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RESEARCH PAPER

Fuel shapes the fire–climate relationship: evidence from Mediterranean ecosystems

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ABSTRACT

Aim To understand how vegetation mediates the interplay between fire and climate. Specifically, we predict that neither the switching of climatic conditions to high flammability nor the sensitivity of fire to such conditions are universal, but rather depend on fuel (vegetation) structure, which in turn changes with productivity.

Location An aridity/productivity gradient on the Iberian Peninsula (Mediterranean Basin).

Methods We defined 13 regions distributed along an aridity gradient, which thus differ in productivity and fuel structure. We then assessed the changes in the temporal fire–climate relationship across regions. Specifically, for each region we estimated three variables: the aridity level for switching to flammable conditions (i.e. climatic conditions conducive to fire), the frequency of these flammable conditions and the area burnt under such conditions. These variables were then related to regional aridity and fuel structure indicators.

Results In mediterranean ecosystems, the aridity level for switching to flammable conditions increased along the aridity gradient. Differences in fire activity between regions were not explained by the frequency of flammable conditions but by the sensitivity of fire to such conditions, which was higher in wetter and more productive regions.

Main conclusions Under mediterranean climatic conditions, fuel structure is more relevant in driving fire activity than the frequency of climatic conditions conducive to fire. At a global scale, fuel also drives the fire–climate relationship because it determines the climatic (aridity) threshold for switching to flammable conditions. Our results emphasize the role of landscape structure in shaping current and future fire–climate relationships at a regional scale, and suggest that future changes in the fire regime (i.e. under global warming) might be different from what it is predicted by climate alone.

Keywords

Climate, fire regime, flammability, landscape structure, productivity gradient, Iberian Peninsula.

INTRODUCTION

Fire is a widespread process in the earth system (e.g., Krawchuk & Moritz, 2011). It has been shaping ecosystems and influencing global biogeochemical cycles since the origin of terrestrial vegetation (Bond *et al.*, 2005; Bowman *et al.*, 2009; Pausas & Keeley, 2009; Bond & Scott, 2010). Nevertheless, current changes in fire regimes are having significant impacts on biodiversity and ecosystem functioning (Cochrane, 2003; Lavorel *et al.*, 2007). Consequently, there is increasing interest in disentangling the drivers of fire regimes world-wide (e.g. Westerling *et al.*, 2006; Marlon *et al.*, 2008; Krawchuk & Moritz, 2011) and implementing this knowledge in predictive tools for environmental management (Lavorel *et al.*, 2007; Flannigan *et al.*, 2009).

Climate controls fire regimes by acting on both fuel moisture (direct effect) and fuel structure (indirect effect). While fuel

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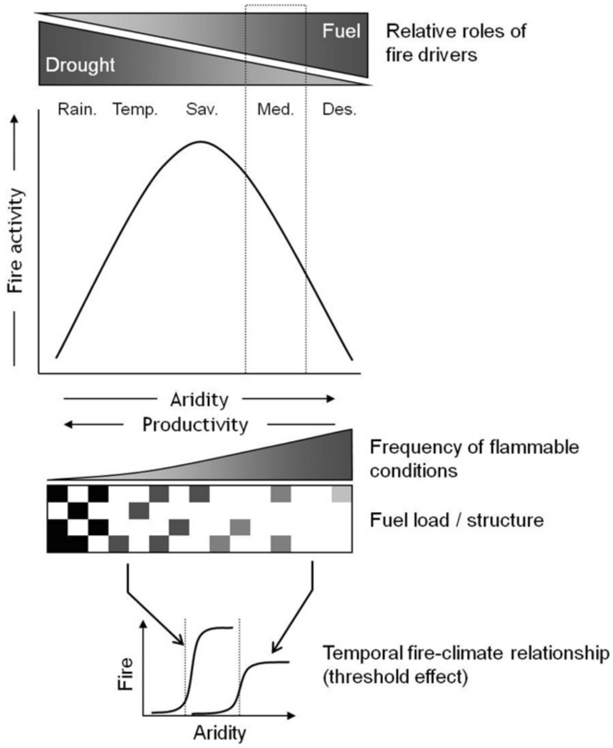

