

**Ecological consequences of drought-driven die-off in *Pinus sylvestris* forests:
Compositional shifts, regeneration filtering, and habitat heterogeneity across
a climatic gradient in Catalonia (NE Spain)**

Faqrul Islam Chowdhury

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Pinus sylvestris forests: Compositional shifts,
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Doctoral Thesis

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To apply for the degree of Doctor

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General abstract

Climate change is increasing the frequency and severity of droughts, triggering widespread tree mortality and raising concerns about potential forest collapse. While the physiological mechanisms of drought-driven tree mortality are well documented, the ecological consequences of post-die-off forest reorganization remain poorly understood, especially in the Mediterranean region. This thesis investigates how drought-induced die-off shapes forest reorganization by examining three core components of forest ecosystems: plant species composition, regeneration dynamics, and habitat complexity (deadwood and tree-related microhabitats or TreMs). We employ a nearly decadal dataset (2013-2022) of twenty paired-plot sites (drought-affected die-off vs. unaffected control) distributed across the regional temperature and precipitation gradient in *Pinus sylvestris* L. dominated forests in Catalonia (NE Spain).

First, for the compositional responses, we integrate field surveys of canopy trees (2013, 2017, 2022) and recruiting trees (2022) and find that drought-induced die-off triggers a compositional shift toward a more diverse community, with the characteristics of a Mediterranean mixed forest. The mortality of the dominant *P. sylvestris* trees reduces competition, releasing previously suppressed recruits of more drought-tolerant broadleaf species (e.g., *Quercus spp.*, *Prunus spp.*, *Acer monspessulanum*, and *Sorbus aria*) - particularly those in an advanced state of regeneration - into the canopy layer. This species turnover is more pronounced at the warmer and drier edges of the climatic gradient. Furthermore, die-off plots exhibit a significantly higher compositional similarity between the tree layer and the recruiting compartment, pointing to a future successional trajectory that is consistent with this compositional shift.

Second, to evaluate the demographic responses of *P. sylvestris* regeneration, we model recruit densities across developmental stages (seedlings, young and old saplings), considering canopy cover conditions (open, defoliated, closed) and the populations' position within the species' climatic niche. We find that *P. sylvestris* regeneration is filtered by the interaction between canopy conditions and the population's distance its climatic niche core, supporting the stress-gradient hypothesis. In climatically optimal sites (niche core), open gaps successfully promote seedling and sapling establishment due to increased light availability. Meanwhile, in climatically marginal sites, regeneration in open gaps fails due to abiotic stress; instead, closed canopy patches

provide microclimatic refugia that buffer local climatic extremes and promote older saplings' persistence. Furthermore, habitats beneath drought-defoliated canopies consistently fail to support regeneration across all developmental stages, even in suitable climates, likely due to severe propagule limitation.

Third, we evaluate deadwood accumulation and its decay stages alongside tree-related microhabitats (TreMs) as proxies for potential biodiversity. Findings show that die-off events support the “disturbance paradox” by significantly enhancing habitat heterogeneity through pulses of deadwood and distinct TreMs. Die-off-affected stands show a substantial increase in the abundance, richness, and diversity of deadwood, which in turn hosts a higher abundance, richness, and diversity of TreMs. However, the persistence and quality of these habitats are influenced by local climate. Wetter and warmer sites likely experience faster decomposition, leading to a high-quality but transient presence of deadwood and TreMs, while limited decomposer activity in colder and drier sites likely provide a more persistent presence.

Combining these findings, we propose a “successional accelerator” model as a consequence of the drought-driven die-off event in these *P. sylvestris* forests. This framework posits that drought-induced die-off does not lead to ecosystem collapse but rather accelerates forest transitions by breaking community inertia, especially at the drier edge of the climatic gradient. Through the increase in tree diversity and the long-term persistence of deadwood substrates and TreMs, these drier sites successfully reorganize vulnerable, climatically mismatched *P. sylvestris* stands into more resilient, structurally complex mixed forests capable of supporting multitaxon biodiversity. From a forest management perspective, the promotion of forest resilience in these forests facing climate-driven drought events would benefit from adopting close-to-nature forest management strategies. These include maintaining continuous cover silviculture, promoting recruits in advanced regeneration and retaining drought-affected weakened trees, deadwood, and emerging TreMs, to ensure forest resilience and biodiversity.

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List of publications and author contributions

This thesis is based on the following peer-reviewed published articles, which correspond to Chapters 2, 3, and 4, respectively.

1. **Chowdhury, F.I.**, Espelta, J.M., Margalef-Marrase, J., Jaime, L., Lloret, F., 2025. Drought-induced die-off triggers species composition shift at warmer and drier edges of climate gradient in *Pinus sylvestris* forests of Catalonia (NE Spain). *European Journal of Forest Research* 144, 727-739.
2. **Chowdhury, F.I.**, Maria Espelta, J., Sánchez-Mejía, T., Margalef-Marrase, J., Jaime, L., Lloret, F., 2026. Canopy cover and species' climatic niche shape *Pinus sylvestris* regeneration after drought-induced die-off. *Forest Ecology and Management* 603, 123438.
3. **Chowdhury, F.I.**, Lloret, F., Jaime, L., Margalef-Marrase, J., Espelta, J.M., 2024. Deadwood and Tree-related Microhabitat's abundance and diversity are determined by the interplay of drought-induced die-off and local climate. *Forest Ecology and Management* 563, 121989.

My contributions (in percentage, %): The three chapters used a decade-long monitoring dataset from twenty paired-plot sites in *Pinus sylvestris*-dominated forests across Catalonia (NE Spain). As the first author of all three publications, I led the primary research activities. I collaborated closely with my supervisors to develop the core ideas, hypotheses, and concepts underlying this thesis (80% in conceptualization). I was also the primary writer for all chapters, leading the drafting the original version and also maintaining collaboration with co-authors during the revision processes for publication (90% in writing and revising). The thesis relies on field data collection. I actively collaborated in the 2022 field data collection campaign with the invaluable assistance of a field team (see acknowledgement section). Following the fieldwork, I processed the dataset and integrated the newly collected data with previous field surveys conducted in 2013 and 2017 (100% in data curation). I customized and optimized existing analytical code to establish the species' climate niche for *P. sylvestris* (90% in model curation and optimization). Finally, I conducted all statistical analyses and generated all figures and tables presented throughout the thesis (100% data analysis and visualization).

Chapter 1: General Introduction

Conceptual framework on drought die-off driven forest reorganization



1. 1. Background

Forest ecosystems are undergoing persistent modifications in response to climate change. Rising global temperatures and altered precipitation regimes are driving more frequent and intense heatwaves and prolonged droughts, imposing acute stress on forest health (Hartmann et al., 2022; International Tree Mortality Network, 2025; IPCC, 2023). Specifically, prolonged periods of heat and water stress reduce tree growth by impairing physiological processes and making forests susceptible to mortality and die-off across diverse biomes and forest types (Adams et al., 2017; Allen et al., 2015; Margalef-Marrase et al., 2020; Senf et al., 2020). While multiple stressors contribute to tree mortality and forest die-off, drought appears as a major cause of tree death and it also intensify the impact of other disturbances, such as wildfire (Van Wees et al., 2021). Notably, drought stress is frequently compounded with the outbreaks of biotic agents, including insect pests and pathogens (Anderegg et al., 2015; Jaime et al., 2022, 2019), transforming localized forest declines into large-scale mortality events (Anderegg et al., 2015; Senf et al., 2020). Accordingly, drought has emerged as a dominant threat to forest ecosystems (Hartmann et al., 2022), with local climatic conditions directly governing ecosystem functions and services (Anderegg et al., 2013). These stressors drive modifications in stand structure and biodiversity (Ruiz-Benito et al., 2013), and triggering compositional shifts that raise concerns over potential ecosystem collapse (Lloret and Batllori, 2021).

1.2. Mechanism of drought-driven tree die-off

Tree mortality and forest die-off under drought conditions occur when physiological processes of the tree are disrupted (Adams et al., 2017). Initially, to limit water loss during drought, trees typically close stomata and/or shed leaves. So, prolonged water deficits may induce hydraulic failure, when xylem embolisms block water transport (Adams et al., 2017), or cause carbon starvation, when respiratory and defensive demands exceed carbon supply (McDowell, 2011), or both may work combinedly, leading to tree death (Mencuccini et al., 2015). Elevated temperatures intensify these stresses by increasing atmospheric water demand (vapor pressure deficit, VPD), making hotter and longer droughts particularly lethal (Park Williams et al., 2013).

At the stand scale, competition among trees may amplify mortality risk; thus, denser stands characterized by higher basal area are generally experiencing higher die-off

(Jump et al., 2017). This structural competition (increase of forest cover and stand density) may be intensified by the decline of traditional management, potentially amplifying tree's vulnerability during drought (Lasanta et al., 2015; Navarro and Pereira, 2012). Eventually, this also weakens the tree's defensive capacity in front of pests and pathogens. Specifically, drought-induced depletion of water and carbon fluxes compromises tree's carbon and chemical defences, while warming also accelerates insect development and outbreak frequencies (McDowell, 2011; Wermelinger and Seifert, 1998). These mechanisms intensify the severity of tree-insect-climate interactions, leading to widespread tree mortality (Figure 1.1; Anderegg et al., 2015).

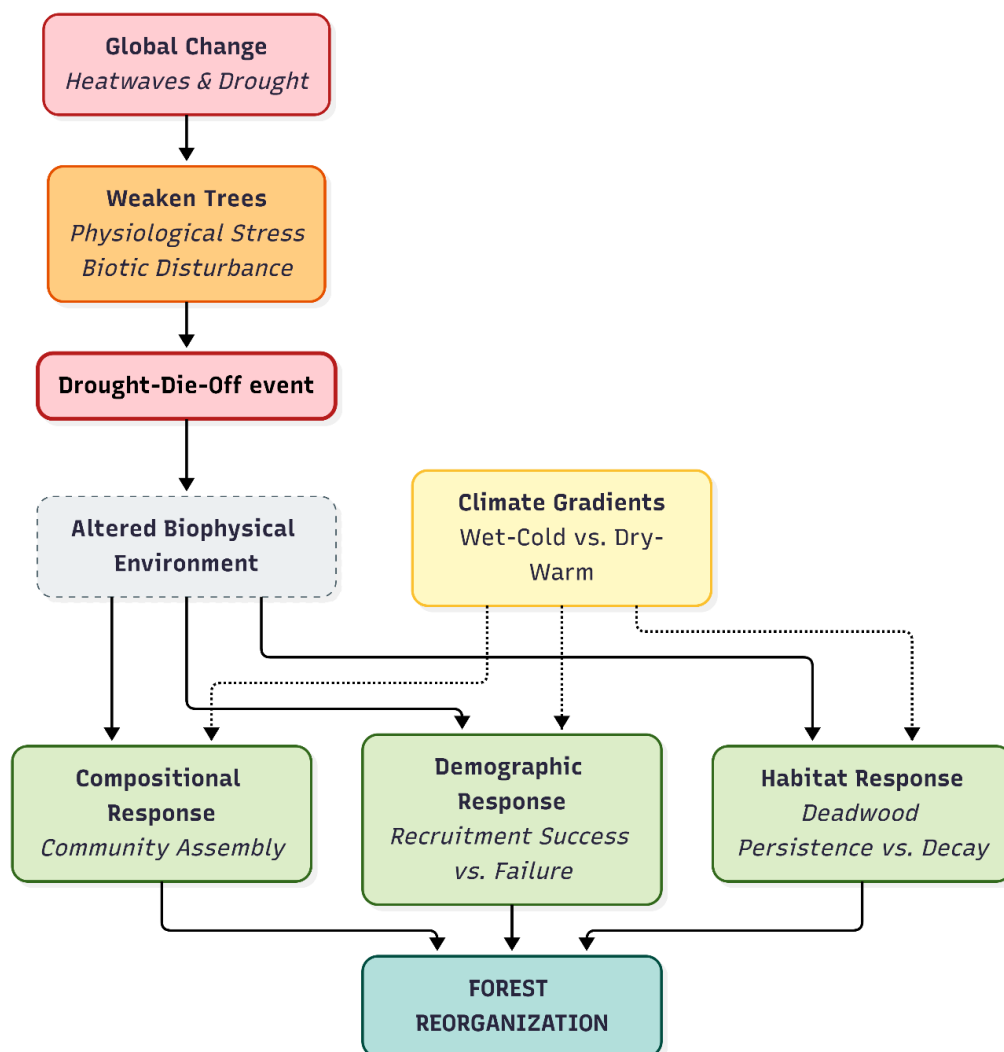


Figure 1.1: Conceptual framework illustrating the progression from global change drivers (heatwaves and drought) to die-off events and their potential effect on forest reorganization. These events alter the biophysical environment and interact with climate

gradients to trigger compositional, demographic, and habitat responses, which collectively drive the reorganization of the forest ecosystem.

