

ORIGINAL RESEARCH



Modeling fuel moisture dynamics under climate change in Spain's forests



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Abstract

Background Current assessments of the effects of climate change on future wildfire risk are based on either empirical approaches or fire weather indices. No study has yet used process-based models over national scales to understand how and where will increases in climate aridity affect the likelihood of fire activity through changes in the moisture content of live (LFMC) and of dead (DFMC) fuels. Here, we used process-based models to forecast changes in LFMC and DFMC under the 21st century climatic conditions projected from moderate and high greenhouse gas emission scenarios (RCP4.5 and RCP8.5). Predictions were performed across broad productivity gradients in peninsular Spain to understand how productivity mediates the effects of climate change on fuel moisture dynamics.

Results LFMC and DFMC were predicted to decline under the climatic conditions projected for the coming decades. Increases in the annual frequency of days with fuel moisture content below wildfire occurrence thresholds were predicted to extend fire season lengths by 20 days under RCP4.5 and by 50 days under RCP8.5. The effects of climate change on LFMC and DFMC varied linearly and negatively with productivity (stronger fuel moisture decreases in least productive environments). Although we observed a significant mitigation effect from rising CO₂ (via increases in water-use efficiency), it was not enough to offset LFMC declining trends induced by increased temperature and aridity.

Conclusions We predicted that the warmer and more arid climatic conditions projected for the 21st century will lead to generalized declines in fuel moisture, lengthening fire seasons, and increasing wildfire danger. The use of process-based models to forecast LFMC dynamics allowed the consideration of plant species capabilities to buffer climate change impacts. Significant increases in the fire season length predicted in the most productive environments, currently with large fire return intervals, would pose an increase of fire danger in major Spanish carbon sinks. Finally, the CO₂ mitigation effect would not be enough to offset climate change-driven declines in seasonal LFMC levels.

Keywords Climate change, Drought, Fuel moisture, Plant hydraulics, Mediterranean

Resumen

Antecedentes Las determinaciones actuales sobre los efectos del Cambio Climático en el riesgo de incendios a futuro están basados en aproximaciones empíricas o en índices de peligro. Ningún estudio hasta ahora ha usado modelos basados en procesos a escalas nacionales para entender cómo y cuándo los incrementos en la aridez del clima afectarán la posibilidad de la actividad del fuego a través de cambios en el contenido de humedad de combustibles vivos (LFMC) y muertos (DFMC). Usamos en este caso modelos basados en procesos para predecir cambios en

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el LFMC y el DFMC bajo las condiciones pronosticadas para el siglo XXI de escenarios de emisiones de efecto invernadero que dan incrementos de moderados a altos (RCP4.5 and RCP8.5). Las predicciones fueron realizadas a lo largo de gradientes muy amplios de productividad en la España peninsular para entender cómo la productividad interviene sobre los efectos del Cambio Climático en la dinámica de la humedad de los combustibles.

Resultados Los resultados predijeron una declinación en los valores de LFMC y DFMC bajo las condiciones climáticas proyectadas para las próximas décadas. El incremento en la frecuencia de días con humedad del combustible por debajo de los umbrales de ocurrencia de incendios fue pronosticado como para extender la estación de fuegos por 20 días bajo el escenario RCP4.5 y por 50 días bajo el escenario RCP8.5. Los efectos del Cambio Climático sobre el LFMC y el DFMC varió lineal- y negativamente, con la productividad (una mayor disminución de la humedad del combustible en ambientes menos productivos). Aunque observamos una mitigación significativa del efecto del aumento del CO₂ (vía incrementos en la eficiencia en el uso del agua), éste no fue suficiente para compensar las tendencias declinantes en el LFMC inducida por el incremento de la temperatura y la aridez.

Conclusiones Predecimos que las condiciones climáticas hacia períodos más cálidos y áridos proyectados para el siglo 21, llevará a declinaciones en la humedad de los combustibles, alargando las estaciones de fuego e incrementado el riesgo de incendios. El uso de los modelos basados en procesos para pronosticar la dinámica del LFMC, permite considerar las capacidades de las especies de plantas para compensar los impactos del Cambio Climático. Los incrementos significativos en la duración de la temporada de incendios predicha para ambientes más productivos, actualmente con largos intervalos de retorno del fuego, va a producir un incremento en el riesgo de incendios en los mayores almacenes de carbono en España. Finalmente, el efecto de las mitigaciones de CO₂ no va a ser suficiente para compensar las disminuciones en niveles de LFMC causados por el Cambio Climático.

Background

Water scarcity is projected to increase in Europe, among other parts of the world, as a result of climate change (IPCC 2021). In ecosystems where plant biomass (i.e., fuel) is abundant enough to sustain fire spread, fire activity is primarily constrained by fuel availability to burn, which is determined by the frequency and duration of hot and dry weather events (Boer et al. 2021). Consequently, climate change may increase wildfire risk and fire season length in many European regions, as fuel moisture declines below critical dryness thresholds for longer periods (Jolly et al. 2015, Resco de Dios et al. 2021, Carnicer et al. 2022). A key aspect for fire prevention and management actions relies in understanding temporal and spatial moisture content variations of both dead and live fuels. Live fuel moisture content (LFMC) shows seasonal variations within and among plant species due to differences in anatomical and physiological traits that interact with environmental conditions (Balaguer-Romano et al. 2022). On the other hand, dead fuel moisture content (DFMC) shows daily scale variations as it responds rapidly to atmospheric changes in temperature and relative humidity, especially in the case of fine fuels as leaves and twigs (Resco de Dios et al. 2015).

Although drought indices derived from fire weather and fire danger rating systems (McArthur 1966, Van Wagner 1987) were not developed to model fuel moisture, they are nonetheless used to estimate LFMC and DFMC dynamics. As these indices are based on daily weather data which can be easily obtained, many studies assessing future wildfire risk by modeling fuel moisture dynamics under climate change projections are primarily based on drought indices estimations (Rigo et al. 2018, Dupuy et al. 2020, Gannon and Steinberg 2021, Ellis et al. 2022). But, while drought indices can reasonably assess future DFMC dynamics (Matthews 2014), they make simplifying assumptions about how LFMC will change under a warming climate. That is, they usually infer LFMC from variations in weather conditions and, consequently, they ignore species-level physiological capabilities to adjust the moisture status of live tissues, potentially leading to future wildfire risk mispredictions.