Figure 1 Changes in fire activity and the relative roles of fire drivers along the productivity gradient (modified from Pausas & Bradstock, 2007). Examples of the location of some biomes along the gradient are also provided (Rain, rainforest; Temp, temperate broad-leaved; Sav, savannas; Med, mediterranean; Des, deserts). In water-limited ecosystems (*sensu* Stephenson, 1990), the productivity gradient is inversely related to the aridity gradient. Notice that the availability of the two fire drivers (fuel structure and flammable conditions) change in opposite directions along the aridity gradient: the frequency of flammable conditions increases towards the arid end of the gradient, while fuels (represented in the fuel diagram by shaded squares) are more abundant (darker) and less fragmented (closer) towards the productive end of the gradient. The model was tested for mediterranean ecosystems (dashed rectangle), which fall within the arid portion of the gradient where drier regions are more fuel-limited and less drought-driven than moister regions.

moisture determines plant flammability (availability to burn), fuel structure refers to the amount and connectivity of burnable resources. Specifically, fuel flammability and fire hazard increase in dry and warm years (Flannigan & Harrington, 1988; Piñol *et al*., 1998; Founda & Giannakopoulos, 2009); fire activity may also increase when moist conditions precede the fire season by promoting fuel build-up (Keeley, 2004; Pausas, 2004; Littell *et al*., 2009; Archibald *et al*., 2010).

It has been proposed that the relative roles of both fuel structure and fuel flammability in determining fire activity change along the global productivity gradient (Pausas & Bradstock, 2007; Fig. 1): in moist and productive regions, fuel is not a limiting factor and fire activity is driven by the frequency with which flammable conditions are attained (drought-driven fire regimes); while in unproductive arid systems, fuel shortages determine fire activity (fuel-limited fire regimes). Several studies comparing regions with presumably contrasting productivity provide some support for this hypothesis (Spessa *et al*., 2005; Archibald *et al*., 2009; Littell *et al*., 2009), and recent findings add further evidence on a global scale (Krawchuk & Moritz, 2011).

Although the frequency of reaching flammable conditions depends primarily on climate, the specific conditions that make vegetation highly flammable should be mediated by the fuel structure. Fire spread depends basically on the balance between the heat released by the flame and the energy needed for the ignition of the surrounding fuel (Thomas *et al*., 1964). Because the heat for ignition is proportional to the fuel moisture, it is primarily related to weather conditions. However, the heat transferred from the flame and the combustion zone changes with fire intensity, which in turn depends on fuel structure and composition (Rothermel, 1972). Therefore, in productive ecosystems, dense fuel packing allows even low-intensity fires to spread easily, while sparse fuel in arid ecosystems requires drier weather conditions for fire propagation. In fact, fires in tropical rain forests occur under moister conditions than in other, drier, systems (Cochrane, 2003). This suggests that fuel determines fire activity, not only because it provides the resources for fire, but also because it modulates fire–climate relationships (i.e. the climatic conditions needed to promote fires).

Our hypothesis is that fuel (i.e. vegetation and landscape structure) shapes the fire–climate relationship at a regional scale. We predict that the climatic conditions that increase flammability, as well as the sensitivity of fire to such conditions, are not universal, but rather depend on fuel structure and thus change along the aridity/productivity gradient. To assess these predictions, we study the inter-annual variability of the fire–climate relationship (temporal scale) along a productivity gradient (spatial scale) under mediterranean conditions. Specifically, we analyse whether the monthly aridity (intensity and frequency) determining fire activity depends on regional climate (productivity), and thus on fuel structure (amount and connectivity), along a climatic gradient on the Iberian Peninsula. In this way, we explicitly test the conceptual model proposed by Pausas & Bradstock (2007) for a portion of the global productivity gradient (i.e. mediterranean conditions) and provide the underlying mechanism driving this fire–climate model on a global scale (Fig. 1).

METHODS

Study area

The Iberian Peninsula (western Mediterranean Basin) provides an excellent framework for evaluating our predictions because it is a clear biogeographic unit with high environmental variability. Climatic conditions range from dry mediterranean in the south-east to temperate in the north-west (Allué, 1990). This climatic variability, combined with the lithological diversity of the area (e.g. sandstone, limestone, granitic rocks and schist), provides a wide range of productivity conditions in a single biogeographic unit (Sánchez Palomares & Sánchez Serrano, 2000; see below).

