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RESEARCH ARTICLE

Diversity modulates above-ground productivity in response to disturbances: The case of Iberian forests

Pedro Rebollo[1,2] | Verónica Cruz-Alonso[1,2] | Paloma Ruiz-Benito[2,3] | María Triviño[4,5] | Julen Astigarraga[2,6] | Patricia González-Díaz[7] | Miguel A. Zavala[2] | Enrique Andivia[1,2]

[1]Departamento de Biodiversidad, Ecología y Evolución, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, Madrid, Spain; [2]Grupo de Ecología y Restauración Forestal, Departamento Ciencias de la Vida, Facultad de Ciencias, Alcala de Henares, Spain; [3]Grupo de Investigación en Teledetección Espacial, Departamento de Geología, Geografía y Medio Ambiente, Alcala de Henares, Spain; [4]Department of Biological and Environmental Sciences, University of Jyvaskyla, Jyvaskyla, Finland; [5]School of Resource Wisdom, University of Jyvaskyla, Jyvaskyla, Finland; [6]Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden and [7]Centro de Investigaciones Sobre Desertificación (CIDE, CSIC-UV-GV), Moncada, Valencia, Spain

Correspondence
Pedro Rebollo
Email: prebollo@ucm.es

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Abstract

1. Disturbances play a key role in forest dynamics globally, with various effects on productivity. Tree diversity is expected to attenuate the negative impact of disturbance on forest productivity, but its overall effect has been little explored and might depend on the functional composition. Here, we analysed whether forest productivity responses to disturbances were modulated by structural and functional diversity, as well as by functional dominance, and whether these responses vary among functional groups.
2. For this, we used 12,075 permanent plots from the Spanish Forest National Inventory spanning the 1986–2019 period and modelled forest above-ground productivity as a function of disturbance occurrence (i.e. harvesting, fire or biotic damage observed in trees) and its pairwise interaction with (i) structural and functional diversity and (ii) functional dominance. We considered the following main functional groups: (i) needle-leaved (50.2% of the data), broad-leaved deciduous (25.8%) and broad-leaved evergreen (24.0%).
3. Harvesting and fire occurrence significantly reduced above-ground productivity of all functional groups, 94.5% and 143.9% on average, respectively. Structural diversity mitigated forest productivity declines associated with harvesting and fire, whereas functional diversity only modulated responses related to harvesting. In general, structural diversity had a more positive effect on forest productivity in disturbed plots than in undisturbed plots. The only exception concerned the impact of fire occurrence on broad-leaved species, which remained similar. In harvested plots, functional diversity increased forest productivity, except for broad-leaved species. Finally, forest productivity decreased in harvested plots

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dominated by broad-leaved deciduous tree species but increased in fire-affected plots.

4. *Synthesis*. Forest diversity can mitigate the negative effects of disturbances on productivity. Higher structural diversity enhanced productivity in both harvested and fire-affected stands, while greater functional diversity maintained productivity in harvested forests. These results highlight the importance of promoting structural and functional diversity as a key strategy to sustain forest productivity and reinforce the role of forests as carbon sinks under increasing disturbance regimes.

KEYWORDS

biotic damage, fire, forest inventory, functional diversity, functional dominance, global change ecology, harvesting, structural diversity

1 | INTRODUCTION

Global change is altering the dynamics of forest ecosystems worldwide (McDowell et al., 2020). Disturbance regimes, defined as the temporal characteristics of events that disrupt forest structure, composition and resource availability, have undergone significant changes in recent decades, with an increased frequency and intensity of wildfires and pest outbreaks (Patacca et al., 2023; Pickett & White, 1985; Senf & Seidl, 2021). Disturbances play a catalytic role in forest dynamics (Holling & Gunderson, 2002), driving community and population-level responses by altering individual demographic rates (McDowell et al., 2020), which in turn determine forest productivity over time (Astigarraga et al., 2020; Ciais et al., 2005). Forest reorganisation after disturbances mainly depends on the type and magnitude of the disturbance, as well as on the species previously present in the stand and their functional traits (Seidl et al., 2024; Seidl & Turner, 2022). For instance gradual disturbances, like pest outbreaks (Coops et al., 2020; Ghazoul et al., 2015), reduce forest productivity but may have a low impact on functional composition, especially if dominant species are highly tolerant to abiotic and biotic stress (García-Valdés et al., 2021). In contrast, abrupt disturbances such as intense thinning and wildfires, may lead to sudden resource releases that can cause shifts in species dominance (Seidl & Turner, 2022). Understanding how disturbances drive forest productivity can help inform climate change mitigation and adaptation policies.

Diversity may enhance forest ecosystem functioning in response to disturbances. Two main, not mutually exclusive, mechanisms have been proposed to explain the positive biodiversity–ecosystem functioning relationship. On the one hand, structural and functional diversity can promote forest productivity through size-mediated or taxon composition-mediated complementarity and niche partitioning, leading to increased efficiency in resource use (Morin et al., 2011). Recent studies have also shown that more structurally diverse forests (i.e. those with higher levels of size heterogeneity) are associated with higher resilience to disturbances as the understorey layer plays a pivotal role in ecosystem recovery (Diaci et al., 2017; Mohr et al., 2024). Further, other studies suggest that disturbances may have a lower impact on forest productivity in mixed and structurally diverse stands, which appear to be more resistant to disturbances (Hantsch et al., 2014; Jactel et al., 2021; Yuan et al., 2018). On the other hand, more functionally diverse forests are likelier to include species featuring traits that favour post-disturbance recovery under specific environmental conditions (i.e. 'selection effect'; Loreau & Hector, 2001). In such cases, the most productive species will become dominant (Cardinale et al., 2007). Therefore, selection effects are based on the mass-ratio hypothesis, which proposes that ecosystem productivity is determined by the functional traits of dominant species (Roscher et al., 2012). Thus, even though diversity has the capacity to sustain ecosystem functioning in response to disturbances, variations in productivity can be expected across dominant functional groups. Despite the growing evidence of positive biodiversity–productivity effects in forests, the role of diversity in stabilising productivity following disturbances and its relations to the dominance of contrasting functional groups have been little explored. Evaluating how disturbances affect above-ground productivity at different ecological levels (i.e. ecosystem and functional group levels) is critical to understand the role of tree diversity in the long-term stability of forest functioning.

As mentioned above, species functional traits can largely explain forest productivity and species-specific responses to disturbances (Barrere et al., 2023). Thus, needle-leaved, broad-leaved deciduous and broad-leaved evergreen species are expected to respond differently to disturbances depending on their dominance (i.e. functional dominance), as these functional groups exhibit distinct traits related to their responses to environmental conditions (Díaz et al., 2016). For instance, Mediterranean needle-leaved species are likely to dominate in the early stages after an abrupt disturbance due to their pioneer traits, such as rapid growth and high seed production and dispersal (Richardson, 2000; Zavala & Zea, 2004). In contrast, broad-leaved deciduous species are more likely to dominate less disturbed areas due to their higher shade tolerance and lower water-use efficiency (Ruiz-Benito, Ratcliffe, Zavala, et al., 2017; Vayreda et al., 2016). Thus, evaluating the interactive effect of disturbances and diversity on the productivity of contrasting functional groups considering their

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dominance can provide further insights into the stabilising mechanisms of biodiversity, which has key implications to understanding forest functioning under forecasted novel disturbance regimes.

Iberian forests represent an excellent case study to assess diversity effects on forest functioning after disturbances along environmental gradients. Changing disturbance regimes are particularly evident in Mediterranean forests as they are highly exposed to climate change (Gazol & Camarero, 2022; Lindner et al., 2010). The frequency and magnitude of fires, extreme drought events, heatwaves and biotic damage have increased in recent decades (Miguel et al., 2024; Seidl et al., 2017). Additionally, rural abandonment and lack of forest management are triggering processes that increase the vulnerability of these forests to disturbances (Vilà-Cabrera et al., 2017). These processes include large biomass accumulations (Cruz-Alonso et al., 2019) due to an increase in forest stand density or tree sizes, which might result in higher competition (Ruiz-Benito, Madrigal-González, et al., 2014).

