

RESEARCH ARTICLE

Fire As a Dynamic Ecological and Evolutionary Force

A three-dimensional approach to general plant fire syndromes

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Abstract

1. Plant fire syndromes are usually defined as combinations of fire response traits, the most common being resprouting (R) and seeding (S). Plant flammability (F), on the other hand, refers to a plant's effects on communities and ecosystems. Despite its important ecological and evolutionary implications, F has rarely been considered to define plant fire syndromes and, if so, usually separated from response syndromes.
2. We propose a three-dimensional model that combines R, S and F, encapsulating both plant response to fire regimes and the capacity to promote them. Each axis is divided into three possible standardized categories, reflecting low, medium and high values of each variable, with a total of 27 possible combinations of R, S and F.
3. We hypothesized that different fire histories should be reflected in the position of species within the three-dimensional space, and that this should help assess the importance of fire as an evolutionary force in determining R-S-F syndromes.
4. To illustrate our approach, we compiled information on the fire syndromes of 24 dominant species of different growth forms from the Chaco seasonally dry forest of central Argentina, and we compared them to 33 species from different Mediterranean-type climate ecosystems (MTCEs) of the world.
5. Chaco and MTCEs species differed in the range (7 syndromes vs. 13 syndromes, respectively) and proportion of extreme syndromes (i.e. species with extreme values of R, S and/or F) representing 29% of species in the Chaco vs. 45% in the MTCEs.
6. In addition, we explored the patterns of R, S and F of 4032 species from seven regions with contrasting fire histories, and found significantly higher frequencies of extreme values (predominantly high) of all three variables in MTCEs compared to the other regions, where intermediate and low values predominated, broadly supporting our general hypothesis.
7. The proposed three-dimensional approach should help standardize comparisons of fire syndromes across taxa, growth forms and regions with different fire histories. This will contribute to the understanding of the role of fire in the evolution of plant traits and assist vegetation modelling in the face of changes in fire regimes.

KEYWORDS

fire ecology, fire regimes, fire response and effect traits, fire-adaptive traits, plant fire syndromes, plant flammability, post-fire resprouting, post-fire seeding

1 | INTRODUCTION

Fire has been part of many terrestrial systems for millions of years (Bond & Scott, 2010; Bowman et al., 2009; Pausas & Keeley, 2009). In the last 20 years, in the context of climate change (IPCC, 2022), there has been a renewed interest in its role as an ecological and evolutionary factor (Lamont et al., 2019a; Lawes et al., 2016). One important focus in this pursuit has been the identification of phenotypic traits recurrently associated with fire in different floras, either in isolation or combined in trait syndromes or strategies. This has been aided by the dramatic expansion of the research field of plant functional traits (Díaz & Cabido, 2001; Lavorel & Garnier, 2002; Violle et al., 2007), and there is now a rich literature on fire-related traits, including, for example, flowering, retention of dead branches (Fidelis & Zironi, 2021; He et al., 2011; Schwilk, 2003), bark thickness, reserve structures, bud position (Paula et al., 2016; Pausas, 2015a; Pausas & Paula, 2019), plant architecture and ramification (Osborne et al., 2018; Schwilk, 2003; Staver et al., 2012) and seed characteristics, such as seed dispersal, dormancy and storage (Lamont et al., 2019b; Pausas et al., 2012).

Plant syndromes in relation to fire have been predominately defined as recurrent combinations of traits that confer the plant the ability to maintain or increase its fitness in the face of fire; in other words, they pertain a plant's specific *response* function sensu (Díaz et al., 2013). One of the most used classifications distinguishes two fire response syndromes: resprouting (R) and seeding (S) (Clarke et al., 2015; Pausas et al., 2004; Pausas & Keeley, 2014), which, respectively, rely on the regeneration from vegetative tissues that survived fire, or on the recruitment of new individuals from seeds. Each of these functions (resprout or regenerate from seed following a fire) is underpinned by multiple traits. Much less common have been studies of traits or trait syndromes that determine a plant's flammability, and thus its individual contribution to a landscape's fire regime (Pausas et al., 2017; Schwilk, 2015). Flammability (F)—broadly defined as the propensity of living or dead plant material to ignite and sustain combustion, also determined by multiple traits, is a specific *effect* function sensu (Díaz et al., 2013) being paid increasing attention (Cui, Paterson, Wyse, et al., 2020; Moreira & Pausas, 2012; Pausas et al., 2017; Poulos et al., 2018; Prior et al., 2018; Schwilk, 2015).

Fire-specific response and effect functions in combination define what a phenotype 'does' both to a fire regime and in response to it. This considering them together has obvious relevance for current discussions within the niche construction (Laland et al., 2014) and contemporary evolution (Hendry et al., 2018) frameworks, that is, plant phenotypes affecting their biotic and abiotic context and at the same time being subject to selective pressures as a result. This is not free of debate, however; the view that flammability has adaptive value, susceptible to directional selection under certain fire regimes, increasing plant fitness (Bond & Midgley, 1995), has been questioned by some (Midgley, 2013), leading to ongoing debates on whether flammability is a fire-selected or an emergent function (Bowman et al., 2014). Beyond these somewhat specialized debates, the practical relevance of flammability at the community and ecosystem

levels, and the importance of considering it in conjunction with tolerance to fire to predict vegetation responses, is undeniable. Yet, flammability has rarely been considered to define fire syndromes, and if so, usually separated from response syndromes. This hampers global modelling efforts of vegetation responses to, and effects on changing fires regimes (Harrison et al., 2021).

Here, we aim to contribute to these efforts by presenting a three-dimensional model that explicitly combines fire-related specific response (resprouting, R, and seeding, S) and effect (flammability, F) functions, allowing the detection of fire syndromes. We claim that these simple and integrated fire syndromes are applicable across floras and growth forms and therefore can contribute to ongoing global efforts in comparative ecology. Each of these three major axes, each representing a specific function sensu (Díaz et al., 2013), is divided into three possible standardized categories, which reflect low, medium and high values of each variable, with a total of 27 possible combinations of R, S and F (Appendix S1). We illustrate our approach with a case study that includes a quantitative assessment of R, S and F for 24 dominant species of different growth forms common in the Chaco seasonally dry forest of central Argentina (Appendix S2). We then explore how the proposed model applies to other regions with contrasting historical fire regimes.

