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Resprouting grasses are associated with less frequent fire than seeders

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Summary

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- Plant populations persist under recurrent fire via resprouting from surviving tissues (resprouters) or seedling recruitment (seeders). Woody species are inherently slow maturing, meaning that seeders are confined to infrequent fire regimes. However, for grasses, which mature faster, the relationships between persistence strategy and fire regime remain unknown.
- Globally, we analysed associations between fire regimes experienced by hundreds of grass species and their persistence strategy, within a phylogenetic context. We also tested whether persistence strategies are associated with morphological and physiological traits.
- Resprouters were associated with less frequent fire than seeders. Whilst modal fire frequencies were similar (fire return interval of 4–6 yr), seeders were restricted to regions with more frequent fire than resprouters, suggesting that greater competition with long-lived resprouters restricts seeder recruitment and survival when fire is rare. Resprouting was associated with lower leaf N, higher C : N ratios and the presence of belowground buds, but was unrelated to photosynthetic pathway.
- Differences between the life histories of grasses and woody species led to a contrasting prevalence of seeders and resprouters in relation to fire frequency. Rapid sexual maturation in grasses means that seeder distributions, relative to fire regime, are determined by competitive ability and recruitment, rather than time to reproductive maturity.

Introduction

Plant species persist in fire-prone environments via two broad strategies: resprouting from surviving tissue or recruiting from seedbanks (Bond & Midgley, 2001; Pausas *et al.*, 2004). The relative benefit of these two strategies ('resprouter' vs 'seeder') varies with fire regime, resulting in patterns of persistence strategies along gradients of fire frequency and intensity, as seen in several woody fire-prone taxa (Keeley, 1986; Bellingham & Sparrow, 2000; Pausas, 2001; Knox & Morrison, 2005; Clarke & Dorji, 2008; Vilà-Cabrera *et al.*, 2008; Pausas & Keeley, 2014). However, for grasses, a globally important plant family whose distribution and success are closely linked to fire (Bond *et al.*, 2005; Keeley & Rundel, 2005; Scheiter *et al.*, 2012; Linder *et al.*, 2018), the relationship between persistence strategy and fire regime has not been explored.

Fire regimes vary spatially and temporally (Gill, 1975; Belcher *et al.*, 2010; Archibald *et al.*, 2013; Keeley & Syphard, 2016) with fire frequency and intensity two fire regime characteristics relevant to understanding strategies of plant growth and

persistence. Fire frequency limits potential periods of plant growth, and therefore resources available to put into organs that may aid resprouting, such as rhizomes. Intensity relates to temperatures experienced, and the potential impact on plant mortality and reproductive success (Moreno & Oechel, 1991; Wade, 1993; McCaw *et al.*, 1997). Fire intensity and frequency are interdependent, as long fire return periods enable the development of significant fuel loads, potentially resulting in high-intensity fires (Bond & van Wilgen, 1996; Archibald *et al.*, 2013). Hence, plant persistence strategies tend to sort along gradients of frequency and intensity (Box 1 panels a and b; Keeley, 1986; Bellingham & Sparrow, 2000; Knox & Morrison, 2005; Pausas & Keeley, 2014). These patterns have been explained by life history theory via the principle of resource allocation (Keeley & Keeley, 1977; Bond & Midgley, 2001), which posits that plants balance the allocation of limited resources among growth, maintenance and reproduction (Silvertown & Charlesworth, 2001). Seeders maximise fitness by allocating relatively more resources than resprouters to fast growth and early reproduction to increase the likelihood of reaching reproductive maturity before the next

fire. By contrast, resprouters maximise fitness by allocating relatively more resources to nonstructural carbohydrate stores and protective structures that will increase the likelihood of survival post fire (Bellingham & Sparrow, 2000).

Fire has played a major role in the historical and contemporary success of the grasses (Keeley & Rundel, 2005; Scheiter *et al.*, 2012; Linder *et al.*, 2018). Large areas of the tropics and subtropics are maintained as grasslands and savannas by fire, despite the climatic potential to support forest (Bond *et al.*, 2005; Beckage *et al.*, 2011). Grasses, in turn, fuel the most frequent fire regimes and the majority of fires on Earth (Mouillot & Field, 2005). There is growing interest in how fire influences and is influenced by grasses (Ripley *et al.*, 2015; Simpson *et al.*, 2016; Wragg *et al.*, 2018; Russell *et al.*, 2019; Simpson *et al.*, 2019). Grasses persist through fire by germinating from soil-stored seed banks or by resprouting from buds (Bond & van Wilgen, 1996). However, how resprouter and seeder grasses sort along gradients of fire frequency and intensity remains untested. Yet, it is important in understanding the consequences of stark differences in life histories that likely underpin relationships between fire regimes and persistence strategies (Pausas, 2001; Box 1 panels c and d).

The plant traits associated with seeder and resprouter strategies of fire-prone woody species are well studied (Paula & Pausas, 2006; Vivian & Cary, 2012), but remain poorly understood in grasses. The C_4 photosynthetic pathway, which has evolved multiple times independently in grasses (Grass Phylogeny Working Group II, 2012) and is highly efficient in warm, high-light environments, such as fire-prone grasslands (Tix & Charvat, 2005; Ratnam *et al.*, 2011), may be important to grass resprouting ability (see Table 1 for specific predictions). A recent study by Moore *et al.* (2019) found that post-fire survival across 52 perennial grasses was associated with C_4 photosynthesis. Likewise, the positioning of resprouting buds is also expected to be crucial (Pausas & Paula, 2020). Buds below the soil surface (rhizomes) are likely better protected from heat than those at the soil surface (crown resprouters or species with stolons; Table 1). Leaf traits probably also differ between seeders and resprouters, as found in woody fire-prone species (e.g. Paula & Pausas, 2006). Leaf traits associated with potential growth rates and resource investment, such as specific leaf area (SLA; Forrestel *et al.*, 2014), and nitrogen (N)-use efficiency (associated with low leaf N content), may be important in fire-prone, N-poor environments (Table 1; Knapp & Medina, 1999; Long, 1999; Sage, 2004; Keeley & Rundel, 2005). Likewise, leaf traits that enhance flammability, such as a high leaf carbon (C) : N ratio, occur in resprouting, shade-intolerant grasses which require frequent defoliation (Table 1; Everson *et al.*, 1988). Life history is likely to be closely linked to resprouting ability, with perennials presumably able to resprout but annuals not (Table 1). Whether this is strictly true, or if there are exceptions to this trend, is unclear.

Here, we explore the global relationship between fire characteristics (frequency and intensity) and the persistence strategies of fire-prone grass species. We predict that patterns of resprouting and seeding with fire characteristics in grasses will differ from those in woody species in the ways outlined in Box 1. Based on *a priori* expectations (Table 1), we also investigate how plant traits

(photosynthetic pathway, life history, bud position, SLA, leaf N content and C : N ratio) relate to resprouting ability.

Materials and Methods

Grass species occurrences

We extracted all georeferenced and dated occurrence records (*c.* 18.6 M records) for Poaceae taxa from the Global Biodiversity Information Facility (GBIF) web portal (GBIF.org (5 November 2019) GBIF Occurrence Download doi: 10.15468/dl.rckugp) via the R statistical computing package `RGBIF` (Chamberlain *et al.*, 2020). This analysis and all statistical analyses were carried out in the R environment (R Core Team, 2019).

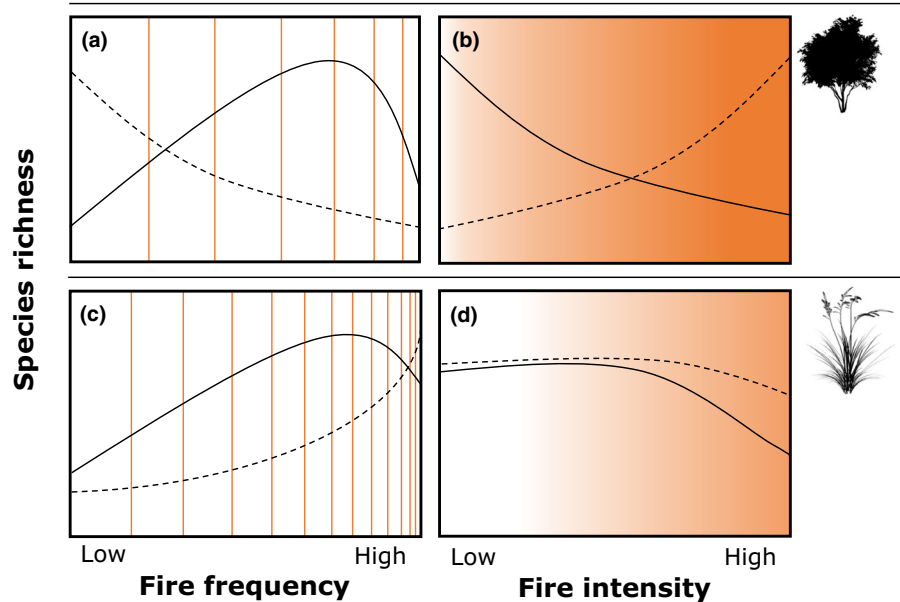
Steps were taken to control the quality and suitability of occurrence records (Supporting Information Table S1 gives the number of records remaining after each cleaning step). Species names were standardised against the Kew Grass Synonymy database (Clayton *et al.*, 2006) using the software package `TAXONOME` (Kluyver & Osborne, 2013), and records were discarded if an accepted name could not be given. Longitude and latitude data were checked to ensure values were sensible using the `COORDINATECLEANER` package (Zizka *et al.*, 2019; for example removal of invalid and nonterrestrial coordinates, duplicated records and

Table 1 Plant traits and their predicted associations with resprouting ability in fire-prone grasses.