One of the key physiological adjustments that may delay or prevent critical dryness transitions in live fuels arises from increasing atmospheric CO_2 concentrations. Stomatal aperture often responds negatively to increasing CO_2 concentrations (Wullschleger et al. 2002), and that may serve as a water conserving mechanism that enhances water use efficiency and thus LFMC. Otherwise, future drier conditions may also alter the demand of living tissues relative to water and carbon fluxes, potentially altering current fuel moisture dynamics (McDowell et al. 2022). There is a wide variety of physiological adjustments that interact with environmental conditions and understanding future variations in LFMC would benefit from process-based modeling in order to improve the biological realism of wildfire danger assessments.

Climate shapes global fire distribution as it constrains the amount and timing of plant available water which, in turn, drives biomass production and fuel dryness, the main conditions for wildfire occurrence (Boer et al. 2021). Fire activity varies unimodally across productivity/aridity gradients, reaching peak values at intermediate productivity levels and decreasing towards extremes. Arid ecosystems may not have biomass high enough to sustain a fire, while very mesic ecosystems may be too wet to sustain fires (Pausas and Ribeiro 2013). Climate change is expected to shift this fire maximum towards more productive ecosystems as climate aridity increases the frequency and intensity of droughts and fuel drying events. Even forested ecosystems with large fire return intervals, currently associated with high fuel moisture contents, may dry out periodically and be subject to large wildfire events in the coming decades (Resco de Dios et al. 2021, Ellis et al. 2022). Whether this switch is likely to occur, depends on the extent to which increasing climate aridity affects fuel moisture dynamics. But current Land Surface Models and Fire-enabled Dynamic Global Vegetation Models (Hantson et al. 2016, Rabin et al. 2017, Teckentrup et al. 2019) cannot yet fully account all relevant climate-vegetation-fire interactions.

General Circulation Models (GCMs), which represent the major climate system components and their interactions (Taylor et al. 2012), together with future greenhouse gas emission and socioeconomic scenarios, as the Representative Concentration Pathways (RCPs; Moss et al. 2010), are the main tools to simulate future climates (Rodríguez and Gutiérrez 2018). Several projections of future wildfire risk under climate change conditions have been conducted using different GCM and RCP, concluding that increased climate aridity would lead to fuel moisture declines and, consequently, to fire seasons lengthening and fire activity increasing during the 21st century (Matthews et al. 2011, An et al. 2015, Abatzoglou, et al. 2019, Varela et al. 2019, Dupuy et al. 2020, Fargeon et al. 2020, Gao et al. 2021, Ma et al. 2021, Vilar et al. 2021, Ellis et al. 2022, Jones et al. 2022). It is important to highlight that even relatively minimum fuel moisture decreases can result in disproportional area burned increases, as the relationship between fuel moisture and fire activity is exponential (Resco de Dios et al. 2022). However, besides the importance of the accurate characterization of fuel moisture dynamics under climate change, no study has so far provided future LFMC estimates using process-based models for a wide range of species and sites distributed across broad climatic and productivity gradients.

Climate-driven fire activity increases have been projected worldwide and have become a major concern in southern Europe (Dupuy et al. 2020). In the last decades, rural land abandonment (Gelabert et al. 2022) together with fire suppression strategies (Stephens et al. 2018) have promoted the increase of forest cover that accumulates huge fuel loads with large spatial connectivity (Resco de Dios et al. 2021). Spain is representative of these changes within southern Europe, with forested land surface increasing by 33% in the last three decades (FAO 2020). More frequent and intense drought events (IPPC 2021), as well as increases in competition for water resources in these densely forested areas, are leading to earlier and longer fire seasons (Vilar et al. 2021). The recent extreme 2022 wildfire season, which has led to abnormally high burned area values in the region, has been related to record-breaking values of fuel dryness (Rodrigues et al. 2023). In this context, the early warming capacity of wildfire danger would benefit from modeling fuel moisture dynamics under a process-based perspective.

Here, we sought to test the general hypothesis that climate change will cause increasing fuel dryness and, consequently, increasing fire season length, across Spain's forest regions during the 21st century. We also hypothesize that climate change effects over fuel dryness will depend on vegetation productivity and that enhanced water use efficiency derived from increased CO_2 effects will not fully compensate for changes in temperature and precipitation. We use different GCM projections during the 21st century under different RCPs (RCP4.5 and RCP8.5) as inputs for LFMC and DFMC process-based models (Resco de Dios et al. 2015, Balaguer-Romano et al. 2022). We then address LFMC and DFMC dynamics and analyze subsequent changes in fire season length by assessing the number of days per year with values below fuel dryness thresholds. We then study how changes in fuel moisture and fire season length vary across gradients of net primary productivity (NPP), to assess whether changes in the potential fire season will be amplified or reduced across productivity gradients. Finally, we analyze CO₂ effects on LFMC dynamics to test the hypothesis that increasing CO₂ concentrations will enhance the water-use efficiency of the vegetation, thus counteracting the negative effects of the increases in water stress due to more frequent and intense water scarcity under global warming. Overall, this represents the first effort to predict fuel moisture dynamics under climate change over broad climate and productivity gradients using processbased models.

Materials and methods

Study sites

We predicted live and dead fuel moisture content variation across many of the contrasting climates and ecoregions of peninsular Spain (Fig. 1). Study site locations correspond with plots from the Third National Forest Inventory of Spain (Alberdi et al. 2016), and they are monospecific stands of six broadleaf species