We hypothesized that environmental filters at the ecosystem level, specifically fire, limit trait space occupation (Pausas & Verdú, 2008). Therefore, the species occurring in a given region should not include all possible combinations of R, S and F values, but rather reflect its fire history. Furthermore, the frequency distribution of fire syndromes within the proposed three-dimensional space should vary among regions with different fire histories (Pausas et al., 2006; Pausas & Verdú, 2005). By assessing the frequency distribution of the categorical values, the proposed three-dimensional approach should allow simple standardized assessment and comparisons of fire syndromes within and among regions with different floras and fire histories.

1.1 | The challenge of comparing fire syndromes

Comparing fire syndromes across regions can be challenging, since there is no universal way of measuring R, S and F. This is because these axes (specific functions) depend on the combination of many underlying functional traits (Bowman et al., 2014; Pausas et al., 2017; Pausas & Keeley, 2014; Poulos et al., 2018), which, in turn, are differentially influenced by multiple factors, fire being a prominent, but not the only one. In addition, it is not uncommon for these traits to show a phylogenetic signal, that is a tendency to be strongly associated or confined to particular clades (Silva & Batalha, 2010; Verdú & Pausas, 2007). Bearing these limitations in mind, one can still consider widely used variables that have a similar ecological interpretation across floras. For example, resprouting has been measured in various ways, from simple estimations of post-disturbance survival percentage at the species level (Pérez-Harguindeguy et al., 2013), to more complex quantitative measures, including ratio of pre- and

post-fire height and basal diameter, number and length of resprouts, post-fire canopy volume and/or plant biomass, among others (e.g. Cruz et al., 2003; Fulbright et al., 2011; Gittins et al., 2011; Gurvich et al., 2005; Moreira et al., 2012; Zizka et al., 2014). Similarly, post-fire seeding regeneration (S axis) can refer to fire-induced released of canopy-stored seeds (Keeley & Fotheringham, 2000; Lamont et al., 2019b) and/or germination capacity in response to fire-related cues (e.g. heat shock, smoke, charred wood and ash; Gorgone-Barbosa et al., 2020; Keeley & Fotheringham, 2000; Moreira et al., 2010). Moreover, examples of flammability measures include, for example, the amount of heat released during combustion, the rate of fire spread, the maximum temperature reached during plant combustion and the amount of biomass consumed (Madrigal et al., 2012; Scarff & Westoby, 2006; Weise et al., 2005).

Fire syndromes resulting from such variables are easier to interpret for R and S, since higher values of any selected variable would usually correlate with higher fitness of plants in the face of fire. In contrast, traits that purportedly influence flammability, while key for ecosystem functioning, are not so obviously related to the fitness of individuals (Bowman et al., 2014). This is particularly the case in regions where fire is not as predictable and/or prevalent in evolutionary terms, where flammability may not be a fire-adaptive trait as it has been described in fire-prone regions with recurring fires (Pausas et al., 2017). A key point to interpret the role of F is how it combines with R and S, and how, in turn, the resulting syndromes are affected by the environmental context of each region, particularly the prevailing fire regime (Keeley et al., 2011; Poulos et al., 2018).

Another key challenge in comparing and modelling fire syndromes across regions is how to simplify the myriad traits that determine their ability to respond to fire, as well as their flammability (Archibald et al., 2018; Poulos et al., 2018), allowing the different fire syndromes to be related to the patterns of fire activity in different regions. These links are pivotal for understanding how particular fire regimes can favour or limit the probabilities of occurrence and dominance of certain syndromes over others (Clarke et al., 2014; Lloret et al., 2005; McLauchlan et al., 2020; Pausas & Verdú, 2008; Rowe, 1983). In ecosystems with a long evolutionary history of recurrent stand-replacing fires, such as Mediterranean-type climate ecosystems (MTCEs), there is a trade-off in the frequency distribution of post-fire regeneration syndromes (i.e. resprouting and seeding), whereby the presence of one syndrome may limit the acquisition of the other (Clarke et al., 2015; Pausas & Keeley, 2014). Therefore, in these regions, a dichotomous measure of presence/absence of resprouting and seeding has proven useful for vegetation prediction and modelling (Loehle, 2000; Noble & Slatyer, 1980; Vesik et al., 2004). Furthermore, in combination with these regeneration strategies, there is evidence that many species have developed characteristics that make them more flammable, increasing the fitness of individual plants (Cowan & Ackerly, 2010; He et al., 2011; Pausas et al., 2012; Pausas et al., 2017; Saura-Mas et al., 2010). Therefore, it is reasonable to expect syndromes combining high values of either R and/or S coupled with high values of F to be comparatively common in these regions (Appendix S1).

There are other regions where fires are not uncommon at present, but whose evolutionary history of fire may not be as long and intense as in MTCEs. A case in point is the Chaco of central-western Argentina. Although Chaco forests have been subjected to fire for centuries to millennia, mainly due to hunting practices of indigenous peoples (Morello & Saravia Toledo, 1959) and also possibly to natural fires produced by lightning during spring/summer storms, there is no evidence of recurring fire as a strong natural selection pressure over longer evolutionary time. However, the marked seasonality and vegetation characteristics of the region (hot, dry weather in early spring, when the vegetation is still dormant, with a high proportion of standing-dead biomass with low water content) make it highly fire-prone. Human-caused fires have been increasing in frequency throughout the region, mainly due to its use as a management tool (Casillo et al., 2006; Kunst et al., 2000, 2015) and the expansion of agriculture and infrastructure (Argañaraz et al., 2015).

Previous studies in the Chaco show that most of the dominant species can tolerate fire of low-to-medium intensity, mainly through resprouting (Bravo et al., 2014; Gurvich et al., 2005; Jaureguiberry et al., 2020; Torres et al., 2014). In addition, seeds of many species can tolerate heat shocks of medium intensity, and some are even stimulated by them (Arcamone & Jaureguiberry, 2018; Ibañez Moro et al., 2021; Jaureguiberry & Díaz, 2015). Such fire tolerance could have evolved as a consequence of the evolutionary pressure exerted by other factors, notably herbivory by large vertebrates (resprouting) and seasonal drought and/or endozoochory (hard seed coats; Charles-Dominique et al., 2016; Dantas & Pausas, 2022; Osborne et al., 2018; Santana et al., 2020), both with long presence in the Chaco (Bucher, 1987; Díaz et al., 1999, 2007). Flammability in the region is largely associated with growth form, ranging from highly flammable grasses to less flammable shrubs and trees (Jaureguiberry et al., 2011; Santacruz-García et al., 2019). Among woody species however, flammability can vary, for example, species with low water content and/or intricate branching patterns are often more flammable (Jaureguiberry, 2012; Ana Carolina Santacruz-García et al., 2019). Furthermore, secondary compounds arguably generated as a strategy to avoid herbivory could also influence flammability (Alam et al., 2019; Ormeño et al., 2009; Owens et al., 1998) and this, in turn, affects resprouting ability (Santacruz-García et al., 2021). However, there is no empirical evidence in the Chaco unequivocally linking the presence of specialized flammability traits with post-fire regeneration strategies. Therefore, although some species in this region could have developed extreme syndromes, the most common should be the syndromes that combine intermediate values of R, S and F.

