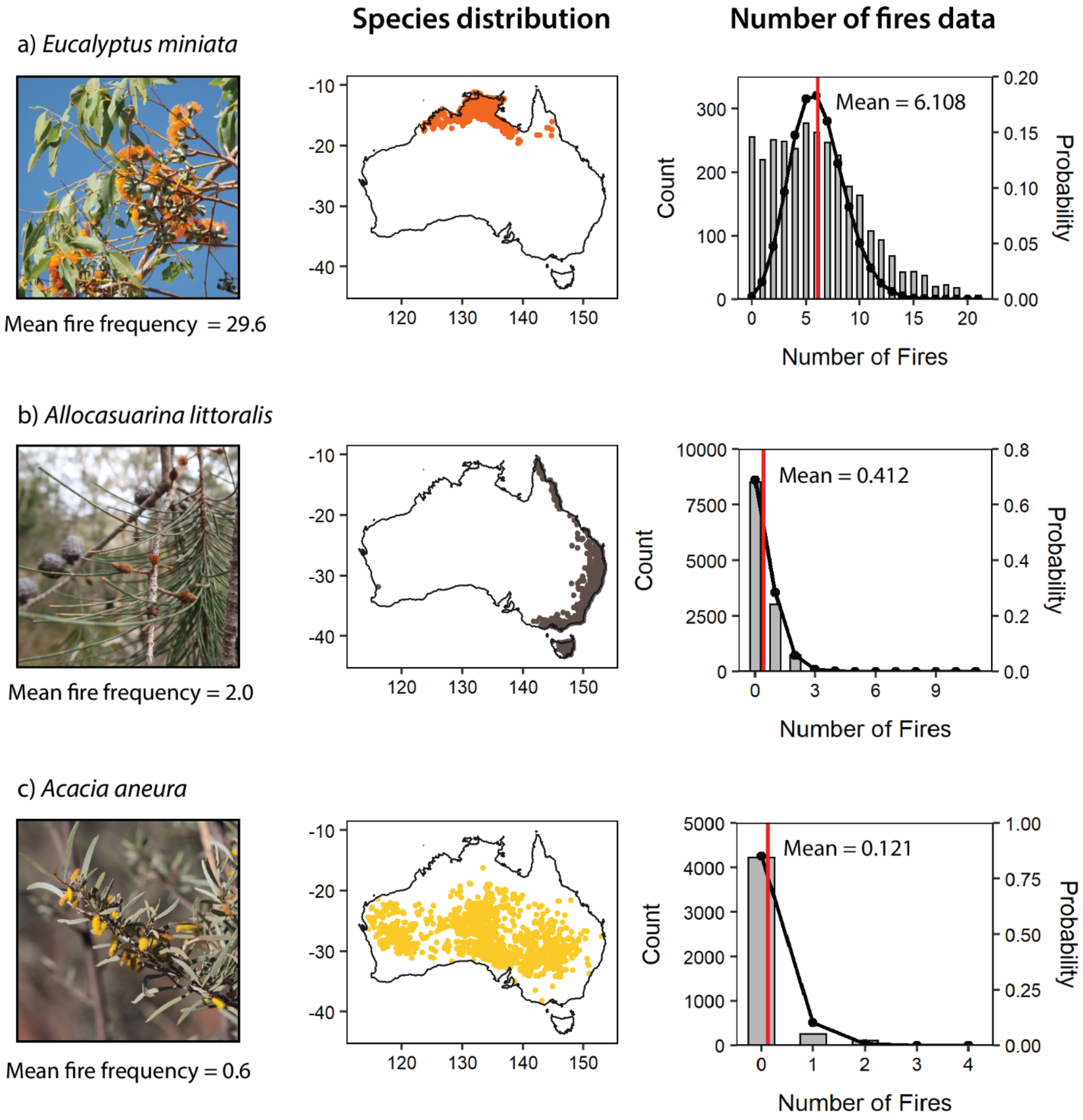