These physiological mechanisms leading to tree death are well established, but the ecological consequences of drought-induced die-off extend beyond mortality itself. Ground-based forest inventories and remote sensing approaches have enabled the detection and monitoring of drought-induced forest decline across broad spatial and temporal scales, while dendroecological analysis of tree growth records provide early warning signals of drought-driven mortality (Allen et al., 2015, 2010; DeSoto et al., 2020; Marbà Vologjanin et al., 2026; Senf et al., 2020). Together, these approaches try to disentangle the biotic and abiotic drivers behind large-scale die-off events, particularly the influence of climatic extremes and biotic disturbances on the patterns and severity of forest mortality events across biomes (Allen et al., 2015; Anderegg et al., 2015; Gao et al., 2025; Hartmann et al., 2022). However, the ecological responses following tree mortality events remain understudied. Specifically, while canopy opening reduces competition and allows understory woody plants species to develop, evidence regarding how drought-induced die-off drives subsequent community dynamics and shapes regeneration trajectories remains insufficient (Figure 1.1). Concomitantly, the accumulation and decay of deadwood may alter habitat heterogeneity, yet it is also unclear how these structural changes interact to support or suppress biodiversity in post-die-off stands (Figure 1.1). Crucially, how climatic gradients modulate successional trajectories (i.e., stands recover to their prior state vs. shift toward alternative community compositions), and how these gradients interact with deadwood decay (i.e., rapid decay vs. long-term deadwood persistence) to shape post-disturbance habitat heterogeneity remains poorly understood (Figure 1.1). This thesis addresses these knowledge gaps to characterize how forests reorganize following drought-induced die-off, thus disentangling the processes that shape post-die-off community assembly and habitat heterogeneity across climatic gradients (Figure 1.1).

1.3. Forest reorganization following drought-induced die-off

Drought-induced die-off drives sharp stand-level declines in canopy cover and carbon storage, initiating changes in the biophysical environment within the stands, disrupting biogeochemical cycles (e.g., carbon, water, and nutrient fluxes) and impacting soil biophysical properties (Figure 1.1; Anderegg et al., 2013). These shifts are driven by

dramatically modified microclimatic conditions that create a new environment characterized by increased light exposure and thermal variability, which may control community assembly and the temporal dynamics of deadwood decay (De Frenne et al., 2019; Greiser et al., 2024; Lenk et al., 2024).

Over time, the loss of dominant canopy trees and subsequent competition release could promote shifts in community composition within die-off-affected stands (Martínez-Vilalta and Lloret, 2016). This canopy opening might facilitates species turnover, often promoting the colonization of drought-tolerant tree and shrub species (Galiano et al., 2013, 2010). Notably, the outcome mostly depends on tree regeneration success of dominant or co-dominant species (Batllori et al., 2020; Martínez-Vilalta and Lloret, 2016). Yet the frequency and intensity of drought-induced die-off might also alter this successional trajectory. While moderate disturbance levels may create heterogeneous niches for higher biodiversity (intermediate disturbance hypothesis in Connell, 1978; also see Viljur et al., 2022), severe and frequent droughts may trigger ecological tipping points (Romanou et al., 2025). These dynamics, combined with stressed biophysical changes following the die-off event, may transform forests into alternative woody shrubland or non-woody communities (Batllori et al., 2020; Lloret and Batllori, 2021).

In parallel, deadwood accumulation and decay following die-off and altered environmental conditions in affected stands create unique opportunities for enhancing biodiversity (disturbance paradox; Thom and Seidl, 2016). These changes effects overall biodiversity components of forest that are critical for maintaining ecosystem functioning, including soil biophysical processes and the regulation of food webs involving antagonistic and facilitative relations (Stein et al., 2014; Stokland et al., 2012; Thom and Seidl, 2016). Notably, deadwood accumulation enhances structural complexity and promotes habitat heterogeneity by providing substrates such as different deadwood decaying stages and tree-related microhabitats (TreMs), which potentially support a wide range of organisms (Asbeck et al., 2021; Bouget et al., 2024; Bouget and Cours, 2025). Meanwhile, their persistence and progressive decay, largely regulated by local climatic conditions, maintain temporal continuity in resource availability and can contribute to niche diversification across climatic gradients (Asbeck et al., 2021; Chagnon et al., 2022; Stokland et al., 2012).

Overall, post-die-off forest reorganization involves complex mechanisms governed largely by three ecosystem components; namely, compositional and demographic responses of the woody species community, and habitat response of the deadwood legacy (Figure 1.1; Bouget and Cours, 2025; Lloret and Batllori, 2021). Moreover, these components are also modulated by the climatic gradient, which determines regeneration success and species selection based on local acclimation, while also regulates the balance between rapid deadwood decay and its structural persistence (Figure 1.1; Batllori et al., 2020; Chagnon et al., 2022).

1.4. Compositional response following drought-induced die-off

Following drought-induced die-off and widespread tree mortality, some forest stands eventually recover to their original composition, while others undergo notable shifts in species composition (Lloret and Batllori, 2021; Martínez-Vilalta and Lloret, 2016). Two main successional trajectories can be identified here. First, self-replacement, which occurs when surviving individuals of the previously dominant species - specifically established saplings and suppressed trees - are released benefiting from the canopy gaps created by the mortality of trees that previously constituted the forest canopy (Margalef-Marrase et al., 2022). This trajectory allows the system to return to its pre-disturbance canopy cover (engineering resilience, sensu Holling, 1996; see Lloret et al., 2024). Second, replacement, which occurs when species that were not previously abundant, eventually achieve dominance in the forest canopy after die-off, either by growing from the understory (Chowdhury et al., 2025) or establishing afterwards through propagule dispersal (Selwyn et al., 2024). This shift represents ecological resilience, where the canopy cover of forest ecosystem reorganizes into a new state better aligned with local climatic conditions (Holling, 1973; Lloret et al., 2024; Walker et al., 2004). Here, drought-induced die-off facilitates the replacement process by breaking community inertia, a state where the climatically mismatched, physiologically stressed canopy tree suppresses the ascent of stress-tolerant understory recruits (Lloret and Batllori, 2021). In this context, the mortality event potentially unblocks the stalled successional trajectory, accelerating the reorganization of forest community composition (Seidl and Turner, 2022).

Interestingly, these successional outcomes are directly shaped by local climate, acting as a filter determining post-drought vegetation dynamics. In favourable sites, where

temperatures remain moderate and soils retain moisture, dominant canopy species can persist and regenerate (Mestre et al., 2017; but see Lloret et al., 2022). Conversely, drier and warmer sites often constrain the establishment of climate-sensitive species, creating opportunities for drought-tolerant taxa to colonize (Petrie et al., 2017). These dynamics can be inferred through the species' climatic niche framework, which defines the climatic conditions under which a species can grow and reproduce, occupying different positions within the niche limit (Grubb, 1977; Pironon et al., 2018). Core populations, situated near the niche optimum, are expected to show vigorous growth and demographic stability, but they may be poorly adapted to extreme events such as severe drought (Pérez Navarro et al., 2019). In contrast, edge populations historically living in marginal climates - with growth constrained by resource limitation - may persist to some extent under extreme climatic events, as they often carry plasticity or acclimation to local conditions (Margalef-Marrase et al., 2022). Thus, both core and edge populations are vulnerable under climate extreme events (Batllori et al., 2025), but for distinct reasons, i.e., population's climate sensitivity at core vs. facing extremity at edge during climatic stresses. Ultimately, climate warming and rising aridity are forcing many species to their climatic edge, i.e., to the limit of their climatic tolerance (Rehm et al., 2015).

Under these climatic constraints, successful replacement is driven by specific functional traits that confer advantages in the post-die-off environment. These replacing species may be light-demanding, shade-intolerant species that take benefit of increased solar radiation following canopy opening (Niinemets and Valladares, 2006; Valladares and Niinemets, 2008). Alternatively, in water-stressed sites, replacing species typically exhibit drought-tolerant traits, such as tree species with high water-use efficiency that allow them to survive the drought period (McDowell et al., 2008) or resprouting species that may gain a competitive advantage through their ability to rapidly restore canopy cover (Zeppel et al., 2015). The compositional shift toward higher tree diversity also optimizes resource utilization through enhanced niche complementarity. Specifically, canopy and understory species can enable coexistence by partitioning resources through differences in rooting depth and phenology (Hooper, 1998; Valladares et al., 2015). Finally, historical legacies such as management abandonment also modify these patterns by altering the available species pool, often contributing to higher stand diversity by the

arrival of animal-dispersed, shade-tolerant species that can wait under the canopy to grow upon gap formation following drought die-off (Selwyn et al., 2024).

Indeed, a diverse overstory provides functional redundancy, ensuring that if one species succumbs to drought, others with different physiological strategies may persist and maintain the forest stand with tree cover (Lloret and Batllori, 2021). However, the response of the understory is equally critical, as severe tree mortality frequently leads to permanent shifts from forest to shrubland or mixed woody communities rather than recovering to tree composition (Batllori et al., 2020). In this context, the shrub community acts as a structural reservoir that could redefine the post-mortality successional trajectory. Once shrubs achieve dominance, their canopies can provide buffer during drought, protecting recruits of climatically vulnerable woody communities, including shrub and tree species (Díaz-Borrego et al., 2024). This process may promote climatic disequilibrium - the mismatch between the observed climate of the site and the optimal climatic requirements of the recruited species (Pérez Navarro et al., 2024). Therefore, characterizing the diversity and spatial arrangement of these co-occurring woody species is critical, as their interactions ultimately dictate whether the ecosystem will recover its forest structure or transition into an alternative state with distinct functional properties (Batllori et al., 2020; Lloret and Batllori, 2021; Martínez-Vilalta and Lloret, 2016).

