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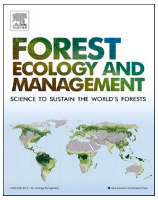

Deadwood and Tree-related Microhabitat's abundance and diversity are determined by the interplay of drought-induced die-off and local climate

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ABSTRACT

Global climate change is increasing the frequency and severity of drought events that cause tree mortality worldwide, particularly in temperate and Mediterranean regions. Researchers have extensively studied the impact of such drought events on forest growth and tree mortality. However, knowledge on the aftermath of such mortality on habitat provision for biodiversity (i.e., abundance, richness, and diversity of deadwood in different decaying stages and tree-related microhabitats) is limited. In this study, we aimed to quantify the impact of drought die-off events on these biodiversity habitat proxies by sampling twenty sites comprised of paired plots (i.e., drought die-off vs control) in Scots pine (*Pinus sylvestris*) dominated forests in Catalonia (NE Spain), also considering the influence of forest structure and local climate. We used deadwood and Tree-related Microhabitats (TreM) as proxies for potential biodiversity, basal area as a descriptor of forest structure, and precipitation and temperature to characterize local climate. We found that die-off plots exhibited higher abundance (83%), richness (23%), and diversity (20%) of deadwood than control ones. We also observed that standing (snags) and downed (logs) deadwood compartment showed high abundance (45% and 56%, respectively), richness (26% and 25%, respectively) and diversity (18% for both snags and logs) of TreM. Yet, we found that the presence of deadwood in different decaying stages was also shaped by local climate factors: i.e., wetter sites contained higher proportion of recent deadwood and lower proportion of decaying deadwood, while colder sites contain higher deadwood abundance. Differences in the timing of tree death together with local climate resulted in higher richness of deadwood types in wetter sites, which can likely support higher biodiversity through the presence of more abundant TreM. However, these benefits may be temporary, due to faster deadwood decomposition in wetter environments. Conversely, the observed more long-lasting presence of deadwood in colder and drier sites, may promote structural complexity to persist, although these more extreme climatic conditions may also hinder this benefit if they affect the species relaying on this resource. Ultimately, our study pinpoints that at least during a certain period following a drought-induced die-off event, forest structure becomes more heterogeneous and complex, potentially supporting higher biodiversity, with local climate further shaping the duration of these beneficial effects. These results may help forest managers in guiding their decision regarding the management of deadwood following die-off episodes, with the aim of promoting heterogeneous forest structures and enhancing biodiversity conservation.

1. Introduction

Climate-induced drought events have emerged globally as important drivers of forest dynamics by promoting tree mortality in various biomes (Allen et al., 2015, 2010). The increase in frequency and severity of droughts (Dai, 2013; Trenberth et al., 2013), often together with heatwaves, has prompted concerns about the vulnerability of forest ecosystems to potential shifts on species composition and structure, and even

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collapse (Lloret and Batllori, 2021), particularly in temperate and Mediterranean areas (Samaniego et al., 2018; Margalef-Marrase et al., 2023). Drought can trigger tree mortality directly via hydraulic failure and/or carbon starvation (Adams et al., 2017), but large-scale mortality events are more often attributable to the combined effect of drought and additional disturbances such as insect pests (Anderegg et al., 2015; Jaime et al., 2022, 2019). The results of this synergistic effect have been thoroughly investigated, including the impact on tree growth and productivity (Babst et al., 2019; García-Valdés et al., 2021), alteration of forest structure and composition (Ruiz-Benito et al., 2013), distribution, and demography (Dyderski et al., 2018; Senf et al., 2021). However, the consequences of drought-induced mortality events on forest biodiversity are still insufficiently explored, in particular for taxa other than tree species (but see Sire et al., 2022).

The aftermath of disturbances in forest ecosystems is complex, as disturbances can negatively impact forest biomass while increasing biodiversity (i.e., “disturbance paradox”, see Thom & Seidl, 2016), provided that disturbances are not too frequent (i.e., “intermediate disturbance hypothesis” see Connell, 1978; Viljur et al., 2022). Tree mortality results in canopy openness and deadwood accumulation, which can modify stand and microclimatic conditions by increasing the penetration of radiation but also retaining moisture (Schmidt et al., 2017; Thom et al., 2020). Moreover, the presence of partly defoliated trees and dead trees in different positions (i.e., snags, stumps, and downed) and decaying stages (i.e., fresh and decomposed deadwood) may increase the overall vertical and horizontal heterogeneity (Vayreda et al., 2019) and the presence of different types of Tree-related Microhabitat (TreM), such as injuries and wounds, insect galleries, fruiting bodies of fungi, bark complexity, among others (Larrieu et al., 2018). Therefore, tree attributes, such as species identity, tree size, health status and deadwood position determine TreMs abundance and richness (Paillet et al., 2017, 2019; Großmann et al., 2018; Asbeck et al., 2021). In turn, these TreMs have been observed to be closely related with the diversity of birds, bats, and invertebrates (Paillet et al., 2018; Basile et al., 2020). Ultimately, the new conditions and resources generated after the drought-induced mortality event may potentially augment both habitat structural complexity and the provision of resources for many species, thereby amplifying forest biodiversity, especially regarding taxa such as birds, small mammals, xylophagous insects, epiphytes, and fungi (Beudert et al., 2015; Thom & Seidl, 2016; Sallé et al., 2020; Bouget et al., 2023). Furthermore, the reduction in competition after tree mortality and the creation of canopy gaps may boost the ingrowth of advanced regeneration and the recruitment of new tree species, initiating a successional process and increasing tree species richness (Lloret et al., 2012; Batllori et al., 2020; García-Valdés et al., 2021). Thus, some of these features (e.g., higher species richness, structural complexity, increase in deadwood, and presence of TreMs) are often included in indices to describe and summarize the biodiversity potential of forests (e.g., IBP by Larrieu & Gonin, 2008; see also Zeller et al., 2022).