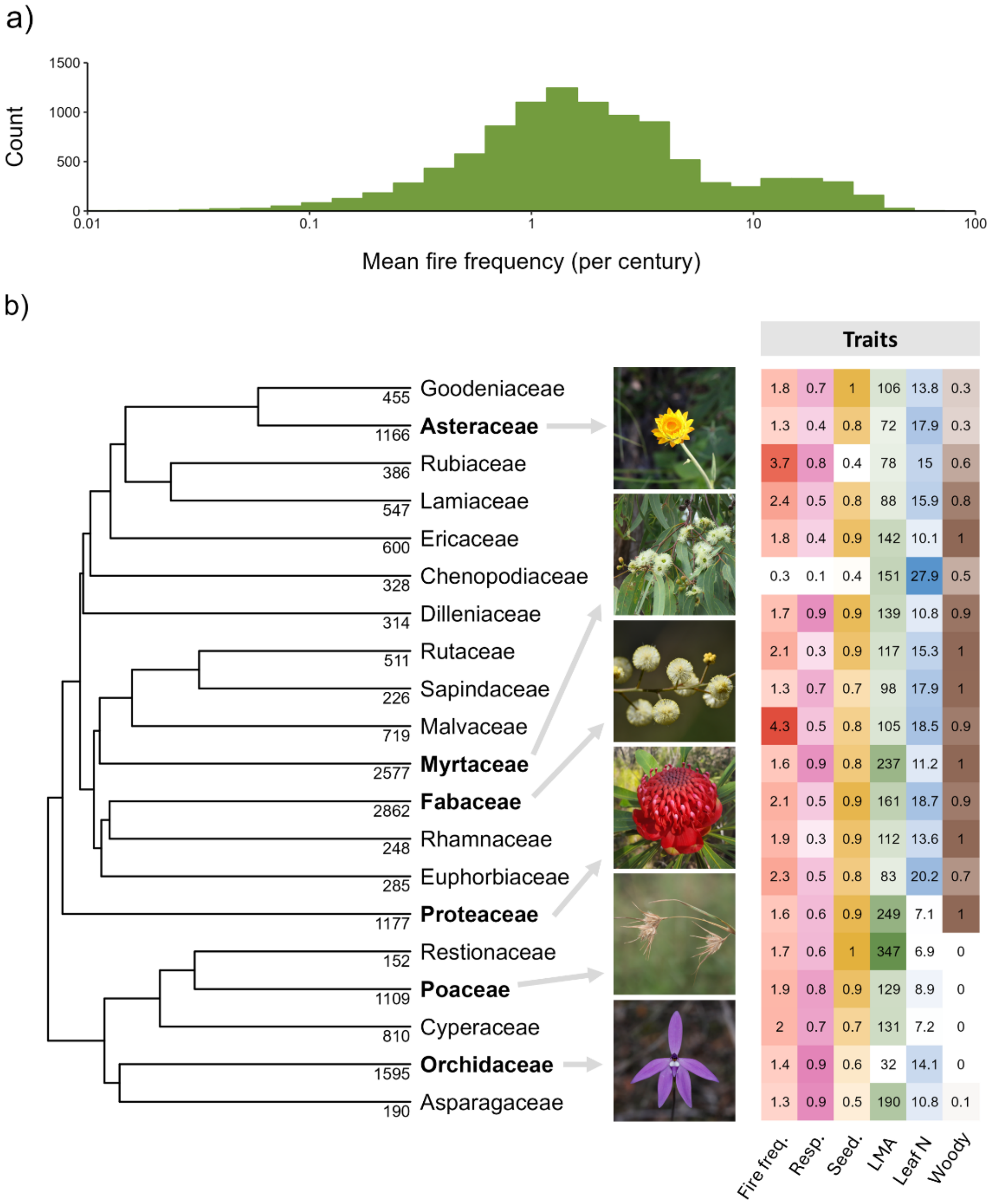