1.5. Demographic response in drought-die-off affected forests

Post-drought recruitment dynamics will ultimately determine the long-term ecosystem stability (Martínez-Vilalta and Lloret, 2016). Specifically, whether forests exhibit resilience and return to their pre-disturbance state (self-replacement) or transition toward new community assemblages (replacement) depends largely on the success of these early life stages (Batllori et al., 2020). In the short term, the vegetation response is primarily driven by the release of advanced regeneration. These established individuals - often belonging to shade-tolerant species - likely exercise a priority effect by rapidly gaining dominance and securing resource acquisition before new colonization can occur (Fukami, 2015). In mid-term, the community composition may be also enriched through seed arrival from surrounding stands (Selwyn et al., 2024). However, the success of this new colonization is also constrained by the timing of arrival, as species arriving later from the regional pool may need to compete with the established individuals that have

already pre-empted local resources (Fukami, 2015). Furthermore, this process is frequently constrained by dispersal limitation, particularly after large-scale mortality events where seed sources are distant, or dispersal agents are absent (Nathan and Muller-Landau, 2000). Also, recruitment success near surviving parent trees may be reduced due to host-specific pathogens or competition (Janzen-Connell effect, Janzen, 1970; Connell et al., 1971; also see Perea et al., 2025), providing free spaces that potentially enhance stand diversity.

Ultimately, these biological mechanisms operate within the constraints of local climate (Lloret et al., 2022; Petrie et al., 2017), which imposes a strict physiological filter on early life stages, as seedlings and saplings operate under a narrower climatic range than adults (Elvira et al., 2021; Grubb, 1977; Jackson et al., 2009). This sensitivity makes regeneration failure one of the earliest signals of climate disequilibrium, indicating the point at which species' realized niches can no longer sustain population regeneration success (Svenning and Sandel, 2013). Nevertheless, recruitment may resume during favourable climatic periods, provided that the species' regeneration capacity is maintained (Grubb, 1977; Pérez Navarro et al., 2021).

In turn, these climatic constraints can be strongly mediated by canopy buffering (De Frenne et al., 2019). Specifically, forest canopies maintain favourable microclimates by filtering direct solar radiation and maintaining humidity, as well as lowering maximum air and soil temperatures (De Frenne et al., 2019; Greiser et al., 2024; Lenk et al., 2024). This canopy cover induced buffering, termed as canopy service, extends to ecological facilitation that creates sheltered refugia where drought-sensitive and shade-tolerant recruits can germinate and survive, even away from their climatic optimum, and, thus, prolong species' persistence before potential local extinction (Alexander et al., 2018; Margalef-Marrase et al., 2025; Pérez Navarro et al., 2024). However, it remains unclear whether drought-driven defoliated trees, which lose substantial foliage but stand alive, can continue to provide buffering service or if foliage loss renders them functionally equivalent to open gaps with no buffering effect. Moreover, in climatically suboptimal sites, excessive defoliation might reduce canopy services, therefore accelerating regeneration failure and state transitions toward alternative vegetation types.

Nonetheless, this facilitation operates in tension with potential inhibitory processes. Specifically, dense shrub layers or ground vegetation may restrict water and nutrient

availability, at least slowing post-drought recovery, and in some cases maintaining persistent shrub- or grass-dominated stands (Petri and Ibañez, 2023). Ultimately, regeneration outcomes are shaped by the balance between facilitative sheltering by the canopy and competitive pressures from the understory or co-existing canopy species. Where canopy buffering prevails, regeneration can sustain original forest structure and enable the coexistence of diverse functional groups, even in stressful sites (Caselli et al., 2021; Pérez Navarro et al., 2024). Conversely, where this buffering weakens, post-drought trajectories may shift toward altered community compositions (Batllori et al., 2020; Martínez-Vilalta and Lloret, 2016). Such limitations can often lead to regeneration failure of tree recruitment (Gazol et al., 2018a) and gradually transform forested stands into open woodlands or shrublands (Batllori et al., 2020; Lloret and Batllori, 2021).

1.6. Habitat response through deadwood accumulation and tree-related microhabitats

Drought-induced tree mortality generates coarse woody debris, regularly supplying both standing deadwood (snags) and downed deadwood (logs) across affected stands (Chagnon et al., 2022). These structural legacies immediately expand habitat resources in ecosystems where deadwood has historically been scarce due to intensive management (Bouget and Cours, 2025). The persistence of deadwood depends on wood chemical traits and structural features (Harmon et al., 1986; Weedon et al., 2009). Dense or resin-rich wood and upright snags decompose slowly, providing long-lasting substrates, whereas downed logs from species with low wood density decay more rapidly, creating a dynamic sequence of decaying stages (Harmon et al., 1986; Weedon et al., 2009). Additionally, local temperature and precipitation regulate the deadwood decomposition and decay, affecting how long these structures remain available in the habitat (Chagnon et al., 2022; Hararuk et al., 2020). Specifically, wood decay generally accelerates with temperature but it may be strongly inhibited by moisture limitation in arid environments (Weedon et al., 2009). The decaying stages of deadwood sustains key ecosystem functions by regulating carbon storage and nutrient cycling, slowly releasing resources that sustains soil fertility over decades (Harmon et al., 1986).

In turn, these decaying stages also enhance vertical and horizontal heterogeneity in forest stands, providing conditions that likely support habitat for both early colonizers

and late-successional species (Asbeck et al., 2021; Bouget et al., 2024; Bujoczek and Bujoczek, 2022). Furthermore, snags and logs buffer temperature and moisture, creating micro-refugia for recruits (seedlings) during drought or in stressful sites (Thom et al., 2023, 2020). They act as nurse logs to facilitate regeneration by providing microsites that enhance seedling establishment under stressful conditions, while protecting propagules from predation (Hagge et al., 2019; Schmidt et al., 2017; Thom et al., 2023). Apart from plants, deadwood sustains a wide range of organisms (Bujoczek and Bujoczek, 2022; Stokland et al., 2012). Interestingly, while inhabiting or modifying deadwood, many of these organisms create or expand distinctive small-scale structures, i.e., biological marks of their activity, commonly recognized as tree-related microhabitats (TreMs; Asbeck et al., 2021; Basile et al., 2020; Larrieu et al., 2018). Together, the presence of deadwood and TreMs provide critical habitats for species that otherwise are excluded from simplified, managed stands (Asbeck et al., 2021; Bouget and Cours, 2025; Bujoczek and Bujoczek, 2022). Cavities excavated by woodpeckers, rot holes, and epiphyte mats are different TreM examples, each offering habitat to specialist organisms during part or full of their life cycle (Larrieu et al., 2018). Because they capture ecological interactions and are relatively easy to quantify, TreMs are widely regarded as effective biodiversity surrogates and reliable indicators of forest naturalness (Asbeck et al., 2021; Larrieu et al., 2018).

From a biodiversity perspective, TreMs potentially supply shelter, nesting sites, and humid substrates that sustain organisms ranging from vertebrates and insects to fungi and bryophytes (Basile et al., 2020, 2020; Larrieu et al., 2022). Moreover, rot holes and bark pockets accumulate organic matter and moisture, likely offering safe germination microsites, while TreM-bearing trees and logs attract seed dispersers that may enhance propagule dispersal (Basile et al., 2020). By maintaining such diverse functions, TreMs link structural complexity with ecological processes, thus, safeguarding biodiversity (Asbeck et al., 2021). In post-disturbance forests, mortality events create new substrates (e.g., deadwood and weaken alive trees) for TreM formation and promote colonization by TreM-dependent taxa, allowing TreMs to sustain multi-taxon diversity even when ecosystem functioning declines (Basile et al., 2020; Bouget et al., 2024).

The occurrence of TreMs depends strongly on tree characteristics such as size, age, species identity, and vitality, and they are especially frequent on large snags and aged trees (Asbeck et al., 2021; Bouget et al., 2024; Großmann et al., 2018; Larrieu et al.,

2018; Paillet et al., 2017). Structurally complex forests or those managed for deadwood retention typically host more TreMs than intensively managed stands (Asbeck et al., 2019; Paillet et al., 2017). Additionally, climate change is expected to accelerate both the creation and loss of TreMs by modifying disturbance regimes and deadwood decomposition processes (Bouget et al., 2024; Chagnon et al., 2022; Chowdhury et al., 2024). Notably, wetter climates may favour TreMs driven by fungal decay (e.g., rot holes), while drier sites may promote abiotic forms like cracks and loose bark, leading to distinct microhabitat assemblages across climatic gradients (Bianco et al., 2024; Chowdhury et al., 2024). However, despite their importance, studies addressing how drought-driven die-off alters deadwood and TreM provision are notably scarce (but see Bouget et al., 2024). More critically, whether these structural legacies persist as long-term biodiversity substrates or rapidly decompose following mortality remains poorly understood, particularly regarding how local climate filters their creation and longevity across climatic gradients (but see Chowdhury et al., 2024).

1.7. Thesis structure

1.7.1. Study system: Drought-driven die-off in *Pinus sylvestris* forests in Catalonia (NE Spain)

Although vegetation in the Mediterranean Basin is generally regarded as drought-adapted, severe die-off episodes have repeatedly followed extreme droughts and heatwaves in recent decades (notably in 1994, 2000, 2005, 2007, 2012, and 2016; Hartmann et al., 2022). These events have affected not only temperate species such as Scots pine (*Pinus sylvestris* L.) but also characteristically drought-tolerant Mediterranean taxa like Holm oak (*Quercus ilex*; see in Hartmann et al., 2022). In Spain, the decline of *P. sylvestris* is especially pronounced at its southernmost distribution limits (Bose et al., 2024), particularly in Catalonia. Here, recurrent droughts have triggered extensive mortality, with the total affected area for this species recorded at 7531, 8743, 5907, and 10,165.0 ha in 2012, 2013, 2017, and 2022, respectively (Figure 1.2; Banqué et al., 2023); also see Margalef-Marrase et al., 2023), a decline often intensified by secondary biotic antagonists (Jaime et al., 2019).

