

Fire regimes shape diversity and traits of vegetation under different climatic conditions

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Abstract

Changes in climate and land use are altering fire regimes in many regions across the globe. This work aims to study the influence of wildfire recurrence and burn severity on woody community structure and plant functional traits under different environmental conditions. We selected three study sites along a Mediterranean-Oceanic climatic gradient, where we studied the fire history and burn severity of the last wildfire. Four years after the last wildfire, we established 1,776 1-m² plots where the percentage cover of each woody species was sampled. We calculated (i) structural parameters of the community such as total cover, alpha species richness, evenness and diversity (Shannon diversity index), and (ii) vegetation cover of each functional group (differentiating life forms, eco-physiological traits and regenerative traits). Focusing on community structure, results showed increases in species richness and diversity as wildfire recurrence increased, but this effect was partially counterweighted in the areas affected by high severity. In relation to functional groups, we found that increases in recurrence and severity fostered transition from tree- to shrub-dominated ecosystems. Non-arboreal life form, high specific leaf area, N₂-fixing capacity, resprouting ability and heat-stimulated germination were advantageous traits under high recurrences and severities, and low seed mass was advantageous under high recurrence situations. We suggest that the strength of the effects of wildfire recurrence and burn severity on vegetation structure and traits might vary with climate, increasing from Oceanic to Mediterranean conditions. In the Mediterranean site, recurrence and severity were strongly related to traits associated with germination (seed mass and heat-stimulated germination), whereas in the Oceanic site the strongest relationships were found with a resprouting-related trait (bud location). This study identifies changes in vegetation structure and composition in scenarios of high recurrence and severity, and provides useful information on plant traits that could be key in enhancing vegetation resilience.

INTRODUCTION

Fire regimes determine vegetation structure and composition in many biomes worldwide (Bond et al., 2004). Fire recurrence (number of fires in a given period) and burn severity (loss of or change in ecosystem biomass) are two of the most important fire-regime attributes in shaping plant communities (Keeley et al., 2011; Fernández-García et al., 2018a; Hart et al., 2019). Generally, vegetation is adapted to certain patterns of fire recurrence and burn severity, but shifts in these variables might result in changes in plant communities (Keeley et al., 2011; Moya et al., 2018). From a scientific point of view, there is growing concern about the possible ecological consequences of expected increases in wildfire recurrence and burn severity arising from warmer and drier climate conditions and increases in fuel load and continuity in many regions of the world (Mouillot et al., 2002; Stephens et al., 2013; Fréjaville and Curt, 2015).

Southern Europe is one of the most vulnerable regions to global change (Giorgi and Gionello, 2008). In this region, climate warming is expected to alter vegetation structure, decreasing diversity, particularly in the transition areas between Mediterranean and continental climates and in mountain ranges (Thuiller et al., 2005). Additionally, rural exodus and extensive monospecific plantations have led to increases in fuel load and continuity, and landscape homogenization in this region (Pausas et al., 2008; Vilar et al., 2016). Understanding the vulnerability of plant community structure to changes in climate and land use is essential to predict modifications in ecosystem functioning (Guiot and Cramer, 2016). However, the indirect effects of climate and land-use change on vegetation through increases in both wildfire recurrence and burn severity are not well understood. Previous studies have focused primarily on the effects of fire-regime attributes on vegetation structure, and have showed highly variable results. For instance, Beckage and Stout (2000) found no effects of wildfire recurrence on species richness and diversity, whereas Tessler et al. (2016) reported significant increases. On the other hand, Blair et al. (2016) found decreases in species richness as burn severity increased, whereas Meyer et al. (2019) found that burning increased richness, so further studies are advisable.

Changes in fire regimes can also modify the composition of plant communities because of differences in species fitness (Keeley et al., 2011; Lamont et al., 2018). Several functional traits have been considered key in determining plant fitness in relation to wildfire recurrence and burn severity, including life form (Pekin et al., 2011; Blair et al., 2016), eco-physiological traits (Anacker et al., 2011; Hart et al., 2019) and regenerative traits (Ojeda et al., 2005; Wright et al., 2016). In relation to life form, wildfire recurrence has been shown to increase the cover of shrubs to the detriment of trees (Tessler et al., 2016; Fernández-García et al., 2018a; Kowaljow et al., 2018), and an analogous pattern has been found with burn severity (Crotteau et al., 2013). However, little is known about the consistency of the relationship between life form and fire regimes under different environmental conditions (Pausas and Bradstock, 2007).

Among plant eco-physiological traits, specific leaf area (leaf area per unit dry mass; SLA) could be affected by changes in fire regimes and environmental conditions in several ways (Macfarlane et al., 2004; Dwyer et al., 2014). Low SLA species invest more dry matter per leaf area, exhibit longer life spans, and have lower growth rates than high SLA species, which are associated with productive habitats (wet and fertile) (Dwyer et al., 2014; Greenwood et al., 2017; Michelaki et al., 2019). Anacker et al. (2011) found shifts in SLA at community level after fire as a result of complex interdependences between fire regimes, climate, and reproductive strategies. Another eco-physiological trait that may be relevant in post-fire regeneration is atmospheric nitrogen- (N_2) fixing capacity (Lajeunesse et al., 2006). Legumes and actinorhizal plants have this ability through symbiosis with *Rhizobia* and *Frankia* bacteria, respectively; it is particularly advantageous in N-deficient areas (Lajeunesse et al., 2006), which can be the case for systems affected by recurrent wildfires or extreme severities (Certini, 2005). However, the potential relationship between N_2 -fixing capacity and fire regime parameters could be modulated by climate, since aridity and low temperatures largely decrease N_2 fixation (Poth, 1982; Lajeunesse et al., 2006). Consequently, research concerning wildfire recurrence and severity effects on SLA and N_2 -

fixing capacity should consider the potential influence of environmental conditions, particularly climate.

Plant regenerative traits are key to post-fire recovery capacity (Calvo et al., 2003; Keeley et al., 2011; Clarke et al., 2013). Several studies in fire ecology differentiate among obligate resprouters (plants whose post-fire regeneration relies on resprouting), obligate seeders (plants whose post-fire regeneration relies on seeding), and facultatives (plants with both mechanisms) (Anacker et al., 2011; Pausas and Keeley, 2014; Pausas et al., 2015). On the one hand, it has been proposed that seeders could be better adapted than resprouters to severe wildfires, where most of the vegetative buds do not survive, particularly those above ground (Clarke et al., 2013). On the other hand, resprouters can have an advantage over seeders in situations of high recurrence, because they are not subjected to immaturity risk (Calvo et al., 2003; Lloret et al., 2005; Pausas and Keeley, 2014). There is evidence indicating that environmental conditions influence regenerative strategies in Mediterranean biomes, with resprouters being more abundant in the most humid areas, as resprouting facilitates rapid regeneration particularly in highly competitive environments (Lloret et al., 2005; Reyes et al., 2009; Pausas and Bradstock, 2007; Pausas et al., 2015). In addition, simulation models suggest that climate can shape the relationship between fire regime attributes and the regenerative strategy (Ojeda et al., 2005), field studies being opportune to corroborate this outcome.