Figure 1 Schematic illustrating how the mean fire frequency (per century) for a species is calculated, for three example species. Centre panels show the known distribution, as represented by observations from GBIF. The right panels show the number of fires data in each 500 by 500 m cell during the period 2000 to 2022, across their range, with fitted Poisson models. Creators of plant images are discoverable on iNaturalist: (a) *Eucalyptus miniata* (Jenny Donald [CC-BY-NC]), (b) *Allocasuarina littoralis* (@cowirrie [CC0]), and (c) *Acacia aneura* (Kym Nicolson [CC-BY]).



		Traits					
		Fire freq.	Resp.	Seed.	LMA	Leaf N	Woody
Goodeniaceae	455	1.8	0.7	1	106	13.8	0.3
Asteraceae	1166	1.3	0.4	0.8	72	17.9	0.3
Rubiaceae	386	3.7	0.8	0.4	78	15	0.6
Lamiaceae	547	2.4	0.5	0.8	88	15.9	0.8
Ericaceae	600	1.8	0.4	0.9	142	10.1	1
Chenopodiaceae	328	0.3	0.1	0.4	151	27.9	0.5
Dilleniaceae	314	1.7	0.9	0.9	139	10.8	0.9
Rutaceae	511	2.1	0.3	0.9	117	15.3	1
Sapindaceae	226	1.3	0.7	0.7	98	17.9	1
Malvaceae	719	4.3	0.5	0.8	105	18.5	0.9
Myrtaceae	2577	1.6	0.9	0.8	237	11.2	1
Fabaceae	2862	2.1	0.5	0.9	161	18.7	0.9
Rhamnaceae	248	1.9	0.3	0.9	112	13.6	1
Euphorbiaceae	285	2.3	0.5	0.8	83	20.2	0.7
Proteaceae	1177	1.6	0.6	0.9	249	7.1	1
Restionaceae	152	1.7	0.6	1	347	6.9	0
Poaceae	1109	1.9	0.8	0.9	129	8.9	0
Cyperaceae	810	2	0.7	0.7	131	7.2	0
Orchidaceae	1595	1.4	0.9	0.6	32	14.1	0
Asparagaceae	190	1.3	0.9	0.5	190	10.8	0.1

Figure 2 (a) The distribution of mean fire frequencies (per century) experienced by Australian species, and (b) Australian plant families with the highest resprouting data coverage, showing fire response and leaf traits in relation to median fire frequency. Native species diversity of each family is indicated below each branch tip, with the top six most speciose families in bold. Example species are indicated by grey arrows: from top to bottom, they are: *Xerochrysum bracteatum* (@gregtasney [CC-BY-SA]), *Eucalyptus tetrodonta* (@nawocnai [CC-BY-NC]), *Acacia terminalis* (@tayloredtotayler [CC-BY-NC]), *Telopea speciosissima* (@vix_ [CC-BY-NC]), *Themeda triandra* (@arista_botha [CC-BY-NC-SA]) and *Glossodia major* (@jimstone54 [CC-BY-NC]) (discoverable on iNaturalist). Traits are summarised and coloured for each family on the right (dark colours indicate higher values). Median fire frequency per century was calculated as the median of all species-level mean fire frequencies in a given family. Mean fire frequencies for each species were the mean number of fires across a species' range from MODIS data (2000 to 2022). Fire response traits were calculated by finding the proportion of resprouters and post-fire seeders respectively in each family. Median leaf mass per area (LMA) (g m^{-2}) and leaf nitrogen (N) (mg g^{-1}) were calculated as the mean LMA and leaf N per species and then finding the median of all species in the family. The tree was built with a dated phylogeny for seed plants by Smith & Brown (2018).

