

# Fire and life history affect the distribution of plant species in a biodiversity hotspot

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## Abstract

**Aim:** Species distribution models (SDMs) provide valuable insights into species–environment relationships and potential climate change impacts on diversity. Most SDMs do not account for the role of natural disturbance regimes such as fire in determining current and future species distributions, or how species traits mediate their response to these stressors. Here, we investigate the importance of fire in determining the distributions of species in fire-prone fynbos vegetation, and how this varies in relation to different life history traits (growth form and fire-response strategy).

**Location:** Cape Floristic Region, South Africa.

**Methods:** We modelled the distribution of 104 plant species with different life history traits, using Maxent. The model included five climatic variables, one edaphic and one fire variable. Post hoc analyses of model output and permutation procedures were conducted to assess variable importance across different life history traits. We accounted for phylogenetic autocorrelation using sister species comparisons.

**Results:** Permutation importance scores identified fire return interval as a major determinant of fynbos species' distributions. Linear mixed effect analyses revealed that seeder species were significantly more sensitive to fire than resprouters. Coefficients from the (linear) response curves of the different predictors indicated that the occurrence of species across all life histories was negatively associated with longer fire return intervals.

**Main conclusions:** Fire and life history traits governing species' response to fire are key factors determining species distributions in our study system. SDMs that ignore the role of fire in driving species distributions, and how this varies across different life history types, compromise our ability to understand species–environment relationships in fire-prone ecosystems. There is great need for better spatial data describing historical, current and future fire regimes and for models that can incorporate different responses based on species life histories, to improve vulnerability assessments for fire-prone ecosystems.

## KEYWORDS

fire return interval, fynbos, life history, Maxent, resprouter, seeder, species distribution model

## 1 | INTRODUCTION

Fire is a pervasive natural disturbance that is well acknowledged as a driver of species distributions and community composition in many ecosystems (Bond & Keeley, 2005; Bowman et al., 2009; Cowling, Holmes, & Rebelo, 1992; Pausas & Verdú, 2008; van Wilgen, Richardson, Kruger, & van Hensbergen, 1992), but the extent and manner in which fire influences species distributions is not fully understood. Fynbos, the dominant vegetation type in the Cape Floristic Region (CFR), is under threat from climate change (Midgley, Hannah, Millar, Rutherford, & Powrie, 2002; Midgley, Hannah, Millar, Thuiller, & Booth, 2003; Slingsby et al., 2017). Projected climate trends for the CFR suggest an increase in temperature (Niang et al., 2014) coupled with a decrease in winter rainfall in the south-west section of the CFR and an increase in rainfall inland and towards the east (Hoffman, Carrick, Gillson, & West, 2009; MacKellar, New, & Jack, 2014). Beyond direct effects on plant species growth and survival, these changes in climate may lead to alterations in the fuel load, fire weather and ignition probability, consequently altering the fire regime (Kraaij, Cowling, & van Wilgen, 2013a; Mouillot, Rambal, & Joffre, 2002; Wilson, Latimer, Silander, Gelfand, & de Klerk, 2010) and impacting on the distribution, composition and function of vegetation (Bond & Keeley, 2005). A sound understanding of the complex relationship between climate, fire and plant species distributions is required to ensure effective conservation and management of fire-prone vegetation, especially in global biodiversity hotspots like the CFR (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000).

Species distribution models (SDMs) enable us to understand and project the effects of climate change on biodiversity, helping guide conservation strategies and policies. To date, most SDMs use only abiotic variables such as climate and soils (Guisan & Thuiller, 2005; Midgley et al., 2003; Parmesan & Yohe, 2003) and/or do not consider the biology of the species being modelled. This limits their ability to detect or predict potential nonlinear ecosystem responses, such as the complex feedback between climate, vegetation and fire. Fortunately, there has been rapid development of SDMs that incorporate species biology over the past decade (Csergő et al., 2017; Franklin, 2010; Keith et al., 2008), and studies in fire-prone ecosystems are increasingly incorporating fire information into SDMs (Crimmins, Dobrowski, Mynsberge, & Safford, 2014; Keith et al., 2008; Merow et al., 2014; Tucker, Rebelo, & Manne, 2012), yet there is still much to be learned. While there is ample observational and experimental evidence regarding the importance of fire in determining the survival of plant species with different life history traits at local sites (Brown, 1993; Keeley, Pausas, Rundel, Bond, & Bradstock, 2011; Kraaij, Cowling, van Wilgen, & Schutte-Vlok, 2013b; Shryock, DeFalco, & Esque, 2014), few studies have scaled up to explore the implications for species global geographical distributions. In particular, studies that include fire data and compare the influence of fire on the distributions of multiple species with different life history traits (Crimmins et al., 2014; Keith et al., 2008; Lawson, Regan, Zedler, & Franklin, 2010) are rare.