Although the regenerative strategy helps to broadly predict vegetation responses to fire regimes (Pausas et al., 2004; Pausas et al., 2015), differences within the resprouter and seeder communities are expected. For instance, Clarke et al. (2013) indicate that among resprouters, those with buds located below ground are the most protected from recurrent and severe wildfires. With respect to seeders, some studies suggest that large seeds can be more resistant to fire and produce more vigorous seedlings (Bond et al., 1999; Delgado et al., 2008; Calvo et al., 2015). Apart from seed allometry, the germination of many obligate seeders is heat-stimulated (Baskin and Baskin, 2014; Tavsanoğlu and Pausas, 2018), and the establishment of heat-stimulated species has been positively related to

wildfire recurrence (Lamont et al., 2018) and burn severity (Wright et al., 2016). Heat-stimulated germination is the consequence of the rupture of physical seed dormancy by high temperatures reached during fire (Baskin and Baskin, 2014) and can be advantageous in fire-prone environments because it promotes germination when conditions for seedling establishment and growth are optimal (Pausas and Keeley, 2014; Lamont et al., 2018). However, potential interaction effects of fire and climate on stimulating germination could be expected, as laboratory studies have indicated that moist heat could promote germination more than dry heat in some species (i.e. hard-seeded legumes) (Wiggers et al., 2017). Consequently, to study the influence of fire regimes on plant traits under different environmental conditions will contribute to better understanding the potential impacts of fire on vegetation as well as to identifying which traits are key for the resilience of the community.

As far as we know, there are no studies analyzing the combined effects of fire recurrence and burn severity on functional traits under different environmental conditions, such as along a climatic gradient. Advances in this knowledge are particularly relevant in the current context of expected increases in wildfire recurrence (Mouillot et al., 2002; Enright et al., 2015; Vázquez et al., 2015) and burn severity (Parks et al., 2016; Stephens et al., 2013). The aim of this work is to study the effects of wildfire recurrence and burn severity of the last wildfire on woody community structure and plant traits along a Mediterranean-Oceanic climatic gradient. Specifically, we want to answer the following questions: (i) Is woody community structure (species richness, total cover, evenness and diversity) related to wildfire recurrence and burn severity four years after fire? (ii) Are plant functional traits (life form, eco-physiological traits, and regenerative traits) related to wildfire recurrence and burn severity four years after fire? We hypothesize that high wildfire recurrence and high burn severity would result in a decrease in species richness, total cover and diversity. Furthermore, the effects of wildfire recurrence and burn severity on vegetation would depend on plant functional traits, which may be intercorrelated among themselves (Anacker et al., 2011). In general, we assume the effects of recurrence and severity to be

aggravated under Mediterranean as compared to Oceanic conditions, as fire impacts in humid climates are, in general, less persistent because of rapid post-fire regeneration (Pausas and Bradstock, 2007; Fernández-García et al., 2018b).

MATERIALS AND METHODS

Study sites

We selected three study sites within the Iberian Peninsula (Fig. 1) representing the Mediterranean-Oceanic gradient, which is the most representative climatic gradient in Southern Europe (Rivas-Martinez and Rivas-Saenz, 2017): the area affected by wildfire in Cortes de Pallás in summer 2012 (297 km²), hereafter the Mediterranean site; the area affected by wildfire in Sierra del Teleno in summer 2012 (119 km²), hereafter the Transition site; and the area affected by wildfire in Monte Pindo in summer 2013 (25 km²), hereafter the Oceanic site. The three wildfires were largely stand-replacing fires which affected serotinous pine forests, the type of forest most affected by wildfires in the Iberian Peninsula (Pausas and Vallejo, 1999; Fernández-García et al., 2019). These wildfires were the last ones occurred in the study sites until field sampling.

The Mediterranean site is located in a mountainous area (120-942 m.a.s.l.) with heterogeneous orography in the eastern Iberian Peninsula. This site is characterized by hot dry summers, averaging four months of summer drought (typical Mediterranean conditions), annual precipitation of 400-600 mm and mean annual temperature of 13-17 °C (Ninyerola et al., 2005). Apart from the large wildfire of June 2012, the Mediterranean site was affected by wildfires in 1978, 1991 and 1994, repeatedly burning *Pinus halepensis* Mill. ecosystems with localized presence of *Pinus pinaster* Ait. and an understory dominated by *Ulex parviflorus* Pourr., *Quercus coccifera* L. and *Rosmarinus officinalis* L. among other Mediterranean shrubs (see Tables A.1, A.2, A.3 for further information on the community composition of the three study sites). Soils are calcareous (8.14 ± 0.06 ; mean pH \pm standard error), with loamy sand and sandy loam texture. Predominant soils are

Haplic Calcisol and Calcari-lithic Leptosol (Jones et al. 2005) according to the World Reference Base for Soil Resources (WRB) classification system.