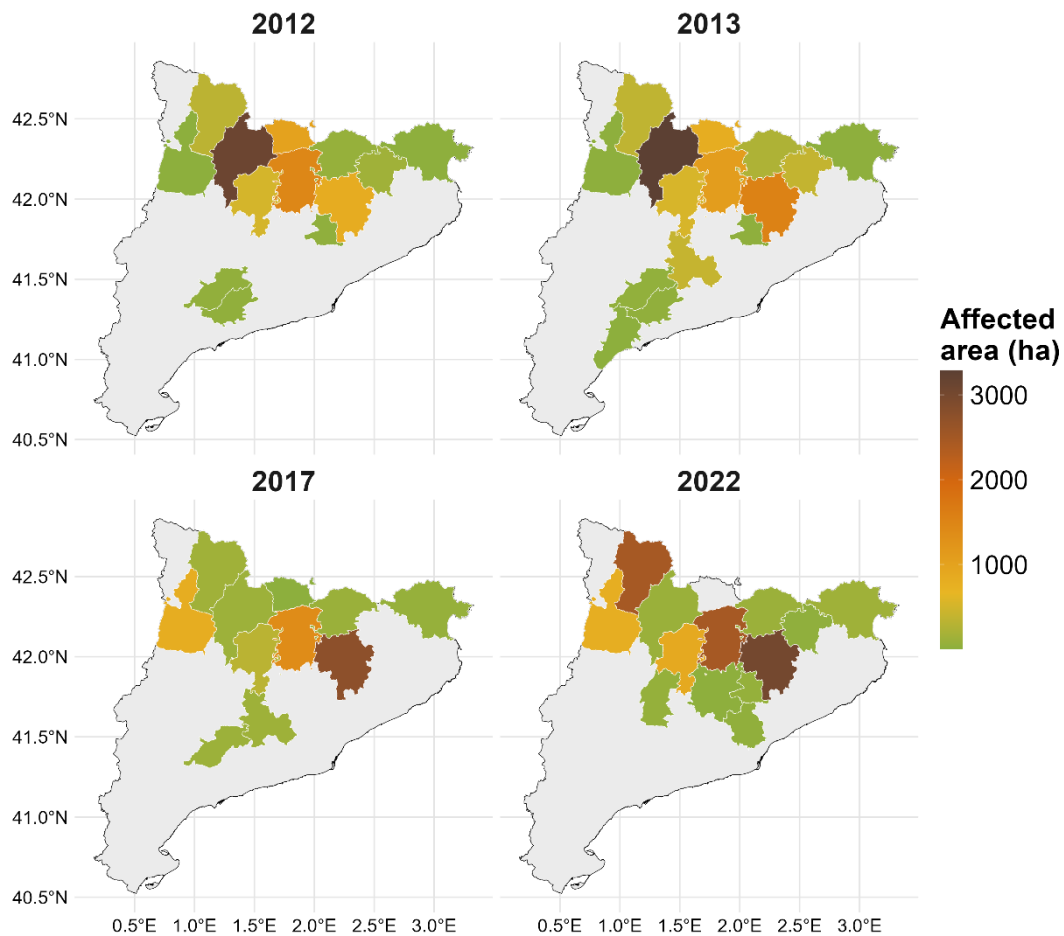


Figure 1.2: Spatiotemporal progression of *Pinus sylvestris* decline across Catalonia (NE Spain) as recorded by the DeBosCat monitoring program (Banqué et al., 2023), showing the total area (ha) affected by drought-induced dieback at the county level. The 2012 panel represents the initial extent of affected forests, while panels 2013, 2017, and 2022 correspond to the specific field data collection periods for this research.

This phenomenon is particularly concerning, as *P. sylvestris* is one of Europe’s most widespread conifers, both ecologically and economically important (Bose et al., 2024). Its current dynamics at these xeric distribution edges potentially provide a focal example of how forest ecosystems may reorganize following drought-induced mortality across climatic gradients. Thus, within this thesis, *P. sylvestris* forests in Catalonia are used as a study system to investigate the forest composition, regeneration, and habitat (deadwood and TreMs) responses to die-off events associated to global climate change.

1.7.2 General and specific objectives

The main objective of the thesis is to elucidate how drought-induced forest die-off changes forest organization regarding three ecosystem components, namely, species composition, regeneration dynamics, and habitat legacies (specifically deadwood and TreMs) in *P. sylvestris* forest across a regional climatic gradient. To do so we conducted three complementary studies focusing these three ecosystem components in *P. sylvestris* forests in Catalonia affected by drought-die-off. Specifically, the objectives were:

- a. To assess compositional changes and diversity patterns in tree and shrub communities across a regional temperature and precipitation gradient.
- b. To evaluate the regeneration dynamics of *P. sylvestris* considering the interplay between the species' climatic niche and canopy-cover conditions.
- c. To quantify how die-off promotes habitat heterogeneity, specifically the abundance and diversity of deadwood and TreMs across climate gradients.

1.7.3. Outline of the thesis

Chapter 1 (General Introduction) provides the conceptual framework of the thesis, outlining the ecological context, key knowledge gaps, and the rationale for investigating the ecological consequences of drought-induced forest die-off in Mediterranean forests.

Chapter 2 (see Chowdhury et al., 2025) examines the compositional response, specifically addressing whether the forest tend to exhibit engineering resilience (recovering its original *P. sylvestris* dominance) or moves towards a state transition (shifting toward a different community composition type). By comparing adult tree surveys over a decade (2013-2022), and recent recruit and shrub community data (2022), we assess whether *P. sylvestris* stands undergo self-replacement, are replaced with drought-tolerant trees, or attain shrub dominance. Crucially, we analyze this trajectory across climatic gradients to determine if local climate interacts with die-off to shape these successional trajectories (Figure 1.3).

Chapter 3 (see Chowdhury et al., 2026) analyzes the demographic responses of *P. sylvestris*, focusing on the regeneration dynamics accounting for the population's position in the species' climatic-niche and canopy cover conditions following die-off. By analyzing recruit densities across developmental stages (seedlings, young and old

saplings) under contrasting canopy conditions (closed, defoliated, and open gaps), we evaluate how canopy-mediated microclimatic buffering interacts with local climatic suitability to determine regeneration success. Specifically, we address the Stress-Gradient Hypothesis to investigate the limits of facilitation, while also determining whether defoliated trees remain effective in mitigating drought stress, or if drought-induced canopy defoliation renders them functionally equivalent to open gaps, leading to a collapse in buffering capacity, especially in suboptimal climates for the species, thereby allowing to assess species' mid-term self-replacement potential (Figure 1.3).

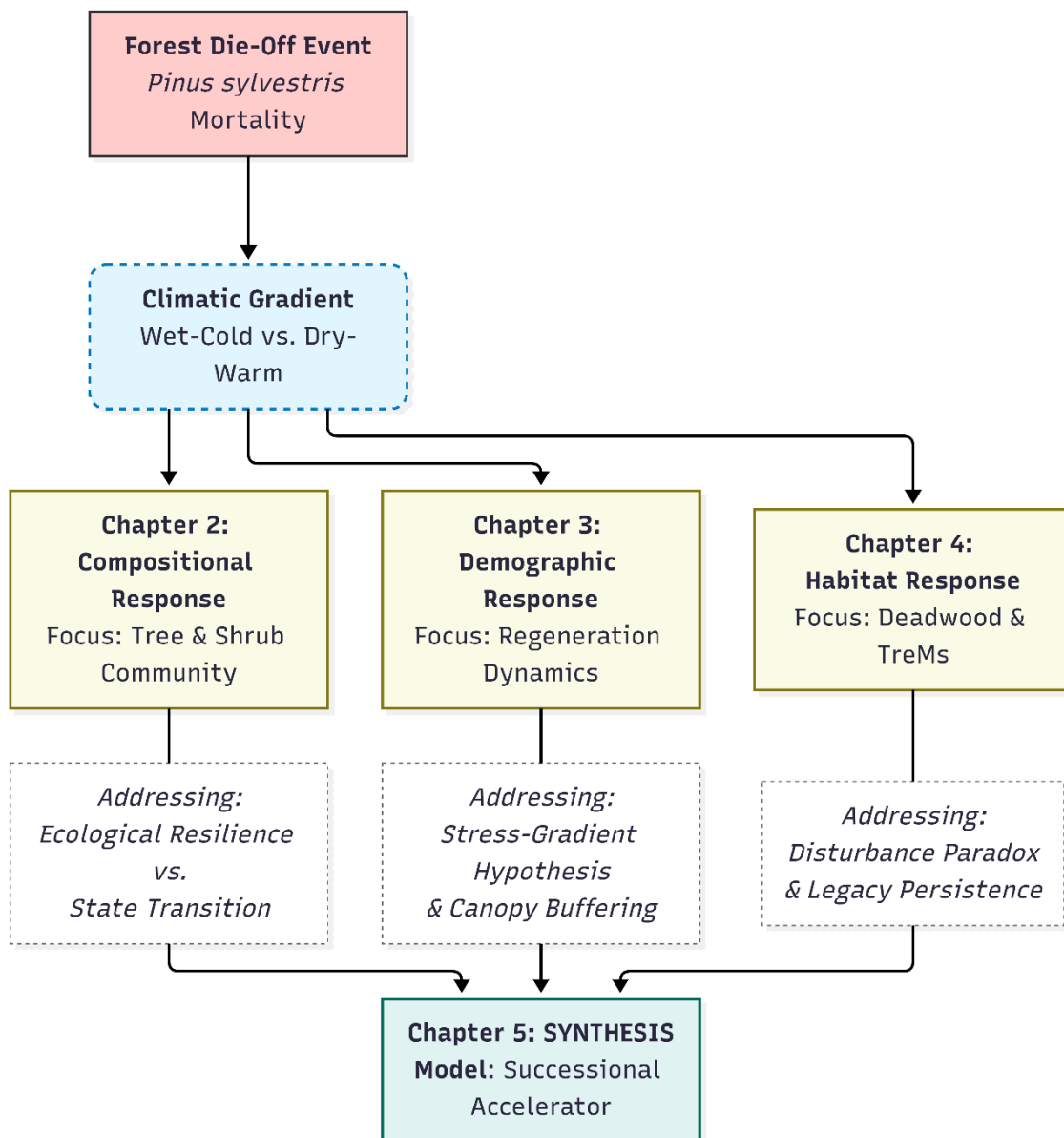


Figure 1.3: Conceptual framework of the thesis, examining how drought-induced mortality interacts with climatic gradients to drive response to three ecosystem

components: compositional changes in the tree and shrub community (Chapter 2), demographic changes on the regeneration success of *P. sylvestris* (Chapter 3), and structural changes involving deadwood and tree-related microhabitats or TreMs (Chapter 4). Integrating these findings, Chapter 5 proposes the “successional accelerator” model to elucidate post-die-off forest reorganization.

Chapter 4 (see Chowdhury et al., 2024) investigates the effects of drought episodes in determining habitat heterogeneity, specifically addressing whether tree mortality generates habitat opportunities for biodiversity. Here, we examined how die-off reshapes two important elements of forest functioning and biodiversity provisioning, namely, the abundance and diversity of deadwood and tree-related microhabitat (TreM). While these elements are essential substrates for biodiversity, their decay dynamics following drought-induced mortality remain poorly understood. By addressing the “Disturbance Paradox” through the changes in deadwood decay stages and TreM diversity across climatic gradients, we aim to identify where post-drought habitat heterogeneity arises and how their persistence is modulated by local climate (Figure 1.3).

Together, these chapters integrate the response of three ecosystem components, namely, compositional turnover, regeneration filtering, and habitat heterogeneity, following a die-off event. This synthesis will improve our understanding of how die-off may function as an active mechanism of forest reorganization (Figures 1.1, 1.3).

Chapter 5 synthesizes these ecosystem responses across climatic gradients to propose the “successional accelerator” framework. This framework explains how the mortality of dominant, drought-sensitive *P. sylvestris* adults at the rear edge of their distribution initiates changes to these ecosystem components that collectively reorganize the forest, potentially creating new opportunities for biodiversity. Furthermore, the thesis examines how local climate modulates these components and discusses the resulting implications for biodiversity (Figures 1.1, 1.3). Also, the chapter explores the perspectives on further potential research, limitations, and adaptive forest management strategies aimed to enhancing future ecosystem resilience. Finally, the thesis highlight the key findings in chapter 6.