Finally, in regions where fire has been historically rare, such as tropical and temperate humid forests, species are likely to be sensitive to fire. However, human-induced changes in climate and land management have made fire a more prevalent factor in these ecosystems over recent decades, urging for their inclusion in fire modelling (Prior & Bowman, 2020). Most of species in these regions have very poor ability to regenerate after a fire, and generally very

low flammability (Hoffmann et al., 2012; Murphy & Bowman, 2012; Pivello, 2011). Therefore, syndromes combining low values of R and S coupled with low values of F should be comparatively more common in these regions. Some species, however, may be sensitive to fire but highly flammable, as is the case of some that avoid fire in regions with infrequent, large stand-replacing fires. For example, *Picea engelmannii* and *Abies lasiocarpa* can be highly flammable, but they avoid fire by growing in fire refugia (Harvey et al., 2016).

2 | MATERIALS AND METHODS

2.1 | Illustrating the proposed model

We focused on 24 dominant species of the seasonally dry Chaco forest of central Argentina (hereafter Chaco), belonging to different growth forms: one forb, six grasses, five shrubs, five trees and seven tree/shrubs (Appendix S2). The flammability, post-fire resprouting and germination capacity after heat shock treatments of these species are known from previous studies by Jaureguiberry (2012), Jaureguiberry et al. (2011, 2020) and Jaureguiberry and Díaz (2015).

Flammability was measured with a specially designed device, which allowed measuring plant portions of up to 70cm long, conserving their architecture. Original measurements included: burning rate, maximum temperature and biomass consumed (see details in Jaureguiberry et al., 2011). However, with the purpose of comparing Chaco species with species from other regions, and considering that burning rate is rarely reported, data of the two latter variables were collected from studies that followed Jaureguiberry et al. (2011). A PCA followed by cluster analysis allowed classifying species into the following categories: 1 = low flammability; 2 = moderate flammability and 3 = high flammability (Appendix S2). Because the dataset included a large number of species and a broad range of growth forms,

this standardization is much more robust than an analysis using classifications from individual studies.

Resprouting capacity was measured in burned sites following the first growing season after the fire (March through June). Although the original study included different quantitative measures of resprouting capacity (e.g. number and diameter of resprouts), in the present conceptual model we focused on the survival percentage recorded for each species (Jaureguiberry et al., 2020) as a proxy for resprouting capacity (Pérez-Harguindeguy et al., 2013). This was because this variable is widely used in fire studies and has a standard scale and range of values, therefore facilitating comparisons between species from different regions. Survival percentages were assigned to one of three possible intervals: 0%–33%; 34%–66% and from 67% to 100%, and then each interval was assigned the value 1, 2 or 3, respectively, indicating low, medium and high values of resprouting capacity.

Germination response to heat shock was measured by subjecting the seeds to dry heat treatments of 70°C for 1h, 100°C for 5 min and 120°C for 5 min, and comparing the germination with a control (i.e. no heat). This allowed classifying the species as heat sensitive (germination lower than the control), heat tolerant (germination similar to the control) or heat stimulated (germination higher than the control; see details in Jaureguiberry & Díaz, 2015). Each of these categories was, respectively, assigned a value of 1, 2 or 3.

Therefore, all data on the three studied axes were standardized to three possible categorical ordinal values: 1, 2 or 3, indicating low, medium and high values of each trait, respectively. Each studied species was then assigned the corresponding ordinal value for each trait (Appendix S2).

We built a three-dimensional figure containing the original data (Figure S1), from which we derived a three-dimensional 'Rubik's Cube' model featuring standardized values of each variable for the 24 studied species (Figure 1a). This figure allows a simple

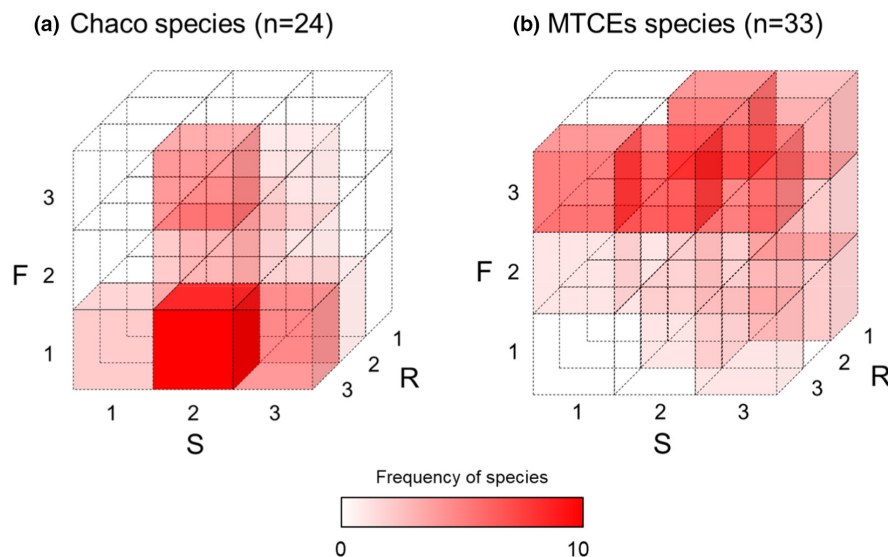


FIGURE 1 Comparison of frequencies of fire syndromes based on standardized categorical values (see text for details) between (a) 24 species from the Chaco region and (b) 33 species from Mediterranean-Type Climate Ecosystems (MTCEs) (Mediterranean Basin, $n = 24$; California, $n = 5$; Southern Australia, $n = 3$; and Southern South Africa, $n = 1$). See list of species in Appendix S4. Each square within the cubes represents one of the 27 possible syndromes (see Appendix S1). The intensity of the colour is proportional to the frequency of species within a given syndrome.

visualization of the pattern and frequency of the fire syndromes of the Chaco region.

2.2 | How do Chaco patterns compare to other regions?