Table 1 Summary of the linear regressions relating fuel load/structure indicators to the mean annual aridity index (AI), the aridity threshold (AT; the switch to high flammability) and the standardized anomaly in area burnt for months drier than the threshold (log-transformed). For the latter, linear mixed models were constructed. Positive relations are shown in bold. When significant spatial autocorrelation of the residuals was detected (i.e. significant Moran's index; Table S6), the *P*-values of the spatially corrected regression are indicated in brackets.

	Annual AI			AT			Anomaly in area burnt	
	R^2	F	P	R^2	F	P	χ^2	P
AET	0.61	17.37	**	0.55	13.56	** (**)	**17.47**	*** (***)
FPP	0.46	9.42	*	0.46	9.20	* (**)	**23.33**	*** (***)
Wildland area	0.40	7.39	*	0.49	10.36	** (ns)	**10.91**	*** (**)
Woodland area	0.46	9.48	* (*)	0.40	7.26	*	**4.48**	* (*)
Wildland + woodland	0.79	19.01	***	0.81	20.74	***	**16.67**	***
Fragmentation	**0.33**	**5.49**	*	**0.40**	**7.27**	*	4.70	* (*)

Productivity and fuel indicators: annual actual evapotranspiration (AET; mm), forest potential productivity index (FPP; log-transformed), proportion of total area occupied by wildland (Wildland area), proportion of wildland area covered by woodlands (Woodland area; tree canopy cover ≥ 30%), landscape fragmentation (Fragmentation; estimated as the mean distance between wildland patches; m).
****P* < 0.001; ***P* < 0.01; **P* < 0.05; ns, non-significant.

The vegetation is dominated by a mosaic of shrublands and low-stature forests that mostly burn in crown-fires (Keeley *et al.*, 2012). Currently, surface fires are rare and mainly restricted to montane (sub-mediterranean) areas (Pausas *et al.*, 2008).

Data sources

Fire data (1968–2007) were obtained from the Spanish Forest Service and include the date, size and location (administrative province) of each wildfire. The data cover the whole of Spain, except for two regions (Basque Country and Navarra), which were poorly represented in the database and thus excluded from the analysis.

The CORINE land-cover map of Spain (CLC2000; Nunes de Lima, 2005) was used to differentiate wildland (woodlands, shrublands, grasslands and agroforestry areas) from non-forested areas (crops, beaches, non-vegetated rocky outcrops, urban areas) and to analyse fuel cover and fragmentation statistics. As an indicator of productivity, we considered the forest potential productivity (FPP) map (1:1,000,000), which is based on Paterson's climatic index of forest growth, modified according to bedrock type (Sánchez Palomares & Sánchez Serrano, 2000).

Monthly actual and potential evapotranspiration (AET, PET) for the period 1968–2007 were obtained from raster layers (grid size 1 km^2) generated by the Spanish government's Environmental Bureau (available at: http://servicios2.marm.es/sia/visualizacion/descargas/). The raw data (temperature and precipitation) used to construct these layers came from more than 5000 weather stations. PET layers were generated from mean temperature data using the Thornthwaite method, and then corrected to infer PET following the Penman–Monteith method (Estrela Monreal *et al.*, 1999). AET layers were obtained by running the SIMPA hydrological model with precipitation and PET data (Estrela Monreal *et al.*, 1999).

To assess the relative climatic variability within and between the studied regions (see below) we used temperature and precipitation records (obtained from 1866 and 2585 weather stations, respectively) for the entire studied area and period (1968–2007). These data, and the mean monthly wind velocity for 78 locations distributed throughout the study area, were provided by the Spanish Meteorological Agency (AEMET).