Chapter 2: Compositional Response

Drought-induced die-off triggers species composition shift at warmer and drier edges of climate gradient in *Pinus sylvestris* forests of Catalonia (NE Spain)

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Abstract

Climate change is increasing the frequency and intensity of drought episodes, with raising forest die-off events globally. Impacts of drought on tree growth and mortality have been extensively investigated, but studies on regeneration after these episodes and their consequences for tree diversity and potential plant composition shifts are still scarce, especially analysing climate gradients. We analyse the impact of drought-induced die-offs on woody plant diversity in *Pinus sylvestris* forests in Catalonia (NE Spain), considering local temperature and precipitation effects. We compared plots affected by die-off to non-affected ones, surveying tree layers in 2013, 2017, and 2022, and tree recruits in 2022. Die-off plots showed greater richness and diversity in tree layer after 5 and 10 years of die-off, particularly in drier sites, while higher evenness was observed in warmer sites. Such pattern indicated a vegetation shift towards a Mediterranean-type forest, with increasing ingrowths of *Quercus*, *Acer*, *Prunus*, and other broadleaf trees which incorporated to tree layer, potentially replacing dead *P. sylvestris*. In die-off plots, species richness and evenness of larger recruits were 36% and 42% higher, respectively, than in non-affected ones. Species in tree layer and recruiting communities showed a 29% higher similarity in die-off plots than in non-affected ones, supporting that die-off provide better opportunities for recruitment by incorporation into the tree canopy and successful establishment of new recruits. These results indicate that drought-induced die-off is triggering forests transition towards a more adapted plant composition to climate change concurrent with ongoing local climate conditions.

Keyword: Biodiversity, climate change, Mediterranean forest; tree mortality; vegetation shift.

2.1. Introduction

Climate change is altering global temperature and precipitation patterns, increasing the frequency and severity of extreme weather events such as floods, heatwaves, windstorms, and droughts (IPCC, 2023). Drought and heatwave episodes are driving large-scale forest die-off and tree mortality in many forest types across biomes (Allen et al., 2015, 2010). Drought-induced tree mortality is associated to plant water and carbon economy, when failure of water and carbohydrate transport (i.e., hydraulic and phloem failure, respectively) and carbohydrate depletion (i.e., carbon starvation) occur concomitantly (Adams et al., 2017; Mencuccini et al., 2015). This is often mediated by stand structure and competition among trees (e.g., stands with higher basal area experience more mortality), and biotic agents (i.e., pathogens and pests), all together interacting with climate (Anderegg et al., 2015; Jaime et al., 2019; Jump et al., 2017). The Mediterranean forest ecosystem is especially vulnerable to drought-related tree die-off and mortality events (Dorado-Liñán et al., 2019), raising concern about potential shifts or even forest collapse (Lloret and Batllori, 2021). Indeed, widespread mortality episodes endanger the future of growth and dynamics of forest ecosystems (Babst et al., 2019; García-Valdés et al., 2021) and their services (Anderegg et al., 2013). However, our understanding on the effects of drought-induced mortality on forest regeneration and potential compositional changes remains largely unknown (Martínez-Vilalta and Lloret, 2016; but see Batllori et al., 2020).

Episodes of drought-induced tree mortality provide opportunities to plant composition shifts as post-drought regeneration may follow uncertain successional trajectories during gap filling (Lloret et al., 2022; Lloret and Batllori, 2021). The replacing individuals could correspond to the ingrowth of recruits (i.e., seedlings or saplings growing into the tree class) in the layer of dominant or co-dominant tree species of already existing recruits in the forest understory (i.e., advanced regeneration) or to propagules arriving from neighbouring forests and successfully establishing in the canopy (Lloret et al., 2022; Selwyn et al., 2024). Indeed, pre-drought dominant tree species can persist after mortality episodes provided their regeneration become successful, or, alternatively, new tree species recruits in the understory can achieve dominance after tree mortality (Batllori et al., 2020). Meanwhile, new species arrival in drought-induced die-off stands could also initiate new successional trajectories, resulting in novel community assemblages (Hobbs et al., 2006). Additionally,

deadwood accumulation after tree mortality may assist in successful regeneration by increasing soil moisture, reducing seed predation, and protecting smaller seedlings from herbivores, while canopy opening alters microclimatic conditions by increasing the sunlight penetration (Schmidt et al., 2017; Thom et al., 2020). Therefore, drought die-off-induced sites provide conditions and resources for tree species turnover that could potentially induce changes in forest structure and composition, thus, determining short- and mid-term resilience (Lloret et al., 2022; Seidl et al., 2017). Accordingly, in the aftermath of drought-die-off episodes, forest structure can become more complex and heterogenous (Chowdhury et al., 2024), while competition release may favour an increase of plant diversity (i.e., “disturbance paradox”, see Thom and Seidl, 2016).

Indeed, compositional dynamics is largely determined by species-specific traits (Batllori et al., 2020; García-Valdés et al., 2021; Lloret et al., 2012). Generally, tree species having higher adaptability to drought, such as resprouting capacity and efficient water use strategy, are considered better self-replacers after drought (Zeppel et al., 2015). Meanwhile, the advanced regeneration of shade tolerant recruits after canopy mortality potentially has better opportunities to become adults (Batllori et al., 2020). Therefore, gap creation in drought die-off sites may favour the germination and growth of seedlings and the ingrowth of shade-tolerant (Galiano et al., 2013, 2010) and drought-resistant species (Niinemets and Valladares, 2006), which could maintain advanced regeneration in the understory. Overall, post-disturbance recruitment primarily sets the stage for long-term trajectory involving ecosystem recovery and community dynamics in forest stands; however, the outcome is difficult to predict as various factors simultaneously effect this successional process.

Plant compositional change during drought and post-drought periods is particularly influenced by local climate as the survival or the regeneration success of any given population is correlated with the species climatic requirements, reflecting species' bioclimatic niche (Grubb, 1977; Pérez Navarro et al., 2019; Pironon et al., 2018). In general, populations located close to species' tolerance limits (i.e. experiencing lower climatic suitability or sited close to the edge of its bioclimatic niche) should exhibit lower regeneration levels, though alternatively may be more resistant to extreme drought episodes due to local acclimation or adaptation (Lloret and Kitzberger, 2018; Margalef-Marrase et al., 2020; Solarik et al., 2018). In contrast, populations living in localities having historical suitable climate may become less tolerant to extreme

climatic fluctuations because of higher demand for resources (Elvira et al., 2021; Pérez Navarro et al., 2019). However, they may maintain successful regeneration when climate become milder after an unfavourable climatic episode. So, compositional changes are expected to be influenced by climatic gradients, reflecting species' environmental requirements (Batllori et al., 2020; Lloret and Batllori, 2021). Yet, this compositional reorganization remains to be better documented at regional scale, considering local species adaptability and niche requirements, particularly across gradients of increasing dryness (Allen et al., 2015; Zhang et al., 2018).

Here we aim to elucidate the potential changes of woody species diversity and composition for a 10-years period following a drought-induced die-off and tree mortality episode (Chowdhury et al., 2024; Jaime et al., 2019; Margalef-Marrase et al., 2023), also considering the effects of local climatic factors through a gradient of precipitation and temperature. We studied woody plant diversity and composition immediately following the event and after 5 and 10 years in forest stands dominated by Scots pine (*Pinus sylvestris*) in Catalonia (NE Spain). We hypothesize that (i) plots affected by die-off will show a higher diversity of trees, recruits, and shrub species than non-affected ones over time, likely due to released competition and changes in environmental conditions following tree death; and (ii) the increase in tree species diversity will be more prominent in the die-off affected plots that experience higher temperature and lower precipitation locally, where species other than *P. sylvestris* adapted to warmer and drier conditions would better resist the drought episode.

2.2. Methods

2.2.1. Study system and experimental design

We conducted this study in forests dominated by *Pinus sylvestris* in Catalonia (NE Spain) that had experienced die-off and tree mortality episodes due to a drought in 2012, exacerbated by bark beetle infestation (Jaime et al., 2019; Margalef-Marrase et al., 2023). In particular, we surveyed twenty different forest sites in 2013, 2017, and 2022 (Appendix A, Figure A1). The average distance between sites was $52.4 \text{ km} \pm 37.7 \text{ km SD}$ (Appendix A, Figure A1). Due to orographic variability, these *P. sylvestris* forests experience different temperature and precipitation conditions, with colder and wetter sites in the Pyrenees and drier and warmer conditions in the Catalan Coastal Range. Overall, the average annual temperature in the study sites is 10.6°C (range: 8.4

to 13.7°C), with annual precipitation accumulation of 734.1 mm (range: 552.0 to 822.6 mm) between 2012-2022 (Appendix A, Figure A2).

In 2013, two paired circular plots with a 10-meter radius (about 314 square meters) were established in each site, ca. 50 to 150 meters apart (Appendix A, Figure A1). Following a visual assessment of the occurrence of *P. sylvestris* mortality, one plot was established in a location affected by drought-induced die-off (hereafter, die-off plot) and the other plot was placed in a non-affected location (hereafter, control plot; see details in Chowdhury et al., 2024; Jaime et al., 2019; Margalef-Marrase et al., 2023). No salvage logging was carried out in the sites after the die-off episode.

To compute woody plant species richness, diversity (Shannon index), and evenness (Pielou index) in each plot, we surveyed species in the tree layer (i.e., alive trees with >2.5 cm dbh), and tree species in the community of recruits with $\text{dbh} \leq 2.5$ cm (i.e., comprising seedlings and saplings), as well as shrub species. Information of the tree layer were collected in all three surveys (2013, 2017, and 2022) from the whole plot, while recruits (seedlings and saplings) information was collected in 2022 by means of transect belts (2 m wide in each side) along two perpendicular transect lines 20 m long (Appendix A, Figure A1). Additionally, shrubs cover information was collected from two transect lines in 2022 (Appendix A, Figure A1).

2.2.2. Quantifying taxonomic diversity in tree layer, tree recruits, and shrubs

In 2013, tree layer species were identified and their dbh were measured (Appendix A, Figure A1, Table A1). We resampled each tree in all plots in 2017 and 2022 using the same standard procedures. In 2017 and 2022, new tree individuals with $\text{dbh} > 2.5$ cm incorporated in the tree layer (i.e., ingrowths) were also identified and measured by comparison to the previous survey (Appendix A, Table A1). We separately calculated tree richness in each plot for the three field-surveys while tree basal area was used as a proxy of abundance to compute diversity (Shannon index) and evenness (Pielou index) (Cruz-Alonso et al., 2021).

In 2022, we identified recruits at species level and counted them in the two transect belts (Appendix A, Figure A1, Table A1). The common area of the transects belts that intersect in the centre of the plot was surveyed only once to avoid duplicate counts. For this sampling, three developmental stages categories were considered: T1: seedlings

under two years-old, T2: saplings older than two years with height < 130 cm, and T3: saplings with height > 130 cm and dbh < 2.5 cm (see for a similar category in LIFE RedBosques, 2019). For age estimation of recruits, we used morphological characteristics based on stem lignification. Specifically, for *Pinus* species, individuals with lignified shoots were classified as two years or older categories. Meanwhile, for broadleaf species, individuals with lignified stems or more than one shoot were classified on the same way. We then computed species richness for the total number of recruits (hereafter, all recruits) and for the three development categories (T1, T2, and T3) per plot. The count information of recruits was utilized to calculate diversity and evenness (Cruz-Alonso et al., 2021).

In 2022, shrub species were also surveyed in the two perpendicular transect lines (Appendix A, Figure A1). Each shrub species in contact with the transect lines that continuously covered at least 30 cm was identified and the cover length was recorded (Appendix A, Table A1). To eliminate duplication, shrub individuals that contacted with both transects were considered only once. In each plot, we also estimated shrub species richness, and the species cover information was used as a proxy of abundance to calculate shrub diversity and evenness.