Trait	Relationship with resprouting ability
Photosynthetic pathway	Resprouters are more likely to be C_4 than C_3 (Moore <i>et al.</i> , 2019). C_4 species are highly efficient in fire-prone environments and may therefore have greater stored resources to resprout (Tix & Charvat, 2005; Ratnam <i>et al.</i> , 2011)
Bud position	Resprouters are more likely to have buds below the soil surface (rhizome resprouters) where they are protected from intense heat (Pausas & Paula, 2020)
Specific leaf area (SLA)	Resprouters will have lower SLA than seeders (Forrestel <i>et al.</i> , 2014). High SLA will aid the rapid growth of seeder species
Leaf nitrogen (N) content	Resprouters will have lower leaf N contents than seeders. Resprouters may experience fire multiple times in their lifetime and thus low-N availability (due to N volatilisation during fire; Reich <i>et al.</i> , 2001; Hernández & Hobbie, 2008). In these conditions, a high N-use efficiency (low leaf N content) may be advantageous (Wedin & Tilman, 1990; Reich <i>et al.</i> , 2001)
Leaf C : N ratio	Resprouters will have higher leaf C : N ratios than seeders. High leaf C : N ratio, which is linked to low decomposition rates and the accumulation of a highly flammable fuel load (Aerts, 1997), may be advantageous to shade-intolerant resprouting species in maintaining an open canopy (by aiding the removal of standing dead and woody biomass; Everson <i>et al.</i> , 1988)
Life history	Resprouters are more likely to be perennial than seeders. Perennial-grass species have buds from which to regrow, which annual species may lack

Box 1 Relationships for woody species.

The predicted relationships between persistence strategy and fire characteristics for fire-prone woody taxa (a and b; solid line in (a) from Bellingham & Sparrow, 2000) and grass taxa (c and d). Solid lines represent the distribution of resprouter species and dashed lines represent seeder species. Fire characteristics are frequency and intensity, and the coloration of plot backgrounds represents typical differences in characteristics between fire regimes fuelled by woody or grassy vegetation (with grass-fuelled fires being more frequent and less intense on average; Archibald *et al.*, 2013).



Relationships for woody species

Fire frequency (a) – Woody seeders (dashed lines) are susceptible to ‘immaturity risk’ (Zedler, 1995), where intervals between fires are shorter than the time taken to reach maturity (e.g. Pausas, 2001). Therefore, the seeder strategy becomes more viable as the interfire period increases and fire frequency decreases. Only seeders with rapid growth and early maturation can exist in very high fire frequencies. By contrast, the cost of storage organs to growth in low fire frequencies means that resprouting (solid lines) is more viable with increasing fire frequency (Bellingham & Sparrow, 2000). However, very high frequencies make maintaining storage organs energetically unfeasible (Vilà & Terradas, 1995; Grady & Hoffman, 2012; Fairman *et al.*, 2019; Day *et al.*, 2020).

Fire intensity (b) – Woody seeders are predicted to be less susceptible to high-intensity fires than resprouters, as the seeds of many fire-prone seeder species are protected from the heat of the fire through insulating seed-storage structures (e.g. serotinous cones from which seeds are released following a fire) or a layer of soil, and are thus much less vulnerable to heat-related damage than adult resprouting plants (Keeley & Fotheringham, 2000; Pausas & Keeley, 2014; Day *et al.*, 2020). The buds of resprouters may be protected to an extent by insulating bark (for epicormic buds) or soil (for basal buds).

Relationships for grass species

Fire frequency (c) – At low fire frequencies, grass resprouters decline because of the energetic costs of maintaining buds when fire is rare. In addition, for clump-forming resprouting species (‘crown resprouters’), the accumulation of detritus due to infrequent fire can lead to individuals becoming moribund (Knapp & Seastedt, 1986), which may be fatal (Zimmerman *et al.*, 2010). At very high fire frequencies, resprouting may decline, as maintaining storage organs becomes less feasible, but will still be common (as resprouting grasses fuel the most frequent fire regimes on Earth; Mouillot & Field, 2005). In contrast to woody seeders, we expect grass seeders to be largely restricted to high fire frequencies when fire return intervals are short. Grasses generally have much shorter generation times than woody species, for example, members of the fire-prone grass lineage, Andropogoneae, flower within months of germination (Estep *et al.*, 2014). Therefore ‘immaturity risk’ is not likely to limit the distribution of grass seeders, even when accounting for the grass-fuelled high fire frequencies. In less frequent fire regimes, we expect seeders will be outcompeted by established resprouters (Zimmerman *et al.*, 2008).

Fire intensity (d) – Grass-fuelled fires tend to be low intensity although there are exceptions (e.g. Spinifex (*Triodia* spp. dominated) grasslands of Australia experience very hot fires; Archibald *et al.*, 2013). Therefore, intensity may not be a relevant fire characteristic in determining the distributions of grass seeders and resprouters, as has been found for other grass traits (Trollope *et al.*, 2002; Uys *et al.*, 2004; Peláez *et al.*, 2013) because it does not represent a strong selection pressure. High fire intensities may cause mortality, particularly in resprouters.

records within biodiversity institutions) and were accurate to at least three decimal places, to represent the small scale over which fire regimes change. Finally, to ensure that records represented individuals from environments subject to ecologically relevant fire regimes, domesticated grass species were excluded (Kluyver, 2013) and all other species' records were checked against Kew GrassBase distributions (Clayton *et al.*, 2006). Records from highly transformed landscapes, where fire regimes are altered through changes in ignition frequency and fuel properties, were also removed. To do this, records from protected areas were identified (using the World Protected Areas map; <http://www.wdpa.org/>) and kept. Otherwise, a human influence index (HII) value was obtained for each record (Sanderson *et al.*, 2002), which indicates how impacted was the landscape by human activities (based on population density, access, land-use and infrastructure). Records with an HII value > 30 are from highly transformed landscapes in terms of fire characteristics (Archibald *et al.*, 2013) and were excluded. Records made before 1980 were removed (a compromise between removing records taken before satellite-derived fire datasets began and not removing a large proportion of the total records). After these cleaning steps, species were excluded if they were sampled by < 50 unique occurrence points.

Fire characteristics

Data from the MODIS satellite were used to characterise the fire regime to which grasses were exposed. This is a *c.* 20-yr dataset, which covers a similar time period as the GBIF location records. Therefore, although current fire regimes might not represent the evolutionary history of fire in that location, they do represent the fire regime to which the species occurring there are exposed and able to persist under.

Fire frequency Fire frequency is characterised as the median fire return interval (FRI; the time between successive fires), with high frequencies associated with short FRIs. The MODIS global monthly burnt area (MCD64A1) satellite data product was used to calculate FRI values. This provides fire data for the Earth's surface at a 500-m resolution. Utilising characteristic changes in surface reflectance following a fire (e.g. charcoal/ash deposits, vegetation loss), as well as active fire detections, the MODIS algorithm identifies recent burn scars and provides an approximate date of burning (Giglio *et al.*, 2009).

Dates of fire occurrence at each GBIF location during the *c.* 20-yr MODIS dataset (April 2000 to January 2020) were extracted and used to quantify all interfire intervals to which each species was exposed (after Archibald *et al.*, 2010). A Weibull distribution was fitted to these interval data for each species using the SURVIVAL R package (R Core Team, 2019). The first and last fires of the MODIS dataset were open tailed (i.e. the limited timespan of the dataset means that the interfire interval before the first fire and after the last fire cannot be determined) and the survival analysis allows these open-tailed intervals to be included to maximise the information provided. Estimations of the Weibull shape and scale parameters were determined for each

species using data from pixels that burnt at least once during the 20-yr period. The shape and scale parameters were used to determine the median FRI using the equation from Moritz *et al.* (2009):

$$\text{FRI} = b(\log_e 2)^{\frac{1}{c}}$$

where *b* is the scale parameter and *c* is the shape parameter. For species in infrequently burnt places (i.e. where the fire return period is much greater than the 20 yr of the MODIS dataset), the above FRI algorithm would converge either on an unrealistically large FRI or not converge at all. We focused on species for which fire is a major disturbance and frequent enough to act as a selective pressure over their range, and hence we defined whether species were 'fire-prone' or not. To do this, the proportion of records that fell within pixels that burned, relative to the total number of records for each species, was used. This proportion was plotted against the number of species and a break-point regression fitted to the curve (Fig. S1) using the SEGMENTED library in R (Muggeo, 2003). An estimated break-point value was calculated (0.26) and species with a proportion burned lower than this value were excluded (i.e. species that had < 26% of their occurrence records in burnt locations were excluded from fire frequency analyses). The impact of any spatial bias in the occurrence records on the proportion burned or the values of FRI was tested by subsetting the records such that there was a maximum of three records per species in each 10 km² grid cell (a grid size that represents a compromise between the finer scale fire characteristic data and not removing a large proportion of the occurrence records). Values of proportion burned and FRI were highly similar between the original and subsetted datasets ($r^2 = 0.99$ and 0.95 , respectively), suggesting that there is no pervasive spatial bias in the original dataset. Finally, any species with fire return intervals that were > 100 or < 1 yr were excluded. The limitations of a 20-yr dataset mean that the results of the survival analysis were not able to resolve these fire regimes sufficiently.