Regions

To define environmentally homogeneous regions on the Iberian Peninsula, we combined the available information with the main Iberian river basins. Fire data (area burnt) were provided by province, and some provinces fell into more than one river basin. In these cases, provinces were assigned to the basin that covered most of the province; if in doubt, climatic similarity was also considered. We finally obtained 13 regions (mean ± SD area: 38,342 ± 24,964 km^2) covering 82% of the Iberian Peninsula: 12 corresponding to the basin of an important river and one to an archipelago (Balearic Islands; see general characteristics in Tables S1 & S2 in the Supporting Information). The climate was more homogeneous within than between regions (Table S3), and thus these regions differed significantly in both productivity and vegetation composition (Table S4). The average climatic conditions of these regions form an aridity gradient that is strongly related to productivity and fuel structure (Tables 1 & S1). Despite the long history of land use in the area (Blondel *et al.*, 2010), the current landscape fragmentation (i.e. the distance between wildland patches; see below) was not related to the mean population density of the last decades (1976–2000), considering either the active or the rural population ($P > 0.1$ in the generalized least squares model corrected by the spatial correlation structure; data provided by the National Statistics Institute of Spain, INE). Therefore, landscape changes along the aridity gradient were mostly related to environmental conditions.

Data analyses

Fuel

To obtain a general characterization of the fuel structure (amount and connectivity) in each region, we considered the following parameters: FPP, proportion of wildland area (including all types of vegetation), proportion of woodland area (i.e. vegetation with tree canopy cover ≥ 30%, which represents the patches with the highest fuel load), and distance between wildland patches (as a proxy for landscape fragmentation). For each region, FPP was calculated as the average of the FPP indices for all patches (forested and non-forested) within the region, weighted by the corresponding patch area. Total wildland and woodland areas were computed by adding up the corresponding patch areas obtained from the CLC2000. Finally, distance between forested patches (assuming the eight-neighbourhood rule from the CLC2000 map) was computed as the distance to the nearest neighbouring patch based on shortest edge-to-edge distance, using FRAGSTATS (McGarigal *et al.*, 2002). We used this measure as it is directly related to fuel continuity across landscapes and thus to fire spread and activity; in fact, this index was correlated with the aridity gradient (see below; Table 1). Other indices of landscape fragmentation, like patch density or patch size (e.g. Duncan & Schmalzer, 2004), were not correlated with the aridity gradient ($R^2 = 0.04$ and $R^2 = 0.11$ respectively; $P < 0.1$ in both cases) and thus they were excluded from the analyses.

Climate

Monthly climatic maps were intersected with the regions to obtain average climatic conditions for each month and region. We then defined an aridity index (AI) as the difference between PET and AET, standardized by PET (Thornthwaite & Mather, 1957). This index reflects the evaporative demand not met by available water and integrates both water and energy supplies, which in turn are the climatic determinants of plant growth and vegetation distribution (Stephenson, 1990). Furthermore, water balance variables are better predictors of area burnt than temperature and precipitation (Littell & Gwozdz, 2011). This AI was computed monthly for each region for the entire study period (1968–2007; monthly AI) and for the average conditions of each region (i.e. mean annual AI, considering the hydrological year from October to September; Table S1). The latter was used to define the aridity/productivity gradient across regions. The advantages of this mean annual AI are that it is based on good quality data, it integrates long-term mean conditions, and it is independent of land use. The mean annual AI was correlated with productivity indicators (FPP and AET) and with variables related to fuel load/structure (Table 1). By contrast, this index was uncorrelated ($P = 0.858$) with mean wind velocity during the fire season, and thus any changes in fire activity along the aridity gradient were not explained by wind patterns.

Fire season

Temporal fire–climate relationships were analysed only for the months of June to September (hereafter, fire season), i.e. the period during which most of the area annually affected by fire burns, especially when considering lightning-fires only (Table S2).

Thresholds

Preliminary analyses showed that, for all regions, the monthly area burnt was higher for months with a high AI. Nevertheless, these two variables were not linearly related, but rather the area burnt increased sharply with monthly aridity beyond a threshold value (Fig. S1). To estimate this threshold, for each region we sorted the monthly area burnt by the monthly AI and estimated the breakpoint with the sequential *F*-test from the *strucchange* library of the R package (Zeileis *et al.*, 2002). The AI associated with this breakpoint was considered to be the aridity threshold (AT) beyond which a switch to flammable conditions occurs. To ensure we cover a wide range of aridity and area burnt, our estimation of the AT was conducted by including all fire season months during all available years. For all regions, there was more variability in area burnt between months (within each year) than between years (Table S2); therefore, the risk of pseudoreplication was low.