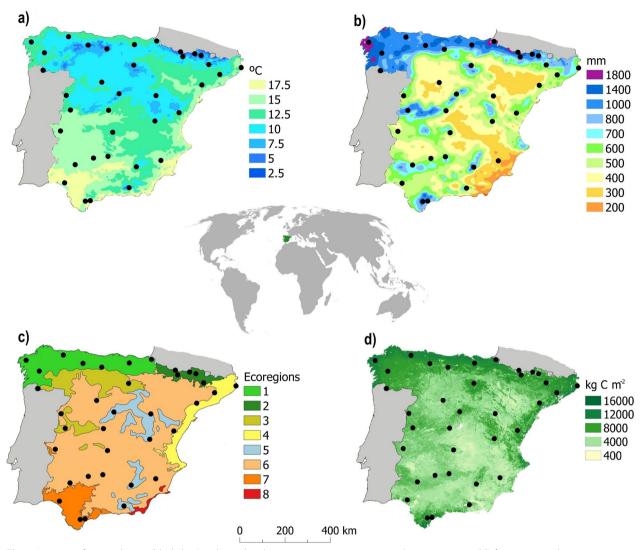


Fig. 1 Location of our study sites (black dots) and main bioclimatic properties: **a** mean annual air temperature (°C), **b** mean annual precipitation (mm), **c** ecoregions, **d** mean annual net primary productivity (kg C m⁻²) between 2010 and 2020. Ecoregion delimitations were obtained from WWF (Dinerstein et al. 2017) and they indicate Cantabrian mixed Forests (1); Pyrenees conifer and mixed forests (2); Northwest Iberian Montane Forests (3); Northeast Spain Mediterranean forests (4); Iberian conifer forests (5); Iberian sclerophyllous and semi-deciduous forests (6); Southwest Iberian Mediterranean sclerophyllous and mixed forests (7); Southeast Iberian shrubs and woodlands (8). Meteorological data is from Chazarra Bernabé et al. (2018) and mean annual net primary productivity values are from Running & Zhao (2019)

(Fagus sylvatica L., Quercus ilex L., Quercus suber L., Quercus robur L., Quercus pyrenaica Willd., or Quercus faginea Lam) and of six conifer species (Pinus halepensis Mill., Pinus nigra Arnold., Pinus sylvestris L., Pinus pinea L., Pinus pinaster Ait., or Pinus uncinata Ramond.), selecting three plots per species which result in 36 study sites (Table S1, Fig. S1). Study sites selection was carried out ensuring that they covered the distribution range of each species (from the least and most productive sites, as well as intermediate), and ensuring that they covered a North-South gradient across peninsular Spain. Across the study sites, mean annual air temperature varied from 10 to 18 °C (Fig. 1a, Table S1) and mean annual precipitation from 375 to 2200 mm (Fig. 1b, Table S1). Vegetation types and ecoregions ranged from xeric sclerophyll or Mediterranean pine forests to the more mesic Cantabrian forests, dominated by temperate deciduous broad-leaf species, or high mountain conifer forests (Fig. 1c). We used an existing MODIS product (MOD17A3HGF, Running and Zhao 2019) with a spatial resolution of 500 m as the estimate of mean annual net primary productivity (kg C m⁻²) between 2010 and 2020. Long-term average annual productivity of study sites ranged

from 3870 to 15,031 kg C m⁻², showing a strong south-north productivity gradient (Fig. 1d, Table S1).

Climate projections

Daily precipitation and daily maximum and minimum air temperature projections from 2010 to 2100 were obtained from the Euro-CORDEX adjusted grid at 0.11° resolution (Kotlarski et al. 2014). We selected four different Global Climate Models (GCM) coupled within Regional Climate Models (RCM), maximizing model spread for relevant variables and avoiding duplications in order to reduce model prediction biases (Table S2, Rodríguez and Gutiérrez 2018). The selected GCMs have been evaluated over Western Europe and exhibit significant differences in predictions of summer temperature and precipitation (Table S2, McSweeney et al. 2015). We considered both moderate and high greenhouse gas emission scenarios (RCPs 4.5 and 8.5) for each GCM. We performed projections bias corrections using standard methods based on daily mean bias for temperature and quantile mapping for precipitation (Ruffault et al. 2014). We use data from the Spanish Meteorological Agency (AEMET) from 2010 to 2020 as reference observational data for GCM projections bias correction and all analyses were performed using the R package meteoland (De Cáceres et al. 2018). Statistical means of GCM climate projections across all study sites showed that, from 2010 to 2100, mean annual temperature is expected to increase by 1.5 °C (min = 0.7 °C, max = 2.15 °C) under RCP4.5 and by 4 °C (min = 3.2 °C, max = 5.7 °C) under RCP8.5, while mean annual precipitation is expected to decrease by 100 mm (min = 87 mm, max = 119 mm) under RCP4.5 and by 150 mm (min = 134 mm, max = 182 mm) under RCP8.5 (Fig. S2). Relative humidity, incoming solar radiation, and potential evapotranspiration were daily predicted using meteoland (De Cáceres et al. 2018). Relative humidity was estimated assuming that dew point temperature equals the minimum temperature. Potential solar radiation was estimated from latitude, slope, and aspect, and incoming solar radiation was then obtained following Thornton and Running (1999). Projections of annual atmospheric CO_2 concentration were obtained for each RCP scenario from Meinshausen et al. (2011).

LFMC modeling

Daily variations in species-level LFMC were predicted following Balaguer-Romano et al. (2022). This processbased model was calibrated and validated with 2512 LFMC data measured from 37 plant species belonging to different functional types, collected between 1996 and 2017 from contrasting climate locations across peninsular Spain. The approach combines MEDFATE, a water balance model for the estimation of speciesspecific daily pre-dawn water potential ($\Psi_{\rm pd}$), and an empirical relationship between Ψ_{pd} and LFMC, established following Nolan et al. (2018). MEDFATE is implemented in an R package, which uses soil, vegetation, and meteorological data to estimate soil water balance and plant water relations (De Cáceres et al. 2015, 2021). The model estimates daily plant transpiration and photosynthesis rates. Stomatal regulation of gas exchange is simulated at sub-daily steps involving detailed calculations of hydraulics, leaf energy balance, and photosynthesis based on Sperry et al. (2017). This approach predicts the trajectory of stomatal responses to changes in the environment across time by considering that at any given instant the stomatal aperture adjusts to maximize the instantaneous difference between photosynthetic gain and hydraulic cost.