The stringent data cleaning process and focus on frequently burned species resulted in a dataset containing 734 fire-prone species (samples per species range = 53–25319; median = 270), whose distribution covers the majority of fire-prone areas, where grasses are an important vegetation component (see Fig. S2 for the distribution of occurrence data).

Fire intensity Values of fire radiative power (FRP), or the rate of radiant energy released, can be obtained from satellite measurements of middle infrared emission over actively burning areas. FRP is frequently used as a proxy for fire intensity (Dwyer *et al.*, 2000; Archibald *et al.*, 2013), and is available globally at 0.5° resolution from the MODIS global monthly fire location product (MCD14ML).

FRP values, measured in megawatts per 1-km pixel, were extracted for all active fire points over the duration of the dataset (2002–2019) for each record. Any FRP values with a detection confidence < 50% were discarded. Data were grouped by species, and the 95th quantile extracted. There is typically a bias towards

low FRP values, due to the high variation in this measurement over the duration of a fire (Dwyer *et al.*, 2000) and low values during the night. The 95th quantile was therefore used, as done elsewhere (Archibald *et al.*, 2013), to indicate the maximum value that a headfire could attain in a particular environment and to avoid errors caused by outliers. The 95th quantile related significantly ($P < 0.001$) with mean ($r^2 = 0.90$) and median ($r^2 = 0.75$) values across all species.

Precipitation and drought

A difficulty in determining the role of fire in driving spatial patterns of plant traits is that fire characteristics are often correlated with climate. High fire frequencies typically occur in areas with high rainfall and long dry seasons, where greater and more spatially connected fuel loads are produced (Pausas & Bradstock, 2007; Pekin *et al.*, 2011). Moreover, droughts influence the success of different grass persistence strategies: both directly, through causing death of perennial grasses and recruitment opportunities for seeder grasses (O'Connor, 1995), and indirectly, through changing the amount and the moisture content of fuels, and thus fire regimes. Drought is therefore expected to be a strong environmental filter (O'Connor, 1995). We used Foley's drought index (FDI; Foley, 1957; Fensham *et al.*, 2009) here to account for the influence of drought on grass persistence strategy that is independent of fire characteristics. The FDI takes the deviations of monthly measurements (i.e. actual rainfall for a period minus the expected rainfall for the same period) from long-term monthly averages and normalises it with respect to average annual rainfall (to allow for comparison across rainfall zones). It is therefore a measure of drought intensity that is not directly correlated with rainfall. To investigate drought at global scales, monthly rainfall values at 0.5 degree scale were used following Lehmann *et al.* (2014). For each grid cell, the FDI was calculated for each month of each yr as actual annual rainfall for 3 yr prior less the expected (long-term average) rainfall for that period, divided by the mean annual precipitation for the period 1901–2003. Monthly values for each location record were averaged per species.

Plant traits

Grass species' persistence strategies through fire were collected from a literature review, drawing upon large plant fire-response databases (e.g. Cook *et al.*, 2005; Crowley *et al.*, 2007; Paula *et al.*, 2009), journal papers (e.g. du Toit *et al.*, 2014; Marais *et al.*, 2014; Moore *et al.*, 2019) and the grey literature (such as Government reports regarding fire management strategies or control of invasive species). Data from sources already known to the authors were extracted first, followed by a targeted approach for species for which we had fire characteristic data. The latter was achieved by using the Web of Knowledge and Google Scholar search engines (to incorporate both the primary and grey literature) for the term '[species name] fire response'. We classed species as either 'seeders' or 'resprouters' based on the response specifically to fire and not to other disturbances, as fire not only

defoliates a plant (similar to other disturbances), but it also has lethal effects on meristem tissues (Pausas *et al.*, 2016). Resprouters were defined in a number of ways depending upon the type of data available. For categorical data, resprouting species were defined as those where resprouting is the main post-fire persistence strategy. In a few cases, the ability to resprout was given in relation to fire characteristics (e.g. 'plants will recover from an occasional, but not annual, fire'), and these were classed as resprouters because they showed an ability to resprout after fire. For quantitative data, species that experienced $< 30\%$ mortality when subjected to 100% leaf scorch were classed as resprouters (*sensu* Crowley *et al.*, 2007). Conversely, a species was classified as a seeder if the main post-fire persistence strategy was germinating from seed (which could be either from a stored soil seedbank or from seeds dispersed into a recently burnt area), or if plants of this species experienced $> 70\%$ mortality when subjected to 100% leaf scorch. In addition, annual species for which no response to fire could be found by searching the literature were assumed to be seeders, unless there was evidence to the contrary ($n = 27$). The seeder/resprouter dichotomy represents the standard way in which a species recovers from fire, but we acknowledge that these strategies are not mutually exclusive, with a number of species able to do both (i.e. facultative seeders; Pausas & Keeley, 2004). The resulting dataset, consisting of 763 taxa, of which 64% of species are classed as resprouters (a similar proportion found in other plant taxa and communities; Clarke, 2002 (71%); Clarke & Dorji, 2008 (60%)), is available via Dryad entry doi: 10.5061/dryad.3bk3j9khn.

Data on plant traits which we thought may be associated with the ability to resprout (Table 1) were collected from a number of sources. Photosynthetic type was acquired from Osborne *et al.* (2014), and bud position from the Kew GrassBase dataset (Clayton *et al.*, 2006). The latter involved the assignment of categories of bud position: belowground buds (species with rhizomes) or buds at ground-level (species with stolons or crown resprouters, defined as caespitose species with neither rhizomes nor stolons). Species-level leaf traits (specific leaf area (SLA), foliar N content and foliar C : N ratio) were obtained from a dataset of 279 grass species (Jardine *et al.*, 2020). A principal components analysis (using the '*princomp*' function; R Core Team, 2019) collapsed the variance in these three leaf traits into two axes that together accounted for 98.7% of total variation (69.1% on dimension 1; 29.6% on dimension 2; Fig. S3). Foliar N content and C : N ratio loaded most heavily on dimension 1, with N content being positively correlated ($r^2 = 0.88$; $P < 0.001$) and C : N ratio being negatively correlated ($r^2 = 0.82$, $P < 0.001$) with this dimension. SLA loaded heavily in dimension 2, and was positively correlated with this dimension ($r^2 = 0.69$, $P < 0.001$; Fig. S3).

Phylogeny To account for evolutionary relationships among grass species, we used a completely sampled, dated Bayesian phylogeny of grasses that incorporates 11 297 grass taxa (Forrestel, 2015) and combined molecular and taxonomic data following the methods of Jetz *et al.* (2012) and Thomas *et al.* (2013). A maximum clade credibility tree was inferred from the resulting distribution of trees using MRBAYES (Ronquist *et al.*, 2012), and

subset to include species in our study (available via Dryad entry doi: 10.5061/dryad.3bk3j9khn).

Data analysis

The relationships between grass persistence strategy and fire characteristics (frequency and intensity) were analysed using phylogenetic logistic regression (Ives & Garland, 2010) implemented in the PHYLLOLM package in R (Ho & Ane, 2014). The response variable was persistence strategy, coded as either 0 (seeder species) or 1 (resprouter species). Either fire frequency or fire intensity was selected as an explanatory variable. The drought index, FDI, was not highly correlated with either fire frequency (Pearson's product moment correlation coefficient = 0.05) or intensity (correlation coefficient = 0.43) and so was included as an additional explanatory variable. Any significant interaction terms between the explanatory variables were included in the final models. Fire frequency and intensity values were log-transformed to improve normality. The 'Logistic_MPLE' (Maximised Penalised Likelihood) method was used, and all analyses were performed with 10 000 bootstrap replicates. Sample sizes are given in Table S2.

To determine how plant traits (photosynthetic pathway, bud position, life history, leaf trait PCA axis one and two) associate

with persistence strategy, phylogenetic binary logistic regressions were fitted (as above) with persistence strategy as the response variable and each plant trait in turn selected as the explanatory variable (see Table S2 for sample sizes).

Relationships between fire frequency, fire intensity and drought were determined using phylogenetic generalised least squares with the 'pgls' function in the CAPER package (Orme *et al.*, 2018).

In these analyses we used species-level data. We recognise that some species show large variability in their traits (e.g. Moreira *et al.*, 2012), and in the environmental conditions they can persist in, but we could not account for within-species variability because the trait data and the location data did not coincide.