In addition to the amount of deadwood resulting from drought mortality events, the presence of TreMs and its potential for biodiversity enhancement will be also determined by deadwood properties. Changes in deadwood characteristics are caused by the combination of physical factors influencing standing and downing of deadwood and the biological activity of invertebrates and fungi driving decay. Immediately after tree death, the factors influencing snag’s tendency to fall depend on species-specific differences in structural strength (e.g. wood density) and tree size, but also on the concurrence of external forces, such as wind (Oberle et al., 2018). At the same time, decay rates of snags and logs also depend on size and species-specific differences in wood characteristics, in addition to be influenced by local environmental conditions, mostly temperature and precipitation, which shape the biological activity of xylophagous insects and fungi (Russell et al., 2015). Indeed, warming may accelerate decomposition (Přívětivý et al., 2016; Hararuk et al., 2020), although reduced precipitation may inhibit this process in snags and logs due to lower deadwood moisture content (Chagnon et al., 2022; Oettel et al., 2023). Therefore, changes in local environmental conditions under climate change may have an important influence on deadwood degradation and decomposition. However, the interplay among the accumulation of deadwood after drought-induced die-off, TreM composition, and the local climatic conditions have rarely been examined, although it is well known that decomposition rates of deadwood can dramatically shift with changes in environmental conditions (see Palmero-Iniesta et al., 2017 for precipitation).

Here, we analysed the effect of a drought event, which resulted on Scots pine (*Pinus sylvestris*) forest die-off in NE Spain in 2012, on the abundance and diversity of deadwood, decaying stages, and TreM across a climatic gradient of temperature and precipitation. Specifically, we hypothesize that after 10 years of the event the structural complexity in terms of the abundance and diversity of deadwood and TreM was higher in drought-affected stands relative to unaffected, control ones, but these differences will be lower in sites with higher precipitation and temperature, owing to their effects on speeding deadwood decomposition.

2. Methods

2.1. Study area and sampling design

We surveyed twenty different forest sites in 2022 across Catalonia (NE Spain, Fig. S1, Table S1) dominated by *P. sylvestris*, which undergone die-off and tree mortality episodes due to a drought event in 2012, in combination with bark beetle infestation (Jaime et al., 2019; Margalef-Marrase et al., 2023). The mean distance between forest sites was 52.4 km (range: 14.7–90.1 km) and elevation approximately ranged from 600 to 1650 m asl. (Table S1). The climate in the studied sites ranges from wet and cold conditions in the Pyrenees to moderate dry and warmer conditions in the Catalan Coastal Range. The range of mean temperature in the study sites after the last drought event (2012) expands from 8.4 to 13.7ºC (mean: ~10.5ºC) while the range of annual precipitation does from 550 to 800 mm (mean: ~730 mm, Table S1).

For the purposes of this study, we benefited from a sampling network established in 2013 including a pair of circular plots of 10-meter radius established in each of the twenty forest sites. One plot was established in a stand that after visual inspection was judged to be affected by drought-induced die-off (i.e. presence of recently dead trees, hereafter, die-off plot), while the other was situated in an unaffected close stand (hereafter, control plot) at approximately 50 – 150 m to each other, to minimize environmental heterogeneity within plots. All pair-plots were free from tree harvesting and extraction of deadwood (see Jaime et al., 2019; Margalef-Marrase et al., 2023 for further details on the survey design). In both 2013 and 2022 inventories, all alive saplings, trees, and standing dead trees (hereafter, snag) with dbh (diameter at breast height) >2.5 cm were labelled and measured. This size range allowed to record TreMs on relatively small individuals (Fig. S2 and Großmann et al., 2018). In the 2022 inventory, downed deadwood (hereafter, log) was also surveyed in two perpendicular transect lines, oriented in a North-South and an East-West directions, intersecting at the centre of the plot following the sampling procedure established by Harmon et al. (2004). Each log (diameter >2.5 cm) in contact with the transects was recorded, and its diameter at the contact point was measured. This information was used to compute the area of the log circumference intersecting the transect line. For maintaining similarity of terms when comparing alive trees and snag trees, we termed it as log basal area in 2022. From the forest inventory performed earlier in 2013 and repeated in 2022, we computed plot basal area immediately after the drought die-off episode and ca. ten years later (hereafter termed as basal area in 2013 and basal area in 2022, respectively), considering the dbh of both alive and dead trees (Table S2).

2.2. Quantifying deadwood and tree-related microhabitat (TreM)

During the survey in 2022, we considered three tree conditions: alive trees, snags, and logs and we established several categories in each condition, according to Vayreda et al. (2019). Thus, we considered two categories for alive trees (healthy or partially defoliated, i.e., with $\geq$50% of leaf loss), seven categories for snags (ranging from newly dead trees to stumps with decomposition signs), and five categories for logs (ranging from fresh downed hard logs/branches to logs/branches with high degree of decomposition), see Table S3A and Fig. S3 for further details. Similarly to Vayreda et al. (2019) and Bouget et al. (2023), for some statistical analyses we have used this extended classification while for others we have used a simplified setting of decaying states, recognizing snags as unbroken and broken, and logs as hard and soft, in addition to alive trees, see details in Table S3B. All these categories were defined based on the survey in 2022.

Following Bouget et al. (2023), to calculate the impact of the drought event experienced by the paired plots (hereafter, mortality extent), we calculated for each plot, the ratio between total deadwood accumulation (sum of snags and logs basal area) in 2022 and basal area in 2013 (sum of alive trees and snags). In turn, to characterize the decay stage of the different tree and deadwood types in the die-off and control plots in 2022, we calculated the proportion of basal area of: i) partly defoliated trees relative to alive trees (hereafter, tree decay), ii) snags or logs relative to total deadwood in 2022 (hereafter, snag and log proportion, respectively), iii) unbroken or broken snag relative to snag basal area in 2022 (hereafter, unbroken and broken snag proportion, respectively), and iv) hard or soft logs relative to log basal area in 2022 (hereafter, hard and soft log proportion, respectively). We used dbh (alive trees and snags) and diameter (logs) information from the field survey in 2022 to compute these respective tree condition's basal areas as a proxy for the abundance of the different tree conditions. In addition, we computed the richness of deadwood types considering the seven categories of snags and the five categories of logs and calculate the diversity (Shannon index) and evenness (Pielou index) indexes, considering basal area as a proxy of the abundance of the different deadwood decaying categories.