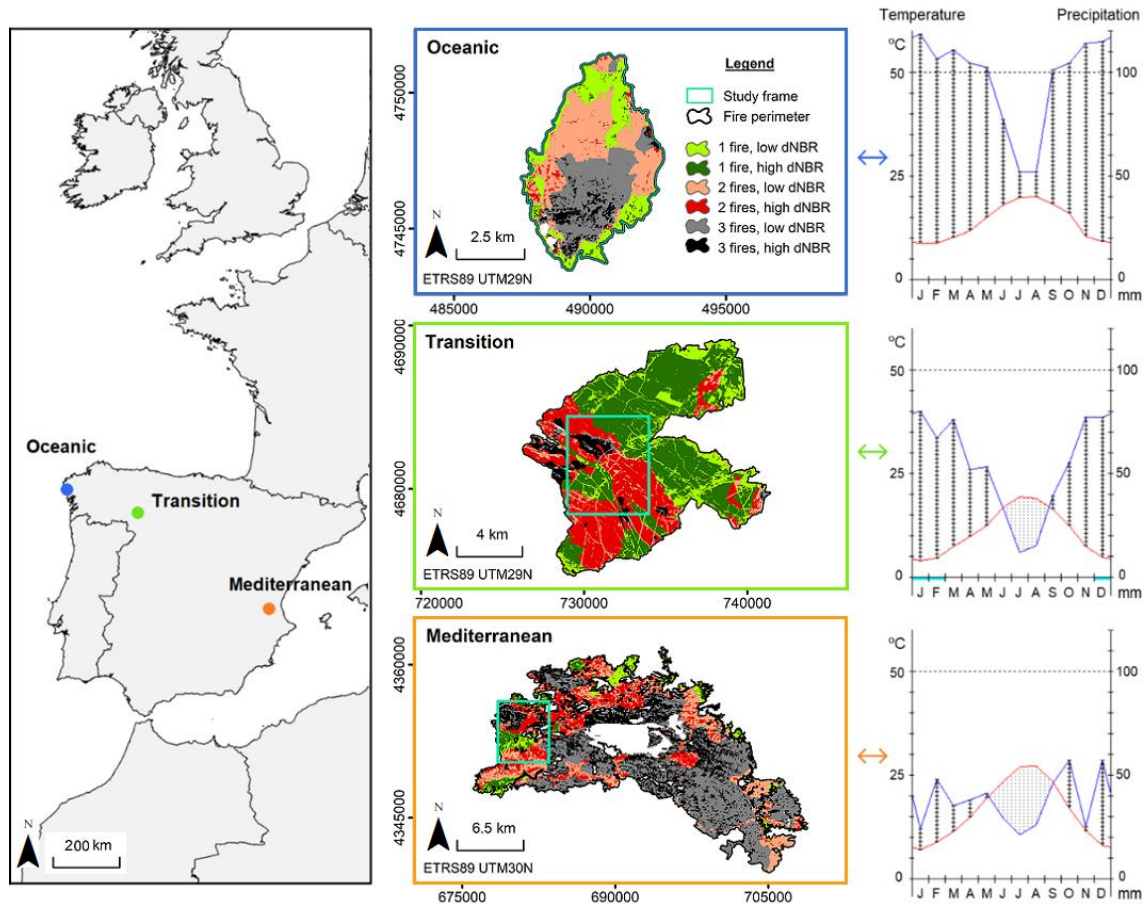


Figure 1. Location of the study sites in the Iberian Peninsula (panel on the left) and perimeters of the last wildfire in each study site with the different wildfire recurrences -1, 2 and 3 fires- and burn severities of the last wildfire -low and high dNBR using 0.55 as threshold- (panel in the centre). Panels on the right show the climate diagrams of the closest meteorological stations for a period ≥ 13 years, based on Rivas-Martinez and Rivas-Saenz (2017).

The Transition site is located in the foothills of a mountain range (836-1,493 m.a.s.l.) in the northwestern Iberian Peninsula. This site has a heterogeneous orography, and climate is characterized by temperate and dry summers with two months of summer drought, annual precipitation of 600-800 mm and mean annual temperature of 8-11 °C (Ninyerola et al., 2005). Part of the area that burned in August, 2012 had previously been affected by large wildfires in 1978, 1991 and 1998. The Transition site is occupied by *Pinus pinaster* ecosystems with a shrubby understory community dominated by *Pterospartum tridentatum* (L.) Willk., *Halimium lasianthum* (Lam.) Spach and *Erica australis* L. Soils are siliceous (pH 4.86 ± 0.14), with a sandy loam texture, and classified as Haplic Umbrisol and

Dystric Regosol (Jones et al. 2005). The Oceanic site is located in Mount Pindo (0-929 m.a.s.l.) in the northwestern Iberian Peninsula. The orography in this site is heterogeneous. Climate is characterized by temperate summers with no drought, annual precipitation of 1700-1800 mm and mean annual temperature of 12-15 °C (Ninyerola et al., 2005). The area affected by the wildfire of September 2013 was partially affected by wildfires that occurred in 2005, 2004, 2001, 2000, 1999 and 1995. The vegetation is dominated by *P. pinaster* and *Eucalyptus globulus* Labill. as invader species from nearby plantations. The understorey community is mostly comprised of *Rubus* sp., *Ulex europaeus* L., *Cytisus scoparius* (L.) Link and *Erica umbellata* Loefl. ex L. Soils are siliceous (pH 5.08 ± 0.10) with frequently exposed bedrock (biotite granite), and mostly classified as Umbrisols (Jones et al. 2005). The land uses in this site are more heterogeneous than in the Mediterranean and Transition ones, comprising natural forests highly variable in tree density, some of them developed over abandoned cropfields and plantations.

Fire regime parameters: recurrence and severity

We mapped wildfire recurrence by delimiting and geoprocessing the fire perimeters in the Mediterranean and Transition sites for the period 1978-2012, and in the Oceanic site for the period 1990-2013 because of the low availability of cloud-free Landsat scenes. In the Mediterranean site, official cartography of fires was available for the entire study period (Alloza et al. 2012). In the Transition and Oceanic sites we digitized the wildfire perimeters using false colour composites from satellite imagery of 80 m to 30 m ground resolution (Landsat 2, 4, 5, 7 and 8) (Earth Explorer, 2019) and aerial orthophotography (see Fernández-García et al., 2018a).

Burn severity was obtained in the three study sites as a continuous variable, by calculating the differenced Normalized Burn Ratio (dNBR) of the last wildfire from Landsat imagery. Landsat 7 scenes from August 22nd, 2011 (pre-fire) and from August 25th, 2012 (post-fire) were used in the Mediterranean site; Landsat 7 scenes from September 20th, 2011 (pre-fire) and September 6th, 2012 (post-fire) were used in the Transition site; and Landsat 8 scenes from August 30th 2013 and September 15th 2013 in the Oceanic site. Images were

atmospherically and topographically corrected and dNBR was calculated, with values ranging from -2 to 2 (see Fernández-García et al., 2018b for a detailed description of the imagery pre-processing and dNBR calculation).

Woody vegetation: sampling, structural parameters and traits

We focused field sampling in a study frame of 3000 ha in the Mediterranean and Transition sites, and in 2500 ha in the Oceanic site (corresponding to the entire wildfire) (Fig 1). These areas were selected because they were formerly dominated by pine ecosystems, with three different wildfire recurrences (one, two and three wildfires) and heterogeneous burn severity. In order to distribute the field plots proportionally to the area of each wildfire recurrence and along the burn severity gradient, we created a recurrence-severity map for each study site (Fig. 1) with six recurrence-severity categories, by combining wildfire recurrence (one to three wildfires) and burn severity classified into low and high severity (using the dNBR value 0.55 as threshold, which is considered moderate burn severity; Fernández-García et al., 2018a, 2018b, 2019). We distributed 30 m x 30 m field plots (corresponding to the spatial resolution of Landsat ETM+ and OLI reflective bands) proportionally to the area of each frequency-severity category, with a minimum of 30 plots per study site, thereby ensuring that all the fire frequency-severity situations were represented. A total of 148 30 m x 30 m field plots were established: 30 plots in the Mediterranean site, 78 plots in the Transition site and 40 plots in the Oceanic site. The minimum distance between plots was 200 m. In each plot we located three 2 m x 2 m subplots, divided into four 1 m x 1 m quadrats. Plot and subplot centres were georeferenced with high precision GPS (RMSE X,Y < 0.5m). Four years after the wildfires (May-June 2016 in the Mediterranean and Transition sites, May-June 2017 in the Oceanic site), we visually estimated the percentage cover of each woody species in each 1 m² quadrat.

Several structural parameters of the woody plant community were studied in each 1-m² quadrat. Specifically, we determined total cover, alpha species richness (S), evenness (J) and diversity (Shannon diversity index, H) according to the following equations:

$$H = -\sum_{i=1}^S p_i \ln p_i$$

where H is the Shannon diversity index (Shannon and Weaver, 1949), S species richness and p_i relative cover of each species i .

$$J = H / H_{\max}$$

where J is the Pielou's evenness index (Pielou, 1966), ranging from 0 to 1; H is the Shannon diversity index and H_{\max} the maximum possible value for H, this is all existing species equally abundant ($\ln S$).