Here, we analyse how structural and functional diversity, as well as functional dominance, mitigate the negative effects of disturbances on above-ground productivity responses over a large spatial scale (mainland Spain) along a 40-year period (three sequential forest inventories). First, we tested the relative importance of each predictor. Second, we examined the mitigating effect of diversity and functional dominance separately for the three main functional groups related to leaf type (i.e. needle-leaved, broad-leaved deciduous and broad-leaved evergreen) that may reflect contrasting productivity rates and different ecological strategies to cope with disturbances. We used 12,075 permanent plots measured in the three censuses of the Spanish Forest Inventory (hereafter SFI) that encompass a bioclimatic gradient ranging from cool temperate to Mediterranean forests. We considered two above-ground productivity estimates: (i) the basal area differences between the 2SFI and the 3SFI, and (ii) the basal area differences observed from the 3SFI and the 4SFI. We expect larger reductions in above-ground productivity in disturbed stands. However, structural and functional diversity will mitigate the impact of disturbances on above-ground productivity, and the magnitude of such mitigation effect will vary depending on disturbance type, the functional group analysed and its dominance. The findings of this study contribute to a better understanding of the role of structural and functional diversity in compensating above-ground productivity losses after disturbances. Integrating both compositional and dominance-related aspects of diversity, our study shows empirical insights into how forest structure and diversity modulate disturbance impacts, thereby advancing understanding of biodiversity's role in ecosystem resilience.

2 | MATERIALS AND METHODS

2.1 | Study area and forest inventory data

The study area covers a large part of the edaphoclimatic gradient of the Iberian Peninsula (37°31′56″ N–43°44′17″ N; 9°14′42″ W–3°13′45″ E; Figure S1.1), from an oceanic climate in the northwestern area to a semi-arid climate in the southeastern part (de Castro et al., 2005). The predominant soil types are siliceous and calcareous in the north and northwest of the peninsula and calcareous and clayey in the east and south (Instituto Geográfico Nacional, 2019). Stands in the study area are still young and in early stages of development (Ruiz-Benito, Madrigal-González, et al., 2014), identifying between 1.3% and 3.4% of the stands as old-growth stands (Astigarraga et al., 2020) and only 0.02% of the forest area as primary forests (Sabatini et al., 2018). The most abundant needle-leaved species in the selected plots are *Pinus sylvestris* L., *P. pinaster* Ait. and *P. halepensis* Mill., comprising 78.1% of all needle-leaved trees (see Figure S1.1). *Quercus pyrenaica* Wild., *Fagus sylvatica* L. and *Quercus faginea* Lam. are the most predominant broad-leaved deciduous species, while *Quercus ilex* L. is the most predominant broad-leaved evergreen species, representing 73.4% and 77.7% of their respective groups (Figure S1.1). The three functional groups are widely distributed throughout the Iberian Peninsula (Figure S1.1).

We used data from the permanent plots in the second (1986–1996), third (1997–2007) and fourth (2008–present) SFI. This dataset contains plots systematically distributed in areas with tree cover greater than 5% on a 1-km^2 grid cell and resampled approximately every 10 years (Villaescusa & Díaz, 1998). The SFI employs variable-radius plots for sampling trees with different diameters at breast height (hereafter d.b.h.): 5 m radius for trees with 7.5–12.4 cm d.b.h.; 10 m radius for 12.5–22.4 cm d.b.h.; 15 m radius for 22.5–42.4 cm d.b.h.; and 25 m radius for >42.4 cm d.b.h. For each sampled tree, species identity, d.b.h., cause and level of damage, and status (alive or dead) are recorded among other variables. We used permanent plots available in the three censuses with at least one adult tree (d.b.h. > 7.5 cm and height > 130 cm) in the 2SFI, resulting in a total of 12,738 plots. Then, we removed plots containing non-native species to the Iberian Peninsula or riparian species to enhance comparability of ecological conditions across the dataset (see Tables S1.1 and S1.2), reducing the total to 12,075 plots. We decided to remove these plots because riparian forests generally experience different disturbance regimes, such as seasonal flooding or erosion (Nakamura et al., 2000), and forests dominated by non-native species have higher growth rates and forest dynamics, which could bias our results (Lara-Romero et al., 2022). Ultimately, we kept a total of 55 tree species (see Table S1.3 for further details).

We quantified above-ground productivity as the difference in basal area, calculated as the sum of the cross-sectional area of the trunk from the d.b.h. of each living sampled individual (m^2 ha^{-1}) and divided by the number of years between consecutive censuses (i.e. 23SFI and 34SFI; m^2 ha^{-1} year^{-1}). We calculated above-ground productivity at two levels: (i) at the forest level, representing the total above-ground productivity of each plot regardless of the functional group; and (ii) by functional group, indicating above-ground productivity of each plot for each functional group (hereafter needle-leaved, broad-leaved deciduous and broad-leaved evergreen species).

2.2 | Disturbances, forest structure and environmental characteristics

We evaluated the effect of harvesting, fire and biotic damage (i.e. fungi, insects, mistletoe and epiphytic plants) on above-ground

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productivity at the forest level and for each functional group. Disturbances were characterised as binary variables (occurrence/absence), representing the occurrence of an event between inventories using the information available in the SFI (Villaescusa & Díaz, 1998). We analysed the effects of disturbances on above-ground productivity during the 23SFI period by using the occurrence of disturbances within the same period, and similarly, assessed the effects in the 34SFI period based on disturbances occurring during that period. This information is recorded for adult trees, with harvesting indicated as the presence of harvested trees and fire and biotic damage as an observed medium to high tree damage due to fire or biotic agents. Despite one plot being affected by more than one disturbance, less than 8% of analysed plots showed multiple disturbances (Table S1.4). We analysed a total of 12,075 plots and 24,017 observations that were filtered by functional group presence if there was at least one adult tree alive of needle-leaved, broad-leaved deciduous or broad-leaved evergreen species (see Table S1.5 for more details). By doing so, we were able to analyse how diversity buffered the impact of disturbances on each target functional group. To characterise the differences in above-ground productivity between disturbed and non-disturbed plots (results in Section 3.1), we calculated the percentage of reduction as:

$$\frac{\mathrm{Prod}_{\mathrm{abs}} - \mathrm{Prod}_{\mathrm{occ}}}{\mathrm{Prod}_{\mathrm{abs}}} \times 100\,(\%),$$

where $\mathrm{Prod}_{\mathrm{abs}}$ is the mean productivity in absence of disturbance and $\mathrm{Prod}_{\mathrm{occ}}$ is the mean productivity when disturbance occurs.

Initial forest structure was characterised as it is strongly correlated with demographic rates, and thus to changes in forest productivity (Kulha et al., 2023). We characterised initial forest structure using 2SFI to estimate above-ground productivity responses during the 23SFI period, and initial forest structure in 3SFI for the 34SFI period. We used: (i) initial stand basal area, calculated as the sum of the basal area of adult trees ($m^2\,ha^{-1}$), (ii) tree density, characterised as the number of adult trees per hectare (no. trees ha^{-1}) and (iii) mean d.b.h., calculated as the mean tree size of adult trees within each plot (mm). We kept structural diversity (i.e. diversity in tree sizes) as a separate variable from forest structure, to specifically test the effect of this component of biodiversity on forest productivity.