For the presence of TreMs in alive trees, snags, and logs, we considered eleven different categories adapted from Kraus et al. (2016) and Larrieu et al. (2018) (see details in Table S4 and Fig. S4). We visually examined each alive tree, snag, and log to determine the presence or absence of each TreM category and summed their abundance across alive trees, snags, and logs, separately and combinedly for each plot (Table S5). Although lying deadwood can be considered an indicator of biodiversity in itself, similarly to Bouget et al. (2023), we also recorded the presence of TreMs because: i) they provide evidence of past processes occurring at earlier stages of the mortality event (e.g. past activity of woodpeckers) and ii) the intimate contact of log with soil and its more advanced decaying stage can promote differences in the abundance of TreMs (e.g. a higher presence of cracks or unspecific holes) in comparison with standing snags. We computed total TreM abundance, TreM richness, TreM diversity (Shannon index), and TreM evenness (Pielou index) separately and combinedly for each tree condition. Furthermore, for the functional description, we re-classified TreMs into saproxylic and epixylic categories, where saproxylic refers to those TreMs that contain deadwood, whereas epixylic does not (details in Table S4, see also Bouget et al., 2023). Finally, we also analysed the abundance of insect galleries and woodpecker cavities as they are the two most species specific and common TreMs in these forests (>50 counts in the total plots in each tree condition) to estimate the effect of the die-off and climate sensitivity on them.

2.3. Extraction of climatic variables

We used temperature and precipitation as climate variables to characterize the climatic gradient of the surveyed sites since seasonal water availability is the main climatic constraint in the studied Mediterranean region and both variables are expected to become more stressful with climate change projections (Buchholz et al., 2016; Haruk et al., 2020). We used *easyclimate* package in R to extract daily minimum and maximum temperatures, as well as daily precipitation from 1 × 1 km resolution raster (Cruz-Alonso et al., 2023), for the forty plots (i.e., 20 sites × 2 plot conditions, die-off and control plots). We extracted the climate data for 2012–2020 on May 2023 to evaluate how climate after the die-off event affected deadwood and TreM. From these data, we obtained mean annual temperature, mean annual maximum temperature, mean annual minimum temperature, and yearly accumulated precipitation as potential explanatory variables. A correlation test (Fig. S5) was performed between these climatic variables, and we eventually selected mean annual temperature (hereafter, temperature) and annual precipitation (hereafter, precipitation) for further statistical analyses.

2.4. Statistical analyses

Regarding deadwood abundance and decay stages, we applied LMMs (Linear Mixed Models), considering separately tree mortality extent, deadwood abundance, richness, diversity (Shannon index), and evenness (Pielou index), and tree and deadwood decay stages, as dependent variables. In the full models, we used plot condition (die-off vs control), temperature and precipitation as explanatory variables, including the interaction terms plot condition × temperature, and plot condition × precipitation. In the case of deadwood abundance, richness, diversity, and evenness, we also included in the model the basal area in 2013, and the interaction term plot condition × basal area in 2013 as explanatory variables, to account for the effects of the forest structure resulting from drought die-off event on deadwood characteristics.

Regarding TreM, we also applied LMMs, considering separately abundance, richness, diversity (Shannon index) and evenness (Pielou index) indices, and abundance of saproxylic, epixylic, and individual TreM (i.e., insect galleries and woodpecker cavity) as dependent variables. For these analyses we also included plot condition (die-off vs control), temperature, and precipitation as explanatory variables, adding the basal area in 2013 as a covariate because its potential effect on TreM. The interaction terms plot condition × basal area in 2013, plot condition × temperature, and plot condition × precipitation were also included as explanatory variables. We performed these analyses for alive trees, snags, logs, and summing all tree conditions together (hereafter, all tree conditions).

In all analyses, we included site as a random factor to account for the paired location of die-off and control plots. For the LMMs we used the *lmer* function from the *lme4* package in R (R 4.3.2) and subsequently used the *dredge* function from the *MuMIn* package to select the best model for each dependent variable based on AIC factor. In each LMM, the continuous explanatory variables were scaled, and the residuals of all models were examined for signs of spatial autocorrelation using the Ljung-Box and the ACF autocorrelation test with the *stats* package in R.

3. Results

3.1. Drought affectation

Tree mortality extent, as inferred from the deadwood accumulated in 2022 and the basal area in 2013, was 83% higher in die-off plots than in control ones (Fig. 1A), but it was not influenced by temperature and precipitation across the studied gradient (Table S6). Aside, the abundance of decaying trees (i.e., partially defoliated) was 56% higher in die-off plots than in control ones, and it was not affected by climate variables either (Table S7).

3.2. Deadwood abundance and diversity

In 2022, die-off plots exhibited a significantly higher abundance (basal area) of total deadwood, snags, and logs than control ones (Fig. 1A; Table 1, S8), with a positive effect of the basal are in 2013 area on the three metrics. The interaction effect between plot condition (die-