Results

Grass persistence strategy relationships with fire characteristics

Both seeders and resprouters can persist in high fire frequencies (i.e. short FRIs; Fig. 1a; modal FRIs: 4.4 yr for seeders and 5.7 yr for resprouters). However, seeders are excluded when fire is infrequent whereas resprouters can tolerate a range of fire

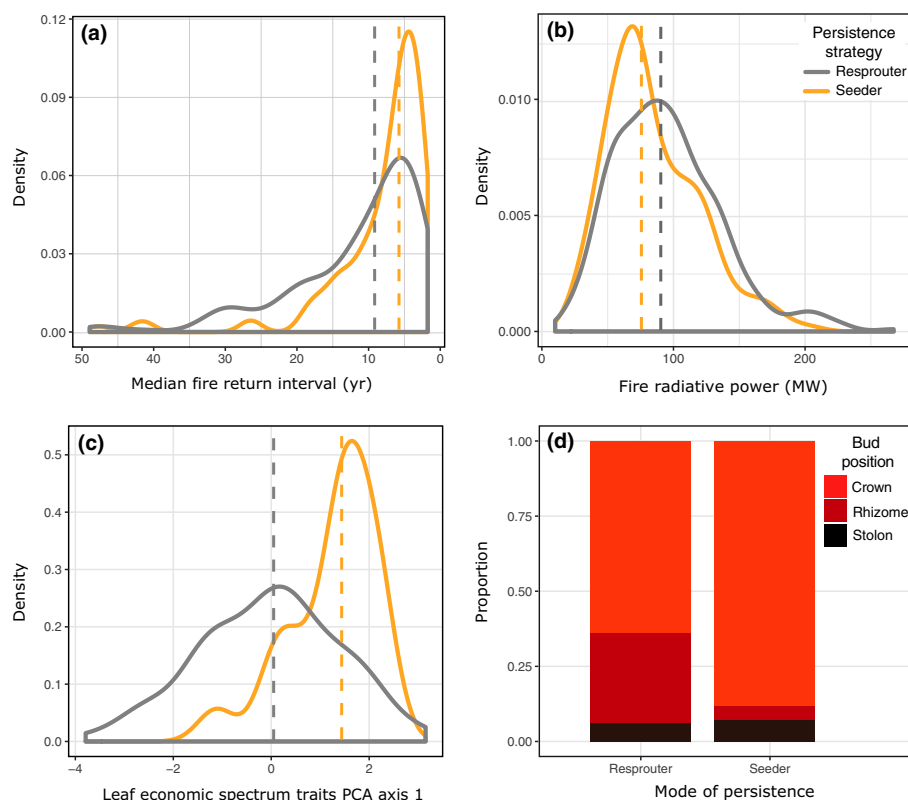


Fig. 1 Fire characteristics and plant traits associated with persistence strategy in fire-prone grass species. (a) Seeders are associated with more frequent fire (i.e. shorter fire return intervals), and (b) lower intensity fire than resprouters (intensity values are 95th percentile of fire radiative power). (c) Resprouters have lower values for leaf trait PCA axis one than seeders (i.e. lower values of leaf N content and higher leaf C : N ratio). (d) A higher proportion of resprouters have buds positioned belowground (in the form of rhizomes) than seeders. Dashed lines in density plots represent median values for either resprouters (grey) or seeders (orange). Sample sizes: (a) 332 species; (b) 550 species; (c) 114 species; (d) 561 species. The x-axis in (a) is reversed (so that high fire frequencies are to the right) and constrained to a maximum of 50 yr for ease of viewing (which accounts for 97% of data).

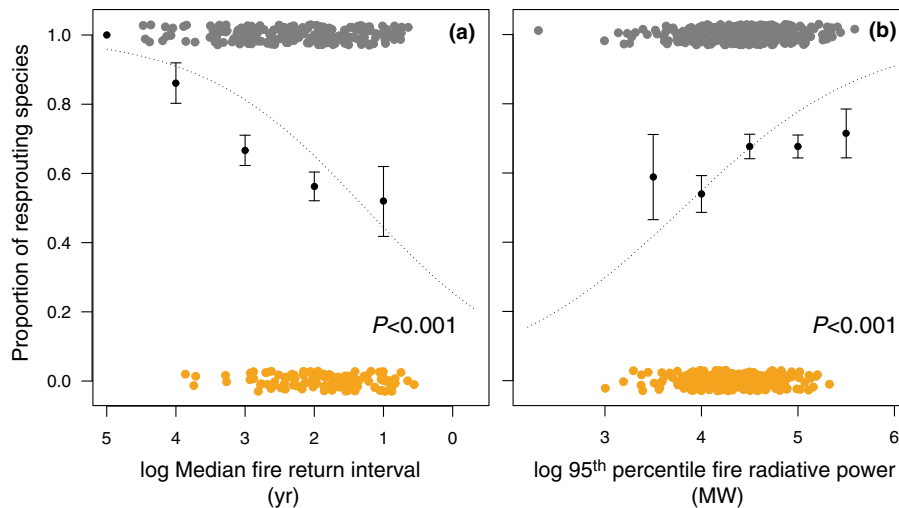


Fig. 2 The proportion of resprouting grass species increases as fire frequency goes down (a) and fire intensity (b) goes up. The dashed line is the relationship as predicted by phylogenetic logistic regression with the effect of drought accounted for. Both fire characteristics are log-transformed to improve normality of the data. Jittered points show the distribution of seeder (orange points) and resprouter (grey points) species. Black points are mean proportion values for data binned by fire characteristic values with each bin representing one log-transformed unit (e.g. in (a), logged fire return intervals are divided into the following bins: 0–1, 1–2, 2–3, 3–4, 4–5). Error bars represent the standard error of the mean for the binned data. The x-axis in (a) is reversed so that high fire frequencies (short fire return intervals) are to the right.

frequencies. This difference means that resprouters are associated with significantly longer FRIs than seeders (coefficient = 0.84, bootstrapped 95% confidence interval (CI): 0.53–1.20; $n = 332$, $P < 0.001$). The median FRIs for resprouters is 8.1 yr (standard deviation (SD): 15.5 yr) in contrast with 5.7 yr for seeders (SD: 7.5 yr; Figs 1a, 2a). This effect was over and above the significant relationship between drought and grass persistence strategy, with resprouters associated with a lower intensity multiannual drought (coefficient = 1.30 (95% CI: 0.42–2.15); $P = 0.007$) than seeders. Resprouting was the predominant persistence strategy across the range of fire frequencies (Fig. 2a). There was no significant interaction between fire frequency and drought, providing evidence that these environmental factors are independently associated with grass persistence strategy.

Grass seeders typically experience lower intensity fire than grass resprouters (coefficient = 1.05; 95% CI: 0.87–1.30, $n = 550$, $P < 0.001$; Figs 1b, 2b). The mean 95th percentile of FRP was 75.1 MW (SD: 35.2 MW) for seeders and 90.3 MW (SD: 40.8 MW) for resprouters. Again, there was also a significant association between drought and grass persistence strategy that was independent of fire (coefficient = 1.61 (95% CI: 0.94–2.30), $P < 0.001$).

Fire characteristics

Fire-prone grasses experience a range of fire frequencies (FRI range: 1.0–94.1 yr; Fig. 3). The species-level median FRI is 6.9 yr, which fits closely with the estimated global mean value for tropical grasslands and savannas (e.g. 6.5 yr for the period 1900–2000; Mouillot & Field, 2005). Species average fire intensity values ranged from 20–267 MW (median = 85 MW) per 1 km pixel (Fig. 3). These values are considered ‘low’ to ‘medium’ fire intensities (category 1 or 2 *sensu* Ichoku *et al.*, 2008), which

is consistent with what is expected from grass-fuelled surface fires (Archibald *et al.*, 2013).

As predicted, fire frequency and intensity are inversely correlated, such that grass species that experience more frequent fire, also experience lower intensity fire ($F_{1,491} = 82.2$, $P < 0.001$, $r^2 = 0.14$; Fig. S4). Intense droughts are associated with the occurrence of very intense fire ($F_{1,548} = 128.5$, $P < 0.001$, $r^2 = 0.19$; Table 2; Fig. S4), and there is some evidence that extreme droughts are also less likely to co-occur with frequent fire regimes ($F_{1,330} = 9.91$, $P = 0.002$, $r^2 = 0.03$; Table 2; Fig. S4).

Plant traits associated with persistence strategy

As predicted, resprouting ability is strongly related to life history (coefficient = 4.61, bootstrapped 95% CI from 4.01 to 5.28, $n = 728$, $P < 0.001$) with the majority of resprouters being perennials (97%) and the majority of seeders being annual species (76%). There are exceptions, however, with 14 annual species able to resprout after fire (e.g. *Panicum verrucosum*, *Agrostis venusta* and *Oplismenus hirtellus*) and 60 perennials persisting through fire only as seeds (e.g. *Digitaria diffusa*, *Paspalum conjugatum*, *Enneapogon lindleyanus*; full list available via Dryad entry doi: 10.5061/dryad.3bk3j9khn). The resprouter strategy was unrelated to photosynthetic pathway (coefficient = 0.21 (95% CI: –0.17 to 0.58), $n = 597$, $P = 0.31$), with 61% of C₃ species and 63% of C₄ species being resprouters. In terms of bud position, resprouters were more likely to have rhizomes (i.e. underground buds) than seeders (30% vs 4%, respectively; coefficient = 2.22 (95% CI: 1.41–3.19), $n = 561$, $P < 0.001$) but did not differ in the proportions of other bud positions ($P > 0.05$; Fig. 1d).