We characterised climate through water availability and drought intensity. Water availability was used as a proxy of the spatial variations in climate across the Iberian Peninsula, as it covers a large gradient from humid and cold to dry and hot climate. Water availability was calculated as the difference between annual precipitation (P) and potential evapotranspiration (PET) divided by potential evapotranspiration ((P – PET)/PET; %) for the period between 2SFI and 4SFI using data from Moreno and Hasenauer (2016), and the *easyclimate* R package (Cruz-Alonso et al., 2023). Lower values of water availability correspond to drier sites, while higher values indicate wetter sites. We did not consider drought intensity as a disturbance per se because we based the disturbance occurrence on field observations, where disturbance effects were recorded at the tree level and that information was not available for drought effects. However, we considered drought intensity as a covariate to control for above-ground productivity reductions that were not associated with the above-mentioned disturbances (i.e. harvesting, fire and biotic damage). Drought intensity was considered as a proxy of the temporal variations in climate due to increasing drought intensity over time (Gazol et al., 2025). Drought intensity was characterised using the minimum Standardised Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2010). SPEI is a normalised drought index based on the difference between precipitation and potential evapotranspiration. We calculated the 12-month minimum SPEI per plot and month for the period between 23SFI and 34SFI, and we selected the lowest value in the time series of the plot between inventories (+2 years to consider for lagged effects) as an indicator of the most intense drought that occurred in the plot. Then, we transformed them to absolute values since all values were negative, so that higher SPEI values correspond to more intense droughts. We used the *easyclimate* R package to download minimum and maximum temperature and precipitation data from 1950 to 2021 (Cruz-Alonso et al., 2023; Moreno & Hasenauer, 2016) and the *SPEI* R package to calculate the minimum SPEI (Beguería & Vicente-Serrano, 2017). Soil characteristics were extracted from the soilgrids database (https://soilgrids.org/) using the *terra* and *geodata* R packages (Hijmans, 2022; Hijmans et al., 2024). Soil data included soil pH (dimensionless) and nitrogen (cg kg^{-1}).

2.3 | Forest diversity measurements

To test the effect of diversity on above-ground productivity (i.e. change in stand basal area between consecutive periods, either 23SFI and 34SFI, or the entire period from 24SFI); we considered structural, functional, taxonomic and phylogenetic diversity in the initial census for each period (i.e. 2SFI for the 23SFI, 3SFI for the 34SFI and 2SFI for the 24SFI). Later, we retained structural and functional diversity because the correlation between functional, taxonomic and phylogenetic was high ($r > 0.7$; see Figure S2.1). We characterised structural diversity as the coefficient of variation of tree size in a plot (i.e. ratio between the standard deviation and the mean d.b.h.; dimensionless). This allowed us to assess whether structural diversity contributed to above-ground productivity through potential complementarity effects mediated by size differences among individuals (Ali, 2019). Similarly, we calculated functional diversity as functional dispersion (Laliberté & Legendre, 2010) using the *FD* R package (Laliberté et al., 2014). We used five traits at the species level which are commonly used to explain productivity differences among woody species and their responses to disturbances. This approach enables us to investigate the responses of functional groups to disturbances, rather than focusing solely on species-specific sensitivities to specific disturbances. The traits used were specific leaf area (SLA, $cm^2\,g^{-1}$), seed mass (SM; log-transformed, mg), wood density (WD, $g\,cm^{-3}$), maximum tree height (MTH, m) and water potential causing 50% loss of hydraulic conductivity (P50, MPa). SLA might be key following canopy openings caused by disturbances, as it is closely related to light acquisition and growth rates (Wright

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et al., 2004). SM differentiates species with high and low seed production and their dispersal capacity influencing seed availability after a disturbance (Seidl & Turner, 2022; Westoby et al., 2002). WD is related to species' tolerance to drought and fires, as it reflects their capacity for water storage (Chave et al., 2009; Wright et al., 2010). MTH is related to species' competitive ability for light resources after canopy openings, and P50 is used as a proxy of drought resistance and xylem safety (Westoby et al., 2002). Trait information for SLA, SM and WD was compiled using the TRY database (https://www.try-db.org/; Kattge et al., 2011) and complementary information from other sources (see Table S2.1). MTH was calculated as the 99.99% percentile of the height distribution for each species in 2SFI, and P50 data was compiled from Choat et al. (2012) database.

To assess how the dominance of a certain functional group influences above-ground productivity (i.e. selection effects), we quantified functional dominance as the community weighted mean of SLA (CWM_{SLA}) in each plot (Lavorel et al., 2008). We explored the collinearity between CWM for each functional trait analysed and found it to be highly correlated for most of them (Figure S2.2). To better distinguish between functional groups, we selected CWM_{SLA} as a representative trait because it reflects key aspects of plants' ecological strategy regarding productivity (i.e. resource acquisitive vs. resource conservative or fast-growing versus slow-growing species; Tilman et al., 1997). In addition, the SLA of the studied species ranged from needle-leaved to broad-leaved deciduous species (Figure S2.3). Thus, low values of CWM_{SLA} reflect a greater dominance of needle-leaved species, and medium to high values represent a higher dominance of broad-leaved species (Ruiz-Benito, Ratcliffe, Zavala, et al., 2017).

2.4 | Statistical analyses to infer the iterative effect of diversity and disturbances on forest productivity

We performed linear mixed models of above-ground productivity between consecutive censuses ($m^2 ha^{-1} year^{-1}$) at the forest level and for each functional group (i.e. needle-leaved, broad-leaved deciduous and broad-leaved evergreen species). Additionally, to account for the fact that disturbance occurrence perception might be affected by the time elapsed between inventories (i.e. lower probability of occurrence if the period is not long enough, Ruiz-Benito et al., 2020), we also fitted the productivity models for the entire period in the permanent plots, that is, 24SFI. The time elapsed between 2SFI and 4SFI is 25 years on average, while analysing the two time periods (i.e. 23SFI and 34SFI) the average time elapsed is 13 years. To assess possible effects of interaction between disturbances on above-ground productivity, we fitted productivity models in plots where more than one disturbance event was recorded (Table S1.4). For the models performed for each functional group, we removed plots where the target group was absent in the consecutive inventories, as above-ground productivity could not be calculated for these cases (i.e. in 2SFI and 3SFI for the 23SFI period, 3SFI and 4SFI for the 34SFI period and in 2SFI and 4SFI for the 24SFI period). As the models were fitted by target group, the same plot could be analysed multiple times if more than one functional group was present (Figure S2.4). We used plot identity as a random effect to account for the temporal autocorrelation resulting from repeated measurements at the same plot as we used two temporal measurements of above-ground productivity (Zuur et al., 2009), from 23SFI and 34SFI. To account for spatial autocorrelation, we added coordinates as covariates (Dormann, 2007). The continuous main effects were standardised to make coefficients more interpretable (Schielzeth, 2010), including as main effects the initial forest structure (i.e. basal area, tree density and mean d.b.h.); climate (i.e. water availability and drought), soil characteristics (i.e. pH and nitrogen); coordinates, the pairwise interaction between disturbances (occurrence of harvesting, fire and biotic damage) and forest diversity (structural and functional diversity), between disturbance and functional dominance (CWM_{SLA}) and between structural and functional diversity, with a total of 10 pairwise interactions (i.e. three disturbance types with two diversity metrics and the CWM_{SLA}; and the interaction between structural and functional diversity; see model details in Equation S2.1). Initial stand basal area, tree density, water availability and diversity were included in the model in quadratic form to consider typical hump-shaped or non-linear relationships between species and environment while allowing monotonic or sigmoidal responses within constrained ranges along either axis (Gómez-Aparicio et al., 2011; Ruiz-Benito, Ratcliffe, Jump, et al., 2017 and exploration in Figure S2.5). Despite the high correlations among water availability and soil variables, we decided to retain both groups because we were interested in explaining both effects (Figure S2.6).

To test the interactive effect between forest diversity and disturbances on above-ground productivity, we fitted a full model containing all the aforementioned variables and compared it to reduced models, each with one interaction term removed. We selected the most parsimonious models based on Burnham and Anderson (2002), choosing the simpler model when the AIC difference between models was less than two units. The process was repeated, comparing the selected model with the supported interactions to candidate models that excluded the main effects, dropping in each model one main effect and selecting the supported variables. We used the *lme4* R package to fit the linear mixed models (Bates et al., 2015) and obtained marginal and conditional R^2 (i.e. for the fixed and fixed plus random effects) to characterise the goodness-of-fit of the most parsimonious model (Nakagawa & Schielzeth, 2013). Finally, we checked the distribution of the residuals of the most parsimonious model both at the forest level and for each functional group (Figure S2.7).

We grouped the explanatory variables into forest structure, climate, soil and disturbances to assess the relative importance of each group of variables. However, diversity-related variables were not grouped in order to evaluate the individual contribution of each diversity metric separately. We used *t*-statistic values obtained from the best models, where the absolute *t*-statistic reflects the significance of each variable (Xie & Luo, 2022). The relative importance of each predictor was calculated as the ratio of the variable's *t*-value to the sum of all *t*-values. The variable importance was calculated using the *caret* R package (Kuhn et al., 2020).