The importance of traits in determining species responses to environmental change in distribution studies is well acknowledged (Dobrowski et al., 2011; Kharouba, McCune, Thuiller, & Huntley, 2013; Syphard & Franklin, 2010; Wiens, 2011). Life history traits describe the adaptations employed by an individual during different stages in its life cycle (i.e., growth, reproduction and survival) in response to environmental conditions (van Wilgen & Forsyth, 1992). Fire-response strategies are a key component of the life history of plants in fire-prone environments such as the CFR. They are often simplified into three categories: obligate seeders, that are killed by fire and recruit from seed in the post-fire environment; facultative resprouters, that both resprout and recruit seedlings from fire-cued seed banks post-fire; and obligate resprouters, that do not have fire-resistant seed banks and regenerate after fire by sprouting from dormant buds (Bell, Hopkins, & Pate, 1984; Keeley, Bond, Bradstock, Pausas, & Rundel, 2012; Marais, Pratt, Jacobs, Jacobsen, & Esler, 2014; Pratt, Jacobsen, Jacobs, & Esler, 2012). All three fire-response strategies are observed in the five growth forms widely used to describe plant species in the CFR, that is trees, shrubs, herbs, geophytes and graminoids (Goldblatt & Manning, 2000).

Fire-response strategy determines the survival of fynbos species under varying fire regimes. For example, seeder species are killed by fire, but recruit rapidly and in typically in large numbers from fire-resistant seed banks (soil or canopy) in order to persist (Le Maitre & Midgley, 1992). Recruitment after a fire significantly depletes these seed banks. For example, Pierce and Cowling (1991) found that more than half of the seed banks belonging to six fynbos shrubs were depleted after a fire. This makes seeder species highly dependent on post-fire conditions (e.g., weather; Slingsby et al., 2017) and fire-free intervals long enough for individuals to germinate, reach maturity and sufficiently replenish their seed banks before the next fire occurs (Pausas, Bradstock, Keith, & Keeley, 2004; Pausas & Keeley, 2014; Pratt et al., 2012). In contrast, obligate and facultative resprouters typically possess defensive structures (bark, buds and storage tissue) that enable them to survive and regenerate after a fire, making fire-free periods less important for individual persistence. However, investment in protective structures and storage tissues, often combined with short-lived fire-sensitive seeds (Keeley, 1992), means that resprouters tend to be slower growing and require longer maturation periods than seeders (Lamont, Enright, & He, 2011; Pausas et al., 2004). Therefore, the stability of resprouter populations may require long fire-free periods so that individuals can establish and transition into adults mature enough to resist fire (Keeley, 1992). In the light of this, we expect that species response to different environmental covariates, particularly fire, should differ according to their respective life histories.

Previous studies that have explored the influence of fire-response strategies on species distributions found that fire-response strategies affect the accuracy of SDMs, with obligate seeders exhibiting greater model accuracy than resprouters (Crimmins et al., 2014; Syphard & Franklin, 2010). These findings are indicative of the mediating effect of fire-response strategies on species-environment responses (Keith et al., 2008; Lawson et al., 2010). Here, we explore

the importance of fire in determining the distribution of fynbos species with different life history traits (growth form and fire-response strategy). We model the distributions of 52 closely related fynbos plant species pairs (104 species), classified across two growth forms (graminoids and shrubs) and their respective fire-response strategies (seeder vs. resprouter). We address the following questions: (1) to what extent does fire determine species distributions relative to climate and soils? (2) Does the importance of fire vary between species of differing life histories? To address these two questions, post hoc analyses of model output and permutation procedures were employed.

## 2 | METHODS

### 2.1 | Study area

Our study focuses on fynbos vegetation within the CFR, a global biodiversity hotspot (Cowling, Pressey, Rouget, & Lombard, 2003; Myers et al., 2000) located on the south-western tip of Africa. Approximately 70% of the  $\pm 9,000$  plant species found in the CFR are endemic to the region (Goldblatt, 1978; Linder, 2003). Fynbos accounts for almost 80% of the vegetation in the CFR and is characterized by four major growth forms: graminoids (restioids), tall shrubs (proteoids), sub-shrubs (ericoids) and geophytes (Cowling & Richardson, 1995). The geology of the CFR is dominated by layers of sandstone and shale, which gave rise to distinct soil types ranging from poor nutrient sandy soils to richer clay soils (Goldblatt & Manning, 2000).

The CFR falls within a predominantly Mediterranean climate (Köppen, 1931), with the west experiencing wet winters and hot, dry summers and bimodal rainfall peaking in March and September in the east (Schulze, 2007; Southey, 2009; van Wilgen et al., 2010). Fynbos is fire-prone (Bond & Keeley, 2005), with natural fires mainly occurring during the dry, hot summer period (Cowling et al., 1992). The average fire return interval ranges between 10–30 years, with few stands surviving beyond 40 to 50 years without burning (Keeley et al., 2012).