Resprouters and seeders differed in their leaf traits relating to N content and C : N ratio (PCA dimension one; coefficient =

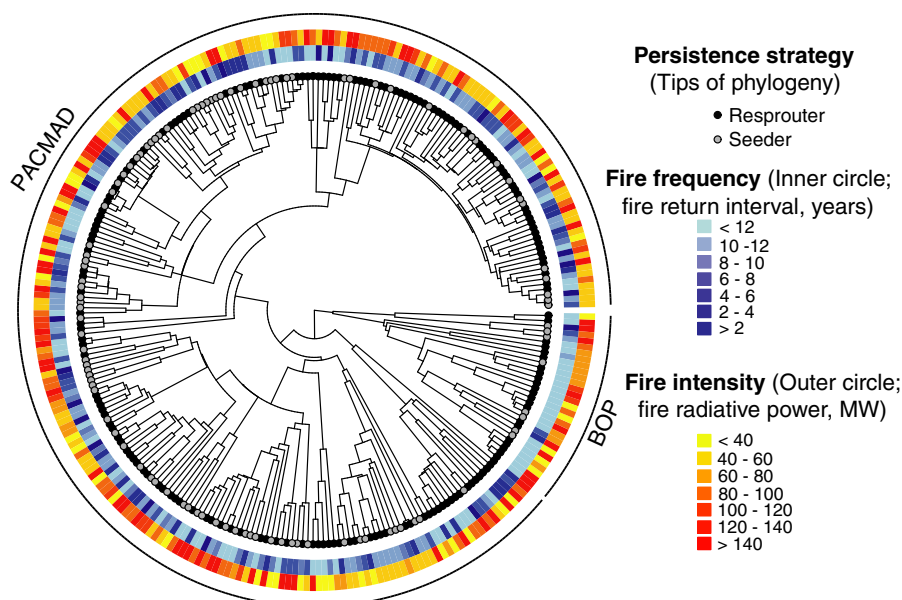


Fig. 3 Fire characteristics and persistence strategies of fire-prone grasses. Phylogeny tips reflect persistence strategy (resprouter/seedler). The inner circle represents fire frequency values, as measured as the median fire return interval in years (darker shades of blue are higher fire frequencies). The outer circle shows values of fire intensity, measured as fire radiative power (MW). The 278 species shown are those with data for both fire frequency and intensity, and persistence strategy. PACMAD and BOP are the two major Poaceae clades

Table 2 Associations of plant persistence strategy (coded either as 0 for seeders or 1 for resprouters) with two fire characteristics, median fire return interval (a measure of frequency; a) and 95th quantile of fire radiative power (a measure of intensity, b), and drought, across fire-prone grass species ($n = 332$ in a; $n = 550$ in b).

(a)	Estimate (bootstrapped 95% CI)	Z value	<i>P</i> -value [†]
Intercept	0.37 (−0.72 to 1.41)	0.62	0.52
Fire frequency	0.84 (0.53–1.20)	4.84	<0.001
Drought [§]	1.29 (0.42–2.15)	2.71	0.006
(b)			
Intercept	−2.30 (−2.89 to −1.79)	−2.53	0.011
Fire intensity	1.05 (0.87–1.30)	4.43	<0.001
Drought [§]	1.61 (0.94–2.30)	3.91	<0.001

[†]Significant model terms ($P < 0.05$) are in bold.

[§]Drought is characterised by the rainfall deficit standardised by mean annual precipitation (Foley's drought index; Foley, 1957), with more negative values representing more extreme drought.

−0.62 (95% CI: −1.13 to −0.21), $n = 114$, $P = 0.007$) but not SLA (PCA dimension two; coefficient = −0.02 (95% CI: −0.54 to 0.61), $n = 114$, $P = 0.91$). Specifically, resprouters were associated with lower leaf N content and higher C : N ratio than seeders (median PCA dimension one scores: 0.04 (resprouter) vs 1.44 (seedler); Fig. 1c).

Discussion

Grasses differ substantially from fire-prone woody species in the sorting of persistence strategies along fire gradients, emphasising the need to develop theory and understanding about plant–fire relationships among diverse life forms that have different patterns

of growth, fecundity and resource allocation (Pausas, 2001). The variable patterns between woody and grassy species persistence strategies related to fire frequency suggests diverse processes shape different fire-prone ecosystems. Whilst ‘immaturity risk’ likely excludes woody seeder species from regions with frequent fire, this was not the case for grasses. Grass seeders are associated with higher relative fire frequencies than grassy resprouters, suggesting that, despite FRIs as short as 1 yr, sexual maturity is reached between fires. The precocious embryo of grass seed, in which root, shoot and haustorial structure are already differentiated (Gibson, 2009), has been credited with the rapid establishment and development of grasses (Linder *et al.*, 2018), with individuals being able to flower in as little as 6 wk (Cope *et al.*, 2009). Seeder establishment is likely limited by high resprouter densities, as the size and storage reserves of resprouters enable rapid occupation of space after fire (Keeley, 1986; Myerscough *et al.*, 1995; Pausas & Keeley, 2014). Consistent with this are observations that resprouter grasses can reach considerable ages within grasslands (e.g. the lifespan of North American resprouting grasses can exceed 30 yr; Lauenroth & Adler, 2008), with seed recruitment rare (Defossé *et al.*, 1997; Milton & Dean, 2000; Zimmerman *et al.*, 2008). By contrast, under very high fire frequencies, resprouting may become energetically inviable, and seeders can dominate, such as in northern Australian savannas dominated by annual *Sorghum* species (Miles, 2003). Our results are consistent with the ‘gap-dependent’ model which has been used to explain patterns of persistence strategy in some woody species (Keeley *et al.*, 2016; but see Cowling *et al.*, 2018). How the lifetime reproductive effort of grass seeders and resprouters differs is unclear. Data from Mediterranean shrubs suggest that seeders are smaller seeded than resprouters (Verdú, 2000), and so might produce more seeds in a limited number of reproductive events.

Grassy resprouters peaked at fire frequencies of *c.* 5 yr return intervals (Fig. 1a), in contrast with woody resprouters typically restricted to fire frequencies of 5–25 yr return intervals in shrublands and woodlands (Le Maitre & Midgley, 1992). For grass resprouters, tolerance of frequent fire is enabled by resprouting from basal meristems. Further, crown resprouters typical in productive ecosystems require regular removal of standing dead biomass to prevent them becoming moribund through self-shading (Everson *et al.*, 1988; Zimmerman *et al.*, 2010) where litter build-up can result in the death of resprouting grasses (Knapp & Seastedt, 1986). Interestingly, although perennial grasses persist at defoliation frequencies of more than 1 yr (Danckwerts & Nel, 1989; Danckwerts, 1993), we found that as in woody plants, very high fire frequencies are correlated with fewer resprouters. It is worth noting that both mammalian grazing and fire typify grassy ecosystems, and whilst we focus on fire, grazing also likely shapes the patterns reported here, with resprouters associated with heavily grazed environments (Solofondranohatra *et al.*, 2020), and where heavy grazing excludes fire (Archibald & Hempson, 2016). In Africa, the intensity of mammalian grazing peaks at lower rainfall values (670 mm MAP) in contrast with the peak of fire frequency at 990 mm MAP (Archibald & Hempson, 2016). As expected, both grass seeder and resprouter species decline under low fire frequencies (although species not considered ‘fire-prone’, because their records primarily occurred in areas unburnt for > 20 yr, were excluded from our analyses), presumably because woody-plant life forms, correlated with lower fire frequencies, dominate landscapes. Consistent with this are abundant observations of forest encroachment into grass-dominated areas upon fire suppression (e.g. Hoffmann *et al.*, 2012).

Differences in fire intensities between grass and woody-plant fuelled fires may explain their contrasting patterns in persistence strategies. Grass-fuelled fires are typically lower intensity than those fuelled by woody species, with temperatures less than 200°C (cf. *c.* 400°C for fires in shrublands/forests; Bailey & Anderson, 1980), due to the low fuel loads of fine vegetation. These differences in fire intensity suggest that grass resprouters may be less vulnerable to heat-induced mortality than woody resprouters. We found that grass resprouters were associated with higher fire intensities than seeders, the opposite pattern to woody species (e.g. Day *et al.*, 2020; although many woody resprouting species can survive and thrive in high-intensity crown fires regimes, see Pausas & Keeley, 2017 and references within). The rapid combustion of grass fuels (Simpson *et al.*, 2016), and resultant low heat residence time, in combination with the cooler fire temperatures, means that resprouting grasses often survive after their aboveground biomass is scorched. Likewise, grass seeds can survive grassland fire temperatures (Gashaw & Michelsen, 2002), or disperse into recently burnt areas using anemochory, epizoochory or autochory (Ernst *et al.*, 1992). Indeed, evidence relating to other grass traits suggests that fire intensity is not an especially strong selection pressure on grasses (Trollope *et al.*, 2002; Uys *et al.*, 2004; Peláez *et al.*, 2013). The association between resprouting and high-intensity fire may result from the ability of resprouters to accumulate more biomass than seeders between fires (e.g. fuel loads in perennial-grass- vs annual-grass-dominated

Australian savannas: *c.* 200 vs 50–100 g m²; Lacey *et al.*, 1982), because they can produce more biomass in a period of time and also have longer intervals between fires. Resprouters may therefore be causing more intense fires rather than being better adapted to surviving them.

Drought was related to grass persistence strategies independently of fire. Studies of woody plants show that resprouters and seeders use alternative regulatory strategies with respect to water status, and are thus affected by water limitation differently (McDowell *et al.*, 2008; Pausas *et al.*, 2016). Resprouters tend to be ‘dehydration avoiders’, which tightly regulate their water status through drought, using strict stomatal control, deep roots and a high-water storage capacity. By contrast, seeders tend to be ‘dehydration tolerators’, which allow their water status to greatly decline through drought because they have shallow roots, weak stomatal control and a limited ability to store water (Clarke & Knox, 2002; Meentemeyer & Moody, 2002; Pausas & Bradstock, 2007; Keeley *et al.*, 2012). They do however avoid injury and are able to continue gas exchange through a water deficit (unlike drought avoiders), providing drought is not too intense. Long droughts are expected to be problematic for drought-avoiding resprouter species, due to the carbon deficits that arise from protracted stomatal closure, resulting in respiratory demands not being met (Plaut *et al.*, 2012). The association of grass resprouters with less intense droughts found here is consistent with these findings from woody species. Studies comparing the rooting depths and plant-water physiology of annual and perennial grasses (as proxies for seeder and resprouter species; Schenk & Jackson, 2002; Vaughn *et al.*, 2011) further support this differentiation of persistence strategy by drought regime. Therefore including drought helped us to explain some of the outliers in our dataset: whilst most seeders are associated with very frequent fire, some seeder species are associated with infrequent fire (20+ yr FRI; Fig. 1a) such as *Cenchrus prieurii* and *Vulpia microstachys*. These species are found in drought-prone environments and the reseeding strategy is probably an adaptation to recovery from extreme drought, rather than infrequent fire (Burkill, 1985).