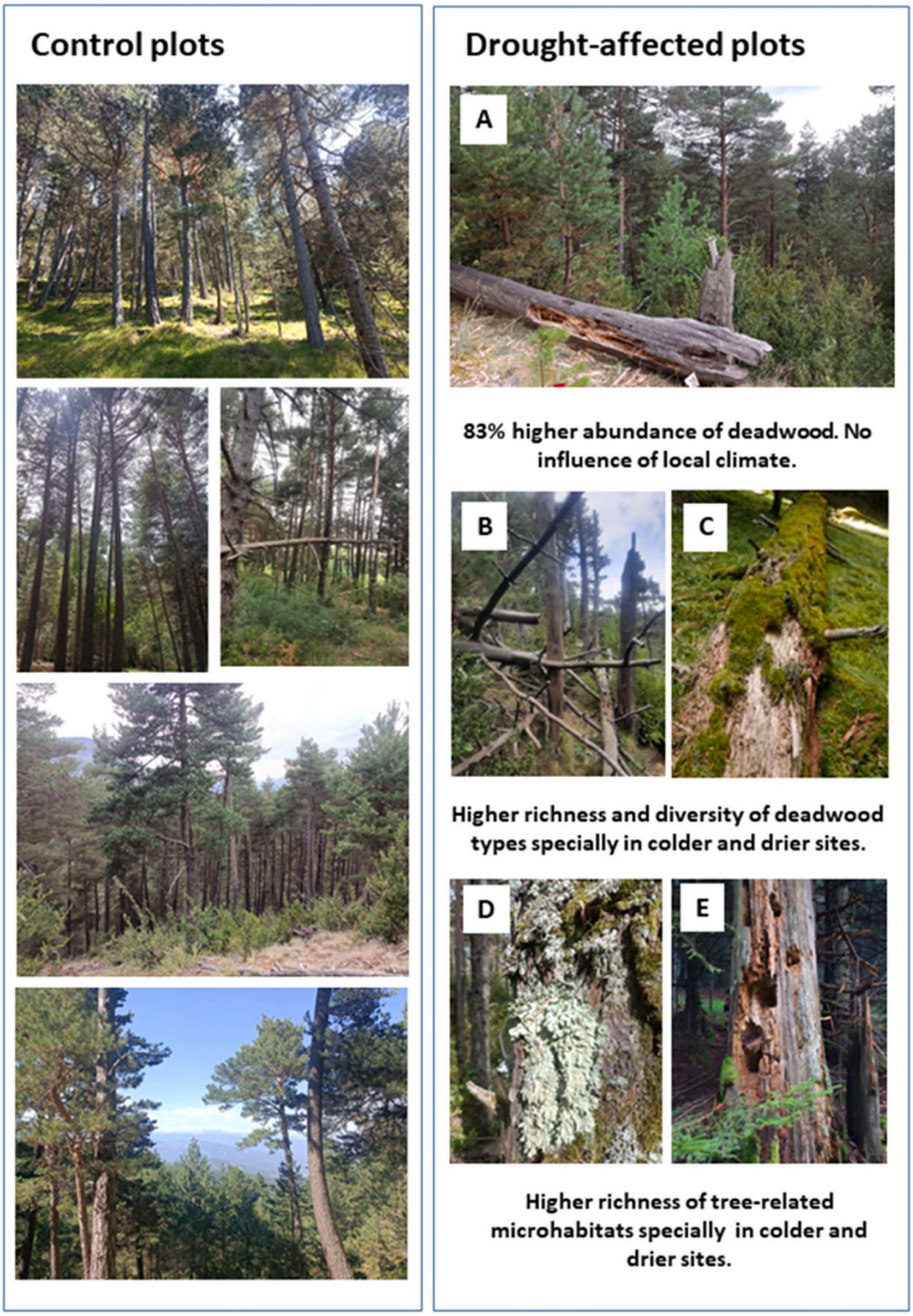

Fig. 1. Infography depicting a general view and the main differences between control and drought-affected die-off plots dominated by Scots Pine (*Pinus sylvestris*) regarding the presence of deadwood and Tree-related Microhabitat (TreM). The left panel shows some general views of Scots pine forests not affected by the drought-induced die-off event while the right panel shows the aspect of forest stands that experienced the die-off together with a brief summary of their main characteristics regarding deadwood (A-C) and TreM (D, E) in inetraction with local climate (i.e. precupitation and temperature).

off vs control) and temperature (Table S8) indicated that the differences between die-off and control plots were higher at the lower range of the temperature gradient while they narrowed at higher temperatures (Fig. 2A-C).

Regarding the different stages of deadwood decay, we did not find significant differences between die-off and control plots for the proportion of snags and logs over total deadwood in 2022 (Table S9). Yet, when we examined the decaying stages for snags and logs separately, the proportion of unbroken snags was significantly lower in die-off than in control plots, while the reverse situation occurred for broken snags (Table 1, S10). As for logs (downed deadwood), the proportion of soft logs was significantly higher in die-off plots compared to controls ones, while no significant differences were observed for hard logs (Table 1, S10). Temperature did not effects deadwood decay stages while precipitation did, i.e., it positively influenced the proportion of unbroken snags, while negatively influenced the proportion of broken snags, and it significantly interacted with plot conditions regarding the proportion of hard and soft logs (Table 1, S10). Thus, the proportion of hard logs was higher in control plots at lower precipitation levels in comparison to die-off ones, while the difference between them narrowed as precipitation

Table 1

Estimates of LMMs determining the effect of drought-induced die-off and climate since the die-off episode (e.g., temperature and precipitation) on different deadwood parameters in *P. sylvestris* forest of Catalonia (SE Spain). Details are presented in supplementary materials.

	Estimates						
Predictors	Deadwood abundance (as basal area)	Unbroken snag proportion	Broken snag proportion	Hard log proportion	Soft log proportion	Deadwood richness	Deadwood diversity
Die-off	22.55***	-0.28**	0.38***	-0.12	0.17*	1.64**	0.26*
Basal area in 2013	4.63***						
Temperature	1.93					-1.23***	-0.32**
Precipitation		0.16*	-0.14*	-0.16*	0.19**	-0.97*	-0.25*
Die-off: Temperature	-5.01*						
Die-off: Precipitation		-0.15	0.14	0.21*	-0.23**	1.36*	0.20