We classified each woody species according to its life form (tree or not tree), ecophysiological traits (low or high SLA -specific leaf area-; with or without N_2 -fixing capacity) and regenerative traits (seeder, facultative or resprouter; presence or absence of underground buds; low or high seed mass; with or without heat-stimulated germination) when there was information available (Tables A.1, A.2, A.3). The information on plant traits was obtained from the BROT 2.0 database (Tavsanoglu and Pausas, 2018), bibliographic review (Cornelissen, 1996; Macfarlane et al., 2004; Reyes et al., 2009; Proença et al., 2010), and field observations in the study sites. SLA and seed mass categories were based on the median value of all the species used in the present study.

We calculated relative cover (RC) of vegetation in relation to functional traits in each 1-m² quadrat as follows: (i) RC of tree species: sum of the cover of tree species/sum of the cover of all species; (ii) RC of species with high SLA: sum of the cover of species with high SLA/sum of the cover of all classified species; (iii) RC of species with N_2 -fixing capacity: sum of the cover of all Fabaceae species/sum of the cover of all classified species; (iv) RC of species with resprouting ability: sum of the cover of resprouters and facultatives/sum of the cover of all classified species; (v) RC of species with underground buds: sum of the cover of resprouters and facultatives with underground buds/sum of the cover of classified resprouters and facultatives; (vi) RC of species with high seed mass: sum of the cover of seeders and facultatives with high seed mass/sum of the cover of classified seeders and facultatives; (vii) RC of species with heat-stimulated germination: sum of the cover of

seeders and facultatives with heat-stimulated germination/sum of the cover of classified seeders and facultatives.

Data analysis

To study the overall similarity of the samples from the three study sites ($n = 1776$) in relation to structural parameters and traits, we performed non-metric multidimensional scaling ordinations (NMDSs) using the *metaMDS* function. A Wisconsin double standardization was applied to the data and Bray-Curtis dissimilarity was used to ordinate the samples. The *envfit* function performed with 1000 random permutations was used to calculate the correlation of the ordination with the external factor study site (Mediterranean, Transition and Oceanic) and with the external variables wildfire recurrence (number of wildfires) and burn severity (dNBR spectral index), obtaining the strength (R^2) and significance (P) of the correlations, using an alpha of 0.05 as the cutoff for significance. In the same way, we calculated the correlation of the NMDSs with the structural parameters and vegetation traits with which the ordination was performed, and vectors were fitted in the NMDSs.

To analyze the effects of wildfire recurrence (number of wildfires) and burn severity (continuous dNBR spectral index of the last wildfire) on the woody community structure and plant traits, we performed generalized linear mixed models (GLMMs) for each study site ($n = 360$ in the Mediterranean; $n = 936$ in the Transition; $n = 480$ in the Oceanic) via penalized quasi-likelihood (*glmmPQL* function) to account for overdispersion. The response variables related to community structure were: (i) woody species richness, (ii) total cover, (iii) evenness and (iv) Shannon diversity index. The response variables related to the woody vegetation traits were: the relative cover (RC) of (i) trees, (ii) species with high SLA, (iii) species with N_2 -fixing capacity, (iv) resprouters, (v) resprouters and facultatives with underground buds, (vi) seeders and facultatives with high seed mass, and (vii) seeders and facultatives with heat-stimulated germination. Following Zuur et al.'s (2009) recommendations, a Gaussian error distribution was used in the GLMMs to fit the continuous response variables (Shannon diversity index), a quasi-Poisson error distribution

for count data and cover (richness and cover), and a quasi-binomial error distribution for the response variables expressed as percentage data ranging from 0 to 1 (species evenness, and relative covers). We used the canonical links for each error distribution family: *identity* for Gaussian, *log* for Poisson and *logit* for binomial. The identities of the 30 m x 30 m and 2 m x 2 m field plots/subplots were included in the models as a nested random factor. The interaction term (Recurrence x Severity) was retained in the models only when it was significant ($P < 0.05$). The generalized R^2 of the GLMMs was obtained via the standardized generalized variance approach.

We tested the significance of the association between the different traits at species level in each study site (n = 49 species in the Mediterranean site; n = 11 species in the Transition site; n = 28 species in the Oceanic site) using Fisher's exact test.

All data analyses were carried out with R (R Core Team, 2017), using *vegan* (Oksanen et al., 2019) *MASS* (Venables and Ripley, 2002), *nlme* (Pinheiro et al., 2017) and *r2glmm* (Jaeger, 2017) packages.

RESULTS

Effects of wildfire recurrence and burn severity on plant community structure

The NMDS ordination (Fig. 2) separated the samples from the three study sites ($R^2 = 0.43$; $P < 0.01$), indicating significant differences in woody community structure among the three climatic conditions. Both recurrence and severity of the last wildfire were significantly related to the ordination ($P < 0.01$). Species richness (S) and Shannon diversity index (H) increased from the Oceanic site to Transition and to Mediterranean sites, whereas evenness (J) was much lower in the Oceanic site compared to the other two sites (Figs. 2,3).

Overall, the GLMMs indicated that the effects of wildfire recurrence and severity of the last wildfire in structural parameters were stronger in the Mediterranean (0.17 ± 0.06 ;

average R^2 of models \pm standard error) than in the Transition (0.04 ± 0.01) and Oceanic sites (0.05 ± 0.01) (see R^2 in Fig. 3).

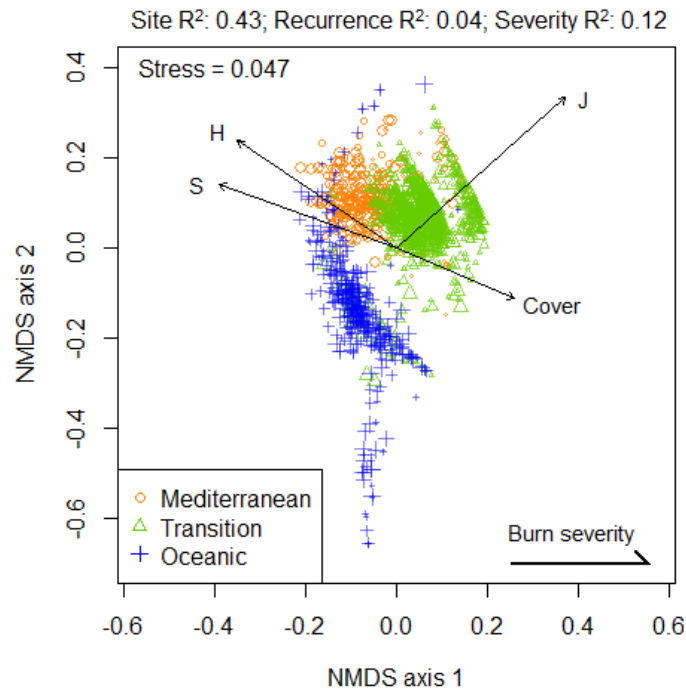


Figure 2. NMDS ordination of the samples from the three study sites (Mediterranean, Transition and Oceanic) according to the structure (total cover, alpha species richness, alpha evenness, and alpha diversity calculated with the Shannon diversity index) of the woody community. R^2 values show the goodness of fit of the ordination to the external parameters study site, wildfire recurrence (number of wildfires) and burn severity (dNBR of the last wildfire) whereas the length of vectors in the panels indicate the goodness of fit of the ordination to the structural parameters. The ordination was rotated, matching burn severity with axis 1. Shape sizes are proportional to the number of wildfires. S: alpha species richness; J: alpha evenness; H: alpha diversity calculated with the Shannon diversity index.