We used soil and vegetation data inputs following previously published protocols (Balaguer-Romano et al. 2022). In short, the soil was divided into four layers (0-10 cm, 10-20 cm, 20-60 cm, and 60-100 cm deep), and data inputs regarding bulk density, the percentage of clay, sand, organic matter, and rock fragment content were extracted for our plot locations from the Soil Grids System at 250 m resolution (Hengl et al. 2017). Vegetation data inputs were species identity, tree density, shrub cover, plant height, tree diameter at breast height, and plant rooting depth. All data except rooting depth were obtained for the selected plots from the Third National Forest Inventory of Spain (Alberdi et al. 2016). Rooting depth, classified as the depth at which cumulative 50% (Z50) and 95% (Z95) of fine roots occur, was set at 20 cm and 100 cm for tree species and at 10 cm and 20 cm for shrub species as previously discussed (Balaguer-Romano et al. 2022). MEDFATE also includes a set of species-specific plant traits covering plant size, plant phenology and anatomy characteristics, and shrub and tree allometric coefficients to predict plant biomass, foliage and small twigs tissue moisture, light extinction, transpiration, and photosynthesis (De Cáceres et al. 2021). We used the default package values (ver. 2.7.3) for each selected species. Following Balaguer-Romano et al. (2022), soil and vegetation data inputs were used along with meteorological projections to estimate daily species-specific Ψ_{pd} values and corresponding daily LFMC for all study sites. To do this we applied Eq. (1):

$$LFMC = 91.87 - 31.12 \log_{10}(-\Psi_{pd})$$
(1)

Finally, we ran a second round of simulations for each species (Table S1), considering a stable atmospheric CO_2 concentration of 386 ppm (2000–2020 mean) in order to

quantify the potential mitigatory effect of CO_2 on LFMC dynamics.

DFMC modeling

Daily minimum DFMC values were predicted from VPD in each study site by applying Eq. (2) derived from the process-based model developed by Resco de Dios et al. (2015):

$$DFMC = DFMC_0 + DFMC_1 e^{(-mVPD)}$$
(2)

where $DFMC_0$ and $DFMC_1$ represent the minimum and maximum moisture content values, respectively, and *m* is the rate of change in DFMC with VPD. Values for $DFMC_0$ (6.79), $DFMC_1$ (27.43), and *m* (1.05) were obtained from (Nolan et al. 2016a), and the Resco de Dios et al. (2015) DFMC model that has been previously used and validated in Spain (Resco de Dios et al. 2022). Daily VPD values were estimated using the plantecophys R package (Duursma 2015) from daily minimum relative humidity and daily maximum air temperature previously obtained from meteorological projections, which leads to the lowest DFMC daily value (Resco de Dios et al. 2015).

Data analyses

Live and dead fuel moisture content were analyzed over three decadal time periods, ranging from 2010 to 2020, from 2040 to 2050, and from 2090 to 2100. Fuel moisture values predicted under each GCM were aggregated into a single daily mean. To analyze fuel moisture content dynamics, we predicted LFMC and DFMC summer mean (from June 21st to September 21st) for each year, as this period concentrates the bulk of the fire activity in peninsular Spain (Resco de Dios et al. 2022). To account for a potential lengthening of fuel-drying events under global warming, we also estimated the lengths of the fire season and low fuel moisture period, as the total number of days per year (days year⁻¹) when predicted fuel moisture content values fell below wildfire occurrence thresholds. LFMC typically ranges between 40 and 150% during the fire season for key woody plant species in peninsular Spain (Nolan et al. 2018, Balaguer-Romano et al. 2022) while DFMC variation ranges between 4 and 30% (Matthews 2014, Nolan et al. 2016b). Here, we followed previous publications that had established the minimum, critical, and extreme threshold values of fuel moisture content associated with fire activity in the Mediterranean and temperate broadleaf and mixed forest ecoregions at 120, 100, and 80% for LFMC and at 12, 10, and 8% for DFMC, respectively (Nolan et al. 2016b, Boer et al. 2017, Ma et al. 2021, Ellis et al. 2022, Resco de Dios et al. 2022). The minimum fuel moisture threshold is defined as the level associated with the onset of wildfire occurrence (Boer et al. 2017, Ellis et al. 2022), while fuel moisture levels below the critical thresholds set the stage for vigorous fire spread (Nolan et al. 2016b, Ellis et al. 2022, Resco de Dios et al. 2022). Lastly, the extreme fuel moisture threshold is defined as the level at which large wildfire events exhibiting exponential growth of the burned area are observed (Nolan et al. 2016b, Ma et al. 2021). Therefore, days recording live and dead fuel moisture values below the minimum thresholds were accounted as fire season days, while days recording values below critical and extreme thresholds were accounted as critically and extremely low fuel moisture periods, respectively.

To assess LFMC and DFMC responses to climate change conditions, we fitted linear mixed-effects models with the lme4 R package (Bates et al. 2015). The fitted models had a double factorial structure with Period and RCPs as fixed factors and Site and Year as random effects, with Year nested in Period. The response variables were summer mean fuel moisture values (%) and the length of the fire season or low fuel moisture period (days year⁻¹). LFMC critical threshold values were squared root transformed in order to meet model assumptions. Results for LFMC extreme fuel moisture threshold data are not shown as the fitted model did not meet normality assumptions. Then, we conducted Bonferroni corrected post hoc comparisons in order to assess pairwise differences between different Period and RCPs fixed factors combinations from the linear mixed-effects models fitted using the emmeans R package (Russell et al. 2023). Then, we correlated moisture content dynamics and fire season lengths with each study site's mean annual net primary productivity (NPP) to assess whether changes in fuel moisture and in the potential fire season length will be amplified or reduced across productivity gradients. Finally, to test for CO₂ effects on LFMC and fire season length, we performed a dependent samples sign test from the R package BSDA (Arnholt and Evans 2022). A nonparametric test was used as linear models fitted with constant and increasing CO₂ database values did not meet normality assumptions. In this way, we assessed whether median LFMC (%) and fire season length (days year⁻¹) values predicted under constant or increasing atmospheric CO₂ concentrations were significantly different. All analyses were conducted considering a significance level of *p* < 0.05.

Results

Fuel moisture content dynamics

Fuel moisture content ranged from 62 to 135% in the case of live fuels and from 7 to 15% in the case of dead fuels, with a mean LFMC of 114% and a mean DFMC of 9%, across all study sites and throughout all time periods while considering both RCP scenarios. Declines in LFMC and in DFMC were recorded in the three decadal

Table 1 Average summer mean moisture content (%) of live (LFMC) and dead fuels (DFMC) predicted across three decadal periods under greenhouse gas emission scenarios RCP4.5 and RCP8.5. 2040–2050 LFMC values predicted under RCP4.5 were not represented as they did not show significant differences with the historical 2010–2020 period

	LFMC (%)		DFMC (%)	
Period	RCP4.5	RCP8.5	RCP4.5	RCP8.5
2010-2020	116	116	10	10
2040-2050	-	112	9.5	9.2
2090-2100	113	106	9	8.5

periods, from 2010–2020 (1^{st} period) to 2040–2050 (2^{nd} period) and from 2010–2020 to 2090–2100 (3^{rd} period) under both RCP scenarios (Table 1).