* p<0.05
** p<0.01
*** p<0.001

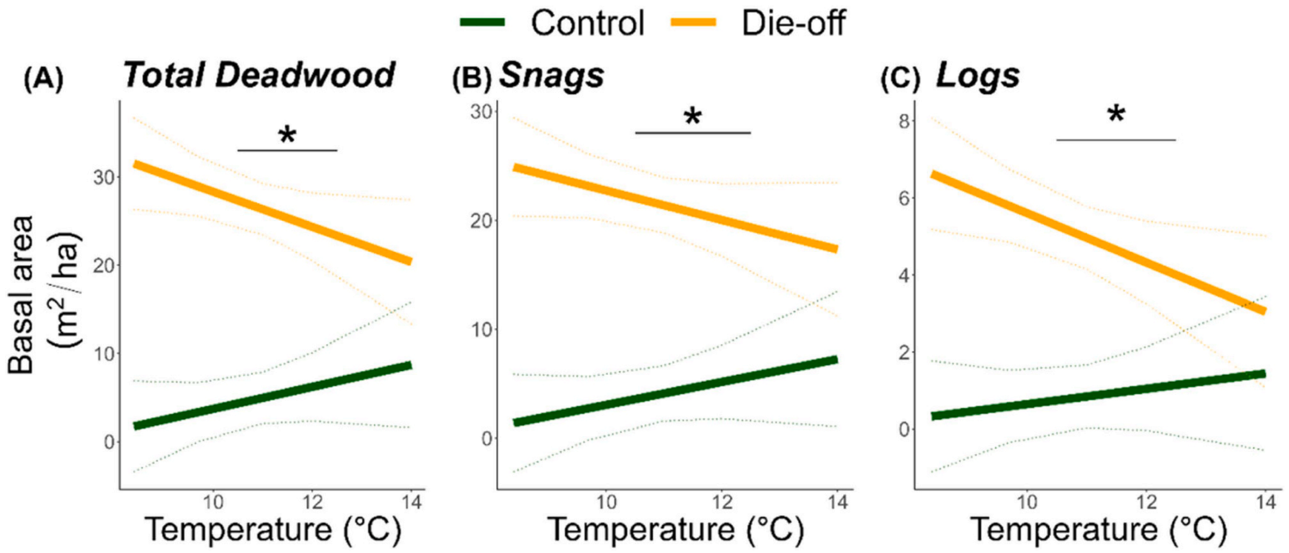

Fig. 2. Interaction effect of forest condition (die-off vs control plots) and local mean temperature on (A) total deadwood basal area in 2022, (B) snags basal area in 2022, and (C) logs basal area in 2022. Asterisk signs indicate the significance level of p-values (*: p<0.05, **: p<0.01, *** p<0.001). The envelopes around effect lines denote 95% confidence interval.

increased (Fig. 3A). The reverse situation was observed for soft logs (i.e., a decrease in die-off plots in wettest sites) (Fig. 3B).

Ultimately the differences in the abundance and decay stages of deadwood between die-off and control plots lead to higher richness and diversity of deadwood types in the die-off plot condition (Fig. 1B-C; Table 1), while there was no significant difference observed in evenness (Table S11). Regarding climatic conditions, both temperature and precipitation had a negative effect on the diversity and evenness of deadwood types (Table 1, S11), but the significant interaction between plot condition and precipitation indicated that the higher richness of deadwood types in die-off plots only occurred in the wettest sites (Fig. S6).

3.3. Tree-related Microhabitat (TreM) abundance and diversity

In line with a greater deadwood abundance and diversity of deadwood types, die-off plots had a significantly higher abundance of total and saproxylic TreM considering all tree conditions, snags, and logs, than control ones, while the abundance of TreM was lower in alive trees in the die-off plots (Fig. 1D, E; Table 2, S12, S13). The abundance of total and saproxylic TreM was positively influenced by the basal area in 2013 (Table 2, S12, S13) while several significant interactions existed with climatic conditions (Table 2, S12, S13). The interaction between plot condition and precipitation indicated that the abundance of total and saproxylic TreM in all tree and deadwood conditions was higher in die-off plots compared to controls in the sites with higher precipitation (Fig. 4A-D). In turn, the interaction effects between plot condition and temperature pointed out to a higher increase in TreM with temperature in die-off plots (Fig. 5A). Furthermore, the interaction between plot condition and basal area in 2013 indicated that the higher abundance of saproxylic TreM in snags in die-off relative to control plots mostly occurred in sites with a higher basal area in 2013 (Fig. S7). Regarding the presence of epixylic TreM, its abundance was also higher in die-off plots for all tree conditions, snags, and logs, while no differences existed for alive trees (Table 2, S14). Besides, we did not observe any effects of climate factors on epixylic TreM (Table 2, S14).

Ultimately, TreM richness and diversity were significantly higher in all tree conditions, snags, and logs in die-off plots compared to control ones, while no significant differences were observed in alive trees (Fig. 1D, E; Table 2, S15, S16). Richness of TreM in all tree conditions and logs was positively influenced by basal area in 2013, while this effect was only observed in TreM diversity in all tree conditions (Table 2, S15, S16). Furthermore, increasing temperature and precipitation had a negative effect on both TreM richness and diversity in snags (Table 2, S15, S16). We only found higher TreM evenness in alive trees in die-off plots than in controls (Table S17).

Regarding individual TreM, insect galleries and woodpecker cavities were significantly higher in all tree conditions, snags, and logs in die-off plots compared to controls (Table S18, S19). Like TreM abundance, the

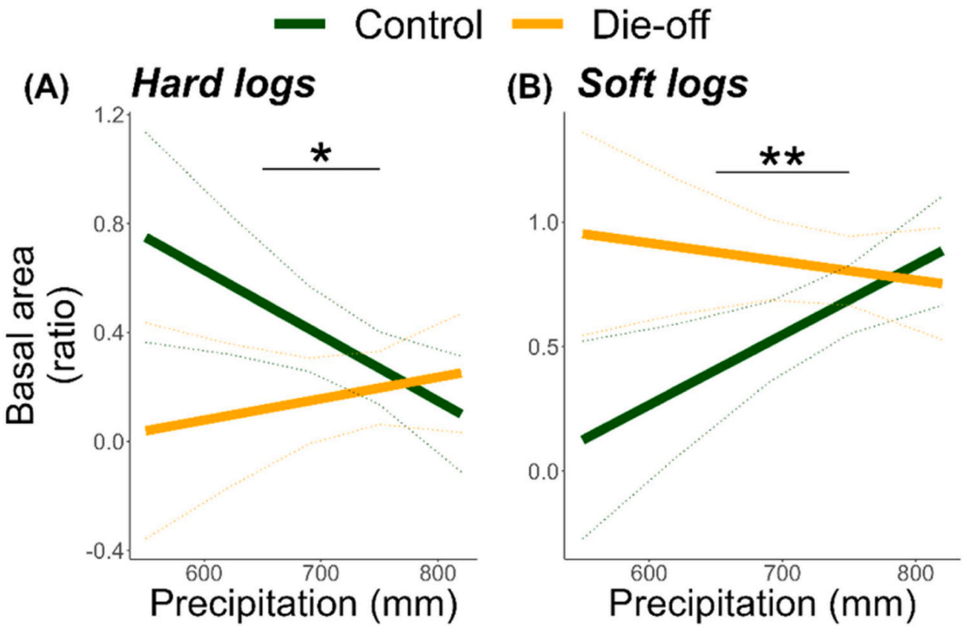

Fig. 3. Interaction effect of forest condition (die-off vs control plots) and local mean precipitation on the proportion of (A) hard logs or (B) soft logs over the total amount of deadwood (basal area ratio). The meaning of asterisk signs and envelopes around effect lines are given at Fig. 2.

interaction between plot condition and precipitation in all tree conditions and logs showed that the abundance of insect galleries was higher in die-off plots compared to controls in the wetter sites (Fig. 4E, F). Interestingly, the interaction between plot condition and temperature in all tree conditions and snags indicated that woodpecker cavities were higher in die-off than in control plots in sites with lower temperature (Fig. 5B, C). Yet, the interaction between plot condition and basal area in 2013 in snags showed that the abundance of woodpecker cavities was higher in die-off than in control plots in sites with a high basal area in 2013 (Fig. S8).