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3 | RESULTS

3.1 | Relationships between disturbances and above-ground productivity

Above-ground productivity decreased in plots that experienced disturbances compared to undisturbed plots, especially for harvesting and fire in needle-leaved species (Figure 1). Harvesting significantly decreased mean above-ground productivity, with reductions of 94.3%, 105.7%, 69.6% and 60.0% at the forest level, needle-leaved, broad-leaved deciduous and broad-leaved evergreen species, respectively (Figure 1a). Above-ground productivity reductions in harvested plots were mainly related to increased mortality (Figure S3.1). Similarly, fire occurrence decreased above-ground productivity at the forest level and for each functional group (144.0% at the forest level, 223.8% for needle-leaved, 33.3% for broad-leaved deciduous and 89.9% for broad-leaved evergreen species; Figure 1b). Above-ground reductions in fire-affected plots were associated with both increased mortality and decreased growth rates (Figure S3.1). The occurrence of biotic damage significantly affected above-ground productivity only in needle-leaved species, leading to a 24.6% reduction (Figure 1c), which was associated with decreased growth rates (Figure S3.1).

3.2 | Biotic and abiotic factors driving above-ground productivity

The best models for predicting above-ground productivity at the forest level and for each functional group included forest structure, soil, climate, diversity, functional dominance, harvesting and fire. However, pest was only included in models at the forest level and for needle-leaved (Table 1). Conditional R^2 ranged from 26% to 33% and marginal R^2 from 14% to 23% depending on the model (Table 1). Forest structure explained between 30% and 48% of the variation, depending on the functional group (Figure 2), being initial basal area the most important forest structure variable in all models, followed by density and mean d.b.h. (see ΔAIC in Table 1). Above-ground productivity decreased with increasing stand basal area at the forest level and for each functional group, but especially for needle-leaved species (Table S3.1; Figure S3.2). In addition, above-ground productivity showed a hump-shaped relationship with tree density at the forest level and for each functional group (Table S3.1; Figure S3.2). Above-ground productivity was negatively associated with mean tree size at the forest level and for each functional group (Table S3.1; Figure S3.2).

Climatic variables explained between 10% and 15% of the variation across all models (Figure 2). Water availability was the most important climatic variable, while drought was included at the forest level and for broad-leaved evergreen species models (Table 1; Figure S3.2). Above-ground productivity decreased with water stress (i.e. lower water availability), especially in needle-leaved species, which showed negative above-ground productivity values in the driest sites (Table S3.1; Figure S3.2). Finally, soil variables explained between 5% and 10% of the variation across all models (Figure 2). Above-ground productivity decreased with pH at the forest level and for needle-leaved and broad-leaved deciduous species, while above-ground productivity increased with high nitrogen content for broad-leaved evergreen species (Table S3.1; Figure S3.2).

Forest structure variables are initial basal area, stand density and mean tree size; climate variables are water availability and drought; soil variables are pH and nitrogen (soil N); disturbance variables are harvesting, fire and biotic damage, and forest diversity variables are structural diversity, functional diversity and functional dominance

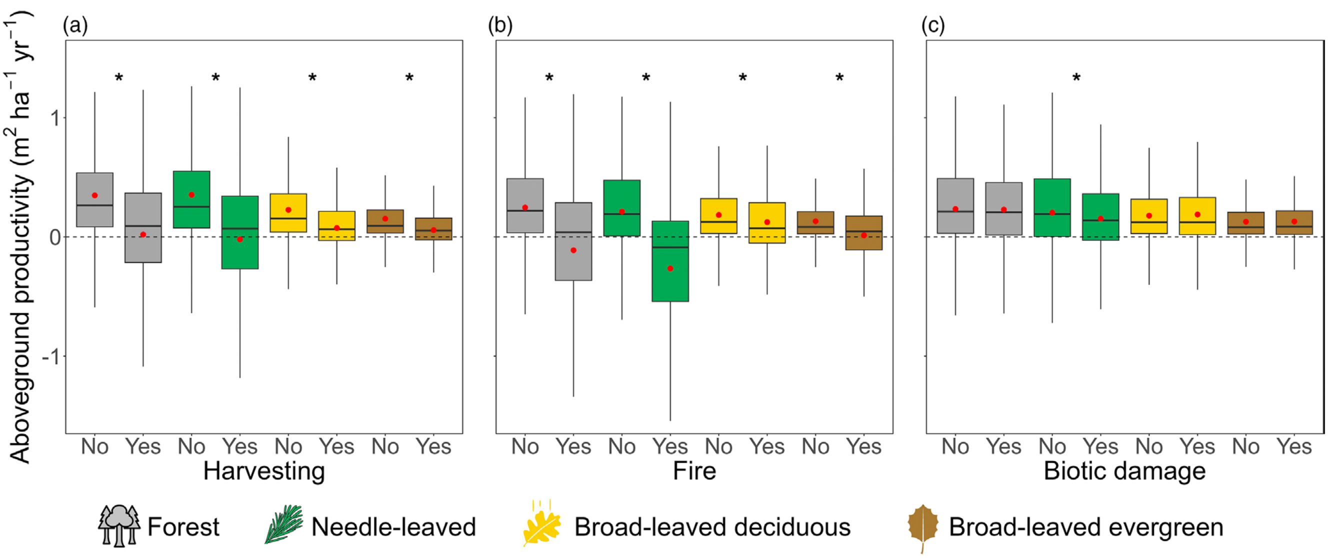

FIGURE 1 Boxplots of the observed above-ground productivity ($m^2\,ha^{-1}\,year^{-1}$) at the forest level (grey), needle-leaved (green), broad-leaved deciduous (yellow) and broad-leaved evergreen (brown) species according to the absence (No) or occurrence (Yes) of (a) harvesting, (b) fire and (c) biotic damage disturbances. Inset asterisks in boxplots indicate significant differences ($p < 0.05$) between the absence and occurrence of disturbances. Red dots indicate the mean values of each group.

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TABLE 1 Two-step model comparisons based on delta Akaike information criterion (ΔAIC) to test pairwise interactions between disturbances and forest diversity, and main effects of forest structure, climate and soil on above-ground productivity for all tree species, needle-leaved, broad-leaved deciduous and broad-leaved evergreen species.

Models	Forest	Needle-leaved	Broad-leaved deciduous	Broad-leaved evergreen
Full model	0	0	0	0
No structural diversity × functional diversity				
No structural diversity × harvesting	44.7	11.1	9.9	16.6
No structural diversity × fire	9.9	4.4	10.4	
No structural diversity × biotic damage				
No functional diversity × harvesting	11.8	12.9	17.0	
No functional diversity × fire				
No functional diversity × biotic damage				
No CWM_{SLA} × harvesting	71.2	124.2	101.3	57.6
No CWM_{SLA} × fire	124.3	45.6		
No CWM_{SLA} × biotic damage	20.3			
Model with significant interactions	0	0	0	0
No harvesting	937.4	773.1	204.6	158.2
No fire	311.4	274.0	13.5	19.5
No biotic damage	22.0	15.4		
No structural diversity	79.9	30.7	76.4	24.2
No functional diversity	11.9	98.7	42.9	7.4
No initial basal area	387.8	447.6	15.2	100.9
No density	200.4	69.4	21.6	108.6
No mean tree size	13.4	17.2	8.4	24.7
No CWM_{SLA}	591.2	381.9	139.0	57.8
No water availability	281.8	180.3	49.2	30.6
No drought	5.2			23.1
No soil pH	126.0	229.2	48.0	
No soil N				8.1
R^2 conditional	0.27	0.33	0.26	0.30
R^2 marginal	0.19	0.23	0.14	0.17

(CWM_{SLA}). The 'No' models exclude the effect of each explanatory variable. The numbers indicate the $\Delta AIC_{reduced\text{-}full}$ between the reduced and the full model. Marginal R^2 (proportion of variance explained by fixed factors) and conditional R^2 (proportion of variance explained by both fixed and random factors) are indicated for the best fitting models.