There was a significant effect of *RCP*, *Period*, and their interactions on LFMC variation (Table S3). Bonferroni corrected post hoc comparisons (Table S4.1) revealed that, under the moderate greenhouse gas emission scenario (RCP4.5, Fig. 2a–c–e), there were only significant differences between the 1st and 3rd decadal periods (p < 0.001) where mean summer LFMC across all sites was predicted to decline from 116% (Fig. 2a) to 113% (Fig. 2e). The trends of declining LFMC were more

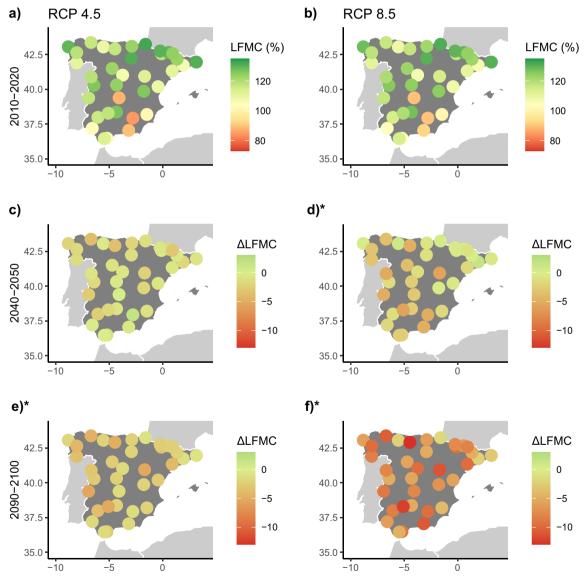


Fig. 2 Predicted changes in mean summer LFMC across Spain for three decadal time periods under RCP4.5 and RCP8.5. LFMC values of each study site for the period 2010–2020 for both RCP 4.5 (a) and 8.5 (b). Differences in LFMC between 2040–2050 and 2010–2020 for RCP 4.5 (c) and 8.5 (d). Differences in LFMC between 2040–2050 and 2010–2020 for RCP 4.5 (c) and 8.5 (d). Differences in LFMC between 2040–2020 for RCP 4.5 (c) and 8.5 (d). Differences between 2040–2020 and 2010–2020 for RCP 4.5 (c) and 8.5 (f). Asterisks after the subplot letter indicate significant LFMC differences between 2010–2020 and future periods

pronounced under high greenhouse emission scenario (RCP8.5, Fig. 2b–d–f), where differences between periods were always significant. We recorded a decline from 116% in 2010–2020 (Fig. 2b) to 112% for 2040–2050 (Fig. 2d) and to 106% for 2090–2100 (Fig. 2f). Regarding RCP comparisons (Fig. S3, Table S4.1), there were nonsignificant differences between predicted mean summer LFMC during the 1st period for both RCPs, and between RCP4.5 for the 3rd period and RCP8.5 for the 2nd period. The rest of pairwise comparisons involving *RCP* and *Period* were significantly different (Fig. 2, Fig. S3, Table

S4.1). Finally, the effect of the random *Site* factor indicated significant and widespread variability across sites (Table S4.2).

DFMC analyses also showed significant effects of *Period, RCP,* and their interaction on DFMC variation (Table S5). Bonferroni corrected post hoc comparisons revealed that all pairwise differences between periods in both RCP scenarios were significant (Fig. S4, Table S6.1). Mean summer DFMC levels across the study sites (Fig. 3) predicted under RCP4.5 showed a decline from 10% in 2010–2020 (Fig. 3a) to 9.5% in 2040–2050 (Fig. 3c), and

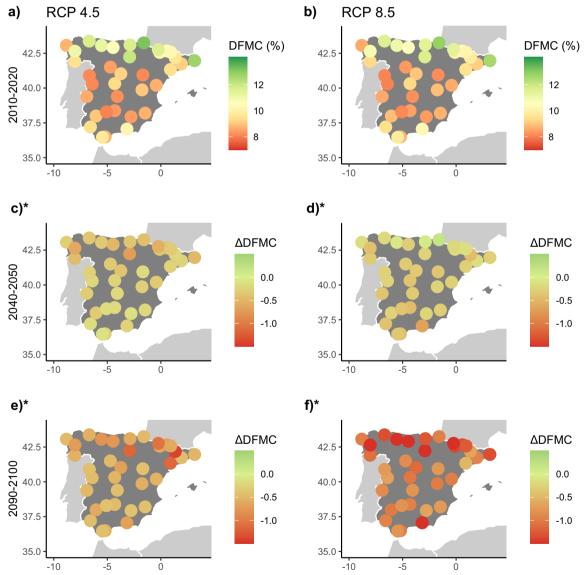


Fig. 3 Predicted changes in mean summer DFMC across Spain for three decadal time periods under RCP4.5 and RCP8.5. DFMC values of each study site for the period 2010–2020 for both RCP 4.5 (a) and 8.5 (b). Differences in DFMC between 2040–2050 and 2010–2020 for RCP 4.5 (c) and 8.5 (d). Differences in DFMC between 2090–2100 and 2010–2020 for RCP 4.5 (e) and 8.5 (f). Asterisks after the subplot letter indicate significant DFMC differences between 2010–2020 and future periods

to 9% in 2090–2100 (Fig. 3e). Under RCP8.5, DFMC showed a decline from 10% in 2010–2020 (Fig. 3b) to 9.25% in 2040–2050 (Fig. 3d), and to 8.5% in 2090–2100 (Fig. 3f). Differences in predicted mean summer DFMC values across all sites between both RCPs for the 2nd periods were not significant, but DFMC was significantly lower in RCP8.5 than in RCP 4.5 in the rest of pairwise comparisons across periods (Fig. S4, Table S6.1). Again, the effect of the random *Site* factor indicated significant and widespread variability across sites (Table S6.2).