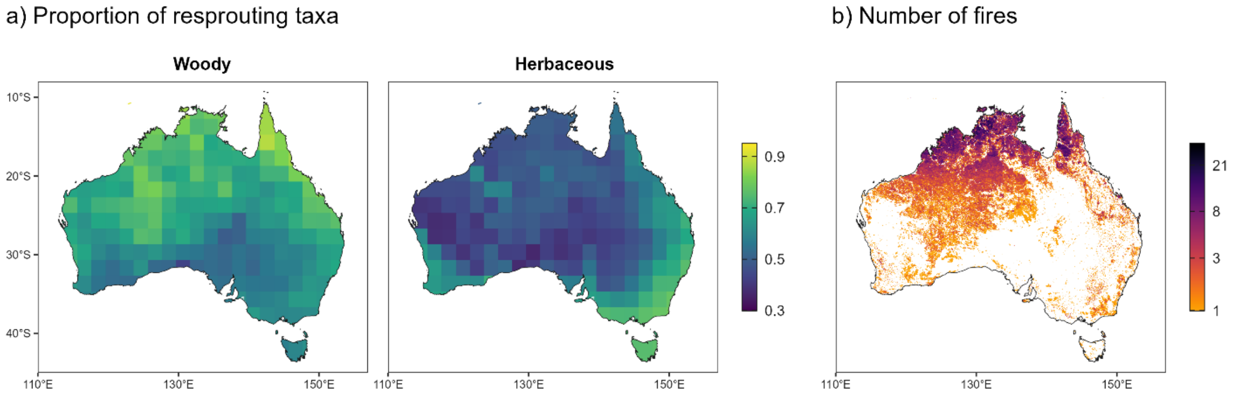


Figure 3 Mapping the distribution of fire response strategies at continental scale, with (a) proportions of resprouters in woody and herbaceous species across Australia and (b) the number of fires that occurred during the MODIS burnt area product (MCD64A1) dataset period (2000 to 2022) (white denotes zero fires), at 500-m resolution. Post-fire seeding was excluded due to lack of data.