4. Discussion

Our study provides evidence of an increase in habitat diversity in terms of deadwood abundance, deadwood types, and TreMs in *P. sylvestris* stands that have experienced events of tree die-off and mortality caused by drought. Importantly, this increase in habitat diversity is positively influenced by the forest structure resulted from the die-off event and local climatic conditions in the aftermath. More specifically, forest stands with a larger basal area in 2013 that were affected by drought-induced die-off event were more likely to transition into a heterogenous forest stand. Meanwhile, temperature and precipitation influenced the decomposition of deadwood, determining richness and diversity of deadwood types. Therefore, our findings indicate that drought-induced die-off episodes initially promote more heterogeneous forest stands. Over time, accumulated deadwood and TreMs experience a complex interplay with local climate conditions. Accordingly, local precipitation positively promotes higher TreM abundance in die-off plots located at wetter sites. Yet, this presence of higher deadwood and TreMs in die-off plots seems to be more transient in sites experiencing higher temperature and precipitation – the two key environmental factors accelerating wood decomposition (Harmon et al., 2004) - thus determining a later decline in TreM richness and diversity. To our knowledge, this is the first time that the association among deadwood produced after drought-induced tree mortality, climate factors, and the abundance and diversity of TreM has been identified, although some previous studies have assessed the association of deadwood decomposition with temperature and precipitation (Hararuk et al., 2020, Chagnon et al., 2022).

4.1. Die-off promotes diversification of deadwood and TreM

The observed higher abundance and diversity of deadwood and TreM in die-off plots is consistent with Bouget et al. (2023), who reported a positive correlation between TreM diversity and disturbance-related forest decline. Indeed, the diversification of deadwood and TreM in drought-induced die-off plots is expected in disturbance-driven heterogenous forest stands (Turner, 2010; Gough et al., 2022). Such heterogeneity could potentially enhance habitat provisioning for biodiversity through different deadwood types and TreMs (Paillet et al., 2018; Basile et al., 2020; Sire et al., 2022). Interestingly, die-off plots showed higher abundances of the two TreM functional groups on which we specifically focused (i.e., saproxylic and epixylic), indicating that TreM increase by die-off events may even occur for those TreMs that do not require a direct association with deadwood (e.g., epiphytes, but see Bouget et al., 2023).

Forest stands bearing a higher basal area (i.e., including alive tree and snags in 2013) are likely to promote higher abundance and richness of deadwood decaying stages, and subsequently to generate abundant and diverse TreMs. Specifically, forest structure resulting from die-off likely enriches forest heterogeneity and potentially host higher biodiversity. Thereby, snags in die-off plots with a higher basal area can temporarily host a higher abundance of saproxylic TreM and woodpecker cavities (Paillet et al., 2019), before progressing to the next tree condition.

4.2. Role of local climate on deadwood characteristics and TreM

The observed higher accumulation of advanced decaying stages (i.e., broken snags and soft logs) in die-off plots indicates that these plots were affected by immediate tree mortality around 2012 due to the intense drought impact coupled with bark beetle attacks (Jaime et al., 2022). That would allow enough time to enhance decay due to active decomposer activity (Oettel et al., 2023). Over time, in sites with higher local precipitation, the proportion of broken snags became lower, which might be attributed to its decomposition sequence. In contrast, trees corresponding to unbroken snags in control plots are likely the ones that suffered lagged mortality, as shown also by the presence of more recent decaying stages of deadwood (i.e., unbroken snags and hard logs).

Table 2

Estimates of LMMs determining the effect of drought-induced die-off and climate since the die-off episode (e.g., temperature and precipitation) on different Tree-related Microhabitat (TreM) in *P. sylvestris* forest of Catalonia (SE Spain) in all Tree Condition (TC), alive tree, snag, and log. Details co-efficient tables are presented in supplementary materials.

			Estimates		
TreM parameter	Predictors	All TC	Alive tree	Snag	Log
Abundance (all)	Die-off	27.08***	-9.08***	10.39*	25.68***
	Basal area in 2013	13.99**	4.78*	-1.28	7.53
	Temperature		0.94	-4.03	
	Precipitation	-12.56*			-8.52
	Die-off: Basal area in 2013			8.80	-6.61
	Die-off: Temperature		4.55*		
	Die-off: Precipitation	17.15**			16.32*
Abundance (saproxylic)	Die-off	21.51**	-9.38***	8.30*	22.57***
	Basal area in 2013	10.84*	5.59*	-0.25	6.23
	Temperature		3.75		
	Precipitation	-12.20*			-8.16
	Die-off: Basal area in 2013	2.05	-0.34	8.03*	-4.19
	Die-off: Temperature		2.16		
	Die-off: Precipitation	19.80**			15.58*
Abundance (epixylic)	Drought	5.38*	0.49	2.08**	3.01**
	Basal area in 2013		0.93	0.84	0.08
	Temperature		-0.23		
	Precipitation	-1.56			0.15
Richness (all)	Die-off	0.60*	-0.57	1.53**	1.67**
	Basal area in 2013	0.57**	0.34		0.84*
	Temperature	0.17	-0.00	-1.19**	0.28
	Precipitation		-0.40	-0.78*	
Diversity (all)	Die-off	0.12*	-0.03	0.28*	0.29*
	Basal area in 2013	0.07*	0.09		0.10
	Temperature	0.04	0.06	-0.31**	0.11
	Precipitation		-0.03	-0.18*	
Insect gallaries (abundance)	Die-off	12.71***	-0.46	3.74**	9.37***
	Basal area in 2013	3.35**			2.36*
	Temperature			0.20	
	Precipitation	-3.70*	-1.20**		-2.03
	Die-off: Temperature			-2.68	
	Die-off: Precipitation	7.84***	0.78		4.73**
Woodpecker cavity (abundance)	Die-off	5.41***		2.44***	3.12***
	Basal area in 2013			0.02	
	Die-off: Basal area in 2013			1.20*	
	Temperature	-0.27		-0.20	-0.53
	Die-off: Temperature	-2.57**		-1.44*	