3.3 | Effects of diversity, functional dominance and disturbances on above-ground productivity

We found that the occurrence of disturbances explained between 16% and 27% of the variance depending on the model (Figure 2; Table S3.1). Harvesting was the disturbance that accounted for most of the variation, followed by fire and biotic damage (Table 1). Structural diversity explained between 1% and 8% of the variation, whereas functional diversity accounted for between 1% and 10%. However, the interaction between both metrics was not included in any model (Table 1).

The interaction between diversity and the occurrence of harvesting and fire was included in models for most of the studied groups, accounting for between 2% and 10% of the variation in above-ground productivity (Figure 2; Table 1). At high levels of structural and functional diversity, above-ground productivity tended to be equal to or higher in plots that experienced harvesting or fire than in undisturbed plots, except for broad-leaved deciduous species in

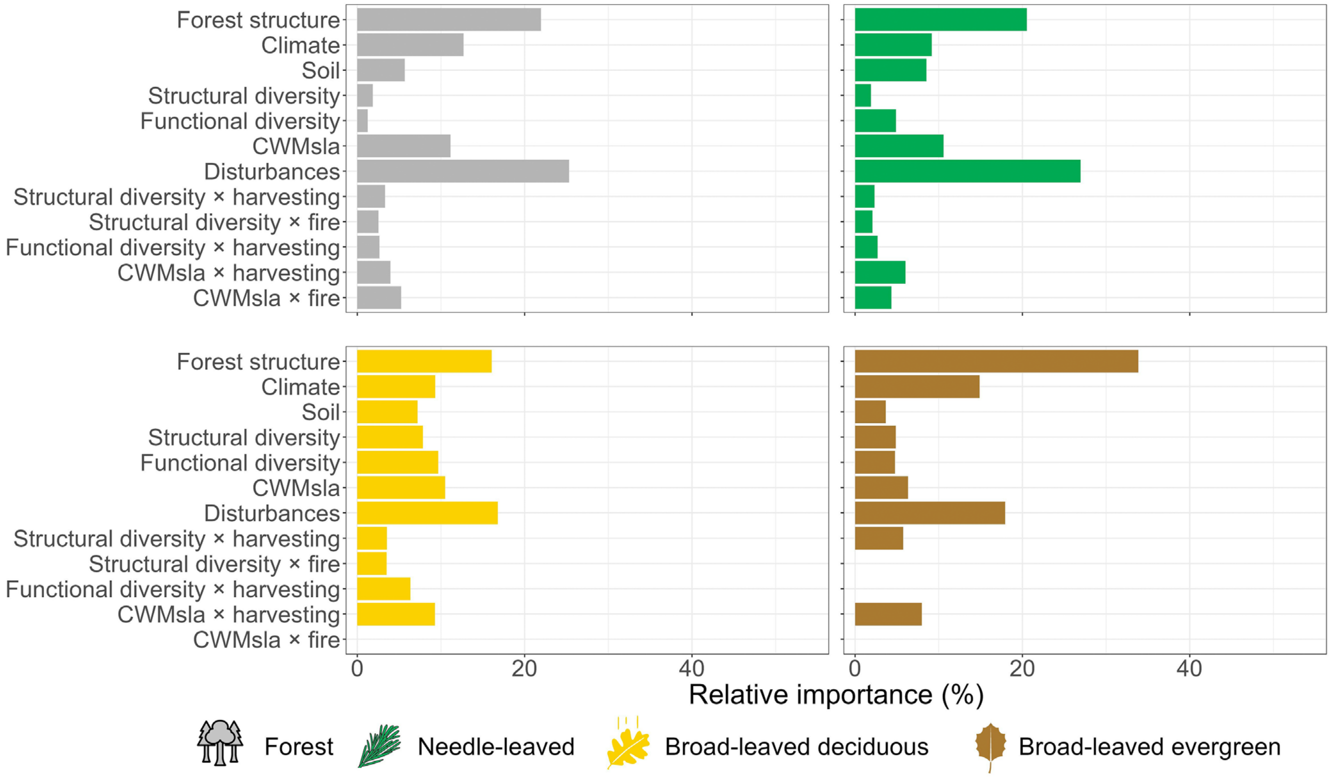

FIGURE 2 Relative importance of forest structure, climate, soil, forest diversity (structural and functional diversity), functional dominance (CWM_{SLA}) disturbances and the interactions between structural and functional diversity, functional dominance and disturbances of the best model at the forest level (grey), needle-leaved (green), broad-leaved deciduous (yellow) and broad-leaved evergreen (brown) species. The interactions without bars in the graph means that it was not included in the best model.

response to fire (Figures 3 and 4; Table S3.1). These patterns were consistent when analysing the entire period 24SFI, except for fires (see Figures S3.3 and S3.4) and when testing multiple interactions (i.e. harvesting and fire; harvesting and biotic damage; fire and biotic damage; see Figures S3.5 and S3.6).

Structural diversity had no effects on above-ground productivity in unharvested plots, but above-ground productivity was greater in harvested than unharvested plots when structural diversity was high (Figure 3a–d). On the contrary, above-ground productivity was higher in unharvested plots when structural diversity showed low to medium values. Above-ground productivity in fire-affected plots did not exceed that of unaffected plots either at the forest level or in each functional group, but above-ground productivity of fire-affected plots was compensated at the highest levels of structural diversity at the forest level and in needle-leaved species (Figure 3e,f). However, above-ground productivity of broad-leaved deciduous species decreased in fire-affected plots with increasing structural diversity (Figure 3g). Finally, structural diversity had no effects on plots with the occurrence of biotic damage.

Functional diversity had varying effects on forest productivity in harvested plots depending on the target functional group (Figure 4; Table S3.1). Above-ground productivity at the forest level and for needle-leaved species in harvested plots was only comparable to that in unharvested forests with highest values of functional diversity (Figure 4a,b). However, the differences in above-ground productivity of broad-leaved deciduous species between harvested and unharvested plots were minimised at medium levels of functional diversity (Figure 4c).

Functional dominance (CWM_{SLA}) explained between 6% and 11% of the variation across models (Figure 2). The interaction between functional dominance and harvesting was selected in all models, accounting between 4% and 10% of the variation in above-ground productivity. In contrast, the interaction between functional dominance and fire was only selected at the forest level and for needle-leaved species, explaining 5% and 4% of the variation, respectively (Figure 2; Table 1). The effects of functional dominance on above-ground productivity varied among the studied functional groups (Figure 5). As CWM_{SLA} increased above-ground productivity generally decreased (Figure 5), especially for needle-leaved species in the absence of disturbances (Figure 5b,f). In contrast, an opposite pattern was found in the absence of harvesting for broad-leaved deciduous species (Figure 5c) and in plots affected by fire (Figure 5e,f), where increased productivity was associated with higher CWM_{SLA}.