Finally, to illustrate the precise species identity involved on species shifts, we recorded and plotted the species that appeared or disappeared in any site in the tree layer (2022 vs. 2013), recruits (2022), and shrub (2022) communities, considering plot condition and the temperature and precipitation gradients.

2.2.3. *Similarity in tree species composition*

We used the Sørensen similarity index (ranging from 0 to 1, indicating no similarity and exact similarity, respectively) to compare the composition of tree layer communities between the surveyed years (2013 vs. 2017, 2013 vs. 2022, and 2017 vs. 2022 comparisons) and between tree layer and recruiting communities in the die-off and control plots in 2022. Additionally, we computed species turnover and nestedness in these communities, which are two different components of β -diversity related to dissimilarity, as captured by Sørensen dissimilarity index (i.e., the opposite of Sørensen similarity index; Baselga, 2010). These components explain two fundamental mechanisms: species replacement (turnover) and species overlap (nestedness),

effectively disentangling overall changes in species composition. We also recorded and plotted the shared species between tree layer and recruiting community to pick their precise species identity in 2022, considering plot condition and the studied climate gradients.

2.2.4. Climate data

We used *easyclimate* package in R to extract daily minimum temperature, maximum temperature, and daily precipitation at 1×1 km resolution raster (Cruz-Alonso et al., 2023), for the forty plots (i.e., 20 sites $\times$ 2 plot conditions, i.e., die-off and control plots) during the period since the drought episode (2012) to the survey data. When the survey was done at the beginning of the year, we considered the climate data until the previous year. So, for the 2013 survey we considered the 2013 climatic data period, for the 2017 survey, we used the 2012-2016 climate data period, and for the 2022 survey we used the 2012-2021 climate data period. Furthermore, for the analysis of the similarity of tree species between 2017 and 2022, we also took the climate data of 2017-2021. Next, we calculated mean annual temperature, mean annual maximum temperature, mean annual minimum temperature, and mean annual precipitation using the daily climatic data. From this climatic dataset, we eventually selected mean annual temperature (hereafter, temperature) and annual precipitation (hereafter, precipitation) for further statistical analyses as these are the more comprehensive climatic variables (Appendix A, Figure A2).

2.2.5. Statistical analyses

To examine the effect of die-off on basal area, species richness, diversity (Shannon index), and evenness (Pielou index) in the tree layer for a specific time, we constructed separate LMMs (Linear Mixed Models) for each response variable for 2013, 2017, and 2022, in which we included plot condition as the sole explanatory variable and incorporated site as a random effect to account for the paired design.

To address the potential effects of the die-off episode and local climate (e.g., temperature and precipitation) across years on the tree layer, we separately applied LMMs, considering richness, diversity, and evenness as response variables. We also built a LMM considering plot tree basal area as response variable in order to analyse changes in forest structure over the years. In all these models, we used plot condition,

year (2013, 2017, and 2022), temperature and precipitation as explanatory variables. Furthermore, interaction terms (plot condition, year, temperature, and precipitation) up to second order were also included as explanatory variables in the full model. For this analysis we included site and plot as random factors to account for the paired design (i.e., die-off and control plots) and repeated measures (i.e., 2013, 2017, and 2022 survey years), respectively.

Regarding tree species recruits, we separately applied LMMs, considering richness, diversity, and evenness indices as dependent variables. For these analyses we included plot condition, temperature, and precipitation as explanatory variables. The interaction terms plot condition $\times$ temperature, plot condition $\times$ precipitation, and temperature $\times$ precipitation were also included as explanatory variables. We performed separate analyses for each recruit stage (T1, T2, and T3), and for all recruits. Similarly, LMM models were also constructed for shrub richness, diversity, and evenness. For both recruit and shrub analyses, we only used site as random factor to account for the paired plots design, while plot was not included as data were only available for the last year survey (2022).

Finally, we used LMMs to assess the similarity, turnover, and nestedness of the tree layer communities between years (2013 vs. 2017; 2017 vs. 2022; and 2013 vs. 2022, separately) as well as between the tree layer and the recruiting communities. In each case, the respective value of Sørensen index, turnover, and nestedness was separately used as the dependent variable. Then, we included plot condition, temperature, precipitation, and the second order interaction terms as explanatory variables. For these analyses, we used site as a random factor to account for the paired plots design.

We used the *lmer* function from the *lme4* package in R to construct the LMMs (Bates et al., 2003; R Core Team, 2024, version 4.3.2). In each LMM, the continuous explanatory variables were scaled and *dredge* function from the *MuMIn* package was used to select the best model for each dependent variable based on AIC factor (Bartoń, 2010).

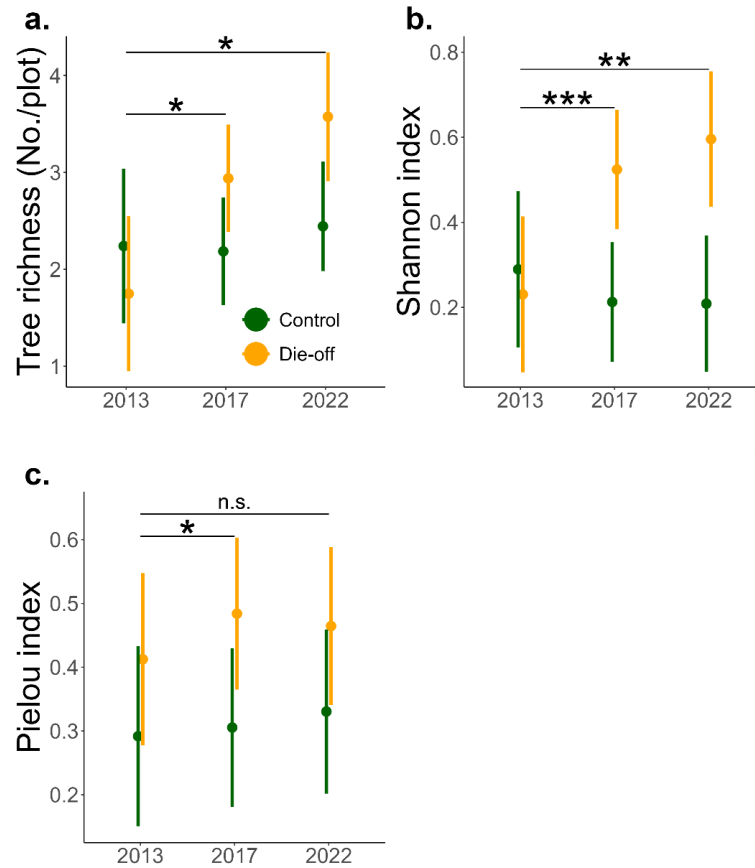


Figure 2.1: Species richness (A), diversity (Shannon index; B), and evenness (Pielou index; C) in tree layer between the plot condition (die-off and control) and across 2013, 2017, and 2022. Asterisk signs indicate significance of p-values (*: $p < 0.05$, **: $p < 0.01$, *** $p < 0.001$), while n.s. denotes not-significant ones.

2.3. Results

2.3.1. Forest structural changes

Basal area was 54%, 53%, and 49% lower in die-off plots than in control ones in 2013, 2017, and 2022, respectively (Appendix A, Table A2). Across years, plot basal area increased by 15% in 2022 compared to 2013 across the study sites, but no significant differences existed between 2013 and 2017 (Appendix A, Table A3). Furthermore, we found that temperature negatively affected basal area. Interestingly, the interaction effects of temperature and precipitation indicated that basal area was higher in sites with lower temperature and higher precipitation (Appendix A, Figure A3).

2.3.2. Changes in tree layer communities

Table 2.1 Estimates of LMMs (Linear Mixed Models) determining the effect of drought-induced die-off (plot condition, die-off vs. control) and local climate (temperature and precipitation) since the die-off episode on richness, diversity (Shannon index), and evenness (Pielou index) of the tree layer (in 2013, 2017, and 2022) in *P. sylvestris*-dominated forest in Catalonia (NE Spain). Temperature and precipitation correspond to mean annual temperature and mean annual precipitation, respectively. m.R² and c.R² denotes to marginal R² (fixed effect) and conditional R² (fixed and random effect), respectively. Details of coefficients are given in Appendix A, Table A6, A7, A9.

Predictors	Estimates		
	Species richness	Shannon index	Pielou index
Year [2017]	-0.06	-0.08	0.01
Year [2022]	0.20	-0.08	0.04
Die-off	-0.49	-0.06	0.10
Temperature	0.46	0.18 **	0.03
Precipitation	0.12	0.07	-0.02
Year [2017] : Die-off	1.24 *	0.37 ***	0.06 *
Year [2022] : Die-off	1.62 **	0.45 ***	0.01
Die-off : Precipitation	-0.82 *	-0.23 **	
Die-off : Temperature			0.12 *
m.R ² / c.R ²	0.29 / 0.83	0.39 / 0.93	0.27 / 0.97

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

Differences between die-off and control plots emerged through time. Thus, richness was 23% and 24% (marginally) higher in die-off plots compared to control ones in 2017 and 2022, respectively (Appendix A, Table A4), while diversity (Shannon index) was 77%, 114%, and 96% higher in die-off plots than controls in 2013, 2017, and 2022, respectively (Appendix A, Table A5). Interestingly, across the years, richness and diversity of the tree layer in die-off plots significantly increased in 2017 and 2022 compared to 2013, while control plots remained steady across the 10-years period (Figure 2.1A, 2.1B; Table 2.1; Appendix A, Table A6, A7). Regarding local climate, temperature showed a positive effect on diversity (Table 2.1). The interaction effects between plot condition (die-off and control) and local precipitation indicated that

richness and diversity in tree layer in die-off plots was lower along the increasing precipitation gradient (Figure 2.2A, 2.2B), while richness remained steady, and diversity increased slightly across the increasing precipitation gradient in control plots (Figure 2.2A, 2.2B). However, evenness (Pielou index) in tree layer was 56% and 60% higher in die-off plots than in controls in 2017 and 2022, respectively (Appendix A, Table A8). Across years, evenness in die-off plots was only significantly lower in 2013 compared to 2017 (Figure 2.1C; Table 2.1; Appendix A, Table A9) while in control plots remained steady across the years (Figure 2.1C). The interaction between plot condition and temperature indicated that the evenness in tree layer was significantly higher in die-off plots compared to control ones only at the warmer edge of the temperature gradient (Figure 2.2C).