2.2.1 | Cobbling together an illustrative dataset

One of the main aims of the proposed model is to explore the distribution patterns of fire syndromes across different regions of the world. To that end, and for illustrative purposes, we performed an unstructured literature review of fire-related traits relevant to our model. Comparable data for a large number of species across regions are surprisingly scarce, mainly due to the multiple methodologies used for measuring R, S and F in different studies. Whenever possible, we searched for the same or similar variables to those used for the Chaco, namely survival percentage, germination response to heat shock and variables related to flammability (e.g. maximum temperature, biomass consumed and burning rate), as proxies for R, S and F, respectively. Importantly, to be consistent to the current most accepted definition of functional traits (Garnier et al., 2016; Pérez-Harguindeguy et al., 2013; Violle et al., 2007), we focused on measures that can be carried out at the individual level, and reflect the behaviour of a particular individual with respect to fire, as opposed to measures that reflect demographic responses at the population level, such as seedling density or seedling-to-parent ratio.

Classification into different R intervals was based either on quantitative data on survival percentage, or on qualitative information from major databases. For example, resprouting capacity reported as 'low' or 'high' (e.g. Tavşanoğlu & Pausas, 2018) were assigned R values of 1 and 3, respectively. Though we acknowledge that this binary classification may bring some bias, it applies to only half of the R data for this region. Furthermore, we tested the proportion of species in each categorical value of R reported here (Table 4) vs. a subset of species for which quantitative data (i.e. survival percentage) was available ($N = 53$ species) (Tavşanoğlu & Pausas, 2018) and they showed a very similar pattern (Table S1). For Southern Australian species, those reported as 'fire killed' and 'weak resprouting' (Falster et al., 2021) were assigned a value of 1, while those reported as 'intermediate resprouting' and 'strong resprouting' were assigned values of 2 and 3, respectively. The vast majority of records in our dataset refer to resprouting of individuals one growing season after the fire. Flammability data for most of the species were based on quantitative measurements that have used the method of Jaureguiberry et al. (2011), which was standardized following the criteria explained earlier. However, for some species, classification was based either on other quantitative measures that followed other methodologies (e.g. measures based on plant parts such as twigs or leaves, or fuel beds) or on qualitative classifications reported in the literature (most of which are, in turn, based on reviews of quantitative measurements from previous studies). We standardized the original data collected for the other regions (Appendix S3) following the same approach as

for the Chaco. We then built contingency tables to analyse each region and to compare between regions (Tables 3 and 4).

Our review resulted in 5377 non-redundant records (i.e. values recorded from independent sources; pertaining any of the three variables). For several species, there was more than one record relevant to one or more of the three variables. In such cases, for the variables R and S, we calculated an average value and we rounded up to the closest standardized categorical value (i.e. 1, 2 or 3). For the variable F, we gave priority to values obtained from the cluster analysis of studies following Jaureguiberry et al. (2011) described in a previous section, and we used average values in the few cases when there were different values from other sources. Therefore, each species in the final dataset was given a unique value for each of the three variables (Table 1; Appendix S3). Species reported as exotic in the original sources were not considered; however, a comprehensive status check of the database was beyond the scope of this study, and there could be a few species that are not strictly native to their assigned regions. The curated total number of records was 4411 (records for R, S and F, were 3399, 678 and 334, respectively) for 4032 species (many species had information on two variables, and very few on the three variables). The database covers a wide taxonomic range, encompassing species from approximately 1250 genera and 180 botanical families, belonging to 10 different growth forms, and coming from seven major regions with a wide range of evolutionary histories of fire, from long and intense (MTCEs) to very recent (New Zealand; Table 1).

2.3 | Completing fires syndromes

Data for all three variables were available for a very limited number of species. With the purpose of completing the fire syndromes of as many species as possible to make cross-regional comparisons more robust, for some species we used traits other than response to

TABLE 1 Summary of records and total number of species obtained through an unstructured literature review for the variables resprouting (R), seeding (S) and flammability (F) for species from different regions with contrasting fire histories. Hyphen indicates lack of data

Region	Records			Total records	Total species
	R	S	F		
California	42	61	7	110	83
Mediterranean Basin	149	303	65	517	414
Southern Australia	2990	142	25	3157	3049
South Africa	69	48	137	254	231
Chaco	36	37	35	108	52
Cerrado	65	87	15	167	121
New Zealand	48	-	50	98	82
Total	3399	678	334	4411	4032

TABLE 2 Frequency of different fire syndromes for 24 species from the Chaco region and 33 species from Mediterranean-type climate ecosystems (MTCEs), obtained from an unstructured literature review, with the corresponding Chi-Square test. Extreme syndromes (i.e. those occupying the corners of the cube in [Figure 1](#)) are highlighted in bold. Full list of species and syndromes are available in [Appendix S4](#).

Fire syndrome	Syndrome number	Chaco	MTCEs	Total	Statistic	Value	df	p
R1-S2-F2	5	0	1	1	Chi-Square Pearson	35.67	15	0.002
R1-S2-F3	6	0	5	5	Chi-Square MV-G2	47.67	15	<0.0001
R1-S3-F1	7	0	2	2	Conting.Coef.Cramer	0.56		
R1-S3-F2	8	0	2	2	Conting.Coef.Pearson	0.62		
R1-S3-F3	9	0	3	3				
R2-S2-F1	13	0	1	1				
R2-S3-F1	16	1	0	1				
R3-S1-F1	19	2	0	2				
R3-S1-F2	20	0	1	1				
R3-S1-F3	21	0	5	5				
R3-S2-F1	22	10	0	10				
R3-S2-F2	23	2	1	3				
R3-S2-F3	24	4	6	10				
R3-S3-F1	25	4	1	5				
R3-S3-F2	26	0	1	1				
R3-S3-F3	27	1	4	5				
Total		24	33	57				

TABLE 3 Frequency of different fire syndromes for 24 species from the Chaco region belonging to two growth forms, with the corresponding Chi-Square test. Extreme syndromes (i.e. those occupying the corners of the cube in [Figure 1a](#)) are highlighted in bold.