[*] p<0.05

[**] p<0.01

[***] p<0.001

Specifically, some trees in wetter sites may have survived the die-off event in 2012, but they were weakened, and subsequently suffer lagged mortality, and the resulting snags have not had enough time to decay and/or break down. Thus, the proportion of unbroken snags (i.e., more recently dead trees) tended to be higher at the wetter sites. Besides the differences in immediate and lagged mortality, snag size and bark presence could prolong snag persistence (i.e., time between tree death and snag fall, see Oettel et al., 2023), thus increasing the proportion of unbroken snags in control plots. On contrary to snags, limited decomposer activity in the drier sites because of lower soil moisture content likely determined the slow decay of logs (Fravolini et al., 2018). As discussed above, the higher presence of soft and hard logs in drier die-off and control plots together with delays in snag fall can also be attributed to immediate and lagged mortality, respectively. Ultimately, the effects of precipitation on snags and logs decay enhanced the richness of deadwood types in die-off plots, particularly in wetter locations.

Similar to the richness of deadwood types, wetter sites that experienced die-off also exhibited higher TreM abundance, particularly of saproxylic TreM. As insect galleries also follow a similar trend, we hypothesize that the die-off plots in wet sites could potentially host more diverse insect communities boosted by the presence of deadwood in different decay stages (Seibold et al., 2016; Sire et al., 2022). This higher abundance of TreM may be especially important because associated species might move to a similar TreM when their previous support disappears (Bütler et al., 2020). For example, insects can take refuge in an existing insect gallery (or excavate new galleries) in more stable decaying deadwood (e.g., unbroken snags or hard logs) when more advanced stages become scarce.

Besides the effects of precipitation on deadwood decaying stages, temperature had a significant influence on the abundance of the different deadwood conditions, maintaining a higher abundance of deadwood in colder die-off plots. Indeed, higher temperatures likely favoured decomposer activities speeding up the decomposition process (Lustenhouwer et al., 2020; Seibold et al., 2021) and therefore reducing the abundance of deadwood, snags, and logs in warmer sites. Faster decomposition in warmer sites may also be responsible for the lower diversity and richness of deadwood types. Interestingly, this can result in a paradox under climate change scenarios. For instance, climate change will increase the amount of deadwood due to the rising frequency of drought-induced die-off events. However, at the same time, the increasing aridity will reduce the decomposition rate, resulting in longer residence time of deadwood.

Similarly, higher deadwood decomposition in warmer sites might be responsible for lower TreM richness and diversity. Yet, the abundance of woodpecker cavities followed a slightly complex trend, since snags in colder die-off plots hosted a higher abundance of woodpecker cavities than controls. In turn, decomposer activities in the warmer sites likely reduce the deadwood amount and subsequently lower TreM within (e.g.,

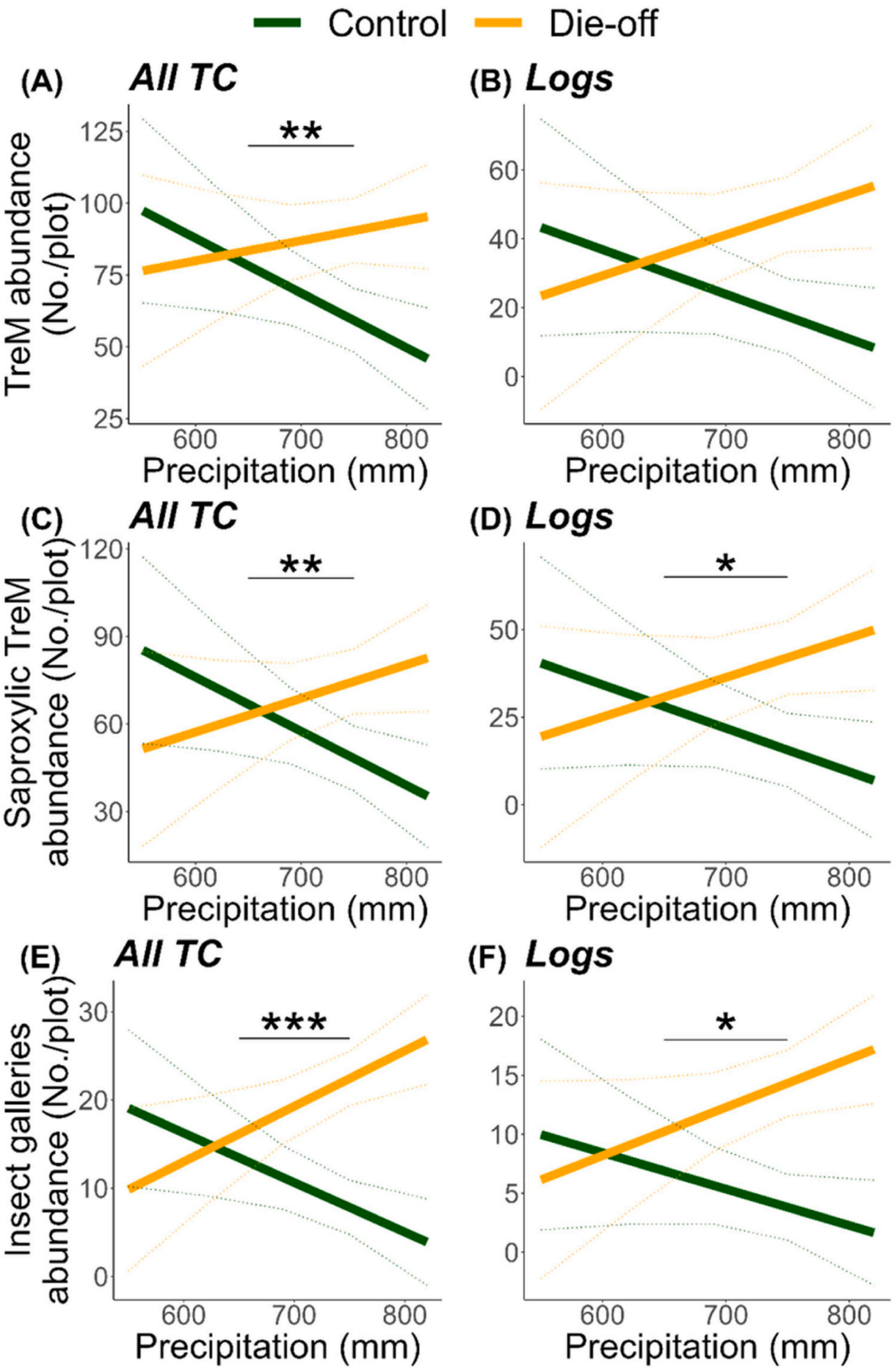

Fig. 4. Interaction effect of forest condition (die-off vs control plots) and local mean precipitation on the abundance (number per plot) of TreM in (A) all tree conditions (TC) and (B) logs, saproxylic TreM abundance in (C) all TC and (D) logs, and insect galleries in (E) all TC and (F) logs. The meaning of asterisk signs and envelopes around effect lines are given at Fig. 2.

woodpecker cavities), potentially lowering biodiversity in such locations.