4 | DISCUSSION

Our findings show a strong impact of harvesting and fires on the above-ground productivity of Iberian forests, particularly for

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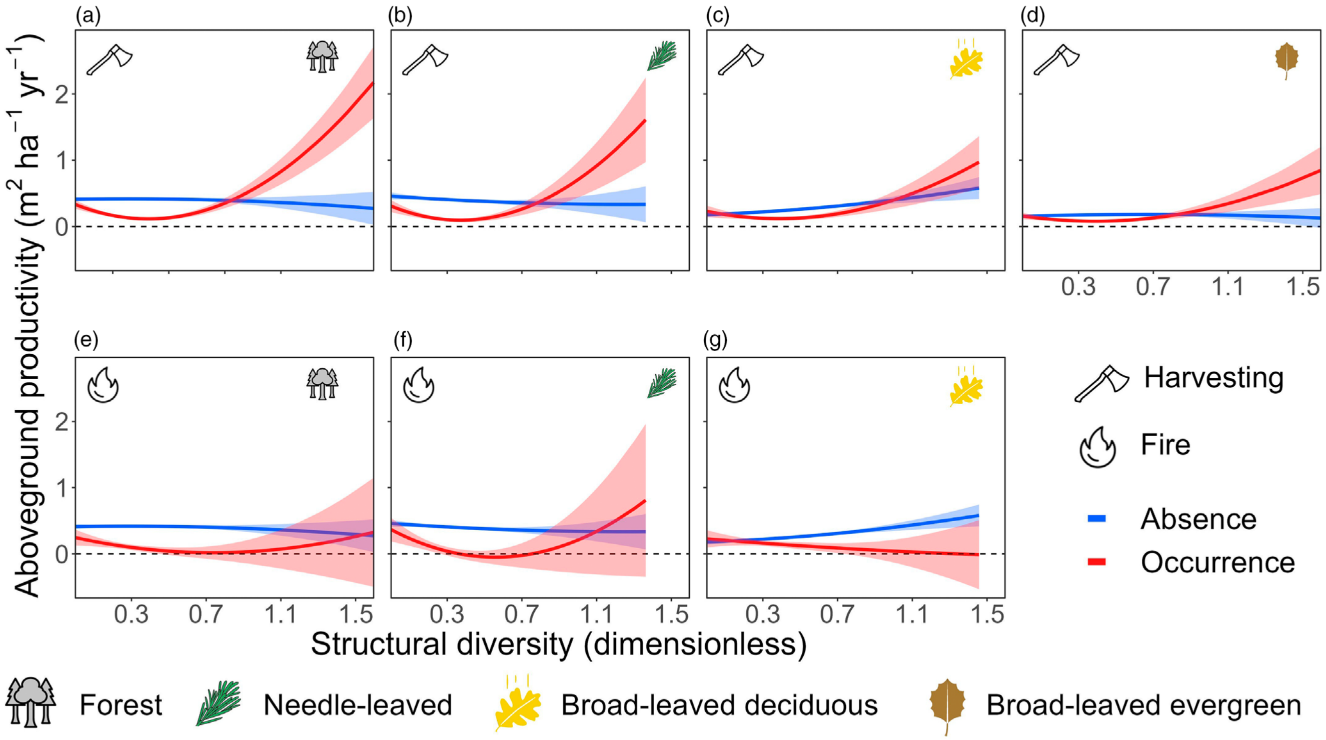

FIGURE 3 Predictions of above-ground productivity (m^2 ha^{-1} year^{-1}) along structural diversity (i.e. coefficient of variation of tree diameters) for: (a, e) the forest level; (b, f) needle-leaved, (c, g) broad-leaved deciduous and (d) broad-leaved evergreen species depending on the occurrence (red) or absence (blue) of harvesting and fire. Only significant interactions for each model are shown.

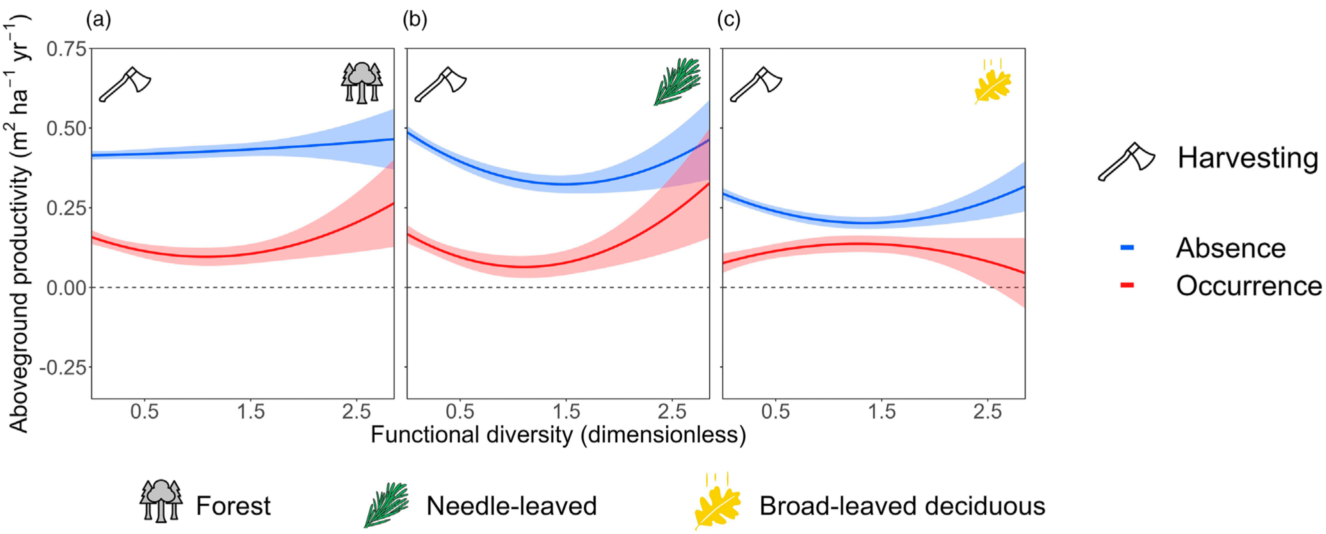

FIGURE 4 Predictions of above-ground productivity (m^2 ha^{-1} year^{-1}) within the range of existing functional diversity (i.e. functional dispersion of key functional traits), for (a) the forest level, (b) needle-leaved and (c) broad-leaved deciduous species depending on the occurrence (red) or absence (blue) of harvesting. Only significant interactions for each model are shown.

needle-leaved species. Interestingly, we found that the negative impact of disturbances on above-ground productivity can be partially mitigated when structural diversity is high. This mitigating capacity was reported at the forest level and for each of the studied functional groups (i.e. needle-leaved, broad-leaved deciduous and broad-leaved evergreen). However, high levels of functional diversity partially attenuated the impact of disturbances only in needle-leaved species, suggesting a more limited capacity of forest ecosystems dominated by broad-leaved species to cope with the impacts of disturbances. Above-ground productivity of each functional group was higher in undisturbed plots where that group was highly dominant, which is consistent with the mass ratio hypothesis. However, the dominance of broad-leaved deciduous species led to decreases in above-ground productivity in harvested plots

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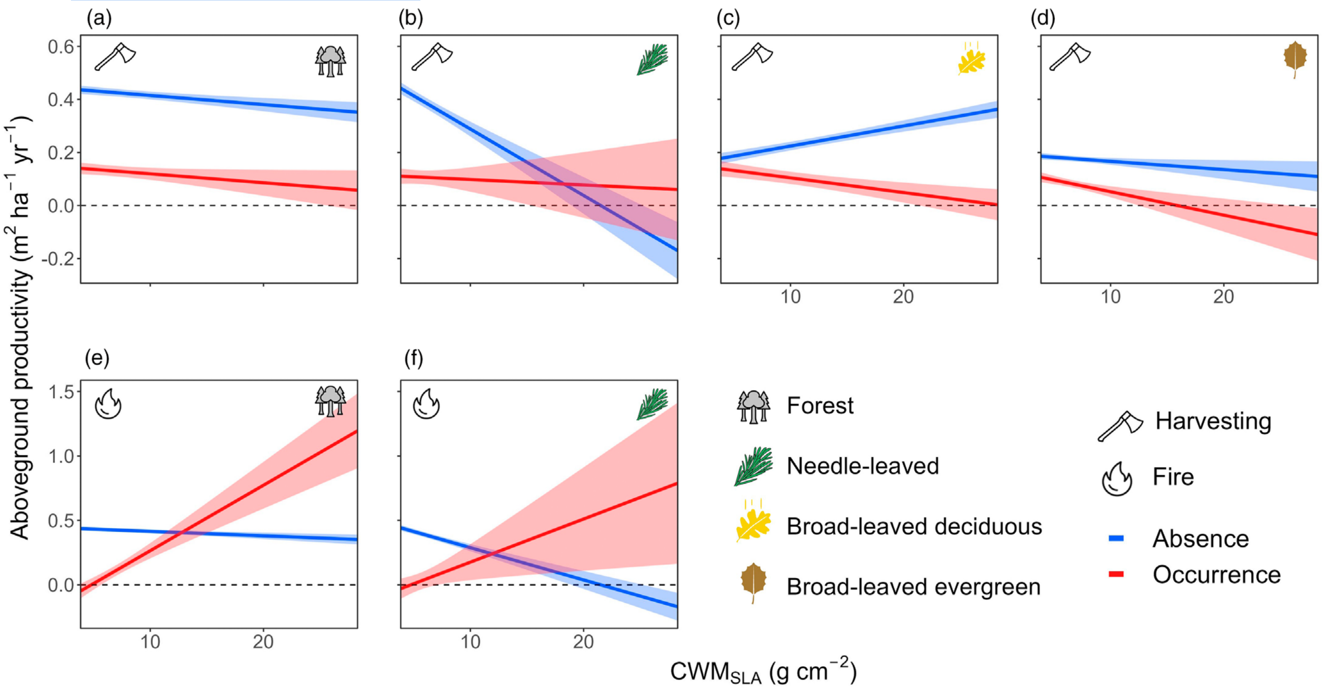