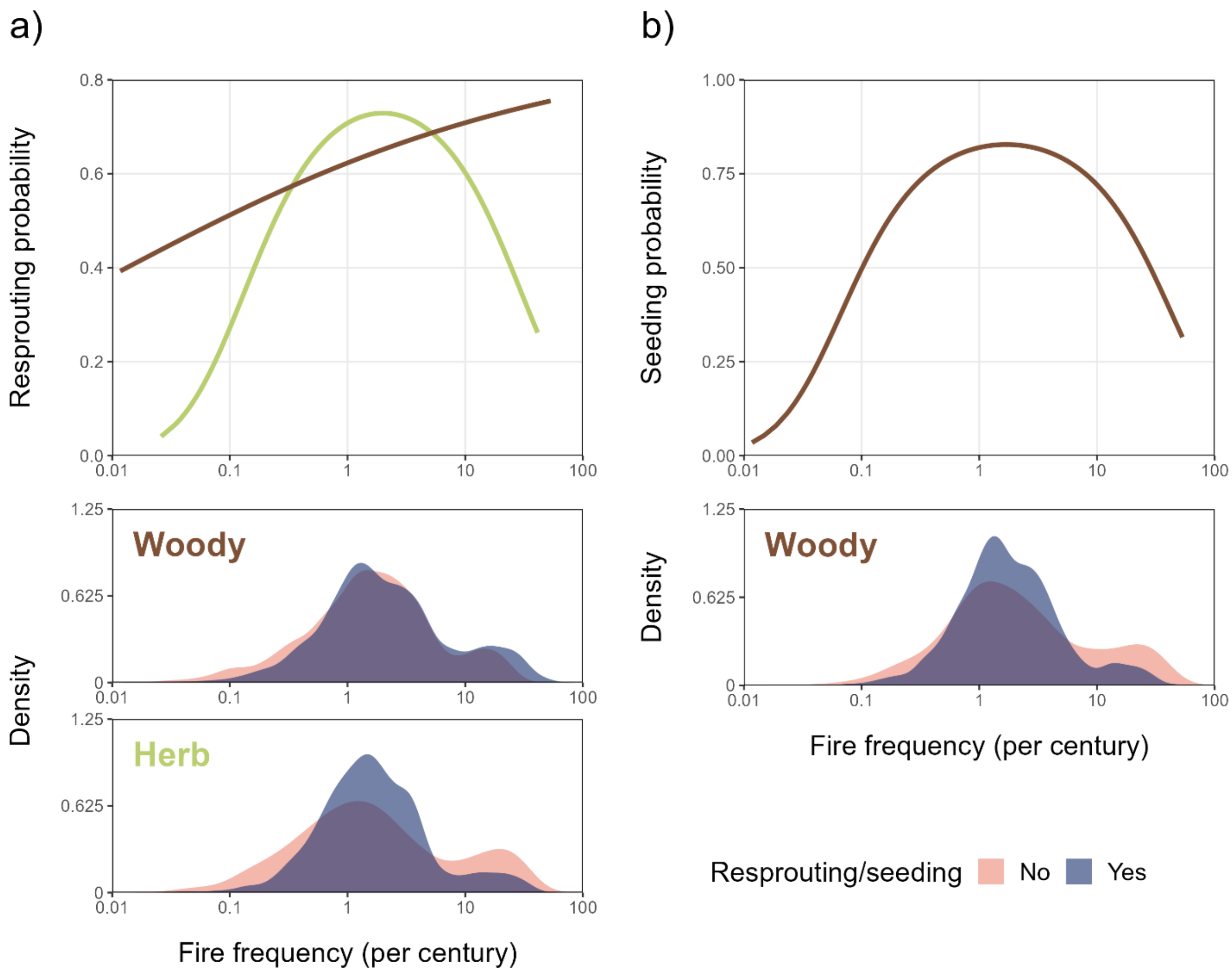


Figure 4 Observed changes in the frequency of two fire-adapted traits with disturbance regime, as indicated by fire frequency. The lines in the top panels show the modelled changes in the proportion of species with either (a) resprouting, or (b) post-fire seeding ability against fire frequency (per century), for woody (brown) and herbaceous (green) species. Herbaceous species were omitted from (b) due to insufficient data. Statistics for these lines are in Table 1 and 2; see text for number of observations in each group. Lowel panels show the density functions for the number of woody and herbaceous species with and without these adaptations, along the gradient. Fire frequency is log-scaled and represents the mean fire frequency across a species' range from 2000 to 2022 (see main text for details).

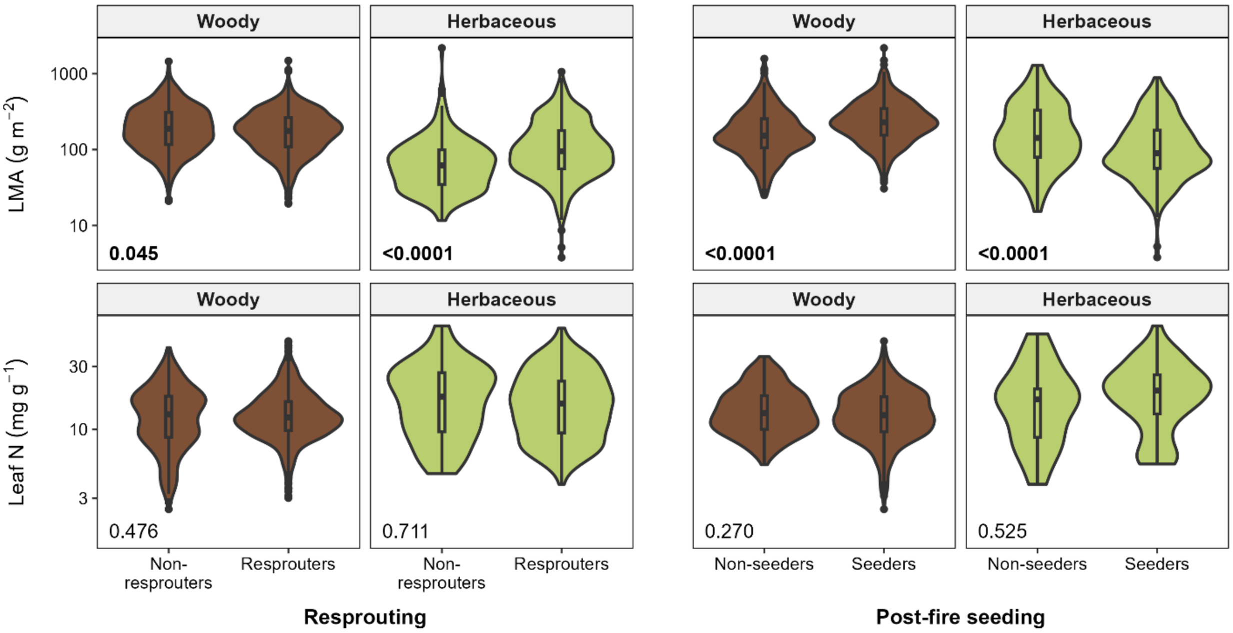


Figure 5 Comparing distributions of two leaf traits, leaf mass per area (LMA) and leaf nitrogen (N) content, among fire-adapted and non-fire-adapted species, within woody (brown) and herbaceous (green) species. Coloured areas show the density distribution of values across all species in each group, with boxplots showing the median, the first and third quartiles (hinges) and the largest/smallest value no further than 1.5 times the interquartile range (whiskers). Outliers (values outside whiskers) are plotted as individual points. P-values indicate results of within group comparisons (see Table 3 for details).