Fire season and low fuel moisture period length

Fire season and low fuel moisture period lengths were estimated from the total number of days per year (days year⁻¹) with predicted LFMC and DFMC values below empirical wildfire occurrence thresholds. For 2010–2020, we estimated a mean fire season length of 112 days (below the minimum LFMC threshold of 120%), and 32 and 2 days with values below the critical (100% LFMC) and the extreme (80% LFMC) thresholds, respectively. Regarding DFMC, we estimated a mean fire season length of 112 days (below the minimum DFMC threshold of 12%), and 70 and 16 days with values below the critical (10% DFMC) and the extreme (8% DFMC) thresholds, respectively.

Estimated fire season and low fuel moisture period length, showed an increasing trend for the 21st century in all study sites for both emission scenarios RCP4.5 and RCP8.5 (Fig. 4, Table 2). There was a significant effect of *RCP*, *Period*, and their interaction on LFMC variation for minimum and critical thresholds (Table S7 and S8) and on DFMC variation for all three thresholds (Table S9–S11). Regarding LFMC values, from 2010–2020 to 2090–2100 fire season length was estimated to increase on average by 15 days year⁻¹ under RCP4.5 and by 50

Table 2 Fire season length represented by the number of days per year (days year⁻¹) with LFMC and DFMC values below wildfire occurrence thresholds (minimum: 120–12% | critical: 100–10% | extreme: 80–8% for LFMC-DFMC, respectively) under scenarios RCP4.5 and RCP8.5. Values for the extreme LFMC threshold of 80% were not represented as the fitted model does not meet normality assumptions

	LFMC		DFMC	
Period	RCP4.5	RCP8.5	RCP4.5	RCP8.5
2010-2020	112 32 2	110 27 2	112 70 16	112 70 16
2040-2050	117 35 -	123 39 -	124 79 23	124 79 23
2090-2100	127 40 -	160 57 -	132 87 31	158 110 49

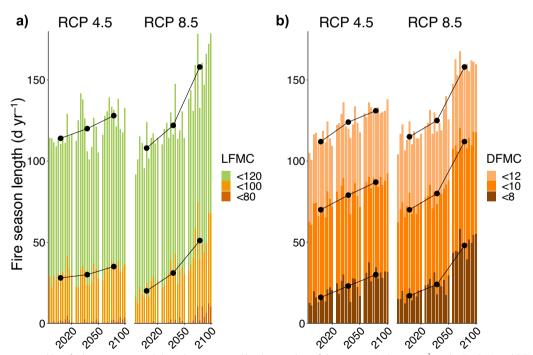


Fig. 4 Fire season and low fuel moisture periods length represented by the number of days per year (days year⁻¹) with LFMC (**a**) and DFMC (**b**) values below wildfire occurrence thresholds (minimum: 120–12%, critical: 100–10% and extreme: 80–8% for LFMC-DFMC, respectively) under scenarios RCP4.5 and RCP8.5. Each bar represents a year within each period (2010–2020, 2040–2050 and 2090–2100). Black dots represent mean values for each period. Mean values for the extreme LFMC threshold of 80% were not represented as the fitted model does not meet normality assumptions

days year⁻¹ under RCP8.5. Meanwhile, critically low fuel moisture periods were estimated to increase by 8 and 30 days year⁻¹ under RCP4.5 and RCP8.5 respectively. Across the same periods and regarding DFMC values, fire season length was estimated to increase by 20 days year⁻¹ under RCP4.5 and 46 days year⁻¹ under RCP8.5. Meanwhile, critically low fuel moisture periods were estimated to increase by 17 and 40 days year⁻¹ under RCP4.5 and RCP8.5 respectively. Finally, extremely low fuel moisture periods were estimated to increase by 15 days year⁻¹ under RCP4.5 and 33 days year⁻¹ under RCP8.5.

Changes across productivity gradients

The effects of climate change on LFMC depended on site productivity, with the decline in LFMC being more marked at the least productive sites. Comparing current LFMC with predicted levels at the end of the 21st century (Δ LFMC, Fig. 5a, c), we observed a negative relationship (p = 0.007, $R^2 = 0.2$), such that Δ LFMC changed from -10 to -2% from the least to the most productive site under RCP8.5. The slope of the relationship was significantly higher (p = 0.001) in conifer

forests, meaning that the future decrease in LFMC could be less marked at broadleaf forest locations. Under RCP 4.5, the change in LFMC with productivity was only marginally significant (p = 0.057) for conifer forests, where the Δ LFMC change across the productivity gradient was from -3 to 1%.

Fire season lengthening was also significantly less in places with higher productivity (Fig. 5b, d). The increase in fire season length (defined from days under the minimum LFMC threshold of 120%) with productivity under RCP8.5, ranged from 100 to 7 days year⁻¹ from the least to the most productive site, and the slope of the relationship was more negative in broadleaf forests (from 80 to 7 days year⁻¹) than in conifer forests (ranging from 95 to 38 days year⁻¹). We observed the same trends under RCP4.5, but less pronounced. The change in fire season length with productivity ranged from 22 to 0 days year⁻¹, being again only significant in conifer forests and with lower slope estimates. Finally, correlations between variation in predicted DFMC and fire season length (regarding DFMC thresholds) against productivity were not significant.

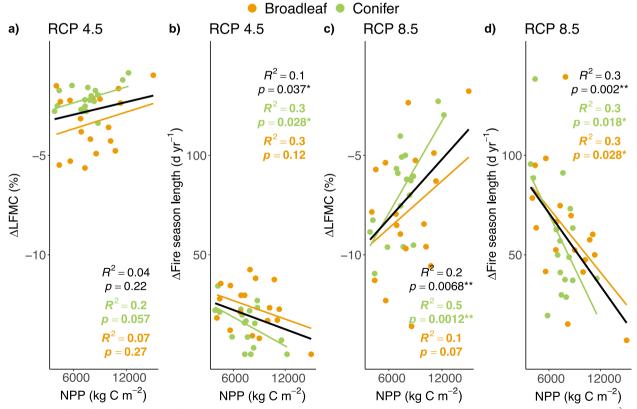


Fig. 5 The effects of climate change on fuel moisture depend on site productivity (2010-2020 mean annual net primary productivity in kg C m⁻²). Correlations between changes in LFMC (Δ LFMC) between 2090–2100 and 2010–2020 and changes in fire season length (minimum threshold of LFMC<120%) as a function of mean annual net primary productivity under RCP4.5 (**a**, **b**) and RCP8.5 (**c**, **d**). R^2 and *p*-values represent the results of linear fitting for all species and separately for conifer forests (blue) and broadleaf forests (orange)