## 2.2 | Data

### 2.2.1 | Species occurrence data

Species occurrence data were acquired from the National Herbarium Pretoria Computerised Information System database (PRECIS, Russell, 1985). All non-indigenous species were removed from the PRECIS dataset, and only perennial species with more than 15 records within intact fynbos, with a location accuracy of <2km, were retained. The data were classified into growth forms and fire-response strategy using information from the Plants of South Africa database (POSA, Germishuizen & Meyer, 2003). Here, obligate seeder species were classified as seeders, while obligate and facultative resprouter species were combined into one class as resprouters. To account for potential phylogenetic autocorrelation, pairs of

species within the same lineage, but with contrasting life history traits, were selected. Phylogenetic autocorrelation is a potential confounding factor when making comparisons among multiple species, because closely related species tend to share similar traits and ecological behaviour, potentially biasing statistical inferences in multispecies models (Blomberg, Garland, & Ives, 2003; Felsenstein, 1985; Peres-Neto, 2006). It is therefore necessary to account for phylogenetic autocorrelation when comparing among species so as to avoid potential type I errors (detection of a relationship between variables that does not exist) or type II errors (not detecting a relationship between variables that does exist) (Abouheif, 1999). As a result, a total of 52 species pairs were selected for the study (see Appendix S2, Table S2.1).

The dataset was examined for spatial sampling bias, a common limitation found in presence-only data where some areas in the landscape are sampled more intensively than others (Phillips, 2009), which could lead to misrepresentation of the real distribution of species (Kadmon, Farber, & Danin, 2004; Reddy & Dávalos, 2003). We compared the species occurrence data and a random sample of points, finding the majority of both to be located within a 1km of a road (see Appendices S1 and S2, Figure S2.2). These results are reflective of the very dense network of roads that exists within the study area, and it is unlikely that our sample is biased with respect to the environmental covariates used in the study.

### 2.2.2 | Environmental variables

Environmental variables were selected based on their capacity to reflect the relationship between species prevalence and the environment, giving due consideration to appropriate scale (Alvarado-Serrano & Knowles, 2014, Table 1). These consisted of five climatic variables: mean annual precipitation; mean January precipitation; Markham's precipitation concentration (Markham, 1970); mean maximum January (summer) temperature; mean minimum July (winter) temperature; one soil variable, representing pH, fertility and texture, and one fire variable, representing fire return interval (Table 1).

Climatic variables were derived from long-term (1950–2000) mean climate data from the South African Atlas of Agrohydrology and Climatology (Schulze, 2007). Markham's precipitation concentration represents precipitation seasonality and ranges from 0% to 100%. A value of 0% indicates equal rainfall throughout the year, while 100% indicates that all precipitation falls in a single month (Markham, 1970; Wilson, Latimer, & Silander, 2015). The soil variable was derived from a 1:250,000 geological map from the Council for Geosciences for which each lithology was classified by experts into fertility (four classes), texture (four classes) and pH classes (three classes) and rasterized (Latimer, Wu, Gelfand, & Silander, 2006). We reduced the dimensionality of the soil data by performing a principal coordinate analysis (PCoA) and retaining only the first PCoA axis, which captured 56% of the variance (see Appendix S1 for details). Low axis scores represent nutrient-poor, coarse-textured, acidic soils, while high axis scores represent fertile, fine-textured, alkaline soils.

**TABLE 1** Details of environmental variables selected for modelling

Variable	Range	Biological significance
Fire return interval (FRI)	0.6–32.7 years	Fire destroys above ground biomass, exterminating species that cannot resprout or do not have a strategy for regenerating from seed (Altwegg et al., 2014; Bond & Midgley, 2001) Fire stimulates various reproductive strategies among fynbos species, many of which are dependent on fire for flowering, seed release or germination (Brown, Staden, Daws, Johnson, & Wyk, 2003; Cocks & Stock, 1997; Keeley et al., 2012; Southey, 2009) Ash from fire acts as a mineralizing agent for fynbos (Stock & Lewis, 1986)
Mean annual precipitation (MAP)	20–3,198 mm	Distribution of fynbos species closely linked to rainfall regime and gradients (Cowling et al., 2005; Goldblatt & Manning, 2000) Temperature affects physiological functioning (e.g., water and nutrient assimilation), as well as growth processes such as germination and bud break (Midgley et al., 2002)
Mean January precipitation (Summer PPT)	0–111 mm	
Mean maximum January temperature (Summer Tmax)	13.1–35.1°C	
Mean minimum July temperature (Winter Tmin)	4.9–10.6°C	
Markham's precipitation concentration (PPT seasonality)	0.5%–51.5%	Rainfall seasonality is closely linked to the persistence of fynbos seeder and resprouter species in response to fire events (Altwegg et al., 2014; Ojeda, 1998; Ojeda, Brun, & Vergara, 2005)
Soils (Soil)	–0.48–0.55 (PC axis 1 scores, see Appendix , Figure )	Fynbos is associated with sandy nutrient-poor soils (Cowling & Holmes, 1992; Cramer et al., 2014), and many species are strongly limited by soil texture and pH (Esler, Staden, & Midgley, 2015)

Our fire variable was derived from a hierarchical Bayesian statistical framework that modelled post-fire recovery based on ten years (2000–2010) of remotely sensed Moderate Resolution Imaging Spectroradiometer (MODIS) 500 m resolution 16-day gridded Normalized Difference Vegetation Index (NDVI) data (Wilson et al., 2015). The variable represents the time required for the vegetation to recover to the point where it can once again carry a fire and has been used in other species distribution modelling studies (Merow et al., 2014). Wilson et al., (2015) corroborated that it is a good proxy for fire return interval by comparing it with a survival model fit with observed fire return times (see Appendix S1 for more details). While other components of the fire regime may also affect species' distributions (e.g., severity/intensity, timing), no such data were available. Fire return interval is perhaps the most important component of the fire regime in the CFR, as most seeder species depend on fires for seed release and/or germination, and require long fire-free intervals to flower and develop seed before the next fire, but not so long that they begin to senesce (Altwegg, de Klerk, & Midgley, 2014; Forsyth & van Wilgen, 2008; van Wilgen et al., 2010).