Patterns along the aridity gradient

We describe the fire–climate relationship within each region (i.e. at temporal scale) by means of the following variables: (a) the AT for switching to flammable conditions (see above); (b) the frequency of flammable conditions (i.e. months drier than the AT), and (c) the anomaly in the area burnt under such conditions (standardized to the mean monthly area burnt for the entire study period). We analysed the changes in these parameters along the aridity gradient by testing their relation to the mean annual AI of each region. First, we tested whether the aridity gradient explained the variability in the AT by means of a linear regression analysis. The analysis was then repeated considering the fire season AI (i.e., the mean monthly AI during the fire season months) as the explanatory variable to assess to what extent the AT was similar to average conditions during the fire season. To analyse changes in the frequency of flammable conditions along the aridity gradient, we used a generalized mixed model (GLMM) with a binomial error distribution and logit link function, which included the mean annual AI as a fixed factor and year as a random factor (i.e. repeated measures analysis). Analogously, we used a linear mixed model with the mean annual AI as a fixed factor and year as a random factor to assess the variability of the standardised anomaly in the area burnt (log-transformed) along the aridity gradient. The latter test was conducted separately for months both drier and wetter than the threshold. For mixed models, model fit and estimation of dispersion was conducted using an analysis of deviance, and maximum likelihood for parameter estimation. The significance of the contribution of the spatial aridity gradient on the variability of mixed models was calculated by comparing the null model (including year as a random factor only) with an alternative one that incorporates the mean annual AI as an explanatory variable by means of a likelihood ratio test. All mixed models were performed with the *lme4* library of the R package (Pinheiro & Bates, 2009). The AT and the anomaly in the area burnt were also related to the indicators of fuel structure

(Table 1) using a similar approach. All regressions were weighted by one minus the *P*-value of the estimated AT to give more weight to those regions for which this value was estimated with less uncertainty. Preliminary tests without considering weight provided the same results (not shown).

Spatial autocorrelation analysis

We assessed the spatial autocorrelation in all the studied variables by means of the Moran's *I* autocorrelation index, with the help of the *ape* library in the R software package (Paradis *et al.*, 2004). For each region, the spatial coordinates were computed as the mean of the spatial centroid of each forest patch, weighted by the corresponding patch area. As expected, most variables were spatially autocorrelated (Table S5). Therefore, we estimated the Moran's *I* of the residuals of each of the regressions considered; for mixed models, we considered the mean of the residuals (by region). In the case of spatially autocorrelated residuals, the regression was repeated by means of a generalized least squares model including a spatial correlation structure (using the *nlme* library of the R software; Pinheiro & Bates, 2009). Gaussian, exponential, linear, rational quadratics and spherical spatial correlation structures were tested, but only those producing the lowest Akaike information criterion (AIC) were used.

RESULTS

The relationship between monthly area burnt and monthly AI showed a threshold pattern in the 13 Iberian regions (temporal scale analysis; Fig. S1). This threshold was located at different aridity levels depending on the environmental conditions of each region (spatial scale analysis). Specifically, the AT was linearly related to the mean annual AI, in such a way that the drier the region, the higher the AT ($R^2 = 0.95$, $F_{1,11} = 200.53$, $P < 0.001$; Moran's index = –0.12, $P = 0.458$). Similarly, the AT was higher for less productive regions, with lower fuel loads and connectivity (Table 1). The AT was also related to the fire season AI (i.e. the mean monthly AI during the fire season months; Fig. 2). The fact that the regression slope was significantly lower than 1 (Fig. 2) indicates that, in drier regions, the AT was closer to the average climatic conditions during the fire season than in more productive regions. In fact, the required change in the fire season AI to attain flammable conditions (i.e. the difference between the mean conditions during the fire season and the AT) was negatively related to the mean annual AI (Pearson's correlation = –0.76, $P = 0.003$). That is, productive regions require a greater reduction in moisture to become flammable (e.g. the change in the AI required to reach flammable conditions in the wettest region is twice the required change for the driest region). The frequency of exceeding this threshold (i.e. the rate of switching to flammable conditions) is also higher in dry environments (Fig. 3a), in spite of their lower climatic variability (the standard deviation of the AI during the fire season is negatively correlated with the mean annual AI; Pearson's correlation = –0.58, P = 0.038; Table S1, Fig. 2).