Fire syndrome	Syndrome number	Herbaceous	Woody	Total	Statistic	Value	df	p
R2-S3-F1	16	0	1	1	Chi-Square Pearson	21.33	6	0.0016
R3-S1-F1	19	0	2	2	Chi-Square MV-G2	24.22	6	0.0005
R3-S2-F1	22	0	10	10	Conting.Coef.Cramer	0.67		
R3-S2-F2	23	1	1	2	Conting.Coef.Pearson	0.69		
R3-S2-F3	24	4	0	4				
R3-S3-F1	25	0	4	4				
R3-S3-F3	27	1	0	1				
Total		6	18	24				

TABLE 4 Contingency tables of relative frequencies (displayed as a gradient of shades of grey based on percentage) of standardized ordinal values of resprouting (R), seeding (S) and flammability (F) for plant species from different regions. Chi-Square tests showed significant differences in the frequencies between regions for the three variables ($p < 0.0001$ in all cases). 'Chaco' refers to Argentine south-western Chaco region. Empty cells indicate lack of data. See [Appendix S6](#) for absolute frequencies and detailed results of Chi-Square tests.

Region	R			S			F		
	1	2	3	1	2	3	1	2	3
California	28	5	67	10	47	43	14	14	72
Mediterranean Basin	27	5	68	5	62	33	12	37	51
Southern Australia	42	6	52	8	44	48	0	8	92
Southern South Africa	6	27	67	4	32	64	20	22	58
Cerrado	6	23	71	2	85	13	53	47	0
Chaco	0	3	97	3	64	33	54	17	29
New Zealand	64	17	19				46	44	10

heat-shock as a proxy for axis S, namely post-fire 'Seedling-to-parent ratio' and 'Fire-cued seeding'. We acknowledge this may pose some limitations to the interpretation of patterns; but overall, all the variables used for this axis (i.e. germination after heat shock, seedling-to-parent ratio and fire-cued seeding) can be similarly interpreted in terms of the effect of fire on plant fitness so that higher or lower values of the variables correlate with higher or lower fitness of individuals in the face of fire. We were able to complete 38 species (which add up to the 24 previously reported for the Chaco, totalizing 62 species with information on all three axes; Appendix S4). Of these 38 species, five belonged to the Cerrado, 24 belonged to Mediterranean Basin, five to California, three to Southern Australia and one to South Africa. For comparative purposes, we grouped species from the latter four regions into the 'grand region' MTCEs. Although these regions are heterogeneous and have ecological differences between them, they present similar fire regimes and many convergences in terms of the characteristics of their floras in relation to fire (Keeley et al., 2012; Keeley & Bond, 1997), justifying their grouping for the broad-scale comparisons made here. We built three-dimensional figures of standardized data to visually explore and compare spatial patterns of fire syndromes between the Chaco region and MTCEs (Figure 1). Cerrado species were not included in the comparison.

3 | RESULTS

3.1 | Fire syndromes in the Chaco

Among the 24 species from the Chaco, we identified seven fire syndromes out of a theoretical total of 27 syndromes (Table 2). The most frequent was syndrome 22 (R3-S2-F1), that is, high resprouting capacity, heat-tolerant seeds and low flammability, which was displayed by 10 species (42%) (Table 2, Figure 1a). Seven species (29%) showed extreme fire syndromes (i.e. one of the eight possible syndromes in the corners of the cubic model in Figure 1). Four corresponded to syndrome 25 (R3-S3-F1), namely *Celtis ehrenbergiana*, *Parkinsonia praecox*, *Maytenus spinosa* and *Prosopis flexuosa*. One grass species, namely *Trichloris* spp. combined high values of all three variables (syndrome 27; R3-S3-F3); while two species, *Castela coccinea* and *Sarcomphalus mistol*, combined high R with low S and F (syndrome 19; R3-S1-F1). The remaining seven species (29%) featured different combinations of high, intermediate or low values of R, S and F (Table 2). Interestingly, there was no combination of extreme low values of R and S simultaneously, nor combined with low F.

Furthermore, the syndromes differed between herbaceous and woody species (Table 3). With the exception of *Larrea divaricata* (woody) and *Justicia squarrosa* (herbaceous), both displaying syndrome 23 (R3-S2-F1), syndromes did not overlap between growth forms (Table 3; Appendix S2). Herbs mostly combined high values of F and R (syndromes 24 and 27), while woody species had low F mostly combined with high R and intermediate or high S (syndromes 22 and 23).

3.2 | Cross-regional patterns of fire syndromes

The 33 species from MTCEs with complete information encompass 13 different fire syndromes (Table 2a; Appendix S5). The most frequent syndromes were 24 (R3-S2-F3), recorded in 6 species (18%), syndrome 6 (R1-S2-F3), and syndrome 21 (R3-S1-F3), recorded in 5 species each (15%). The frequency of syndromes differed significantly from those observed in the Chaco species (Figure 1; Table 2). Extreme syndromes represented 45% of species in the MTCEs, whereas in the Chaco they represented only 29% (Appendix S5).

Furthermore, analyses of frequencies of R, S and F in the full dataset showed significant differences between regions for all three axes (Table 4). Species from Southern Australia, California and the Mediterranean Basin had predominantly either high or low values of R, with very few species showing intermediate value, supporting the validity of the classic seeder vs resprouter classification used in these regions. Although the Chaco and Cerrado both showed a predominance of high values of R, they differed significantly overall (Chi-square = 9.63; $p = 0.0081$), since several species from the Cerrado showed intermediate values, and some had low values (Table 4), while Chaco species did not show low values, and only one species had intermediate value. Conversely, most of species from New Zealand had low R values, with only a few showing intermediate or high values (Table 4). Regarding the S axis, high values predominated in South Africa and Southern Australia. Intermediate values were the most frequent in the remaining regions, but the proportions differed. While in California, high values were almost as frequent as intermediate ones, and some species had low values, in the Cerrado very few species had either high or low values. The Mediterranean Basin and Chaco had similar proportions of species in the three categories, with almost two-thirds in the intermediate values, one-third in the high category and only few species with low values. Finally, the F-axis showed a clear predominance of high values in MTCEs, while low values and intermediate to a lesser extent, predominated in Cerrado, Chaco and New Zealand (Table 4).