A test for collinearity (level of dependence) among the selected variables established that none of the variables were correlated at  $r > |0.7|$  (see Dormann et al., 2013), therefore all seven variables were retained. All data were trimmed to the extent of untransformed fynbos in the CFR (40,966.1 km<sup>2</sup>), because our fire variable could not be derived for transformed areas and because our species locality information was likely biased towards untransformed areas. All data were resampled to 1 min (~1.55 x 1.85 km) to match the lowest resolution data source; the soil data.

## 2.3 | Model settings and outputs

The Maxent (maximum entropy) software package (<http://www.cs.princeton.edu/~schapire/Maxent/>; Phillips, Anderson, & Schapire, 2006; Phillips et al., 2006) was used to develop species distribution models (SDMs), and to measure the relative contribution of each variable for predicting each species' distribution (Phillips et al., 2006). Maxent is a machine-learning model that was preferred over other approaches due to its robust method in handling presence-only, non-stratified data (Phillips et al., 2006). The Maxent algorithm estimates the probability distribution with the maximum entropy, that is the distribution that is most spread out, or closest to uniform after all constraints are taken into consideration (Phillips et al., 2006), by contrasting environmental conditions at the locations of presence data against those at the background location points where presence/absence is not measured (Merow, Smith, & Silander, 2013).

We fitted the model with seven predictor variables (i.e., map, Summer PPT, PPT seasonality, Winter Tmin, Summer Tmax, Soil and FRI) and ran ten replicates of the model. Using a random split, 70% of the occurrence records were set aside to train the model, and 30% as test data. Background samples were set at the default of 10,000 points. Only linear features were selected, as the use of simple models is more suitable when investigating the importance of predictors (Merow et al., 2013). It avoids complex interactions among variables and the response curves are easier to interpret, making the models more suited to hypothesis testing about key drivers of species distributions. Excluding quadratic features (i.e., unimodal relationships between species occurrence and covariates) was justified because comparison of AIC from logistic

regression models, where each covariate was fitted as a linear feature only versus as a quadratic feature for each species, indicated preference for the linear model ( $\Delta\text{AUC} > 2$ ) or did not distinguish between models ( $\Delta\text{AUC} < 2$ ) in >90% of comparisons (see Appendix S2, Table S2.2).

### 2.3.1 | Importance of environmental predictors

To evaluate the importance of fire in predicting species distributions relative to climate and soil, we considered Maxent's jackknife analysis of the area under the receiver operator curve (AUC) and permutation importance values. These outputs measure the extent to which each variable contributes to the model outcome, that is indicate the strength of the relationship between a particular variable and the distribution of the species (Phillips et al., 2006).

The jackknife test estimates the change in AUC when each variable is removed from the model, and when each variable is used in isolation. The AUC value indicates the effectiveness of each variable in predicting species presence in the model. These values range from 0 to 1, where <0.5 indicates a relationship worse than random, 0.5 indicates that the model has no predictive power (no better than random), and 1 signifies a perfect model prediction (Elith et al., 2006). Models with AUC values of >0.9 are interpreted as very good to excellent, 0.7–0.9 as moderate to good; and <0.7 as fair to poor (Swets, 1988). Models with AUC < 0.5 were excluded from our study.

Maxent provides other estimates of variable importance such as permutation importance. Permutation importance is measured by randomly permuting the values of each environmental variable against training presence and background data (Phillips, 2009). The resulting decrease in training AUC indicates the extent to which the model depends on that variable, that is the greater the decrease in training AUC, the greater the explanatory capacity of the variable. Permutation importance scores are normalized and expressed as percentages (Phillips et al., 2006).