Table 1 Association of (a) resprouting and (b) post-fire seeding with mean fire frequency (per century). Both response variables were coded as TRUE or FALSE, with separate models run for each trait. Values show the odds ratio of the response for a change in each predictor[1]. We also included growth form (woody or herbaceous) as a predictor for resprouting ability, , but not for post-fire seeding due to lack of data. Mean fire frequency was log-transformed to reduce skewness. Number of observations and R^2 Tjur value are listed.

Predictors	*Odds Ratios*	*CI*	*P*
(a) Resprouting			
(Intercept)	2.42	2.24 – 2.62	**<0.001**
Mean fires [log10]	2.01	1.73 – 2.36	**<0.001**
(Mean fires [log10])^2	0.31	0.26 – 0.36	**<0.001**
Woody or herb [woody]	0.68	0.62 – 0.76	**<0.001**
Mean fires [log10] * Woody or herb [woody]	0.76	0.62 – 0.92	**0.005**
(Mean fires [log10])^2 * Woody or herb [woody]	3.11	2.56 – 3.79	**<0.001**
Observations	10012		
R^2 Tjur	0.031		
(b) Post-fire seeding			
(Intercept)	4.54	4.05 – 5.11	**<0.001**
Mean fires [log10]	1.62	1.26 – 2.07	**<0.001**
Mean fires [log10]^2	0.35	0.28 – 0.44	**<0.001**
Observations	2576		
R^2 Tjur	0.039		

[1] The odds ratio is the ratio of the probability of responding to the probability of not responding for a unit change in the predictor. Values (<1 indicates a lower likelihood of responding compared to not responding with an increase in the predictor.

Table 2 Associations of (a,b) mean leaf mass per area (LMA) (g m^{-2}) and (c,d) mean leaf nitrogen (N) content (mg g^{-1}) with resprouting and post-fire seeding, including woody or herbaceous growth form as an explanatory factor and any interactions. Values are fitted parameters from a linear model. Number of observations and R^2 values are listed below each model.

	Estimates	*CI*	*P*
(a) Mean LMA [log10] versus resprouting			
(Intercept)	1.79	1.75 – 1.84	**<0.001**
Resprouting	0.20	0.15 – 0.25	**<0.001**
Woody or herb [linear]	0.47	0.42 – 0.52	**<0.001**
Resprouting * Woody or herb [linear]	-0.24	-0.30 – 0.18	**<0.001**
Observations	2840		
R^2 / R^2 adjusted	0.171/0.170		
(b) Mean LMA [log10] versus seeding			
(Intercept)	2.08	2.01 – 2.14	**<0.001**
Seeding	-0.18	-0.25 – -0.10	**<0.001**
Woody or herb [linear]	0.02	-0.05 – 0.10	0.584
Seeding * Woody or herb [linear]	0.32	0.24 – 0.41	**<0.001**
Observations	1498		
R^2 / R^2 adjusted	0.162/0.161		
(c) Mean leaf N content [log10] versus resprouting			
(Intercept)	1.21	1.16 – 1.26	**<0.001**
Resprouting	-0.03	-0.09 – 0.03	0.287
Woody or herb [linear]	-0.13	-0.18 – -0.07	**<0.001**
Resprouting * Woody or herb [linear]	0.05	-0.01 – 0.11	0.118
Observations	1636		
R^2 / R^2 adjusted	0.025/0.023		
(d) Mean Leaf N content [log10] versus seeding			
(Intercept)	1.17	1.09 – 1.27	**<0.001**
Seeding	0.07	-0.03 – 0.18	0.174
Woody or herb [linear]	-0.04	-0.13 – 0.06	0.416
Seeding * Woody or herb [linear]	-0.10	-0.21– 0.01	0.068
Observations	869		
R^2 / R^2 adjusted	0.029/0.026		

Supporting Information

Fig. S1 Comparison of two methods for estimating average fire frequency for an example species.

Fig. S2 Comparison of mean fire frequencies estimated using Poisson generalised linear model and survival analysis methods.

Fig. S3 Relationships between resprouting or seeding versus fire frequency per century, as predicted by phylogenetic logistic regression.

Table S1 Woodiness trait values from AusTraits divided into woody, herbaceous, semi-woody and ambiguous categories.

Table S2 Association of resprouting and seeding with fire frequency and woody or herbaceous growth form, as fit by phylogenetic logistic regression.

Table S3 Associations of leaf mass per area and leaf nitrogen content with resprouting and post-fire seeding, fit by phylogenetic linear regression.