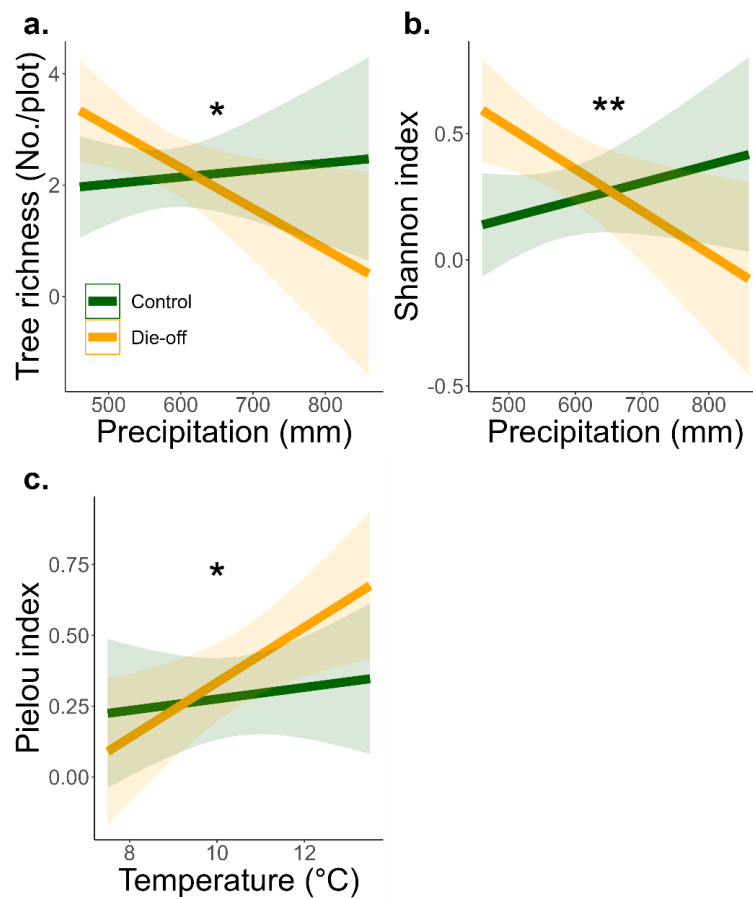


Figure 2.2: Interaction effects of plot condition (die-off and control) and mean annual precipitation on adult tree species richness (A) and diversity (Shannon index) (B), and plot condition and mean annual temperature on tree evenness (Pielou index) (C), across 2013, 2017, and 2022. Asterisk signs indicate the significance level of p-values (*:

$p < 0.05$, **: $p < 0.01$, *** $p < 0.001$). The envelopes around effect lines denote 95% confidence interval.

Specifically, *Quercus ilex*, *Quercus humilis*, *Acer monspessulanum*, *Crataegus monogyna*, *Fraxinus excelsior*, *Phillyrea latifolia*, *Prunus mahaleb*, and *Sorbus aria* appeared in new die-off affected plots in 2022 compared to 2013, mainly in drier and warmer sites (Figure 2.3; Appendix A, Figure A4, A5).

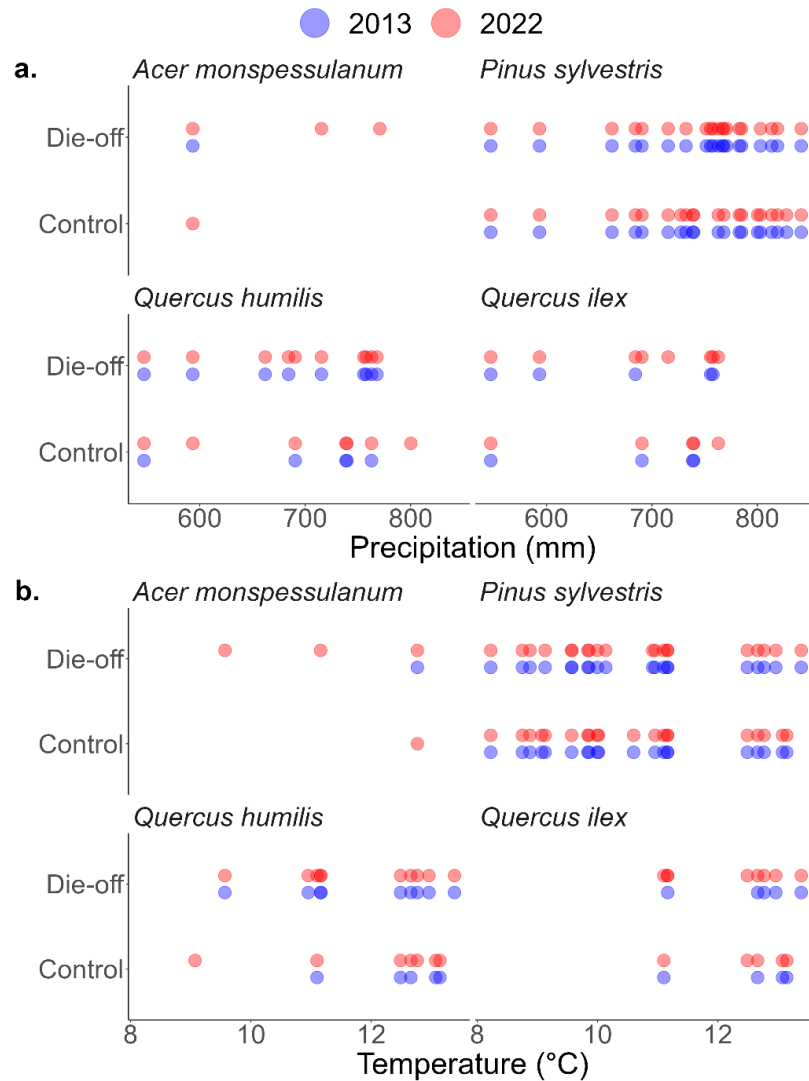


Figure 2.3 Presence of selected species in tree layer that showed changes across the precipitation (mm; A) and temperature (°C; B) gradients in die-off and control plots. Tree species that newly appeared in the edge(s) of climate gradients are shown here. Presence of all tree layer species are given at Appendix A, Figure A4 and A5.

2.3.3. Changes in recruiting communities

We did not find any significant difference between plot condition or local climate in the richness, diversity, and evenness of tree recruits, when considering the three stages of development together, and for the younger T1 and T2 stages, separately (Table 2.2; Appendix A, Table A10-A12). However, for the T3 stage (i.e., larger recruits), species richness and evenness were significantly higher in die-off plots compared to control ones, while no difference was observed for diversity (Table 2.2; Appendix A, Table A13). We also observed significant positive effect of temperature on richness, diversity, and evenness of these recruits (Table 2.2; Appendix A, Table A13). Specifically, larger recruit class of *Q. humilis*, *Q. ilex*, and *S. aria* newly appeared in the sites with warmer Mediterranean climate, thus promoting *Quercus spp.* to become dominant in about 35% of the total plots (Appendix A, Figure A6). Meanwhile, the absence of the largest recruit class of *P. sylvestris* in warmer die-off plots was also apparent (Appendix A, Figure A6). The absence of large recruits of *P. sylvestris* was recorded in approximately 50% of the die-off and control plots, separately, while the presence of recruitment (considering all recruits stages) was observed in only 25% of the die-off plots and 40% of the control ones, especially in drier sites (Appendix A, Figure A6).

Table 2.2: Estimates of LMMs (Linear Mixed Models) determining the effect of drought-induced die-off (plot condition, die-off vs. control) and climate (temperature and precipitation) since the die-off episode on richness, diversity (Shannon index), and evenness (Pielou index) of recruiting tree species (all recruits, and T1, T2 and T3 stages; see more in Methods) in *P. sylvestris*-dominated forest of Catalonia (NE Spain). Temperature and precipitation correspond to mean annual temperature and mean annual precipitation, respectively. $m.R^2$ and $c.R^2$ denotes to marginal R^2 (fixed effect) and conditional R^2 (fixed and random effect), respectively. Details of coefficients are given in Appendix A, Table A10-A13.

Recruit components	Predictors	Estimates		
		Species richness	Shannon index	Pielou index
All recruits	Die-off	0.03	-0.04	-0.01
	Precipitation	-0.24	-0.17	-0.03
	Temperature	-0.17	-0.13	

			Die-off	: 0.09	-0.02	-0.07
			Precipitation			
			Die-off	: 0.05	0.11	
			Temperature			
			m.R ² / c.R ²	0.05 / 0.81	0.08 / 0.72	0.07 / 0.73
Recruit stage	in	T1	Die-off	-0.11	-0.03	0.09
			Temperature	-0.11	-0.11	-0.00
			Precipitation	-0.18	-0.21	-0.08
			Die-off	: 0.08		
			Temperature			
			Die-off	: 0.06		
			Precipitation			
			m.R ² / c.R ²	0.04 / 0.75	0.07 / 0.64	0.10 / 0.53
Recruit stage	in	T2	Die-off	0.25	0.534	-0.03
			Temperature	-0.65	0.340	0.06
			Precipitation	-0.87	0.200	-0.01
			Die-off	:		-0.05
			Temperature			
			Die-off	:		-0.03
			Precipitation			
			m.R ² / c.R ²	0.08 / 0.73	0.06 / 0.67	0.07 / 0.23
Recruit stage	in	T3	Die-off	0.68 *	0.18	0.35 *
			Temperature	0.50 *	0.20 **	0.25 *
			Die-off	:		-0.16
			Temperature			
						m.R ² / c.R ²
* $p<0.05$ ** $p<0.01$ *** $p<0.001$						

2.3.4. Changes in shrubs communities

Similar to recruits, shrub richness, diversity, and evenness did not show significant difference between die-off and control plots (Table 2.3; Appendix A, Table A14). However, there was a significant interaction between plot condition and precipitation (Figure 2.4; Table 2.3; Appendix A, Table A14). The interaction indicated that die-off

plots had significantly higher species richness, diversity, and evenness of shrubs compared to control ones at the drier edge of the precipitation gradient, while the differences disappeared as precipitation increases (Figure 2.4A-2.4C). Meanwhile, temperature negatively affected shrub evenness (Table 2.3; Appendix A, Table A14). Regarding composition, *Buxus sempervirens* was the dominating shrub species in die-off and control plots across the climate gradient (Appendix A, Figure A7). However, several shrub species such as *Erica scoparia*, *Ligustrum vulgare*, and *Rosa spp.* newly appeared in sites having drier Mediterranean climate regime among the die-off plots (Appendix A, Figure A7).

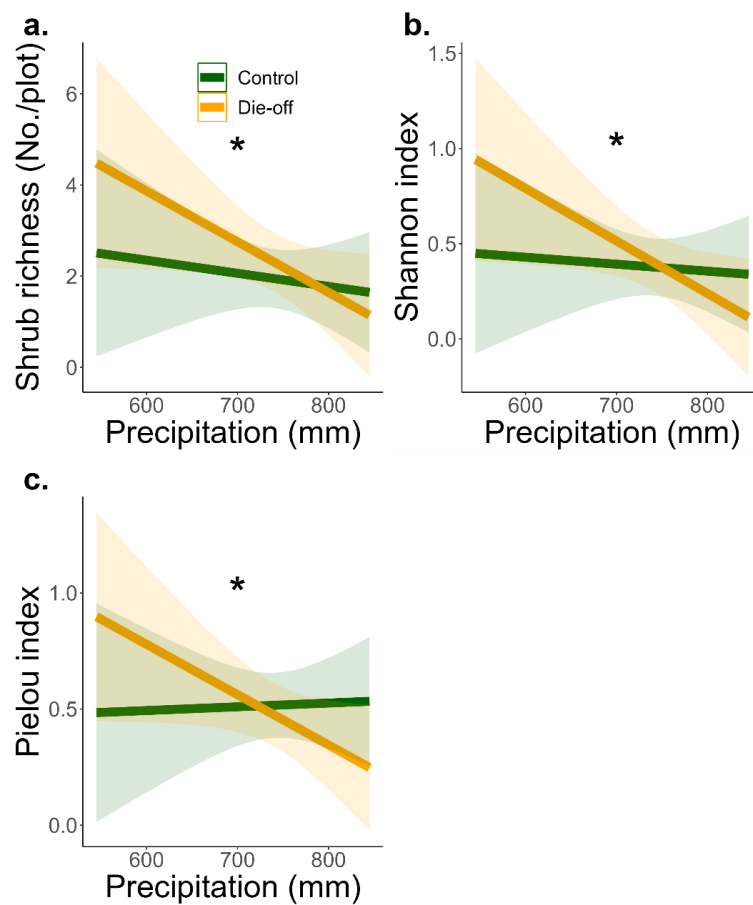


Figure 2.4: Interaction effect of shrub species richness (A), diversity (Shannon index) (B), and evenness (Pielou index) (C) between plot condition (die-off and control plots) and mean annual precipitation. Asterisk signs indicate the significance level of p-values (*: $p < 0.05$, **: $p < 0.01$, *** $p < 0.001$). The envelopes around effect lines denote 95% confidence interval.