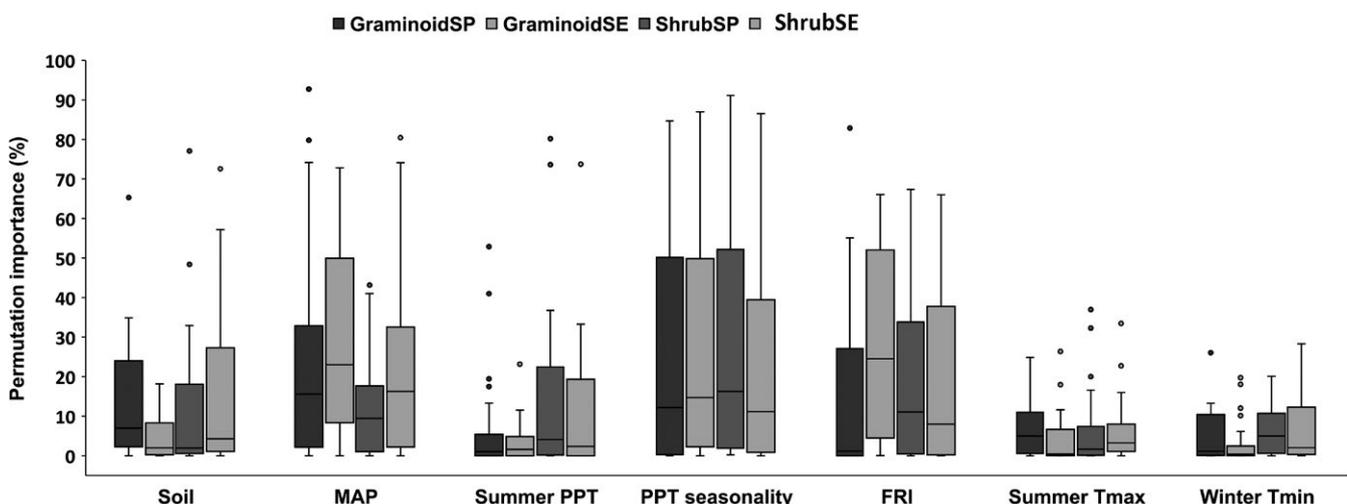
Using the coefficients of the response curves for each predictor variable (i.e., lambda values) we assessed the direction of the relationship between each environmental variable and species across the different life histories.

To test whether species responses to each environmental variable depends on their life history traits, we fitted linear mixed effect models using the 'lme4' package (Bates, Mächler, Bolker, & Walker, 2014; Bates et al., 2014) in R (R Development Core Team, 2015). Permutation importance values were extracted from the Maxent output and modelled as a function of species life history traits. Growth form and fire response were assigned as fixed effects with an interaction term, while contrasting species pairs were set as the random effect to account for phylogenetic autocorrelation. Linear mixed effect models were fit separately for each environmental variable due to sample size constraints.

## 3 | RESULTS

### 3.1 | Jackknife scores

The full model (all seven variables) achieved good accuracy (median AUC = 0.88, interquartile range = 0.8–0.94) in determining the distribution of species across all four life history types, despite variability among species within and between life history types (see Appendix S2, Figure S2.1). The AUC remained generally high across all life histories regardless of the omission of any of the seven variables. While this may vary by species, the lack of trend suggests that no variable consistently contributed important unique information across all species within a life history type that was not already present in the other six. The observed AUC values when the model is based on a single variable, however, do show variation in the relative strengths of each variable as a predictor of fynbos species distributions (see Appendix S2, Figure S2.1). Most univariate models



**FIGURE 1** Variable importance as described by permutation importance for resprouter graminoids (GraminoidSP), seeder graminoids (GraminoidSE), resprouter shrubs (ShrubSP) and seeder shrubs (ShrubSE)

**TABLE 2** Linear mixed effects model summary describing the importance of each environmental variable (measured as permutation importance) as a function of growth form and fire-response strategy

	FRI <sup>b</sup>			MAP <sup>c</sup>			PPT seasonality <sup>d</sup>			Summer PPT <sup>e</sup>			Summer Tmax <sup>f</sup>			Soil <sup>g</sup>			Winter Tmin <sup>h</sup>		
	B	SE	p	B	SE	p	B	SE	p	B	SE	p	B	SE	p	B	SE	p	B	SE	p
(Intercept)	14.52	4.53	0*	24.67	4.4	0*	26.88	5.59	0*	6.99	3.08	0.03*	7.66	1.66	0*	14.37	3.09	0*	4.91	1.41	0*
Seeder	15.27	6.41	0.02*	6.93	5.83	0.24	-2.6	7.9	0.74	-4	4.36	0.36	-3.68	2.13	0.09	-10.06	4.37	0.03*	-1.87	2	0.36
Shrub	4.24	6.29	0.5	-12.17	6.09	0.05*	3	7.75	0.7	6.57	4.28	0.13	-1.7	2.3	0.46	-2.39	4.29	0.58	2.45	1.97	0.22
Seeder - Shrub	-14.5	8.9	0.11	2.17	8.09	0.79	-4.43	10.96	0.69	1.15	6.05	0.85	3.87	2.96	0.2	12.16	6.06	0.05*	-0.43	2.79	0.88

<sup>a</sup>Note: Bolditalic entries indicate a statistical significance, \* $p < .05$  \*\* $p < .01$ . <sup>b</sup>Fire return interval. <sup>c</sup>Mean annual precipitation. <sup>d</sup>Markham's precipitation concentration. <sup>e</sup>Mean January precipitation. <sup>f</sup>Mean maximum January (summer) temperature. <sup>g</sup>Soil pH, fertility and texture. <sup>h</sup>Mean minimum July (winter) temperature.

had AUC scores >0.5, suggesting that almost all variables have some power to predict the distribution of our focal species.