The effect of climate on TreM only mediated the saproxylic TreMs but not the epixylic one. Although die-off events increased epixylic TreMs, the local climate factors show no effects on such TreM functional group, suggesting that the presence of epixylic TreMs are relatively independent of the environmental characteristics that influence the decay of wood.

Contrary to deadwood, TreM abundance in alive trees increased positively with temperature, likely associated with higher biodiversity in warmer sites (Coelho et al., 2023). The loss of tree vigour is likely associated with higher TreM abundance (Larrieu et al., 2022), so in warmer die-off plots decaying alive trees would encourage associated animal species to generate specific TreM, eventually resulting in higher TreM evenness.

For both precipitation and temperature, it must be highlighted that

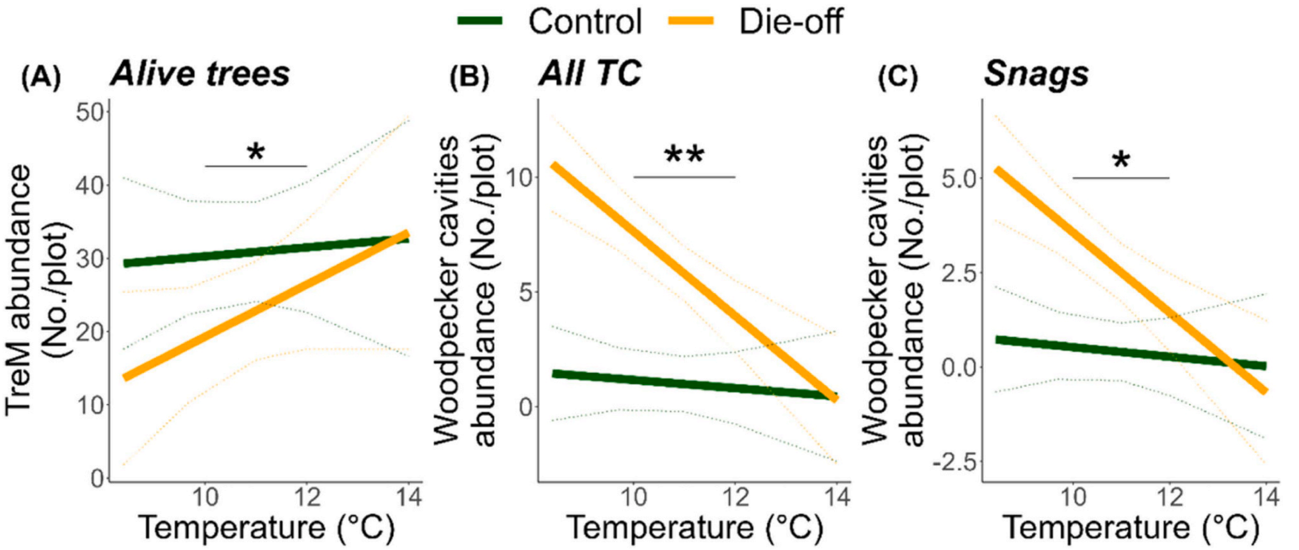

Fig. 5. Interaction effect of forest condition (die-off vs control plots) and local mean temperature on the abundance (number per plot) of TreM in (A) alive trees and abundance of woodpecker cavities in (C) all tree conditions (TC) and (D) snags. The meaning of asterisk signs and envelopes around effect lines are given at Fig. 2.

our results were obtained in a relatively reduced climatic gradient. This, taken together with our limited number of replicates, incorporates a certain stochastic uncertainty in our interpretations, which should be taken with caution when extrapolating them to wider climatic contexts, particularly those derived from climate change.

5. Concluding remarks

The intense drought-induced die-off occurred in 2012 resulted in similar mortality levels across Scots pine forests in the whole studied gradient of temperature and precipitation. This disturbance produced an important increase in the abundance and diversity of deadwood, ultimately resulting in a higher forest structural heterogeneity and presence of TreM in die-off stands, which will potentially be beneficial for forest biodiversity. Nevertheless, the observed ongoing lagged mortality occurred in control plots indicates that the creation of forest heterogeneity still continues, though with a smaller extent than immediately after the drought episode. Thus, from a management perspective, aside from maintaining deadwood in plots that have experienced the die-off event, our results highlight the importance of retaining weakened trees in non-affected sites to promote structural heterogeneity and the presence of TreM in the future. We also observed that the presence of deadwood follows a complex interplay with local climate factors (i.e. temperature and precipitation) shaping the differences in the abundance and diversity of the various stages of deadwood decay and TreMs between die-off and control plots. Interestingly, our results suggest that the potential benefits resulting from the increased presence of deadwood and TreMs in die-off plots may be somewhat temporary in sites with a wetter local climate, where decomposition occurs faster. Conversely, in colder or drier sites, deadwood and TreMs in die-off plots seems to persist for a longer period, although their beneficial role should be further investigated, as species associated to these TreMs may be also limited by these colder or drier conditions. Ultimately, the reported importance of climate suggests the need to adapt the management of deadwood following die-off episodes to the local environmental conditions, with the aim of ensuring the maintenance of forest structure heterogeneity and TreMs to enhance forest biodiversity conservation.

CRediT authorship contribution statement

Faqrul Islam Chowdhury: Writing – review & editing, Writing – original draft, Visualization, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Francisco Lloret:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Luciana Jaime:** Writing – review & editing, Methodology, Data curation. **Jordi Margalef-Marrase:** Writing – review & editing, Methodology, Data curation. **Josep Maria Espelta:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of Competing Interest

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

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121989.

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