FIGURE 5 Predictions of above-ground productivity (m^2 ha^{-1} year^{-1}) within the range of existing functional dominance (CWM$_{SLA}$), for (a, e) the forest level, (b, f) needle-leaved, (c) broad-leaved deciduous and (d) broad-leaved evergreen species depending on the occurrence (red) or absence (blue) of harvesting and fire. Only significant interactions for each model are shown.

for all the studied functional groups. Overall, our results provide information to better understand the role of different components of forest diversity in the stability of above-ground productivity to disturbances, as well as its implications for forest dynamics and dominance shifts.

4.1 | Disturbance impacts on above-ground productivity differ between species functional groups

Disturbances exert a strong influence on forest dynamics by increasing tree mortality, ultimately leading to a reduction in above-ground productivity (McDowell et al., 2020). This is particularly the case for abrupt disturbances such as harvesting or fire (Turner & Seidl, 2023). The negative impacts of disturbances may be influenced by forest structure and climate. For instance, high basal area is associated with more intense competition (Rosas et al., 2021), which may explain the strong decrease in productivity under disturbance occurrence and at high basal area for needle-leaved species. Our findings align with other studies highlighting the greater vulnerability of needle-leaved species to disturbances compared to broad-leaved species in Mediterranean forests (Barrere et al., 2023). Their fast growth and intensive management for timber, often in high-density plantations (Ruiz-Benito et al., 2012), may increase susceptibility to fire due to fuel accumulation (Pausas & Ribeiro, 2013) and exacerbate competition, reducing regeneration and productivity (Ruiz-Benito, Madrigal-González, et al., 2014; Zavala & Zea, 2004). In contrast, the functional characteristics of Mediterranean broad-leaved species, including high wood density, high capacity to cope with water stress and their resprouting ability, combined with their comparatively less intensive exploitation for timber purposes relative to needle-leaved species, could explain the lower impact of fire and harvesting on these species (Barrere et al., 2023; Hanewinkel et al., 2013).

Needle-leaved species also showed significant reductions in above-ground productivity in response to biotic damage. The fact that a high proportion of needle-leaved forests are monospecific plantations might underlie their increased susceptibility to host-specific pests (Jactel et al., 2021). Furthermore, increased frequency and intensity of drought events under warming conditions in the Mediterranean region may increase tree vulnerability to pests (Gallego-Tévar et al., 2024; Rebollo et al., 2024). For example, bark beetles generally attack weak trees (i.e. water-stressed) and the interaction between climate and biotic damage may lead to large tree mortality events and consequently to reduced above-ground productivity of needle-leaved species (de la Mata et al., 2017; Trugman et al., 2021). Finally, the lack of data from Andalusia (Southern Spain), a region severely affected by *Phytophthora* (Corcobado et al., 2014; Serrano et al., 2024), may underestimate the biotic impacts on broad-leaved species.

4.2 | Structural and functional diversity underlined disturbance effects on forest productivity

Our results show how structural and functional diversity reduced the negative effects of disturbances on above-ground productivity

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in Iberian forests. However, both diversity components attenuated the negative effects of disturbances differently, and their mitigating potential varied among the functional groups studied. We found that structural diversity had a stronger effect than functional diversity in shaping productivity responses to fire and harvesting disturbances. This is in line with previous studies that suggest that size heterogeneity promotes complementarity in the use of resources more strongly than changes in functional traits between species (Aponte et al., 2020; Zhai et al., 2024). High tree-size heterogeneity could increase above-ground light interception and below-ground resource utilisation, increasing productivity (Williams et al., 2021). In addition, structural diversity also plays a key role in forest recovery after abrupt disturbances as it allows the presence of saplings and juveniles in the understorey due to enhanced light capture (Diaci et al., 2017; Sapijanskas et al., 2014). Thus, when a disturbance such as the harvesting of overstorey trees occurs, individuals in the understorey can grow rapidly due to competition release (Bartels & Macdonald, 2023). Furthermore, intensive managing practices lead to decreases in soil nutrients such as nitrogen due to increases in solar radiation and temperature in the soil following vegetation removal (Ameray et al., 2021; Merino et al., 1998). In this regard, evergreen species have higher nutrient use efficiency than deciduous species due to their longer leaf lifespan and lower nutrient loss rates, showing higher productivity rates than broad-leaved species after abrupt disturbances (Aerts, 1995).

Structural diversity also diminished the negative effects of fire on above-ground productivity. At the forest level and for needle-leaved species, high structural diversity buffered post-fire above-ground productivity losses, whereas broad-leaved deciduous species showed reduced productivity across the entire structural diversity gradient. On the one hand, structural diversity might attenuate environmental stress in small trees by reducing water loss from evapotranspiration (Ma et al., 2023). On the other hand, more diverse forest structure promotes fuel load accumulation and continuity, thus increasing fire intensity and frequency (Fernandes, 2009; González & Pukkala, 2007), aggravating fire impacts on productivity when biomass and homogeneity are high (Zhai et al., 2022). In the last decades, fire severity has increased in Iberian forests, especially in needle-leaved-dominated stands (Miguel et al., 2024). Our results suggest that the negative impacts of fire on productivity in needle-leaved species may be mitigated when structural diversity is high, possibly due to the presence of fire-adapted species and resource release after fire (Oliver, 1980).

On the contrary, functional diversity exhibited a more limited capacity to mitigate the negative impacts of disturbances at the forest level. Moreover, compensation of above-ground productivity loss due to harvesting in needle-leaved species occurred at a high level of functional diversity, while in the case of broad-leaved deciduous it occurs at intermediate levels. This result is consistent with previous research suggesting the high resilience of *Pinus* species in response to abrupt disturbance in the Mediterranean region, which has been linked to the serotinous characteristics of some species and their capability to take advantage of the gaps created after disturbances, being a pioneer tree species in disturbed forest ecosystems (Guo et al., 2019; Holling & Gunderson, 2002; Vacek et al., 2021). Thus, a higher level of functional diversity can partly compensate above-ground productivity loss due to abrupt disturbances, but at the expense of increasing the dominance of needle-leaved over broad-leaved species in sites where both groups coexist (Seidl & Turner, 2022).

In the context of global change, an increase in compound disturbances is anticipated, including the combination of natural events followed by management interventions such as post-disturbance thinning (Kleinman et al., 2019; Leverkus et al., 2018). These interacting disturbances have the potential to alter forest recovery trajectories and compromise ecosystem resilience (Bigler et al., 2005). Our findings indicate that forest diversity may play a crucial role in buffering the effect of such compound events, highlighting its potential as a key component in enhancing forest resilience under increasingly complex disturbance regimes.

Beyond its role in resilience, tree diversity also holds important implications for climate mitigation efforts. Previous studies have shown that increased tree diversity enhances carbon storage (Ruiz-Benito, Gómez-Aparicio, et al., 2014). Building on this, our results show that promoting structural and functional diversity may not only maintain forest productivity but also support more stable carbon sinks by mitigating the impacts of disturbances (Aponte et al., 2020). Thus, tree diversity should be carefully considered in forest management practices aiming to maximise carbon sequestration and the stability of key ecosystem services (Anderegg et al., 2020).