4 | DISCUSSION

4.1 | A contribution to modelling in fire ecology

The proposed model, based on resprouting, germination and flammability, is a step forward with respect to previous classification because it incorporates not only specific response, but also specific effect functions of plants with respect to fire. This model is of special interest in ecosystems prone to disturbances (such as fire, herbivory and extreme drought), where the stability of the system depends on feedback loops involving not only the response of plants but also the marked influence of plants on their own environment through effect traits (Wigley et al., 2020). In such ecosystems, R, S and F are more likely to be correlated, as opposed to them being independent. Previous studies focusing on a binary perspective (i.e.

presence or absence) of resprouting and seeding have highlighted how selective pressures under predictable fire regimes have influenced the frequency of these persistence syndromes, particularly in Mediterranean regions (Pausas et al., 2004, 2006; Pausas & Verdú, 2005), and how, in turn, regeneration strategies could be related to plant flammability, increasing plant fitness (Bond & Midgley, 1995; Kerr et al., 1999; Schwilk & Kerr, 2002). Although there is experimental evidence supporting these theoretical models at different levels (Burger & Bond, 2015; Cowan & Ackerly, 2010; He et al., 2011; Pausas et al., 2012; Poulos et al., 2018; Saura-Mas et al., 2010; Scarff & Westoby, 2006; Schwilk, 2003; Schwilk & Ackerly, 2001), testing how R, S and F relate to each other across regions has remained a pending issue. Our model is an ideal tool to test this hypothesis at a broad scale, allowing the comparison of fire syndromes of a large number of species from regions with markedly different floras and contrasting disturbance regimes, particularly fire.

The illustrative database compiled here covers a wide range of families and growth forms, including dominant species from all the studied regions, therefore making it sufficiently robust to reflect the general patterns of their respective floras. We recognize, however, that the expansion of this database, including more species and regions, will help produce a more comprehensive picture, and will allow exploring patterns at finer scales. Furthermore, given that key aspects of fire regimes, such as fire intensity, may influence plant response and that such response may be phylogenetically determined, the inclusion of phylogenetic analyses in future studies will also bring further insights to the patterns presented here.

While acknowledging that they are simplifications of more complex underlying processes, and that they involve trade-offs between simplicity and scope, models are essential for interpreting patterns at a broad ecological scale. Our model represents a greater synthesis effort than previous works in three prominent ways: first, by including response an effect axes, each with three levels, it is more sensitive to capture variations of fire syndromes across regions with contrasting fire regimes, broadening the scope of previous models (e.g. Pausas et al., 2004, 2017; Pausas & Lavorel, 2003; Schwilk, 2015). Second, it is not limited to particular growth forms or taxa (e.g. Archibald et al., 2019; Pausas, 2015b). Third, we focused on the performance of the plant in relation to the three proposed axes or functions, regardless of the underlying traits that determine them.

Our approach does not necessarily intend to replace pre-existing classifications or models. Rather, it can enrich them or make them more applicable to specific regions. We mention two examples: First, it could help improve models addressing relationships between fire frequency, regeneration strategies and environmental gradients (e.g. precipitation gradients) that use binary classifications of R and S (Harrison et al., 2021). This is particularly relevant in regions where a binary classification of fire syndromes does not adequately describe the dominant strategies. For example, in the Chaco, where the vast majority of species resprout after fire, a categorical approach like the one proposed here, which better captures the R and S gradient, would capture changes in plants' strategies that tend to be

missed by models based on binary classifications. Second, it could help refine pre-existing vegetation classifications with respect to fire. Specifically, Archibald et al. (2013) have proposed five major types of fire regimes or *pyromes* at a global level, showing that the spatial dominance of each pyrome is not always correlated with the type of biome and/or the climate. These pyromes are defined on a very recent timeframe, and therefore do not necessarily reflect ancient fire patterns that gave rise to fire syndromes in today's species. However, exploring fire syndromes defined with our approach through the lens of Archibald's model could tell us, for example, if particular fire syndromes are more frequent in certain pyromes, or to what degree these are independent. Although a full answer to these questions is beyond the scope of this study, a general overview at the complete syndromes obtained here (Table 2) in relation to biomes and pyromes shows that in *Mediterranean vegetation* (sensu Archibald et al., 2013), infrequent fires of high and medium intensity (i.e. pyromes RIL and RCS), compatible with crown fires characteristic of these ecosystems, are more prominent than in other biomes relevant to this study, such as *Tropical grasslands and shrublands*. This is consistent with the higher frequency of extreme fire syndromes observed here for MTCEs. However, other biomes of relevance to this study, such as *Xeric vegetation* and *Temperate grasslands and shrublands* also have considerable presence of RIC and RCS pyromes. Moreover, the pyrome ICS (see Table 1 and fig. 2 in Archibald et al., 2013), considered by the authors as largely defined by human influence on fire regimes globally, is pervasive across most vegetation types, making it difficult to establish clear patterns between pyromes and fire syndromes at this scale. Having spatially explicit data for the syndromes proposed here, and a higher spatial resolution for pyromes, would be key to make a stronger link between these two models in the future.

4.2 | Ecological and evolutionary implications

The fire syndromes reported here represent an 'average' of the performance of each species facing a given fire regime in its natural distribution area, on which the consulted bibliography focused. The response capacity of a given species (i.e. R and S values) could change depending on many variables, fire intensity being a very important one, such that a species with high resprouting and/or seeding capacity under low intensity fires could have low values under high intensity ones (Keeley et al., 2008; Moreno & Oechel, 1991, 1993; Pausas et al., 2016; Trabaud, 1994). Likewise, plant flammability of a given species can also vary depending on the environmental context (Krix & Murray, 2018; Murray et al., 2013; Pausas et al., 2012; Wyse et al., 2016).

Although many species are able to adjust their performance to changes in one or more aspects of the fire regime, the performance of many other species will be affected, leading to changes in the prevalence of certain fire syndromes over others. For example, species with the syndrome R1-S3-F3, such as many flammable sclerophyllous shrubs in the Californian Chaparral, are adapted to

infrequent, intense crown fires (Keeley et al., 2012). Such species take advantage of the low competition for space generated in the post-fire environment to recruit new individuals from seed (Keeley et al., 2008; Keeley, Fotheringham, et al., 2005). Increased fire frequency due to human activities in the last centuries has led shrubs to be replaced by herbaceous vegetation which are highly flammable strong resprouters (i.e. syndrome R3-S1-F3), well adapted to frequent low to medium intensity surface fires (Keeley, Baer-Keeley, et al., 2005; Syphard et al., 2018).

Conversely, a species with the syndrome R1-S2-F3, for example *Pinus nigra* in eastern Spain, a thick-barked tall tree with self-pruning of lower branches, is adapted to rather frequent low-severity surface fires, in which its flammable canopy is kept away from fire (Fulé et al., 2008). Mismanagement in the region, including dense plantations and fire suppression, has changed the fire regime towards less frequent high-intensity crown fires, leading to the extirpation of this species in some areas (Pausas et al., 2008; Retana et al., 2002). Analogous examples can be mentioned for other syndromes and/or growth forms, the underlying message being that the performance of each syndrome is dependent on the characteristics of the fire regime, such as intensity, frequency and seasonality (Franklin et al., 2004, 2001). Our model is thus a promising tool to test not only the dominance of certain syndromes under different environmental contexts (particularly fire regimes), but also how environmental changes can affect species via changes in fire regimes.