Focusing on each structural parameter, we observed that species richness (Fig. 3a) and Shannon diversity index (Fig. 3d) significantly increased with wildfire recurrence in the Mediterranean and Transition sites, the Oceanic site showing the same pattern but without statistical significance. Woody species cover also increased with recurrence in the Transition site (Fig. 3b). The effects of burn severity on the structural parameters were not significant, but a common trend was found in the three sites, with decreasing richness, evenness and Shannon diversity index (Fig. 3a, c, d; Table A.4) as severity increased.

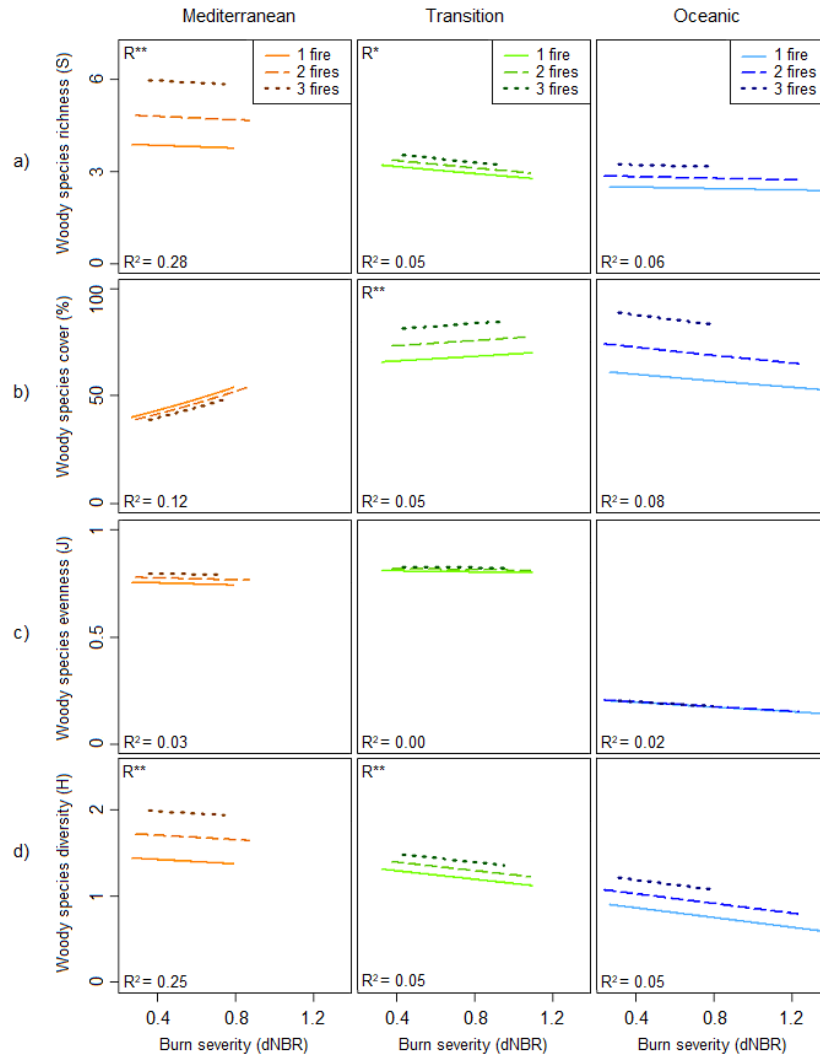


Figure 3. Mean predicted (a) alpha species richness (S), (b) total cover (%), (c) alpha evenness (J), and (d) alpha diversity calculated with the Shannon diversity index (H) of the woody community in relation to wildfire recurrence (number of wildfires) and burn severity (dNBR of the last wildfire). R^2 values indicate the standardized generalized variance (mean generalized R^2) explained by the GLMMs. The significance of model predictors (recurrence: R, severity: S) is represented as * ($P < 0.05$) and ** ($P < 0.01$).

Effects of wildfire recurrence and burn severity on plant traits

The NMDS ordination based on functional traits (Fig. 4) did not show a clear clustering of samples. Study site, wildfire recurrence, and burn severity of the last wildfire were significantly related to the ordination ($P < 0.01$).

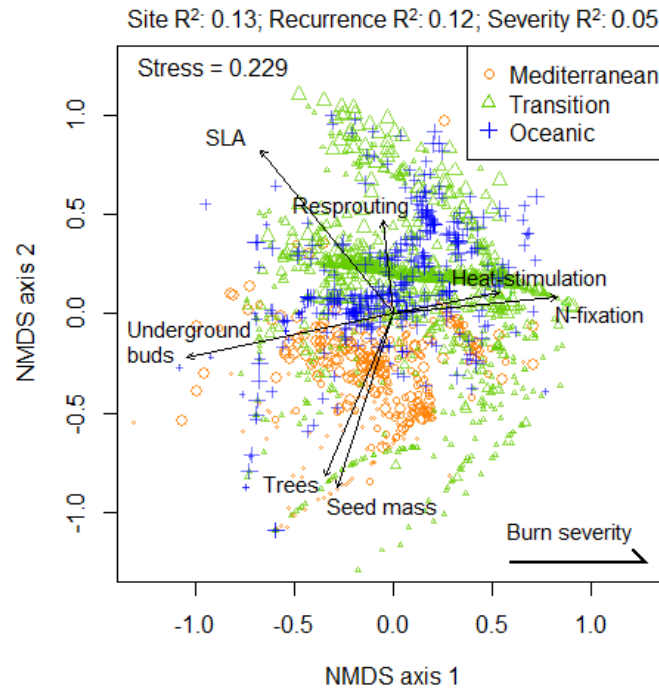


Figure 4. NMDS ordination of the samples from the three study sites (Mediterranean, Transition and Oceanic) according to the functional traits of the woody community. R^2 values show the goodness of fit of the ordination to the external parameters study site, wildfire recurrence (number of wildfires) and burn severity (dnBR of the last wildfire), whereas the length of vectors in the panels indicates the goodness of fit of the ordination to the functional traits. The ordination was rotated, matching burn severity with axis 1. Shape sizes are proportional to the number of wildfires. SLA = specific leaf area.

In general, we did not find significant correlations among plant traits (Table A.5), except for N_2 -fixing capacity and seed mass in the Mediterranean site, and N_2 -fixing capacity and heat-stimulated germination in the Oceanic site.