We found no evidence of significant spatial bias in our dataset, although temporal bias cannot be excluded. If sampling of a species is temporarily constrained (such as a resprouter that initially dominates, but after successive frequent fire is outcompeted by a seeder), it may falsely be recorded as absent. Changes in fire frequency can alter the composition and abundance of resprouting grass species (Forrestel *et al.*, 2014) but how the abundance of grass seeders/resprouters relates to fire frequency remains unknown. In a study of Mediterranean shrubland communities (which include several grasses), the relative abundance of resprouters (vs seeders) increases with fire frequency, whilst the actual abundance of both resprouters and seeders decreases (Vilà-Cabrera *et al.*, 2008).

We found that the ability to resprout post-fire was not significantly associated with either C₃ or C₄ photosynthetic pathways, matching previous work using a smaller sample (Pausas & Paula, 2020). As in that work, we found that bud position was indeed related to resprouting ability, with a significantly higher

proportion of resprouting species having buds belowground in the form of rhizomes as predicted. Resprouting from the crown was the most common strategy overall in fire-prone grasses, suggesting that the tightly packed leaf bases of caespitose grasses effectively protect buds from intense heat (or that buds may be positioned below the soil surface, as in some *Andropogoneae* species) and stolons are rare, possibly because of the high vulnerability of their buds to fire (above, at, or just below the soil surface). As expected, life history was strongly related to resprouting ability, but interestingly there are exceptions with seeder perennials and disturbance-tolerant annuals. This latter group was a mixture of C_3 and C_4 species, and had crown buds (where we had data). The ecological and environmental causes of these 'exceptions' could be an interesting line of study.

Leaf traits relating to N content, but not SLA, were significantly associated with persistence strategy, with resprouters having lower leaf N contents and higher C : N ratios. Due to its low temperature of volatilisation in comparison with other macronutrients (Neary *et al.*, 1999), N is selectively lost during fires resulting in typically N-poor soils (Vitousek & Howarth, 1991; Pellegrini *et al.*, 2015). As resprouters may experience fires and low-N conditions multiple times during their lives, high N-use efficiency may be under selective pressure, resulting in their lower leaf N contents in comparison with seeders (as has also been found Mediterranean-climate woody species; Paula & Pausas, 2006; but see Vivian & Cary, 2012). However, these differences could also reflect differences in resource uptake, such that seeders and resprouters segregate along the leaf economics spectrum, with seeders adopting a more resource acquisitive strategy (associated with rapid growth, high photosynthetic rates, short leaf-life spans and low investment in leaf structure; Wright *et al.*, 2004) than resprouters. In addition, differences in drought regimes experienced by seeder and resprouter species could explain this variation in leaf N. Species growing in drier sites, like grass seeders, often show higher leaf N content (Reich *et al.*, 1999; Wright *et al.*, 2001, 2005), possibly because greater investment in N-rich photosynthetic machinery may permit higher photosynthetic rates for a given stomatal conductance (Wright *et al.*, 2001). The high C : N ratio of grass resprouters enhances their flammability, by reducing decomposition and allowing an accumulation of biomass (Simpson *et al.*, 2016). The growth and survival of these species may be enhanced by high flammability, which aids the removal of standing dead and woody biomass (Everson *et al.*, 1988; Zimmerman *et al.*, 2010).

Fire and drought regimes are changing worldwide. Climate change and human activity have greatly altered global fire, and significantly led to the suppression of fire in grassy environments (Andela *et al.*, 2017). Increasing temperatures and vapour pressure deficit means that many areas currently affected by drought will become more arid, and rainfall variability will increase (IPCC, 2014). How these multiple, changing factors will combine to impact grass species distributions is unclear (Settle *et al.*, 2014), although our results suggest grass species responses will depend upon their persistence strategy.







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Author contributions

KJS, GHT, CERL, SA and CPO designed the study. KJS, ECJ, EJF and SA generated the data. KJS, GHT and CPO analysed and interpreted the data. KJS wrote the paper with the help of all the authors.

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Data availability

Plant trait data: Species-level values for persistence strategy, photosynthetic pathway, bud position, life history and leaf trait PCA scores will be made available in Dryad entry doi: 10.5061/dryad.3bk3j9khn.

Fire and drought characteristic data: Species-level values for fire frequency and intensity, and FDI will be made available in Dryad entry doi: 10.5061/dryad.3bk3j9khn.

Phylogeny: The maximum clade credibility tree of the study species will be made available in Dryad entry doi: 10.5061/dryad.3bk3j9khn

R code: An example R code to extract and clean occurrence data, extract fire and drought characteristic data, and carry out the phylogenetic logistic regression will be made available in Dryad entry doi: 10.5061/dryad.3bk3j9khn.

References

- Aerts R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79: 439–449.
- 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.
- Archibald S, Hempson GP. 2016. Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371: 20150309.
- Archibald S, Lehmann CER, Gomez-Dans JL, Bradstock RA. 2013. Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences, USA* 110: 6442–6447.