An outstanding question is whether species differ in their flexibility to 'adapt' their fire syndromes to the different habitats where they occur. The fact that many cosmopolitan or wide-ranging species occur across regions with different historical fire regimes suggests that it might be easier for such species to 'adjust' their fire syndromes to other habitats outside their natural distribution, while species with more restricted natural distributions might have more difficulty to establish in other regions. An obvious further point from this reasoning is that changes in fire regimes could affect species differentially, a topic of particular relevance given the increasing role of humans in the modification of fire regimes at the global level (Bowman et al., 2011).

From the evolutionary point of view, the studied regions show clear differences both in the comparison of complete syndromes (Chaco vs. MTCEs; Table 2, Figure 1) and in the frequency of R, S and F values (Tables 3 and 4). We argue that these differences are largely explained by differences in the historical fire regimes of these regions. Supporting this general hypothesis, our results show that the frequency of values of the three axes is significantly associated with the region (Table 4). In MTCEs, a bimodal pattern (either low or high) of R predominates, with intermediate forms comparatively less frequent (Bond & Midgley, 2001; Keeley et al., 2012). This dichotomy could be rooted in the lability of underlying resprouting traits, which have made them prone to repeated disruptive selection (Altwegg et al., 2015; Lamont et al., 2011), favouring extreme values over intermediate ones. Values of S also differed between regions, with MTCEs showing a higher percentage of high values compared to the other regions, where intermediate values prevailed (Table 4).

While resprouting is considered ancestral in most plant lineages as a common strategy to cope with disturbances, and has proven effective for many species in fire-prone environments, the seeding strategy is more tightly linked to regions where fire is a preponderant and predictable evolutionary factor (Keeley & Pausas, 2022; Lamont et al., 2019b). In such regions, such as the MTCEs, the dominant historical fire regime, predictable within the life span of the dominant species and unfavourable for many post-fire resprouters, led many species to depend on fire for sexual reproduction or even to lose their ability to resprout (Pausas et al., 2006; Pausas & Keeley, 2014). Beyond the historical dominant fire regime, factors, such as soil fertility, variability in water availability and physiological characteristics of species, influence the prevalence of seeders vs resprouters, as well as the coexistence of both strategies (Cowling et al., 2018; Keeley et al., 2016; Vilagrosa et al., 2014). This is reflected in the interregional variation in the frequency of R and S values (Table 4; Appendix S6). While the process of losing the resprouting capacity is not physiologically (mechanistically) linked to the process of acquiring the capacity of postfire seeding (Pausas & Keeley, 2014), the two strategies may show a negative evolutionary correlation (Pausas & Verdú, 2005). Here, in line with these arguments, syndromes showing opposite extreme values of R and S (namely 7, 9, 19 and 21 in Table 2) were recorded in 10 species from MTCEs, representing a third of the 33 species described, compared to only two species in the Chaco. This supports the hypothesis that trade-off between R and S is more common in MTCEs species. Finally, the higher frequency of high flammability values in MTCEs species is likely an indicator that many species benefit from burning readily and at the same time having strong regeneration strategies, particularly seeding (He et al., 2012; Pausas et al., 2017; Saura-Mas et al., 2010; Schwilk & Ackerly, 2001). This increases their performance and provides them with an advantage in a context where fire is a key ecological and evolutionary factor (Keeley & Pausas, 2022).

Patterns in non-Mediterranean regions (i.e. Cerrado, Chaco and New Zealand) were also broadly consistent with their disturbance histories. Evidence suggests that Cerrado lineages are strongly associated with adaptations to fire, evolving in situ via recent and frequent adaptive shifts to resist fire (Simon et al., 2009), which is reflected in the dominance of strong resprouters, but also in the presence of some species with alternatives strategies. Our results suggest a more limited variety of strategies of Chacoan species compared to the Cerrado. While this may be an artefact due to a greater spatial restriction of the Chaco data, there is evidence of Cerrado species strategies such as fire-stimulated flowering (Fidelis & Zironi, 2021), thick bark and root sprouting adapted to intense fires (Simon & Pennington, 2012), while such strategies are yet to be empirically explored in the Chaco. However, and with our review being only illustrative, a deeper analysis of the literature is required to draw more definitive conclusions. Chacoan species have also shown to be highly tolerant to fire, despite its fire history being arguably shorter and less intense and predictable than the Cerrado's. These complex patterns of differences and similarities may be reflecting the history of disturbances other than fire. Both the Cerrado

and Chaco have been historically subjected to disturbances such as herbivory by large mammals (Dantas & Pausas, 2022) and seasonal drought (Werneck, 2011). A stronger evolutionary role of herbivory in the Chacoan flora, as suggested by its higher general soil fertility and the historical distribution of extinct herbivore megamammals (Gallo et al., 2013), as well as cross-regional differences in historical climatic shifts (Ab'Sáber, 1977; Vuilleumier, 1971) may have led many Chacoan species to develop traits of adaptive value to cope with fire, compensating for the less strong historical role of fire as a direct evolutionary agent compared to the Cerrado.

The clear predominance of species with low resprouting capacity in New Zealand is compatible with the history of fire in the region, almost exclusively linked to anthropic factors and very recent in evolutionary terms (Lawes et al., 2014; Perry et al., 2014). Other ecological factors with possible influence on fire-related traits of this flora, such as grazing or browsing pressure, have been also historically scarce in this region. The few species with intermediate or high resprouting (e.g. *Discaria* spp., *Cordyline* spp.) are closely related to eastern Australian species and have been present in New Zealand's flora since at least the Pliocene (Mildenhall, 1980). Some species, however, had high flammability, and a considerable proportion had intermediate flammability. This could be due to the trade-off between traits related to resource-use strategy that indirectly affect flammability, such as leaf morphology traits (Mason et al., 2016). Another cause behind this pattern could be the changes in species dominance due to human activities in recent centuries, including more frequent fires, which may have led to a greater presence of species and/or growth forms that are more tolerant to fire and/or more flammable compared to earlier times (Cui, Paterson, Alam, et al., 2020; Mason et al., 2016).