The GLMMs indicated that the strength of the relationships (R^2) between fire regime attributes (wildfire recurrence and severity) and plant functional traits decreased from the Mediterranean (0.33 ± 0.06 ; average R^2 of models \pm standard error) to the Oceanic site (0.12 ± 0.05), being intermediate in the Transition site (0.21 ± 0.04) (see R^2 in Fig. 5). In the Mediterranean site, the strongest relationships were found with traits related to germination (relative cover -RC- of species with high seed mass and RC of species with heat-stimulated germination) and N_2 -fixing capacity, whereas in the Oceanic site wildfire recurrence and severity were strongly related to the resprouting-related trait (RC of resprouters and facultatives with underground buds) and N_2 -fixing capacity. In the Transition site, models performed with the traits related to life form (RC of trees) reached the highest R^2 . We also found that fire regime attributes affected a higher number of traits in Mediterranean and Transition sites (all traits significantly affected) than in the Oceanic one (two traits significantly affected) (Fig. 5; Table A.6).

The RC of trees decreased from the Mediterranean to the Oceanic climate (Fig. 5a). Common trends were found in the three study sites, the RC of trees decreasing as wildfire recurrence and severity increased (Fig. 5a). The effects of wildfire recurrence were significant in the Mediterranean and Transition sites, whereas the effect of burn severity was significant in the Mediterranean site.

SLA increased from the Mediterranean to the Oceanic climate (Fig. 5b). SLA significantly increased with wildfire recurrence in the Mediterranean and Transition sites, and with burn severity in the Mediterranean site. N_2 -fixing capacity increased with severity in the Mediterranean site, with wildfire recurrence in the Transition site, and a significant interaction between recurrence and severity was detected in the Oceanic site (Fig. 5c).

There was a clear increase in the RC of species with resprouting ability from the Mediterranean to the Oceanic site (Fig. 5d). RC of resprouters significantly increased with wildfire recurrence in the Mediterranean site, and with both recurrence and severity in the Transition site (Fig. 5d).

Among the species able to resprout (resprouters and facultatives), those with underground buds dominated the Mediterranean site (Fig. 5e). The RC of resprouters with underground buds did not show a consistent pattern along the climatic gradient in relation to recurrence and severity (Fig. 5e). Wildfire recurrence and severity decreased the RC of resprouters with underground buds in the Mediterranean site; severity increased them in the Transition site; and there was a significant interaction between recurrence and severity in the Oceanic site.

Among the species that regenerate by seeds (obligate seeders and facultatives), those with high seed mass dominated the extremes of the climatic gradient (Oceanic and Mediterranean sites) (Fig. 5f). We found a common trend in the three sites, with seed mass decreasing as wildfire recurrence increased (Fig. 5f), the effects being significant in the Mediterranean and Transition sites. Positive relationships between burn severity and seed mass were found in the Mediterranean site, particularly after two and three wildfires. Conversely, both wildfire recurrence and severity tended to increase the RC of vegetation with heat-stimulated germination along the climatic gradient, with significant effects of severity in the Mediterranean site and significant interaction between recurrence and severity in the Transition site.

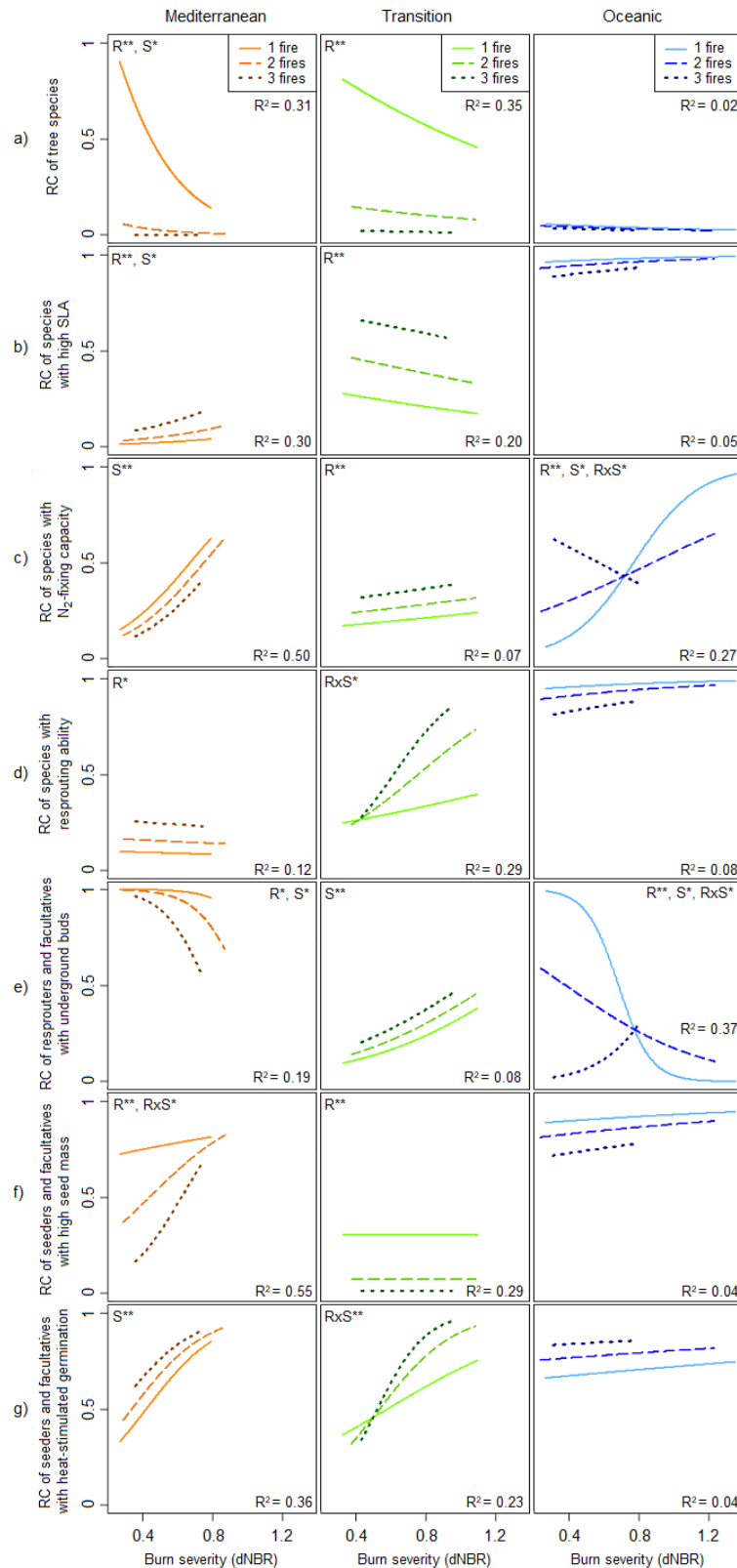


Figure 5. Mean predicted relative cover (RC) of (a) trees, (b) species with high specific leaf area (SLA), (c) species with N₂-fixing capacity, (d) species with resprouting ability, (e) resprouters and facultatives with underground buds, (f) seeders and resprouters with high seed mass, and (g) seeders and resprouters with heat-stimulated germination of the woody community, in relation to wildfire recurrence (number of wildfires) and burn severity (dNBR of the last wildfire). R^2 values indicate the standardized generalized variance (mean generalized R^2) explained by the GLMMs. The significance of model predictors (recurrence: R, severity: S, and their interaction: R x S) is represented as * ($P < 0.05$) and ** ($P < 0.01$).