4.3 | Functional dominance modulated forest productivity in response to harvesting and fire

We found that selection effects determined above-ground productivity to harvest and fires, explaining between 4% and 10% of the variance. Selection effects reflect the advantage of certain traits under prevailing environmental conditions leading to increased forest productivity (Loreau, 2000). In absence of disturbances, we found that productivity decreased as the CWM_{SLA} increased, except for broad-leaved deciduous species. These results support the mass-ratio hypothesis as we expect that the highest productivity is at the lowest values of CWM_{SLA} for needle-leaved species, at intermediate values for broad-leaved evergreen species and at the highest values for broad-leaved deciduous species (Figure S5). Our result agrees with previous suggestions of the highest productivity and carbon storage when the target trait dominates, with fast-growing Mediterranean species being the most sensitive to selection effects (Ruiz-Benito, Gómez-Aparicio, et al., 2014).

In harvested plots, above-ground productivity responses to selection effects were lower in needle-leaved and broad-leaved deciduous species (i.e. see lower slope when harvesting is absent than present, Figure 5b,c). The lowest effect of selection effects on forest productivity due to harvesting occurrence could be due to the fact that the most dominant species is the one that has the highest probability of being harvested (Suvanto et al., 2025). Harvesting the most dominant species could be underlying the more similar responses of forest productivity observed along the range of CWM_{SLA}, therefore, decreasing the magnitude of the observed selection effect in each functional group. We did not find a very contrasted response in harvested plots for broad-leaved evergreen species, which might be underlined by the lowest exploitation (Vadell et al., 2022; see also that 25.8% were affected by harvesting, compared to 42.5% and 30.2% in needle-leaved and broad-leaved deciduous species, respectively; Table S1.5).

We only found significant differences in forest productivity along functional dominance in the presence and absence of fires for needle-leaved species (Figure 5f). Furthermore, under fires, forest productivity decreased as the dominance of the target group increased (i.e. when CWM_{SLA} is low, the stand dominated by needle-leaved species, Figure 5f). The observed response only in needle-leaved species suggests that they are particularly vulnerable to fires (Lloret et al., 2002), which could be partially due to the high resprouting capacity of some deciduous oaks (Espelta et al., 2003).

4.4 | Limitations of the study

In this study, we used field data from the Spanish Forest Inventory to evaluate the effect of disturbances (i.e. harvesting, fires and biotic damage) on above-ground productivity at large spatial extents, but we acknowledge several limitations. Firstly, reliance on forest inventory data limits our ability to infer causality, as unmeasured confounding factors may influence productivity. For example, prior land-use history or unrecorded disturbances may influence productivity through legacy effects (Vilà-Cabrera et al., 2023). Secondly, focusing only on the occurrence of disturbances limits our ability to investigate how forests respond to different disturbance intensities, frequencies and extents (Turner & Seidl, 2023). Further understanding of the role of disturbances on above-ground productivity requires a higher temporal resolution of observations such as those provided by remote sensing data (Kulha et al., 2025). Finally, other confounding factors may interact with the disturbances studied here, including climatic extremes, such as droughts and heatwaves, that are playing an increasing role in vegetation dynamics (Tijerín-Triviño, Lines, et al., 2025). The identified limitations on our study preclude the inference of causal mechanisms and highlight the need for studies incorporating experimental manipulations, high-resolution temporal data and mechanistic modelling to disentangle the multifaceted interactions between disturbance regimes, diversity components and forest functioning under changing climate.

5 | CONCLUSIONS

This study underscores the critical role of forest diversity in buffering the impacts of disturbances on above-ground productivity, offering valuable insights into ecosystem resilience under changing environmental conditions. Abrupt disturbances (i.e. harvesting and fire) strongly decreased above-ground productivity of Iberian forests in the last decades. Our results suggest that the impacts of abrupt disturbances on above-ground productivity can be diminished by increasing forest diversity. Specifically, high structural diversity increased above-ground productivity in harvested and fire-disturbed stands. High functional diversity also increased productivity in harvested stands, suggesting that it might also be a key mitigation measure. In addition, we observed strong selection effects in the absence of disturbances, suggesting increased productivity when the target species dominate (i.e. low CWM_{SLA} in needle-leaved species or high CWM_{SLA} in broad-leaved deciduous species). These selection effects disappeared with harvesting, whereas fires showed the opposite patterns in needle-leaved species (i.e. decreased productivity when the target species dominate). Taken together, all the results suggest that promoting structural diversity should be a priority measure to further enhance the role of forests as carbon sinks and for the maintenance of forest productivity. Furthermore, the altered selection effects under disturbances suggest that measures towards trait selection can further determine forest productivity and responses to disturbances.

Our approach, grounded in extensive forest inventory data and tree functional traits, provides a robust framework for assessing forest productivity responses to disturbances across broad bioclimatic gradients. Future research could extend the applied approach by incorporating the effect of different dimensions of disturbance regimes (i.e. disturbance intensity, frequency and extent; Senf & Seidl, 2021) on forest productivity (i.e. Tijerín-Triviño, Serra-Maluquer, et al., 2025). Moreover, generalising how functional and structural diversity maintains forest productivity in other biomes would enhance our understanding of the role of biodiversity in buffering negative impacts of disturbance on forest productivity, with direct implications for forest management and conservation planning. Ultimately, our findings advocate for integrating structural and functional diversity into adaptive forest management schemes to enhance the role of forests as carbon sinks and sustain forest productivity in the face of shifting disturbance regimes.

AUTHOR CONTRIBUTIONS

Pedro Rebollo, Enrique Andivia, Verónica Cruz-Alonso and Paloma Ruiz-Benito planned the research. Verónica Cruz-Alonso, Paloma Ruiz-Benito, Julen Astigarraga, Miguel Ángel Zavala and Patricia González-Díaz processed the data and Pedro Rebollo, Enrique Andivia, Verónica Cruz-Alonso and Paloma Ruiz-Benito analysed the data. Pedro Rebollo, Verónica Cruz-Alonso and María Triviño designed and performed the graphical representation. All authors contributed to the final version through several revisions.

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el Reto Demográfico). Pedro Rebollo is funded by an assistant professor grant from the Complutense University of Madrid. Verónica Cruz-Alonso was supported by the Ministry of Universities, Spain, and Next Generation-EU, with a 'Maria Zambrano' fellowship. Paloma Ruiz-Benito was supported by the Community of Madrid Region under the framework of the multi-year Agreement with the University of Alcalá (Stimulus to Excellence for Permanent University Professors, EPU-INV/2020/010). María Triviño was supported by the Kone Foundation (application 202206136). Julen Astigarraga, Verónica Cruz-Alonso, Pedro Rebollo, Paloma Ruiz-Benito, María Triviño and Miguel Ángel Zavala have been funded by the Science and Innovation Ministry, AEI (Agencia Estatal de Investigación) (subproject LARGE, No. PID2021-123675OB-C41). Miguel Ángel Zavala and Paloma Ruiz-Benito were also supported by grant VERDAT; MITECO (Organismo Autónomo de Parques Nacionales, Ref. 2794/2021). The Spanish National Forest Inventory is available thanks to the Spanish Ministry for the Ecological Transition and the Demographic Challenge (https://www.miteco.gob.es). We are also grateful to Niko Kulha, Georges Kunstler and Julien Barrere for their valuable discussions.

CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available in https://doi.org/10.5281/zenodo.17140641 (Rebollo, 2025). The Spanish National Forest Inventory data were provided by the Spanish Ministry for the Ecological Transition and the Demographic Challenge (MITECO) and were obtained at https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional.html.

ORCID

Pedro Rebollo https://orcid.org/0000-0001-9448-7507
Verónica Cruz-Alonso https://orcid.org/0000-0002-0642-036X
Paloma Ruiz-Benito https://orcid.org/0000-0002-2781-5870
María Triviño https://orcid.org/0000-0002-2420-3537
Julen Astigarraga https://orcid.org/0000-0001-9520-3713
Patricia González-Díaz https://orcid.org/0000-0003-3664-2913

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SUPPORTING INFORMATION

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

Appendix S1. Further details of the Spanish Forest Inventory.

Appendix S2. Further modelling details.

Appendix S3. Complementary results.

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