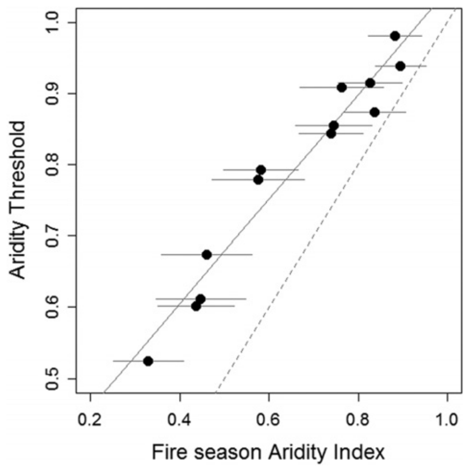

Figure 2 Relationship between the fire season aridity index (i.e. the mean monthly AI during the fire season months) and the estimated aridity threshold (AT) above which area burnt increases abruptly for 13 mediterranean regions located on the Iberian Peninsula (see Fig. S1). The continuous line represents the fitted linear regression [$R^2 = 0.95$, $F_{1,11} = 192.63$, $P < 0.001$; confidence interval for the estimated slope (0.62,0.85)]. The dashed line represents the values for which the AI matches the AT (1:1 line). Horizontal bars represent the inter-annual variability (SD) in AI. The residuals of this regression were not spatially autocorrelated (Moran's index = –0.08, $P = 0.955$). The relationship is also highly significant using the mean annual (regional) AI as an independent variable ($R^2 = 0.95$, $F_{1,11} = 200.53$, $P < 0.001$; Moran's index = –0.12, $P = 0.458$).

In the range of conditions tested, fire activity was negatively related to the aridity of the region (the Pearson's correlation between mean annual AI and proportion of wildland area annually burnt was –0.58, $P = 0.037$), in such a way that productive regions burnt more than arid regions. However, this negative relation was not explained by the frequency of flammable conditions (see above; Fig. 3a), but by the total area burnt under such conditions. That is, for dry months (drier than the AT), the standardized anomaly in area burnt decreased along the aridity gradient (closed symbols in Fig. 3b). This contrasts with the absence of a pattern during wet periods (i.e. months wetter than the AT; open symbols in Fig. 3b). Accordingly, the standardized anomaly in area burnt during dry months increased with fuel amount and connectivity (i.e. towards the mesic regions; Table 1) suggesting that, in the studied part of the global aridity gradient, fuel structure is a more relevant factor than the frequency of drought (Fig. 1).

DISCUSSION

Fuel structure and flammability have both been proposed as alternative drivers of fire regimes (e.g., Minnich, 1983; Keeley *et al.*, 1999; Keeley & Zedler, 2009). Here we show evidence that both drivers may act simultaneously, and not necessarily over the same (temporal/spatial) scale. Under the range of conditions analysed, climate shapes fire activity on a temporal scale by