DISCUSSION

Effects of wildfire recurrence and burn severity on plant community structure

We found that fire regime attributes (wildfire recurrence and burn severity of the last wildfire) determine woody community structure, particularly in the Mediterranean and Transition sites. Increases in wildfire recurrence increased alpha diversity (Shannon index) and species richness, whereas increases in burn severity tended to counteract this shift. Although results in the literature are variable (e.g. Peterson and Reich, 2008; Pekin et al., 2011), many previous studies are in agreement with our results, reporting increases in species diversity with wildfire recurrence (Beckage and Stout, 2000; Tessler et al., 2016; Meyer et al., 2019), because fire prevents competitive exclusion (Schwilk et al., 1997; Beckage and Stout, 2000). Accordingly, decreases in tree cover with wildfire recurrence can contribute to increased diversity of the understory community (Peterson and Reich, 2008; Tessler et al., 2016; Meyer et al., 2019), but when tree canopy cover is completely depleted, further increases are not expected (Beckage and Stout, 2000). On the other hand, we found a decreasing trend in the Shannon diversity index from low to high severities. This pattern can be related to pre-fire canopy structure, as the highest severities usually occur in areas with high tree abundance (Safford et al., 2009; Shive et al., 2013; García-Llamas et al., 2019), which have, in general, a less diverse understory (Beckage and Stout, 2000; Peterson and Reich, 2008; Tessler et al., 2016). We also found increases in total vegetation cover in the three study sites from the least (one wildfire and lowest severity) to the most disturbed scenario (three wildfires and highest severity). This shift can be attributed to faster recovery of shrubs, expected to dominate the most disturbed areas, than trees (Taboada et al., 2017; Fernández-García et al., 2018a). Thus, differences in structural parameters with recurrence and severity may be associated with the transition from forest to shrub-dominated ecosystems.

Effects of wildfire recurrence and burn severity on plant traits

The influence of wildfire recurrence and burn severity of the last wildfire on life forms supports the assumptions expressed above, since we found significant decreases in the relative cover (RC) of tree vegetation. Previous studies in different ecosystems have found similar trends in relation to fire recurrence (Blair et al., 2016; Tessler et al., 2016; Kowaljow et al., 2018) and burn severity (Crotteau et al., 2013; Fernández-García et al., 2018a). This result was expected because many shrub species in the study sites (e.g. Ericaceae and Cistaceae) find their optimal growth at short fire return intervals (5-10 years) (Fernández-García et al., 2018a) and are better colonizers of gaps created by high severities than trees (Crotteau et al., 2013). In contrast, pines, which are the dominant trees in the three study sites, need longer periods to reach maturity and produce viable seed banks to ensure natural regeneration (Santana et al., 2010), particularly in Mediterranean climates (Calvo et al., 2013). In fact, pine seedling density decreased from the one wildfire and low severity (dNBR < 0.55) to the three wildfires and high severity (dNBR ≥ 0.55) situations in all study sites, specifically: (i) from 12.04 ± 1.57 (pines $\text{m}^{-2} \pm$ standard error) to 0 in the Mediterranean, (ii) from 3.47 ± 0.47 to 0.35 ± 0.08 in the Transition and (iii) from 0.38 ± 0.13 to 0.24 ± 0.06 in the Oceanic site).

In relation to eco-physiological traits, we found that the RC of species with high SLA increased towards the humid side of the climatic gradient (Oceanic site) as well as in areas of high recurrence and severity, mainly due to the effect of wildfire recurrence. Anacker et al. (2011) found similar patterns three years after fire in chaparral ecosystems, with SLA increasing in the most humid and frequently burned sites. Regardless of climate and soil, these authors attributed this result to the positive relationship between SLA and resprouting ability at species level. However, in our study sites we did not find such a significant correlation, so results could be the consequence of different resource-use strategies between low and high SLA species (Dwyer et al., 2014; Michelaki et al., 2019). Thus, high SLA could be advantageous under high recurrence and severity regimes, because these species are characterized by low investment per leaf area, short life-leaf

spans and rapid growth, reaching maturity early (Dwyer et al., 2014; Dirks et al., 2017; Greenwood et al., 2017). Likewise, we found that species with N₂-fixing capacity were favored in the most disturbed situation compared to the least disturbed one. Increases in N₂-fixing vegetation abundance after fire have been detected previously (Cleveland et al., 1999; Reich et al., 2001), and can be related to soil N limitations for plant growth (Certini, 2005; Lajeunesse et al., 2006) and to raised N demands for rapid regrowth under frequent disturbance regimes (Sheffer et al., 2015). However, we found that N₂-fixing capacity was correlated with seed mass and with heat-stimulated germination, because in the Mediterranean site seeds of Fabaceae species (N₂-fixers) were predominantly heavy, and in the Oceanic site most Fabaceae species were facultatives with heat-stimulated germination.

The dominant regenerative strategy varied along the climatic gradient from obligate seeders in the Mediterranean site to vegetation able to resprout (resprouters and facultatives) in the Oceanic site. We suggest that this difference could be attributed to higher tolerance of obligate seeders to tissue dehydration, making them generally more resistant to drought than resprouters (Pausas et al., 2004; 2015), as well as to the limitation of available gaps for post-fire seedling recruitment in highly competitive environments (moist and fertile) such as the Oceanic site (Clarke et al., 2013; Pausas and Keeley, 2014). In the Mediterranean and Transition sites we confirm resprouting ability as a favourable trait to deal with high wildfire recurrence. This can be attributed to the capacity of resprouters to rapidly recover after fire, taking advantage of their surviving biomass (Calvo et al., 1998; Pausas and Keeley, 2014), and because their regeneration does not depend on seed production, which requires time to reach maturity (Pausas and Vallejo, 1999; Calvo et al., 2003).

Presence of underground buds was not clearly advantageous for resprouters throughout the climatic gradient. In this sense, Clarke et al. (2013) indicated that the number of buds as well as available resources must be taken into consideration along with bud location to understand the behavior of resprouting species. This assumption may support the positive

effect of severity on species with underground buds in the Transition site, represented only by *Erica australis* (Table A.2), as this species has a high number of buds in a lignotuber where it stores carbohydrates and mineral nutrients for resprouting (Calvo et al., 1998; Tavsanoğlu and Pausas, 2018).

Germination-related traits were among the most relevant in the Mediterranean side of the gradient. Nevertheless, light seeds and heat-stimulated germination were advantageous traits for seeders and facultatives along the entire gradient under combined increases in wildfire recurrence and burn severity. In general, seed mass was inversely related to wildfire recurrence, and heat-stimulated germination directly related to burn severity. Light seeds seem to be useful for colonizing burned areas because they have a high dispersion capacity (Delgado et al., 2008), and they show better fitness than heavy seeds in typical luminous conditions after fire (Dirks et al., 2017). Furthermore, the correlation between species' seed mass and time to reach maturity (Moles and Westoby, 2006) suggests that light-seeded species are at an advantage in recurrent crown fire regimes. The positive effect of burn severity on the RC of species with heat-stimulated germination can be attributed to massive germination caused by thermal shock at temperatures between 60 °C and 100 °C (Baskin and Baskin, 2014).