CO₂ effects

Results of the dependent samples sign test showed that median LFMC values predicted under an increasing atmospheric CO_2 concentration were significantly greater (p < 0.001) than median LFMC values predicted under a constant [CO₂]. Differences between constant and increasing atmospheric [CO₂] predictions were greater for RCP8.5 (1.5%) than for RCP4.5 (0.75%). LFMC levels under RCP4.5, from 2010-2020 to 2090-2100, were predicted to decline by about 4% under increasing atmospheric [CO₂], and by about 5% under stable atmospheric [CO₂]. For RCP8.5, predicted declines were larger for the same periods, with a LFMC decline of 10% under increasing atmospheric [CO₂], and a decline of 13% under constant atmospheric [CO₂] conditions. Estimated fire season lengthening was approximately 10 days year⁻¹ lower in simulations conducted under increasing atmospheric [CO₂]. Thus, the estimated lengthening under RCP8.5 between 2020 and 2100 was 50 days year⁻¹ under increasing atmospheric [CO₂], while under constant $[CO_2]$ conditions lengthening was 60 days year⁻¹ for the same RCP, period and thresholds (Table S.12).

Discussion

By applying process-based models and considering climate change conditions derived from moderate and high greenhouse gas emission scenarios (RCPs 4.5 and 8.5), we predicted that warmer and more arid climatic conditions will lead to declining trends of LFMC and DFMC, consequently increasing the annual frequencies of days recording fuel moisture values below wildfire occurrence thresholds, lengthening the fire seasons and increasing wildfire danger. LFMC and DFMC values were predicted to decrease by 3% and 1%, respectively, extending annual fire season length by 20 days under projected climatic conditions for RCP4.5 by 2100. LFMC and DFMC values were predicted to decrease by 10% and 1.5%, respectively, causing the annual fire season length to increase by 50 days under RCP8.5 projected climatic conditions for RCP8.5 by 2100, compared with the current fire season. Despite predicted declines in LFMC and DFMC (10 and 1.5%, respectively) were relatively small, it is important to consider that the relationship between fuel moisture and burned area is exponential. Longer periods with low fuel moisture values increase available fuel connectivity at landscape scales by affecting wet local areas, as valley bottoms, that could act as natural fire breaks (Resco de Dios et al. 2022). Thus, considering that current fuel moisture values in large European areas are already close to the limit of wildfire occurrence thresholds (Carnicer et al. 2022, Resco de Dios et al. 2021), even minimum decreases in fuel moisture can lead to large wildfire events that exponentially increase the burned area surface (Nolan et al. 2016b). In this context, is also crucial to consider future changes in socioeconomic factors and land use policies that influence burned area, as that could affect the relationship between LFMC and burned aea (de Diego et al. 2023).

DFMC showed proportionally steeper declining trends than LFMC. We found more study sites with fuel moisture values below wildfire occurrence thresholds for DFMC (Fig. 3) than for LFMC (Fig. 2), and DFMC predictions showed more days per year with values below critical and extreme thresholds (70 and 16 days year⁻¹, respectively) than LFMC (32 and 2 days year⁻¹). These observed differences would not arise if future moisture dynamics of both fuel types were predicted by applying commonly used drought indices, as process-based models allowed to consider species-level physiological capabilities to adjust the moisture status of live tissues. The predicted misalignment between live and dead fuel moisture declines could modify fire regimes by affecting fire behavior and fire spread. Further studies should assess how physiological plant responses to climate change conditions (e.g., vulnerability to cavitation) will increase the proportion of dead particles in tree canopies, and, consequently, crown fire risk (Van Wagner 1977).

We found a productivity gradient effect over the predicted fuel moisture trends, with the largest declines at the least productive sites (Fig. 5). But, despite low productivity southern study sites recorded the minimum predicted moisture content values (Figs. 3 and 4), high productivity northern sites showed significant increases in the fire season length. Furthermore, it is in northern study sites where we predicted greater DFMC declines (Fig. 3e, f). Northern Spain climatic conditions favor the development of forests dominated by temperate deciduous broad-leaf species (Fig. 1c). These ecosystems are highly productive and hold huge amounts of biomass (Fig. 1d) being the major Spain's forest carbon sinks (Alberdi et al. 2016). Several decades of land abandonment have promoted the encroachment of forest into former pastures and croplands increasing fuel accumulation and forest continuity (Gelabert et al. 2022). These vast amounts of forest biomass have formed fuel arrays of high vertical and horizontal continuity in relatively humid environments with large fire return intervals (Resco de Dios et al. 2021). However, predicted fuel moisture declines driven by projected climate aridity increases would largely increase fire danger in Spain's major forest carbon sinks (Anderegg et al. 2020).

Predictions conducted with increasing atmospheric CO_2 concentrations showed significantly higher LFMC values compared to predictions conducted with stable CO_2 concentrations. Under RCP 8.5, the CO_2 mitigation effect caused an average increase of 3% in LFMC values,

which was not enough to compensate for a net LFMC decline of 13% expected by the end of the century as a result of increasing temperature and decreasing precipitation. Also, fire season lengthening was 10 days year⁻¹ lower under increasing $\rm CO_2$ concentration predictions, but again not enough to overcome a net increase of 60 days year⁻¹ estimated as a result of climate change alone. Our model of $\rm CO_2$ effects over LFMC only accounted for water savings through stomatal conductance, and it did not include negative LFMC feedbacks through, for instance, increasing leaf area index which would increase transpiration and, hence, soil water depletion (McDowell et al. 2022). Our results thus present a "best-case scenario" regarding the mitigation effect of increasing $\rm CO_2$ concentration over LFMC declines.