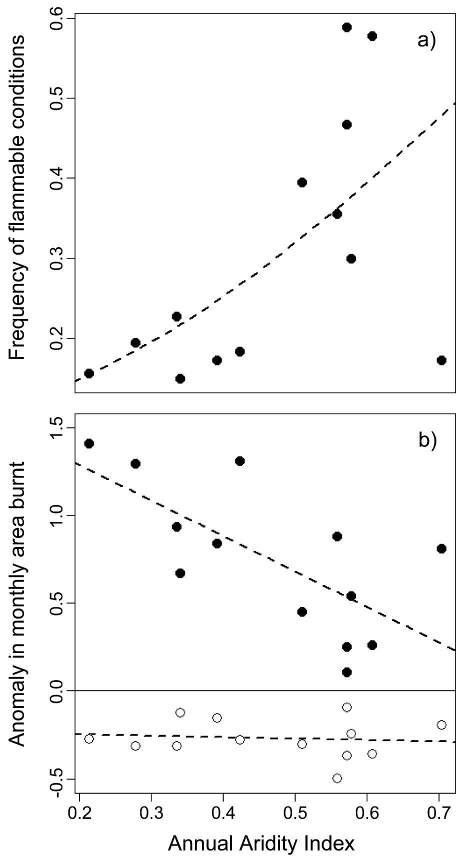

Figure 3 Fire–climate relationships along the aridity gradient of the studied area (see Fig. 1 for their location on the global aridity gradient). (a) Relationship between the regional (mean annual) aridity index (AI) and the mean frequency of fire-prone months [i.e. months drier than the aridity threshold (AT) during the fire season]. The dashed line represents the fitted logistic mixed model ($\chi^2 = 93.58$, $P < 0.001$). The residuals were not spatially autocorrelated (Moran's index = –0.02; $P = 0.291$). (b) Relationship between the regional AI and the anomaly in area burnt (standardized to the mean area burnt during the fire seasons) for months drier (closed symbols) and wetter (open symbols) than the AT. The dashed line represents the fitted linear mixed models (closed symbols: $\chi^2 = 20.56$, $P < 0.001$; open symbols: $\chi^2 = 0.14$, $P = 0.711$). The residuals were not spatially autocorrelated for wet months (Moran's index = –0.05; $P =$ 0.555), although they were for dry months (Moran's index = 0.09; $P = 0.004$). However, the results did not change ($P < 0.001$) when the spatial structure was included in the model. See Table S7 for further details on the results of the mixed models.

modifying fuel flammability (i.e. more fire during dry years) and on a spatial scale by affecting fuel structure (i.e. more fire in productive regions). That is, although dry conditions are necessary to achieve high flammability, changes in fire activity along our aridity gradient are not controlled by the frequency of flammable conditions (they are negatively related; Fig. 3), but rather by the fuel structure. The change in fire activity between dry (i.e. flammable) and wet (non-flammable) months decreases along the aridity gradient (Fig. 3b), indicating that the sensitivity of fire activity to dry conditions increases with productivity. In other words, switching to flammable conditions has a greater effect on fire activity in productive systems than in dry ones. These results suggest that our study area is located within the fuel-limited section of the global aridity gradient (the right end of Fig. 1). On the opposite end of the global gradient (highly productive ecosystems; the left end of Fig. 1), fire activity should be driven by the frequency of flammable conditions (i.e. months drier than the AT); for instance, in tropical rain forests and temperate ecosystems, fire is associated with infrequent severe droughts (Cochrane, 2003; Westerling *et al.*, 2011). Even over the relatively short gradient considered in this study (Fig. 1), the relative role of each fire driver changes spatially with regional aridity: in mesic regions, fuel is less limiting and fire depends on the occurrence of climatic conditions conducive to ignitability and fire propagation (drought-driven fire regime; Fig. 3a); in drier regions, in spite of the high frequency of flammable conditions, area burnt is low due to the low fuel load and connectivity (fuel-limited fire regime; Fig. 1).

On a temporal scale, fire and climate are not linearly related, but there is a critical aridity level (i.e. the climatic threshold; AT) above which fuels become highly flammable and area burnt increases sharply (Fig. S1; see also Flannigan & Harrington, 1988 and Westerling & Bryant, 2008). This threshold acts as a climatic switch for fire (*sensu* Bradstock, 2010), in such a way that if the climatic conditions are drier than the threshold, the climatic switch is turned 'on', and fire will occur depending on the status ('on/off') of other switches, such as fuel availability (load and connectivity). The AT is not universal, but rather intrinsic to an ecosystem (i.e. to its landscape structure). This ecosystem-dependent switch is analogous to the intra-specific variations in the response to lethal thermal doses in a wide range of organisms (e.g., Fangue *et al.*, 2006; Sorte *et al.*, 2011), including humans (Davis *et al.*, 2003; García-Herrera *et al.*, 2005). In our study area, the drier the region, the higher the dryness level needed for switching from non-flammable to flammable conditions (Fig. 2), suggesting that the AT is mediated by fuel. In productive regions, an ignition may lead to a fire under conditions of relatively high moisture (compared to drier regions) due to the high fuel load and connectivity. However, this does not mean that these regions burn more frequently or require less drought to burn, because their AT is further away from their average conditions (Fig. 2) and is rarely exceeded (Fig. 3a). On the contrary, in dry regions, wildfires are more fuel-limited, so more extreme climatic conditions (higher aridity than in more mesic regions) are needed for fires to spread successfully; but as these extreme conditions are not far from average conditions, dry regions become flammable more frequently than wetter regions (Fig. 2, Fig. 3a).