Influence of environmental conditions on the effects of wildfire recurrence and burn severity

The three study sites have different environmental conditions (soil type, elevation, land uses, fire history and climate) that may affect vegetation structure and traits in different ways, potentially interacting with wildfire recurrence and burn severity. Nevertheless, we found that the strength of the effects of recurrence and severity on the structure and traits of woody vegetation varied with climate, increasing from the Oceanic to the Mediterranean site in most cases. We suggest that this pattern could arise from any one of several underlying factors: (i) fast post-fire recovery in humid climates, which rapidly attenuates fire impacts (Pausas and Bradstock, 2007; Fernández-García et al., 2018b). (ii) The high productivity in humid climates, which could counteract the effects of wildfire

recurrence on traits linked to growth speed and time to reach maturity (e.g. SLA, resprouting ability, seed mass) (Enright et al., 2015). (iii) Soil moisture content attenuates temperatures reached during fire (Certini, 2005), thus potentially reducing the heat-stimulation of germination in upper layers of soil in humid climates. Moreover, moisture facilitates thermal transmissibility (Certini, 2005), likely increasing seed mortality in deep layers at high severities. (iv) Differences in competition, which are more relevant in highly productive environments, such as Oceanic sites, than in drier environments (Clarke et al., 2013; Pausas and Keeley, 2014), potentially masking the effects of recurrence and severity on vegetation. (v) Heat-stimulated germination is considered advantageous for withstanding both droughts and fires (Pausas et al., 2004; Keeley et al., 2011), and thus could be doubly relevant on the Mediterranean side of the gradient, where water deficits can be aggravated after fire (Certini, 2005). As a result, our findings suggest that the relationship between fire regime and plant traits requires a simultaneous consideration of climatic conditions (Pausas and Bradstock, 2007), although we recommend further evaluations to confirm this first evidence.

Concluding remarks

Changes in climate and land-use will modify fire regimes across the globe, and it is necessary to know the behavior of vegetation under these new scenarios to increase the resilience of ecosystems. In this sense, our study provides valuable information that anticipates future shifts in woody vegetation diversity and traits. Our results also indicate that these shifts could be more intense in warm climates with summer drought such as the Mediterranean and Transition climates than in Oceanic climates.

Among the effects of fire regimes on the woody community structure, we detected increases in alpha richness and diversity of woody species with wildfire recurrence, partially counteracted in areas where the severity of the last wildfire was high. Focusing on plant traits, our findings indicate that high wildfire recurrence and burn severity contribute to the loss of forests, facilitating the transition from tree- to shrub-dominated ecosystems. Our results also revealed that woody vegetation with non-arboreal life form, high SLA, N₂-

fixing capacity, resprouting ability and heat-stimulated germination is favored in regimes of high wildfire recurrence and burn severity, and that woody vegetation with low seed mass is favoured in regimes of high recurrence.

We provide valuable information to better understand the effects of shifts in wildfire recurrence and burn severity on vegetation structure and traits in a global change context. We highlight that shifts in fire regimes modify diversity and composition of woody species in post-fire environments, and we recommend maintenance of plant trait diversity at the community level to enhance ecosystem resilience in a changing world.

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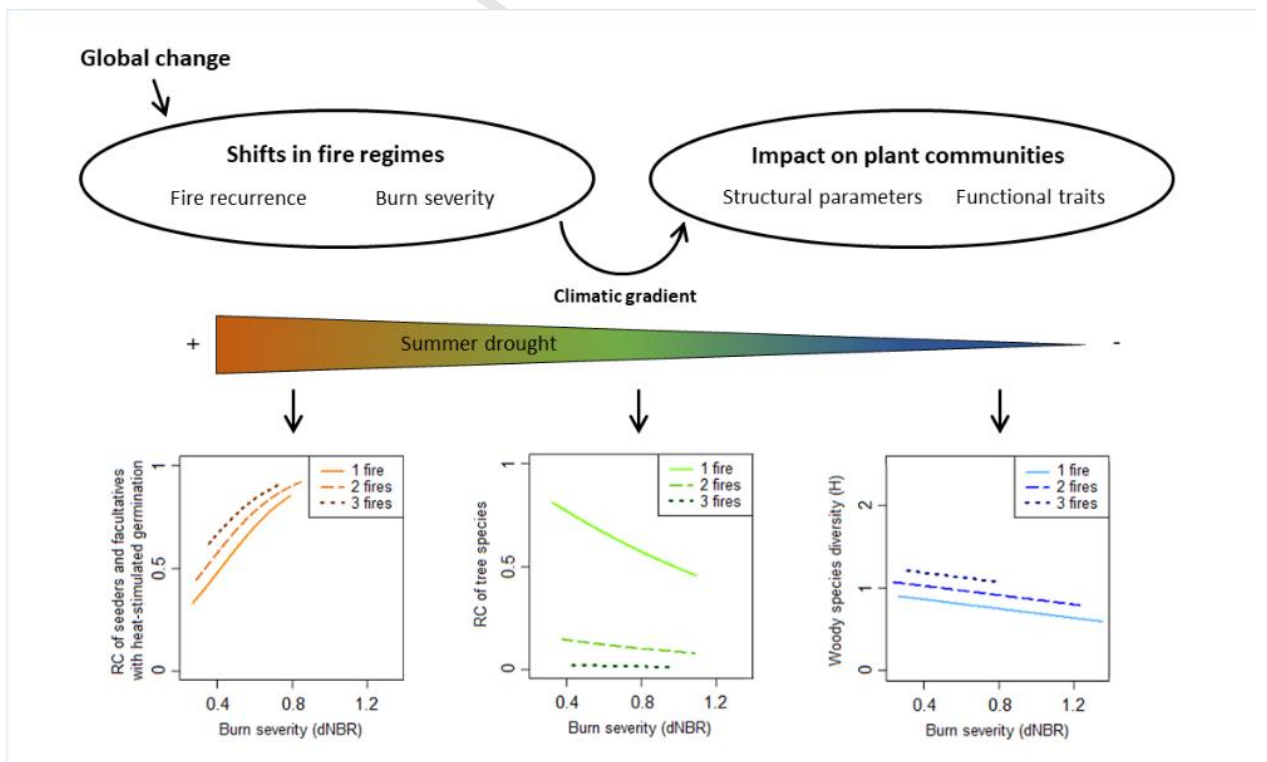
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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Graphical abstract



Highlights

Wildfire recurrence and burn severity modify plant species richness and diversity

High recurrence and severity fosters transition from forests to shrublands

Several plant traits are advantageous in fire regimes of high recurrence and severity

Fire recurrence and severity effects on vegetation may vary with climatic conditions

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