### 3.2 | Permutation importance

Permutation importance, representing the normalized change from the AUC for the optimal model with all variables for each species, revealed that there were significant differences in the importance of variables across all species ( $F = 21.83$ ,  $df = 6$ ,  $p < 0.001$ ), with *FRI*, *MAP* and *PPT seasonality*, generally being the strongest determinants of fynbos plant species distributions (see Appendix S2, Table S2.3), although this varied among life histories (Figure 1).

The linear mixed effects analysis exploring variation in the permutation importance scores for each variable revealed significant differences among species with different life history in response to *FRI* (Table 2). Seeders were significantly more sensitive to fire than resprouters ( $p < 0.05$ ), likely driven by the large difference between seeder graminoids (median = 24.5%) and resprouting graminoids (1.2%). For the climate variables, shrub species were significantly less sensitive to *MAP* than graminoids ( $p \leq 0.05$ ). For soils, seeders were significantly ( $p < 0.05$ ) less sensitive to soil properties than resprouters, but there was a significant ( $p \leq 0.05$ ) interaction between the shrub growth form and seeder strategy, suggesting that seeder shrubs are more sensitive to edaphic conditions than resprouter shrubs.

### 3.3 | Response curves

The response curves indicate the direction of the relationship between species and the different environmental variables used (Figure 2). We observed that species across all life histories have a negative response to increasing fire return interval (Figure 2); that is a longer fire return interval results in the reduced probability of occurrence of all species. This negative relationship was also apparent for *Soil*, *Summer PPT*, *Winter Tmin* and *Summer Tmax* (i.e., hotter, more fertile conditions with higher summer rainfall), while a positive relationship was noted for *MAP* (higher rainfall) and *PPT seasonality* (stronger seasonality), generally representing the dominant environmental conditions in the mountains of the CFR ( $F = 8.376$ ,  $df = 6$ ,  $p < 0.001$ ).

The linear mixed effect analysis on the slopes of the response curves revealed that there was a significantly more negative relationship between seeders and fire return interval as compared to resprouters ( $p < 0.05$ , Table 3), although the interaction term suggested that seeder shrub species were less affected. The inverse was true for the soil variable, with seeders showing significantly a less negative relationship ( $p < 0.05$ ), but seeder shrubs showing little response. This may suggest that seeder species do better in sites characterized by more fertile soils and shorter fire return intervals than resprouters. There were significant ( $p \leq 0.05$ ) interactions between the shrub growth form and seeder strategy in response to fire return interval (positive) and soils (negative), indicating that seeder shrubs are better suited to longer fire return intervals and more fertile soils than other functional types.