The fact that the AT is intrinsic to the ecosystem emphasizes the importance of landscape structure in determining fire–climate relationships along the climatic gradient (spatial scale): the climatic control of fire activity is exerted through fuel structure, because fuels are not only burnable resources, but they also determine the climatic conditions that drive the switch to high flammability (Table 1, Fig. 2). Fuel structure, which forms the basis for different fire regimes (Pausas & Keeley, 2009), also shapes the fire–climate relationship on a temporal scale. The influence of antecedent climate on fire activity (through fuel build-up) has been detected in regions where surface fires are common (Kitzberger *et al*., 1997; Veblen *et al*., 1999; Grau & Veblen, 2000; Littell *et al*., 2009; Archibald *et al*., 2010), and fire depends on fast-growing fine fuels that are highly sensitive to a single wet period. In ecosystems characterized by crown-fires that burn slow-growing fuels, as is the case for our system, fire activity should be less sensitive to precedent climate. Consequently, only exceptionally wet years may have an important effect on fuel availability and only very long time-series will be able to detect any significant effects of preceding climatic conditions on fire activity (e.g. Keeley, 2004; Pausas, 2004).

Global models predicting future wildfires under scenarios of climatic change show high spatial variability, with increased, decreased or even no changes in fire activity (Flannigan *et al*., 2009). Increased fire activity is predicted in highly productive regions (Scholze *et al*., 2006), where fires are currently limited by the occurrence of flammable conditions (Fig. 1). Our results provide the underlying mechanism for these findings, because we found that the fire–climate relationship changes along the productivity gradient and that wetter systems become flammable under wetter conditions compared with drier regions (Fig. 2). In highly productive regions, a small reduction in moisture might not have a significant effect on productivity (i.e. a decrease in fuel load and connectivity). However, if this small climatic change increases the probability of exceeding the AT, then it would have important fire impacts on the ecosystems – impacts far greater than direct climatic effects (Littell *et al*., 2010; Westerling *et al*., 2011). On the contrary, in low-productivity regions, where fires are limited by fuels, aridification may exacerbate fuel limitations and thus fire activity will decrease (Pausas & Bradstock, 2007). That is, fuel structure not only plays a key role in shaping current fire regimes world-wide (Pausas & Keeley, 2009), but it will also drive the direction of future fire regimes. In fact, projections of global fire distribution under future climate conditions differ depending on whether shifts in vegetation tracking climate change are considered or not (Krawchuk *et al*., 2009). However, vegetation shifts would not only respond to direct climatic changes (e.g. Cramer *et al*., 2001), but also to other global change factors. For instance, elevated CO_2, the spread of exotic plants and changes in decomposition rate all have the potential to change fuel structure and thus fire regimes (D'Antonio & Vitousek, 1992; Bond *et al*., 2003). Furthermore, negative feedbacks in fire–climate–vegetation interplay can be expected under the climate change scenario, since a shorter fire return would preclude fuel build-up and ultimately diminish fire activity (Krawchuk & Cumming, 2011). That is, climate warming might shift some ecosystems from drought-driven to fuel-limited systems.

Fuel structure does not depend exclusively on environmental conditions (e.g. aridity/productivity); shifts in fire activity have also been related to changes in land use (Guyette *et al*., 2002; Marlon *et al*., 2008; Pausas & Fernández-Muñoz, 2012) and fire-suppression policies (e.g. Minnich, 1983; Covington & Moore, 1994). Gradual historical shifts in land use may produce abrupt changes in fuel structure across landscapes, and thus in fire activity (Pausas & Fernández-Muñoz, 2012). Therefore, the fire–climate relationship changes not only spatially with fuel along the aridity gradient but also temporally (and abruptly) in response to different land uses and management practices. Consequently, in many ecosystems, landscape management may have a stronger influence on future fire regimes than the direct effects of climate change.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Climatic characteristics of the studied regions.
Table S2 Fire statistics for each of the studied regions.
Table S3 Climatic variability between and within regions.
Table S4 Tests for homogeneity comparing forest potential productivity and vegetation among regions.
Table S5 Spatial autocorrelation for the variables studied.
Table S6 Spatial autocorrelation of the residuals of the linear regressions.
Table S7 Results of the mixed models.
Figure S1 Relation between monthly area burnt and monthly aridity for each Iberian region.

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