4.3 | The way forward

Feedbacks between fire regimes, biodiversity and ecological processes are increasingly being recognized in the fire ecology research agenda (Bowman et al., 2014, 2016; He et al., 2019; McLauchlan et al., 2020; Pausas & Keeley, 2021; Rogers et al., 2020). In this context, models such as the one presented here are a fundamental contribution to interpret and/or predict the vegetation dynamics under the increasingly complex current and future scenarios posed by global change, particularly in relation to its effects on fire regimes. However, the amount of information on fire-related functional traits that could inform the development and refinement of such models remains scarce. We therefore call for an international coordinated effort to build open communal databases of fire-specific traits involved in the three dimensions presented here. Such undertaking could add to, or be modelled on the example of ongoing successful efforts such as TRY (Kattge et al., 2020), CESTES (Jeliazkov et al., 2020) and GRooT (Guerrero-Ramírez et al., 2021), among others. It should help address outstanding questions regarding plant fire syndromes, for example how the observed syndromes relate to different characteristics of the fire regimes across regions (e.g.

frequency, type, seasonality and intensity); how does the proposed three-dimensional space relate to other plant traits of potential fire-adaptive value, such as bark thickness and wood density; how do fire syndromes vary when species are outside their native habitats and how this, in turn, affects the patterns of fire syndromes in such habitats; how could the combination of response and effect traits offer a new ground to test phylogenetic relationships of fire syndromes across different floras. In summary, the generalizing standard approach presented here is a step forward towards building a synthesis of the evolution of fire-related plant syndromes at the global scale.

AUTHOR CONTRIBUTIONS

Pedro Jaureguiberry and Sandra Díaz conceived the ideas and designed the methodology; Pedro Jaureguiberry collected and analysed the data; Pedro Jaureguiberry led the writing of the manuscript; Sandra Díaz contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflicts of interests to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.j6q573njb> (Jaureguiberry & Díaz, 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Comparison of frequency of species (expressed as percentages) of species within each categorical value of resprouting (R) (i.e. 1, 2 or 3) for species from the Mediterranean Basin, based on data from Tavşanoğlu & Pausas (2018). (a) Analysis considering only quantitative data (i.e. post-fire survival percentage) (N=53 species); (b) Analysis considering both quantitative data and binary data (i.e. “low” and “high” classifications, assigned to categories 1 and 3, respectively) (N=148 species). Post-fire survival percentage was assigned to one of the three categories as follows: 0–33%=1; 34–66%=2; and 67%–100%=3. Note that the percentages in each category are similar between the two approaches, supporting the use of combined binary and quantitative data for analyses.

Figure S1. Three-dimensional model showing the pattern of fire syndromes among 24 dominant species from the Argentine south-western Chaco region. The position of species is based on the following original data: axis R shows percentage of survival (Jauregui et al., 2020); axis F shows the flammability index ranging from 0 (i.e. minimum flammability) to ~3 (i.e. maximum flammability) (Jauregui et al., 2011); and axis S shows a categorical classification of germination response to heat-shock treatments (Jauregui & Díaz, 2015), where heat-sensitive germination = 0.5; heat-tolerant germination = 1.5; and heat-stimulated germination = 2.5. The frequency of fire syndromes based on standardised categorical ordinal data (see details on its calculation in the text) is shown in Figure 1a. Species references: (1) *Aloysia gratissima*; (2) *Aspidosperma quebracho-blanco*; (3) *Castela coccinea*; (4) *Celtis ehrenbergiana*; (5) *Parkinsonia praecox*; (6) *Condalia microphylla*; (7) *Geoffroea decorticans*; (8) *Larrea divaricata*; (9) *Maytenus spinosa*; (10) *Mimozyanthus carinatus*; (11) *Prosopis chilensis*; (12) *Prosopis flexuosa*; (13) *Prosopis torquata*; (14) *Sarcomphalus mistol*; (15) *Senegalia gilliesii*; (16) *Senegalia praecox*; (17) *Vachellia aroma*; (18) *Vachellia caven*; (19) *Justicia squarrosa*; (20) *Aristida mendocina*; (21) *Neobouteloua lophostachya*; (22) *Papophorum vaginatum*; (23) *Setaria pampeana*; (24) *Trichloris* spp.

Appendix S1. Thricotomous key of the 27 possible combinations (i.e. syndromes) of resprouting (R), seeding (S) and flammability (F). Extreme syndromes (i.e. those occupying the corners of the cube in Figure 1) are highlighted in light blue.

Appendix S2. List of 24 species from the Chaco region, with their corresponding taxonomical information, original values recorded for resprouting (R), seeding (S) and flammability (F), standardised categorical ordinal values, and corresponding fire syndromes. See key to fire syndromes in Appendix S1. Nomenclature follows the Catálogo de las Plantas Vasculares del Cono Sur (Zuloaga, Morrone, & Belgrano, 2008) and online updates (<http://www.floraargentina.edu.ar/>). *These values correspond to Axis 1 of a PCA performed with quantitative data on maximum temperature and biomass consumed; while standardised values were obtained with a cluster analysis (see Methods).

Appendix S3. Full list of records of standardised values of resprouting (R), seeding (S) and flammability (F) obtained for species from different regions, through an unstructured literature review. Ordinal categorical values 1, 2 and 3 indicate low, intermediate

and high values of the corresponding variable. Total number of records=4411; total number of species=4032.

Appendix S4. List of species for which data on resprouting (R), seeding (S) and flammability (F) was obtained, with their corresponding standardised values and associated fire syndrome. The grouping by region and grand region used to compare the syndromes is also detailed. Chaco refers to the Argentine south-western Chaco region; MTCEs= Mediterranean-type climate ecosystems. Extreme syndromes (i.e. those occupying the corners of the cube in Figure 1) are highlighted in light blue.

Appendix S5. Frequency of different fire syndromes [i.e. recurrent combinations of categorical ordinal values of resprouting (R), seeding (S) and flammability (F)] of dominant species from the Chaco region (n=24) and from Mediterranean Type Climate Ecosystems (MTCEs) (n=33), the latter including species from the Mediterranean Basin (n=24), California (n=5), Southern Australia (n=3) and Southern South Africa (n=1) (full list of species in Appendix S4).

Extreme syndromes (i.e. those occupying the corners of the cube in figure 1) are highlighted in light blue. At the bottom of the table, the percentage of species with extreme syndromes in each region is reported. The intensity of the red colour indicates the frequency of the syndromes.

Appendix S6. Contingency tables of absolute frequencies of standardised ordinal values of resprouting (R), seeding (S) and flammability (F) for species from different regions, with their corresponding Chi-Square tests.

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