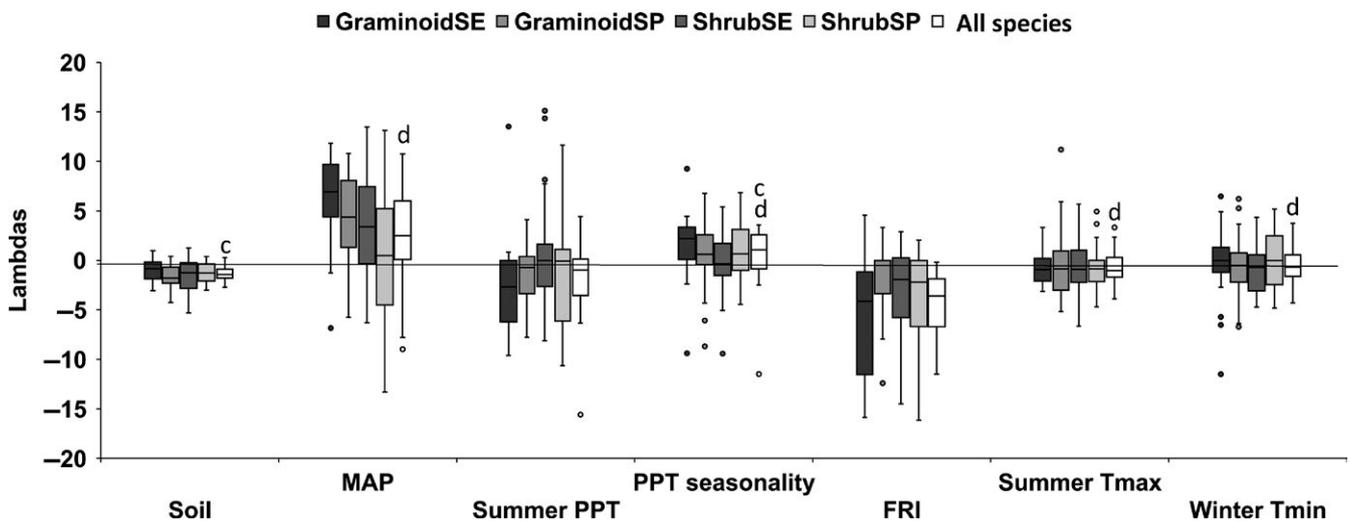
## 4 | DISCUSSION

Species distribution models (SDMs) are central to improving our understanding of how species may respond to climate change. Various studies allude to the need to incorporate more non-climatic variables and consider functional trait differences among species when modelling their distributions (Austin & van Niel, 2011; Enright, Fontaine, Lamont, Miller, & Westcott, 2014; Franklin, Serra-Diaz, Syphard, & Regan, 2016; Heikkinen et al., 2006; Syphard & Franklin, 2010; Yates et al., 2010). Such modifications to traditional SDMs (typically exclusively based on climate and soils) are suggested to be necessary for the detection of underlying complex species–environment relationships, as well as the improvement of model accuracy in predicting species distributions. Given that fire is a significant driver of vegetation dynamics in Mediterranean-type ecosystems such as the CFR (Bond & Keeley, 2005; Keeley et al., 2012; van Wilgen & Forsyth, 1992), we hypothesized that fire would be a significant predictor of plant species distributions and therefore its inclusion in SDMs was warranted. We further hypothesized that the distribution of fynbos plant species would vary across life histories, with differences in the distribution of species stemming from underlying trait-driven responses to environmental conditions.

Output from our models confirms the importance of fire as a determinant of fynbos plant species distributions and highlight the complementary roles of rainfall and fire in the reproductive and physiological processes that occur in fynbos species (Cowling & Heijnis, 2001; Cowling, Ojeda, Lamont, Rundel, & Lechmere-Oertel, 2005; Keeley et al., 2012; Procheş, Cowling, & Preez, 2005; van Wilgen et al., 1992). For instance, dry season fires initiate flowering and/or seed release, and break seed dormancy, in many fynbos species (Brown, 1993; Keeley et al., 2012), while winter rainfall facilitates

germination and the growth of new seedlings. Furthermore, a demographic study by Treurnicht et al., (2016) found that while climate had a dominant effect on the recruitment of 26-shrub species (Proteaceae), fecundity was mostly fire-driven. In other studies; Lawson et al., (2010) and Regan, Crookston, Swab, Franklin, and Lawson, (2010) used spatially explicit stochastic population models to show that changes in fire return interval have significant effects on population abundance relative to other threats such as climate change and land use. Demonstrating the influence of fire on the distribution of plant species further cements concerns not only for the impacts of climate change but for changing fire regimes on biodiversity in fire-prone environments, and a need for models that capture the interaction of fire and climate (Abbott & Le Maitre, 2009; Yates et al., 2010).

The importance of fire as a determinant of fynbos distributions was more apparent among seeder species than resprouters, confirming the variation in sensitivity of resprouters and seeders to fire regimes cited by other studies (Bond & Midgley, 2001; Enright et al., 2014; Keith et al., 2008; Wilson et al., 2010). Seeder species are highly dependent on the timing and frequency of fire (Altwegg et al., 2014; Pausas & Keeley, 2014). Most seeders require fires to release seed and/or germinate and depend on fire-free intervals long enough for individuals to establish and mature, but not so long that they begin to senesce (Pratt et al., 2012). In contrast, resprouters exhibit greater resilience in their interaction with fire, with rapid regrowth and defensive structures (e.g., thick bark) facilitating continued persistence under a range of fire return intervals (Lamont et al., 2011). While seeder species were significantly limited in their distribution by fire return interval, edaphic conditions had greater influence on resprouters. This finding supports other studies that allude to the dominance of either resprouters or seeders along fire and edaphic gradients



**FIGURE 2** Species response to environmental variables based on slopes of the Maxent response curves for resprouter graminoids (GraminoidSP), seeder graminoids (GraminoidSE), resprouter shrubs (ShrubSP), seeder shrubs (ShrubSE) and all species. Positive lambda values indicate a positive relationship between the life history trait and corresponding variable, a negative lambda value indicates a negative relationship. Letters indicate significant differences among variables based on an ANOVA on all species ( $F = 8.38$ ,  $df = 6$ ,  $p < 0.001$ ; Table 3)

**TABLE 3** Linear mixed effects model summary indicating the direction of the relationship between species and the selected environmental variables represented by the slope of the Maxent response curves as a function of growth form and fire- response strategy

	FRI <sup>b</sup>			MAP <sup>c</sup>			PPT seasonality <sup>d</sup>			Summer PPT <sup>e</sup>			Summer Tmax <sup>f</sup>			Soil <sup>g</sup>			Winter Tmin <sup>h</sup>			
	B	SE	p	B	SE	p	B	SE	p	B	SE	p	B	SE	p	B	SE	p	B	SE	p	
(Intercept)	-2.07	0.94	0.03*	4.21	2.19	0.06**	0.66	1.12	0.56	-2.17	1.8	0.23	0.68	0.54	0.24	0*	-1.72	0.24	0*	-0.43	0.6	0.48
Seeder	-3.77	1.34	0.007*	1.93	3.1	0.54	-0.89	1.5	0.56	-0.33	2.4	0.89	0.77	0.61	0.31	0.01*	0.8	0.31	0.01*	0.02	0.85	0.98
Shrub	-1.46	1.34	0.28	-5.15	3.1	0.1	0.33	1.58	0.83	-2.4	2.54	0.35	0.44	0.77	0.33	0.13	0.5	0.33	0.13	0.31	0.85	0.72
Seeder - Shrub	3.95	1.89	0.04*	-3.26	4.38	0.46	-0.38	2.11	0.86	4.8	3.37	0.16	0.63	1.08	0.43	0.02*	-1.03	0.43	0.02*	-0.78	1.2	0.52

<sup>a</sup>Note: Boldfalic entries indicate a statistical significance, \* $p < .05$  \*\* $p < .01$  <sup>b</sup>Fire return interval. <sup>c</sup>Mean annual precipitation. <sup>d</sup>Markham's precipitation concentration. <sup>e</sup>Mean January precipitation. <sup>f</sup>Mean maximum January (summer) temperature. <sup>g</sup>Soil pH, fertility and texture. <sup>h</sup>Mean minimum July (winter) temperature.