We applied process-based models to predict fuel moisture dynamics, quantifying annual time periods with values below fire danger thresholds. Fuel moisture declines and fire season lengthening trends found in this study are consistent with projections for southern Europe by previous studies (Abatzoglou et al. 2019; Dupuy et al. 2020; Ellis et al. 2022; Jones et al. 2022; de Rigo et al. 2017). However, it is important to consider that these previous studies were based on fire weather indices such as the Canadian Fire Weather Index (FWI; Van Wagner 1987). Weather indices ignore species-level physiological capabilities to adjust the moisture status of live fuels, which would explain why we observed a less pronounced fire season lengthening than previous studies (i.e., Jones et al. 2022 predicted a fire season lengthening of 60 days year⁻¹ from 2020 to 2100 under RCP8.5 conditions while we report a lengthening of 50 days year⁻¹). It is important to note that even minimum fuel moisture prediction biases could lead to large uncertainties. Thus, we suggest that the use of process-based approaches for modeling fuel moisture would benefit the prediction of annual and seasonal dynamics, enhancing fire danger monitoring from local to landscape scales.

Conclusions

We predicted that the warmer and more arid climatic conditions projected for the 21st century will lead to generalized declines in fuel moisture, lengthening fire seasons, and increasing wildfire danger. The use of process-based models to forecast LFMC dynamics allowed the consideration of plant species capabilities to buffer climate change impacts, beneficiating wildfire danger assessments. Significant increases in the fire season length, as predicted for the most productive environments, currently with large fire return intervals, would pose an increase of fire danger in major Spanish carbon sinks. Finally, our results indicated that the CO_2 mitigation effect on plant water relations and LFMC (via increases in water-use efficiency) would not be enough to offset climate change-driven declines in seasonal LFMC levels.

Limitations

The process-based fuel moisture dynamics modeling attempts carried out in this study show limitations. In the case of LFMC modeling, we have considered vegetation communities to be static, that is, we have not accounted for the climate-driven vegetation changes that may occur over the 21st century, in order to reduce modeling complexities when simulating the climatic influence on live fuel moisture. In this context, we also have only considered tree species. Future research efforts should include shrub species and more complex communities. Finally, we have not taken into account the effect of seasonal changes in dry weight. Given the importance of phenological variations in dry weight driving LFMC dynamics (Brown et al. 2022; Griebel et al. 2023; Nolan et al. 2020), it should be at the forefront of our future research efforts. In the case of DFMC modeling, we have not accounted for the precipitation effect as we applied a VPD-based approach. However, as dead fuel moisture will reach the saturation point (25–30%) after as little as 2 mm of rain (Viney 1991), VPD will sharply drop as relative humidity approaches 100%. Therefore, the effect of precipitation on DFMC model performance is very limited (Resco de Dios et al. 2015).

Abbreviations

LFMC Life fuel moisture content DFMC Dead fuel moisture content VPD Vapor pressure deficit Ψ_{pd} Predawn leaf water potential GCM Global Climate Model RGM Regional Climate Model RCP Relative Concentration Pathway [CO₂] CO₂ concentration

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-023-00224-0.

Additional file 1: Table S1. Location, IFN3 plot selection and target species for each sampling site. Latitude and Longitude (°), Altitude (m), Spanish region, plot ID, target species, mean annual temperature, mean annual precipitation and net primary productivity. Sites followed by an asterisk (*) were used for a second simulation round considering stable CO2 atmospheric concentration across the century. Figure S1. Study site's location. Northern sites overlap: Pu01 and Ps01. Southern sites overlap: Pp03. Table S2. Global Climate Models (GCM) and Regional Climate Models (RCM) couples selection and temperature for Europe according to McSweeney et al. (2015). Figure S2. Mean annual temperature (°C) and mean annual precipitation (mm) projections of each Global Climate Model (GCM) for each greenhouse gas emission scenario (RCP4.5 and RCP8.5). Table S3. Analysis of variance table for fixed effects in the linear mixed-effects model fitted with annual summer mean LFMC as response

variable. Figure S3. LFMC mean values across the three decadal periods (1:2010-2020; 2:2040-2050 and 3:2090-2100) in both RCP scenarios (4.5 in red and 8.5 in blue). Bars represent standard deviation (SD). Table S4.1. Pairwise differences between different Period (1:2010-2020; 2:2040-2050 and 3:2090-2100) and RCP (4.5 and 8.5) fixed factors combinations from the linear mixed-effects model fitted with annual summer mean LFMC as response variable. Table S4.2. ANOVA-like table for Site and Year (as a replicate of Period) random-effects from the linear mixed-effects model fitted with annual summer mean LFMC as response variable. **Table S5.** Analysis of variance table for fixed effects in the linear mixed-effects model fitted with annual summer mean DFMC as response variable. Figure S4. DFMC mean values across the three decadal periods (1:2010-2020; 2:2040-2050 and 3:2090-2100) in both RCP scenarios (4.5 in red and 8.5 in blue). Bars represent standard deviation (SD). Table S6.1. Pairwise differences between Period (1:2010-2020; 2:2040-2050 and 3:2090-2100) and RCP (4.5 and 8.5) from the linear mixed-effects model fitted with annual summer mean DFMC as response variable. Table S6.2. ANOVA-like table for Site and Year random-effects from the linear mixed-effects model fitted with annual summer mean DFMC as response variable. Table S7. Analysis of variance table for fixed effects in the linear mixed-effects model fitted with the number of days per year when LFMC < 120 % as response variable. Table S8. Analysis of variance table for fixed effects in the linear mixed-effects model fitted with the number of days per year when LFMC < 100 % (square root transformed) as response variable. Table S9. Analysis of variance table for fixed effects in the linear mixed-effects model fitted with the number of days per year when DFMC < 12 % as response variable. Table S10. Analysis of variance table for fixed effects in the linear mixed-effects model fitted with the number of days per year when DFMC < 10 % as response variable. Table S11. Analysis of variance table for fixed effects in the linear mixed-effects model fitted with the number of days per year when DFMC < 8 % as response variable. Table S12. Fire season lengthening median values (d yr⁻¹) regarding minimum (<120%) and critical (<100%) LFMC thresholds for wildfire occurrence under increasing and constant atmospheric [CO₂] conditions for both RCPs (4.5 and 8.5) and in all periods (2010-2020, 2040-2050, 2090-2100).

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Authors' contributions

RBR, RDS, MDC, JV, MB, and VRD conceptualized and designed the project. RBR and JV held statistical data analysis. RBR wrote the manuscript with critical revisions from RDS, MDC, JV, MB, and VRD. All authors read and approved the final manuscript.

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Availability of data and materials

All data analyzed during this study are included in this published article [and its supplementary information files]. The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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