- Archibald S, Scholes RJ, Roy DP, Roberts G, Boschetti L. 2010. Southern African fire regimes as revealed by remote sensing. *International Journal of Wildland Fire* 19: 861–878.
- Bailey AW, Anderson ML. 1980. Fire temperatures in grass, shrub and forest communities of Central Alberta. *Journal of Range Management* 33: 37–40.
- Beckage B, Gross LJ, Platt WJ. 2011. Grass feedbacks on fire stabilize savannas. *Ecological Modelling* 222: 2227–2233.
- Belcher CM, Mander L, Rein G, Jervis FX, Haworth M, Hesselbo SP, Glasspool IJ, McElwain JC. 2010. Increased fire activity at the Triassic/Jurassic boundary in Greenland due to climate-driven floral change. *Nature Geoscience* 3: 426–429.
- Bellingham PJ, Sparrow AD. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* 89: 409–416.
- Bond WJ, Midgley JJ. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution* 16: 45–51.
- Bond WJ, Van Wilgen BW. 1996. Population and community biology series, 14. Fire and plants. *Population and Community Biology Series. Fire and plants* 14: 34–50.
- Bond WJ, Woodward FI, Midgley GF. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525–537.
- Burkill HM. 1985. *The useful plants of West Tropical Africa, vol. 1. Families A-D*. London, UK: Royal Botanic Gardens at Kew.
- Chamberlain S, Barve V, Mcglinn D, Oldoni D, Desmet P, Geffert L, Ram K. 2020. rgbif: Interface to the Global Biodiversity Information Facility API. R package version 3.2.0.
- Clarke PJ. 2002. Community insularity and fire response traits: evidence from a sclerophyll archipelago. *Oecologia* 132: 582–591.
- Clarke PJ, Dorji K. 2008. Are trade-offs in plant resprouting manifested in community seed banks? *Ecology* 89: 1850–1858.
- Clarke PJ, Knox JE. 2002. Post-fire response of shrubs in the tablelands of eastern Australia: do existing models explain habitat differences? *Australian Journal of Botany* 50: 53–62.
- Clayton WD, Vorontsova MS, Harman KT, Williamson H. 2006. onwards. *GrassBase – the online world grass flora*. [WWW document] URL <http://www.kew.org/data/grasses-db.html>.
- Cook BG, Schultze-Kraft R, Pengelly BC, Taylor M, Jones C, Burkart S, Peters M. 2005. *Tropical Forages: an interactive selection tool*. Brisbane, Australia: CSIRO, DPI&F(Qld), CIAT and ILRI. [WWW document] URL <http://www.tropicalforages.info> [accessed February 2020].
- Cope T, Gray AJ, Tebbs M, Ashton P. 2009. *Grasses of the British Isles*. London, UK: Botanical Society of the British Isles.
- Cowling RM, Gallien L, Richardson DM, Ojeda F. 2018. What predicts the richness of seeder and resprouter species in fire-prone Cape fynbos: rainfall reliability or vegetation density? *Austral Ecology* 43: 614–622.
- Crowley G, Gardener M, Marrinan M. 2007. *Tropical savannas fire response database*. Darwin, Australia: Tropical Savannas Cooperative Research Centre.
- Dankwerts JE. 1993. Reserve carbon and photosynthesis: their role in regrowth of *Themeda triandra*, a widely distributed subtropical graminaceous species. *Functional Ecology* 7: 634–641.
- Dankwerts JE, Nel LO. 1989. The effect of frequency of defoliation on *Themeda triandra* in the False Thornveld of the Eastern Cape. *Journal of the Grassland Society of Southern Africa* 6: 32–36.
- Day NJ, White AL, Johnstone JF, Degré-Timmons GÉ, Cumming SG, Mack MC, Turetsky MR, Walker XJ, Baltzer JL. 2020. Fire characteristics and environmental conditions shape plant communities via regeneration strategy. *Ecography* 43: 1–11.
- Defossé GE, Robbrecht R, Bertiller MB. 1997. Seedling dynamics of *Festuca* spp. in a grassland of Patagonia, Argentina, as affected by competition, microsites, and grazing. *Journal of Range Management* 50: 73–79.
- Dwyer E, Pinnock S, Gregoire JM, Pereira JMC. 2000. Global spatial and temporal distribution of vegetation fire as determined from satellite observations. *International Journal of Remote Sensing* 21: 1289–1302.
- Ernst WHO, Veenendaal EM, Kebakile MM. 1992. Possibilities for dispersal in annual and perennial grasses in a savanna in Botswana. *Vegetatio* 102: 1–11.
- Estep MC, McKain MR, Vela Diaz D, Zhong J, Hodge JG, Hodkinson TR, Layton DJ, Malcomber ST, Pasquet R, Kellogg EA. 2014. Allopolyploidy, diversification, and the Miocene grassland expansion. *Proceedings of the National Academy of Sciences, USA* 111: 15149–15154.
- Everson CS, Everson TM, Tainton NM. 1988. Effects of intensity and height of shading on the tiller initiation of 6 grass species from the highland sourveld of natal. *South African Journal of Botany* 54: 315–318.
- Fairman TA, Bennett LT, Nitschke CR. 2019. Short-interval wildfires increase likelihood of resprouting failure in fire-tolerant trees. *Journal Environmental Management* 231: 59–65.
- Fensham RJ, Fairfax RJ, Ward DP. 2009. Drought-induced tree death in savanna. *Global Change Biology* 15: 380–387.
- Foley JC. 1957. Droughts in Australia. Review of Records from Earliest Years of Settlement to 1955. Bulletin No. 47. Bureau of Meteorology, Commonwealth of Australia, Melbourne, Australia.
- Forrestel EJ. 2015. *Biogeographic influences on grassland community structure and function*. PhD thesis, Yale University, CT, USA.
- Forrestel EJ, Donoghue MJ, Smith MD. 2014. Convergent phylogenetic and functional responses to altered fire regimes in mesic savanna grasslands of North America and South Africa. *New Phytologist* 203: 1000–1011.
- Gashaw M, Michelsen A. 2002. Influence of heat shock on seed germination of plants from regularly burnt savanna woodlands and grasslands in Ethiopia. *Plant Ecology* 159: 83–93.
- Gibson DJ. 2009. *Grasses and grassland ecology*. Oxford, UK: Oxford University Press.
- Giglio L, Loboda T, Roy D, Quayle B, Justice CO. 2009. An active-fire based burn area mapping algorithm for the MODIS sensor. *Remote Sensing of Environment* 113: 408–420.
- Gill AM. 1975. Fire and the Australian flora: a review. *Australian Forestry* 38: 4–25.
- Grady JM, Hoffmann WA. 2012. Caught in a fire trap: recurring fire creates stable size equilibria in woody resprouters. *Ecology* 93: 2052–2060.
- Grass Phylogeny Working Group II. 2012. New grass phylogeny resolves deep evolutionary relationships and discovers C₄ origins. *New Phytologist* 193: 304–312.
- Hernández DL, Hobbie SE. 2008. Effects of fire frequency on oak litter decomposition and nitrogen dynamics. *Oecologia* 158: 535–543.
- Ho LST, Ane C. 2014. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Systematic Biology* 63: 397–408.
- Hoffmann WA, Geiger EL, Gotsch SG, Rossatto DR, Silva LCR, Lau OL, Haridasan M, Franco AC. 2012. Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters* 15: 759–768.
- Ichoku C, Martins JV, Kaufman YJ, Wooster MJ, Freeborn PH, Hao WM, Baker S, Ryan CA, Nordgren BL. 2008. Laboratory investigation of fire radiative energy and smoke aerosol emissions. *Journal of Geophysical Research* 113: 1–11.
- Intergovernmental Panel on Climate Change (IPCC). 2014. Climate change 2014: synthesis report. In: Pachauri RK, and Meyer LE, Core Writing Team, *Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change*. Geneva, Switzerland: IPCC.
- Ives AR, Garland T. 2010. Phylogenetic logistic regression for binary dependent variables. *Systematic Biology* 59: 9–26.
- Jardine EC, Thomas GH, Forrestel EJ, Lehmann CER, Osborne CP. 2020. The global distribution of grass functional traits within grassy biomes. *Journal of Biogeography* 47: 553–565.
- Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and time. *Nature* 491: 444–448.
- Keeley JE. 1986. Resilience of Mediterranean shrub communities to fires. In: Dell B, Hopkins AJM, Lamont BB, eds. *Resilience in mediterranean-type ecosystems*. Dordrecht, the Netherlands: Springer, 95–112.
- Keeley JE, Bond WJ, Bradstock RA, Pausas JG, Rundel PW. 2012. *Fire in Mediterranean ecosystems: ecology, evolution and management*. Cambridge, UK: Cambridge University Press.
- Keeley JE, Fotheringham CJ. 2000. Role of fire in regeneration from seed. In: Fenner M, ed. *Seeds: the ecology of regeneration in plant communities*. Wallingford, UK: CABI, 311–330.
- Keeley JE, Keeley SC. 1977. Energy allocation patterns of resprouting and seeder species of sprouting and non-sprouting species of *Arctostaphylos* in the Californian chaparral. *American Midland Naturalist* 98: 1–10.

- Keeley JE, Parker VT, Vasey MC. 2016. Resprouting and seeding hypotheses: a test of the gap-dependent model using resprouting and obligate seeding subspecies of *Arctostaphylos*. *Plant Ecology* 217: 743–750.
- Keeley JE, Rundel PW. 2005. Fire and the Miocene expansion of C_4 grasslands. *Ecology Letters* 8: 683–690.
- Keeley JE, Syphard AD. 2016. Climate change and future fire regimes: examples from California. *Geosciences* 6: 37.
- Kluyver T. 2013. *A global perspective on the origins of agriculture: the importance of unconscious selection*. PhD thesis, University of Sheffield, UK.
- Kluyver TA, Osborne CP. 2013. Taxonome: a software package for linking biological species data. *Ecology and Evolution* 3: 1262–1265.
- Knapp AK, Medina E. 1999. Success of C_4 Photosynthesis in the field: lessons from communities dominated by C_4 plants. In: Sage RF, Monson RK, eds. *C_4 plant biology*, vol 8. San Diego, CA, USA: Academic Press, 251–283.
- Knapp AK, Seastedt TR. 1986. Detritus accumulation limits productivity of Tallgrass Prairie. *BioScience* 36: 662–668.
- Knox KJE, Morrison DA. 2005. Effects of inter-fire intervals on the reproductive output of resprouters and obligate seeders in the Proteaceae. *Austral Ecology* 30: 407–413.
- Lacey CJ, Walker J, Noble IR. 1982. Fire in Australian Tropical Savannas. In: Huntley BJ, Walker BH, eds. *Ecology of tropical savannas. Ecological studies (analysis and synthesis)*, 42. Berlin, Germany: Springer, 246–272.
- Lauenroth WK, Adler PB. 2008. Demography of perennial grassland plants: survival, life expectancy and life span. *Journal of Ecology* 96: 1023–1032.
- Le Maitre DC, Midgley JJ. 1992. Plant reproductive ecology. In: Cowling RM, ed. *The ecology of fynbos: nutrients, fire and diversity*. Cape Town, South Africa: Oxford University Press, 135–174.
- 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.
- Linder HP, Lehmann CER, Archibald S, Osborne CP, Richardson DM. 2018. Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat transformation. *Biological Reviews* 93: 1125–1144.
- Long SP. 1999. Environmental responses. In: Sage RF, Monson RK, eds. *C_4 plant biology*. San Diego, CA, USA: Academic Press, 215–249.
- Marais KE, Pratt RB, Jacobs SM, Jacobsen AL, Esler KJ. 2014. Postfire regeneration of resprouting mountain fynbos shrubs: differentiating obligate resprouters and facultative seeders. *Plant Ecology* 215: 195–208.
- McCaw WL, Smith RH, Neal JE. 1997. Prescribed burning of thinning slash in regrowth stands of karri (*Eucalyptus diversicolor*). I. Fire characteristics, fuel consumption and tree damage. *International Journal of Wildland Fire* 7: 29–40.
- McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG *et al.* 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* 178: 719–739.
- Meentemeyer RK, Moody A. 2002. Distribution of plant life history types in California chaparral: the role of topographically-determined drought severity. *Journal of Vegetation Science* 13: 67–78.
- Miles G. 2003. Fire and spear grass: a case for wet-season burning in Kakadu. *Savanna Links* 25: 6–7.
- Milton SJ, Dean WRJ. 2000. Disturbance, drought and dynamics of desert dune grassland, South Africa. *Plant Ecology* 150: 37–51.
- Moore NA, Camac JS, Morgan JW. 2019. Effects of drought and fire on resprouting capacity of 52 temperate Australian perennial native grasses. *New Phytologist* 221: 1424–1433.
- Moreira B, Tormo J, Pausas JG. 2012. To resprout or not to resprout: factors driving intraspecific variability in resprouting. *Oikos* 121: 1577–1584.
- Moreno JM, Oechel WC. 1991. Fire intensity effects on germination of shrubs and herbs in southern California chaparral. *Ecology* 72: 1993–2004.
- Moritz MA, Moody TJ, Miles LJ, Smith MM, de Valpine P. 2009. The fire frequency analysis branch of the pyrostatistics tree: sampling decisions and censoring in fire interval data. *Environmental and Ecological Statistics* 16: 271–289.
- Mouillot F, Field CB. 2005. Fire history and the global carbon budget: a $1^\circ \times 1^\circ$ fire history reconstruction for the 20th century. *Global Change Biology* 11: 398–420.
- Muggeo VMR. 2003. Estimating regression models with unknown break-points. *Statistics in Medicine* 22: 3055–3071.
- Myerscough PJ, Clarke PJ, Skelton NJ. 1995. Plant coexistence in coastal heaths: floristic patterns and species attributes. *Australian Journal of Ecology* 20: 482–493.
- Nearly DG, Klopatek CC, DeBano LF, Ffolliott PF. 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology Management* 122: 51–71.
- O'Connor TG. 1995. Transformation of a savanna grassland by drought and grazing. *African Journal of Range and Forage Science* 12: 53–60.
- Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearce W. 2018. *caper: Comparative analyses of phylogenetics and evolution in R*. R package v.1.0.1. [WWW document] URL <https://cran.r-project.org/web/packages/caper/index.html>.
- Osborne CP, Salomaa A, Kluyver TA, Visser V, Kellogg EA, Morrone O, Vorontsova MS, Clayton WD, Simpson DA. 2014. A global database of C_4 photosynthesis in grasses. *New Phytologist* 204: 441–446.
- Paula S, Arianoutsou M, Kazanis D, Tavsanoğlu Ç, Lloret F, Buhk C, Ojeda F, Luna B, Moreno J m, Rodrigo A *et al.* 2009. Fire-related traits for plant species of the Mediterranean Basin. *Ecology* 90: 1420.
- Paula S, Pausas JG. 2006. Leaf traits and resprouting ability in the Mediterranean basin. *Functional Ecology* 20: 941–994.
- Pausas JG. 2001. Resprouting vs seeding – a Mediterranean perspective. *Oikos* 94: 193–194.
- 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. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist* 204: 55–65.
- Pausas JG, Keeley JE. 2017. Epicormic resprouting in fire-prone ecosystems. *Trends in Plant Science* 22: 1008–1015.
- Pausas JG, Paula S. 2020. Grasses and fire: the importance of hiding buds. *New Phytologist* 226: 957–959.
- 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.
- Pekin BK, Wittkuhn RS, Boer MM, Macfarlane C, Grierson PF. 2011. Plant functional traits along environmental gradients in seasonally dry and fire-prone ecosystem. *Journal of Vegetation Science* 22: 1009–1020.
- Peláez DV, Andrioli RJ, Elia OR, Bontti EE, Tomas MA, Blazquez FR. 2013. Response of grass species to different fire frequencies in semi-arid rangelands of central Argentina. *Rangeland Journal* 35: 385–392.
- Pellegrini AFA, Hedin LO, Staver AC, Govender N. 2015. Fire alters ecosystem carbon and nutrients but not plant nutrient stoichiometry or composition in tropical savanna. *Ecology* 96: 1275–1285.
- Plaut JA, Yopez EA, Hill J, Pangle R, Sperry JS, Pockman WT, McDowell NG. 2012. Hydraulic limits preceding mortality in a pinon-juniper woodland under experimental drought. *Plant, Cell & Environment* 35: 1601–1617.
- R Core Team. 2019. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. [WWW document] URL <https://www.R-project.org/>.
- Ratnam J, Bond WJ, Fensham RJ, Hoffmann WA, Archibald S, Lehmann CER, Anderson MT, Higgins SI, Sankaran M. 2011. When is a 'forest' a savanna, and why does it matter? *Global Ecology and Biogeography* 20: 653–660.
- Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80: 1955–1969.
- Reich PB, Peterson DW, Wedin DA, Wragg K. 2001. Fire and vegetation effects on productivity and nitrogen cycling across a forest–grassland continuum. *Ecology* 82: 1703–1719.
- Ripley B, Visser V, Christin P-A, Archibald S, Martin T, Osborne C. 2015. Fire ecology of C_3 and C_4 grasses depends on evolutionary history and frequency of burning but not photosynthetic type. *Ecology* 96: 2679–2691.

- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MRBAYES 3.2: Efficient Bayesian phylogenetic inference and model selection across a large model space. *Systems Biology* 61: 539–542.
- Russell ML, Vermeire LT, Ganguli AC, Hendrickson JR. 2019. Fire return interval and season of fire alter bud banks. *Rangeland Ecology & Management* 73: 542–550.
- Sage RF. 2004. The evolution of C₄ photosynthesis. *New Phytologist* 161: 341–370.
- Sandersen EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G. 2002. The human footprint and the last of the wild. *BioScience* 52: 891–904.
- Scheiter S, Higgins SI, Osborne CP, Bradshaw C, Lunt D, Ripley BS, Taylor LL, Beerling DJ. 2012. Fire and fire-adapted vegetation promoted C₄ expansion in the late Miocene. *New Phytologist* 195: 653–666.
- Schenk HJ, Jackson RB. 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* 90: 480–494.
- Settele J, Scholes R, Betts R, Bunn S, Leadley P, Nepstad D, Overpeck JT, Taboada MA *et al.* 2014. Terrestrial and inland water systems. In: Field CB, Barros VR, Dokken DJ, Mach KJ, Mastrandrea MD, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, eds. *Climate change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. Contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change*. Cambridge, UK and New York, USA: Cambridge University Press, 271–359.
- Silvertown JW, Charlesworth D. 2001. *Introduction to plant population biology*. Malden, MA, USA: Blackwell Science.
- Simpson KJ, Olofsson JK, Ripley B, Osborne CP. 2019. Frequent fires prime plant developmental responses to burning. *Proceedings of the Royal Society B: Biological Sciences* 286: 20191315.
- Simpson KJ, Ripley BS, Christin P-A, Belcher CM, Lehmann CER, Thomas GH, Osborne CP. 2016. Determinants of flammability in savanna grass species. *Journal of Ecology* 104: 138–148.
- Solofondranohatra CL, Vorontsova MS, Hempson GP, Hackel J, Cable S, Vololoniaina J, Lehmann CER. 2020. Fire and grazing determined grasslands of central Madagascar represent ancient assemblages. *Proceedings of the Royal Society B: Biological Sciences* 287: 20200598.
- Thomas GH, Hartmann K, Jetz W, Joy JB, Mimoto A, Mooers AO. 2013. PASTIS: An R package to facilitate phylogenetic assembly with soft taxonomic inferences. *Methods in Ecology and Evolution* 4: 1011–10.
- Tix D, Charvat I. 2005. Aboveground biomass removal by burning and raking increases diversity in a reconstructed prairie. *Restoration Ecology* 13: 20–28.
- du Toit JCO, Van der Berg L, O'Connor TG. 2014. Fire effects on vegetation in a grassy dwarf shrubland at a site in the eastern Karoo, South Africa. *African Journal of Range and Forage Science* 32: 1–8.
- Trollope WSW, Trollope LA, Hartnett DC. 2002. Fire behaviour a key factor in the fire ecology of African grasslands and savannas. In: Viegas, ed. *Forest fire research and wildland fire safety*. Rotterdam, the Netherlands: Millpress, 1–15.
- Uys RG, Bond WJ, Everson TM. 2004. The effect of different fire regimes on plant diversity in southern African grasslands. *Biological Conservation* 118: 489–499.
- Vaughn KJ, Biel C, Clary JJ, de Herralde F, Aranda X, Evans RY, Young TP, Savé R. 2011. California perennial grasses are physiologically distinct from both Mediterranean annual and perennial grasses. *Plant and Soil* 345: 37–46.
- Verdú M. 2000. Ecological and evolutionary differences between Mediterranean seeders and resprouters. *Journal of Vegetation Science* 11: 265–268.
- Vilà M, Terradas J. 1995. Effects of competition and disturbance on the resprouting performance of the Mediterranean shrub *Erica multiflora* L. (Ericaceae). *American Journal of Botany* 82: 1241–1248.
- Vilà-Cabrera A, Saura-Mas S, Lloret F. 2008. Effects of fire frequency on species composition in a Mediterranean shrubland. *Ecoscience* 15: 519–528.
- Vitousek PM, Howarth RW. 1991. Nitrogen limitation on land and in the sea – how can it occur. *Biogeochemistry* 13: 87–115.
- 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.
- Wade DD. 1993. Thinning young loblolly-pine stands with fire. *International Journal of Wildland Fire* 3: 169–178.
- Wedin DA, Tilman D. 1990. Species effects on nitrogen cycling – a test with perennial grasses. *Oecologia* 84: 433–441.
- Wragg PD, Mielke T, Tilman D. 2018. Forbs, grasses, and grassland fire behaviour. *Journal of Ecology* 106: 1983–2001.
- Wright IJ, Reich PB, Cornelissen JHC, Falster DS, Garnier E, Hikosaka K, Lamont BB, Lee W, Oleksyn J, Osada N *et al.* 2005. Assessing the generality of global leaf trait relationships. *New Phytologist* 166: 485–496.
- Wright IJ, Reich PB, Westoby M. 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology* 15: 423–434.
- 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.
- Zedler PH. 1995. Are some plants born to burn? *Trends in Ecology & Evolution* 10: 393–395.
- Zimmermann J, Higgins SI, Grimm V, Hoffmann J, Linstädter A. 2010. Grass mortality in semi-arid savanna: the role of fire, competition and self-shading. *Perspectives in Plant Ecology, Evolution and Systematics* 12: 1–8.
- 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.

Supporting Information

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

Fig. S1 Proportion of grass species occurrence records that fell within burnt pixels against species frequency.

Fig. S2 Occurrence data for 734 fire-prone grasses.

Fig. S3 Principal components analysis biplot for leaf economic spectrum traits.

Fig. S4 The relationships between fire characteristics and drought.

Table S1 Number of occurrence records and species represented remaining after each cleaning step.

Table S2 Sample sizes for analyses representing the overlap of species data for each named trait with data on resprouting ability.

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