(Wisheu, Rosenzweig, Olsvig-Whittaker, & Shmida, 2000; Wuest et al., 2016). For example, Wisheu et al. (2000), found that there was a dominance of resprouters on fertile soils, while seeders dominated sites with nutrient-poor soils and frequent fires. The dominance of seeder species was attributed to their ability to make use of nutrients (released by the fire) just below the surface that resprouters, with deeper root systems, were not able to access.

While our results show that fire is an important determinant of fynbos species' distributions, models that excluded fire, and many that were based on single climatic variables, generally showed good predictive accuracy (AUC > 0.75). These results agree with those of Tucker et al. (2012), who found that fire variables did not greatly improve predictions of shrub species presence in the CFR. In a related study based in California, Crimmins et al. (2014) also found that fire occurrence generally did not improve model accuracy in predicting the distribution of a set of vascular plant species. The corroboration between our results and those of Tucker et al., (2012) and Crimmins et al., (2014) is not surprising given that fire is inherently a weaker determinant of fynbos distributions when compared to climate. This is likely to be due to the dependence of fire on climate, resulting in shared explanatory ability between fire and climate-related covariates (Tucker et al., 2012). Fire regimes are typically a function of rainfall seasonality, which affects the occurrence of fire weather and fuel moisture content (flammability) and precipitation (build-up of fuel load) (Ellis, Verboom, van der Niet, Johnson, & Linder, 2014; Pausas & Paula, 2012; Wilson et al., 2010). Fire regime, however, holds the potential to change in a nonlinear manner, with negative implications for species distributions and vegetation composition. Changes in fire regime may be affected through changes in fuel properties due to shifts in species composition (e.g., grasses or invasive alien trees), increased frequency of extreme fire weather, or direct human alterations in probability of ignition and fire spread (i.e., from fire suppression or habitat fragmentation). Therefore, fire information may not be essential for predicting historical fynbos distributions, but are likely to become crucial for achieving a more accurate understanding of how fynbos distributions may change in future.

Although our study only focuses on fire return interval, we do acknowledge the ecological importance of other components of the fire regime in driving plant species distributions in fire-prone ecosystems. For example, Altwegg et al. (2014) highlight the differential effects of fire seasonality and fire intensity on resprouters and seeders that result in the dominance of one life history over the other in a given space. In their study, Altwegg et al. (2014) predict resprouters to have greater resilience against out of season fires, or fires followed by unfavourable conditions for establishment (e.g., unpredictable rainfall), while high-intensity fires are predicted to favour seeder species. In the light of this, there is a need for better estimates of more components of the fire regime for input into SDMs. Such estimates would provide a more holistic understanding

of species responses to fire regime, and ultimately improve predictions of how changes in fire regime will influence future species distributions.

Anticipating the impacts of climate change on biodiversity in fire-prone ecosystems requires an approach where not only the interactions between plant species and climate, but also disturbance factors such as fire, form the basis of vulnerability assessments. Furthermore, the role of life history traits in driving the sensitivity of plant species to changes in ecological regime should also be considered. Despite the general assumption that species distributions are more strongly limited by climate as compared to edaphic conditions and or disturbance, our study indicates that disturbance variables such as fire have the capacity to add to our understanding of plant species distributions in fire-prone ecosystems, particularly in the case of seeder graminoids and shrubs. The variation in species' response to environmental covariates across different growth forms and fire-response strategies shows that life history traits are crucial to the identification of vulnerable species. By accounting for disturbance factors such as fire, and functional differences among species that may affect their response to disturbance, SDMs become better equipped to generate more accurate and appropriate information to guide future biodiversity conservation. Our study further highlights the need for better spatial estimates of fire regime parameters, and how these may be altered under global change, to support vulnerability assessments of vegetation in fire-prone ecosystems.

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## DATA ACCESSIBILITY

The authors confirm that all data underlying the findings are fully available without restriction. Data available upon reasonable request from corresponding author (nyasha.magadzire@gmail.com).

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## BIOSKETCH

**Nyasha Magadzire's** research interests involve understanding how changes in ecological regime (especially fire regimes) affect species distributions across time and space, through the use of remote sensing, GIS and species distribution models. Interests of the team of authors include spatial analysis, ecology, biogeography and drivers of change in Mediterranean-type ecosystems. JS conceived the study, NM & JS performed data analysis, HdK & KJE contributed to the design and implementation of research, verifying analytical methods and interpreting results NM wrote the manuscript and KJE, JS and HdK contributed and edited it.

## SUPPORTING INFORMATION

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

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