Table 2.3: Estimates of LMMs (Linear Mixed Models) determining the effect of drought-induced die-off (plot condition, die-off vs. control) and climate (temperature

and precipitation) since the die-off episode on richness, diversity (Shannon index), and evenness (Pielou index) of recruiting shrub species in *P. sylvestris*-dominated forest of Catalonia (NE Spain). Temperature and precipitation correspond to mean annual temperature and mean annual precipitation, respectively. $m.R^2$ and $c.R^2$ denotes to marginal R^2 (fixed effect) and conditional R^2 (fixed and random effect), respectively. Details of coefficients are given in Appendix A, Table A14.

Predictors	Estimates		
	Species richness	Shannon index	Pielou index
Die-off	0.36	0.02	-0.04
Precipitation	-0.22	-0.03	0.01
Temperature	-0.47	-0.18	-0.19 *
Die-off : Precipitation	-0.62 *	-0.18 *	-0.17 *
$m.R^2 / c.R^2$	0.13 / 0.64	0.19 / 0.58	0.30 / 0.41

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

2.3.5. Similarity between tree layer and recruiting communities

We did not find any significant differences in the overall similarity, nestedness, and turnover of tree species composition between die-off and control plots across the three surveyed periods (i.e., between 2013 vs. 2017, 2013 vs. 2022, and 2017 vs. 2022; Appendix A, Table A15-A17) indicating an overall high similarity of tree layer composition in affected and non-affected plots across the survey years. Local climate conditions did not have significant effects either. However, the similarity between tree layer and recruiting communities was higher in die-off plots than in control ones in 2022 (Figure 2.5A, 2.5B; Appendix A, Table A18). Furthermore, temperature showed a positive effect on the similarity of tree layer and recruit composition between die-off and control plots, specifically due to the presence of *A. monspessulanum*, *Arbutus unedo*, *Prunus avium*, *Q. ilex*, and *Q. humilis* in both layers (Figure 2.5A, 2.6; Appendix A, Figure A8; Table A18). This pattern is consistent with the observation that the turnover component of Sørensen dissimilarity was significantly (but marginally) lower in die-off plots (0.21) than in control ones (0.39), while no differences were found for nestedness (0.25 and 0.20, respectively; see Figure 2.5C, 2.5D).

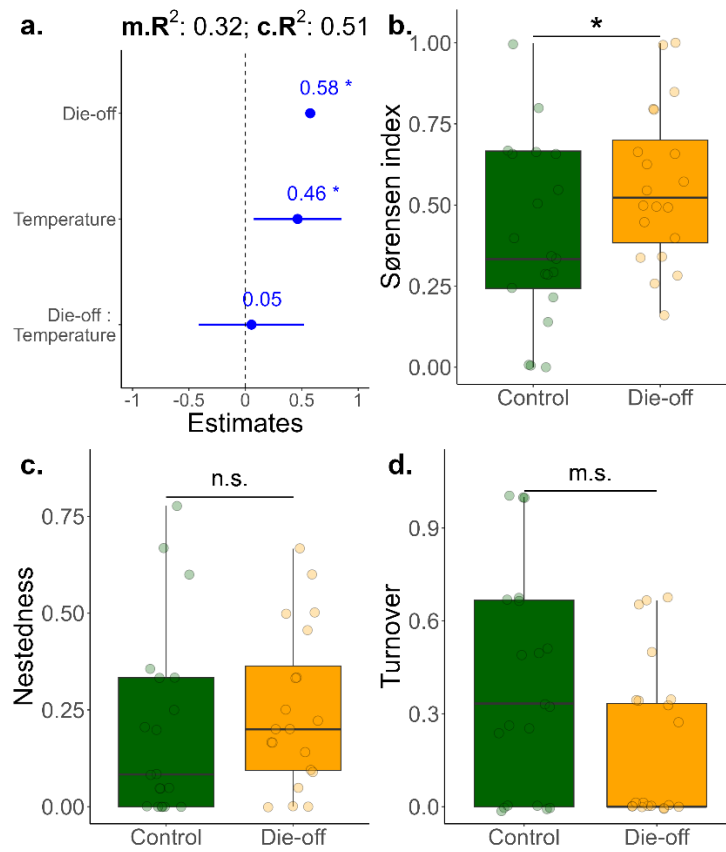


Figure 2.5: Estimates of the models of similarity of tree composition (Sørensen index) between tree layer and recruiting communities in relation to plot condition (die-off and control plots) and mean annual temperature (A), and box plot of Sørensen index (B), nestedness (C), and turnover (D) in die-off vs. control plots. Asterisk signs indicate the significance level of p-values (*: $p < 0.05$, **: $p < 0.01$, *** $p < 0.001$), while m.s. and n.s. denote marginal- and not-significant p-values, respectively. The $m.R^2$ and $c.R^2$ in denotes marginal and conditional R^2 of the model respectively (A). Details of coefficients tables are given in supplementary materials (Appendix A, Table A18).

2.4. Discussion

Here we report that forest stands of *Pinus sylvestris* that experienced die-off and tree mortality due to drought and associated bark beetle attacks (Chowdhury et al., 2024; Jaime et al., 2019; Margalef-Marrase et al., 2023) exhibited higher plant diversity, considering tree layer and large recruits. Importantly, sites in the drier and warmer edges of Mediterranean-type climatic conditions showed higher diversity changes in tree layer, being this trend also present for shrub species. The opening of forest canopy due to die-off in drier and warmer sites likely provided better opportunities for

advanced regeneration (i.e. suppressed tree saplings) belonging to species other than *P. sylvestris* to replace dead *P. sylvestris* trees, thus increasing diversity in the tree layer. The die-off episode affecting *P. sylvestris* thus triggered shifts of tree species composition favouring *Q. ilex*, *Q. humilis*, *A. monspessulanum*, *S. aria*, and other broadleaf trees. Additionally, the die-off plots also exhibited higher richness and evenness of larger recruits likely due to an increase on survival, thanks to competition release after tree death. Also, the increase of habitat complexity, after the accumulation of standing and downed deadwood (Chowdhury et al., 2024), could aid tree seeds of different species to achieve successful germination and maintain their growth. Ultimately, this resulted in higher similarity between the tree layer and the recruiting community in die-off plots relative to control ones, pointing that the increased diversity driven by the die-off episode reflects to different life-history stages of tree species (i.e., canopy adults and recruits).

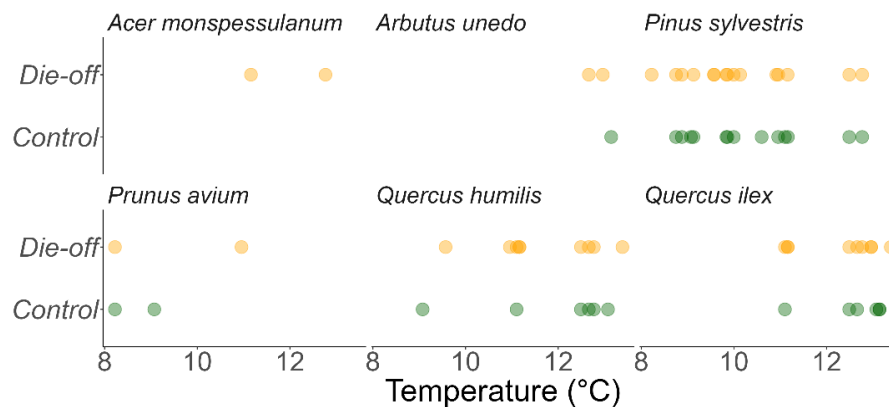


Figure 2.6: Presence of selected tree species that appeared in both tree and recruiting communities across the temperature gradient in the die-off and control plots in 2022. Status of all tree species are given at Appendix A, Figure A8.

Our findings indeed indicated a reduction of basal area in the die-off plots. This would correspond to open spaces and likely releasing competition. This facilitated previously suppressed tree individuals that maintained advanced regeneration and persisted in sub-canopy to grow (i.e. ingrowths), occupying the canopy layer in the following years after the event. Interestingly, the newcomers that fill the canopy gaps in die-off plots were often new tree species in the canopy compared to the pre-drought stand, resulting in higher diversity in the tree layer. Importantly, tree diversity also varied across the climate gradient. Higher tree diversity and evenness was found in the die-off plots

located closer to the drier and warmer edges of the studied Mediterranean area. This may be attributed to *P. sylvestris* sensitivity towards drier-warmer sites (Bose et al., 2024; also see Appendix A, Figure A3), which explain the sudden die-off-induced basal area reduction in 2013 (Appendix A, Table A3; Chowdhury et al., 2024). Ultimately, this is leading a community shift in the tree layer of the *P. sylvestris*-dominated forests with Mediterranean type climate.

Indeed, shade tolerant species present in Mediterranean and Sub-Mediterranean forests, such as *Q. ilex*, *Q. humilis*, *A. monspessulanum*, and other broadleaf species were likely to stay in the understory before the die-off event. After the event, they got the resources and spaces to achieve the canopy, particularly in relatively drier sites, thus contributed to the increase the richness and diversity of tree layer (Figure 2.3A; Appendix A, Figure A4). These species were also growing abundantly in relatively warmer sites and increased tree evenness therein (Figure 2.3B, Appendix A, Figure A5). In fact, the increase of *Quercus* spp. co-dominance with *P. sylvestris*, agrees with previous observations in Mediterranean-type forests (Galiano et al., 2013, 2010; Rigling et al., 2013). Here we expand these observations to other species, mainly broadleaf trees (e.g., *A. monspessulanum*, *C. monogyna*, *F. excelsior*, etc.; see Figure 2.3A, 2.3B; Appendix A, Figure A4 and A5 for details) many of them relatively adapted to drought conditions. For instance, shade-tolerant species such as *Quercus* spp. and *A. monspessulanum* possess drought-related functional traits such as deep root systems, high specific leaf mass, and efficient water use strategies, enabling them to thrive in drier-warmer sites and contribute to the successful establishment in the canopy layer after the die-off event (González De Andrés et al., 2024; Italiano et al., 2024). On the other hand, wetter and colder sites that were affected by the die-off episode showed self-replacement of *P. sylvestris* and those sites remained less diverse and uneven.

When considering the different recruiting stages, exposed canopy trees that survived in die-off plots or those living closely had likely experienced better conditions for reproduction. Accordingly, they would have produced abundant seeds that can disperse and eventually germinate, thereby increasing the richness and evenness of tree species in the regeneration compartment where they were previously absent or scarce (Selwyn et al., 2024). However, differences between smaller seedlings and larger sapling were apparent. On one hand, similar abundance and richness of the smaller recruit categories in die-off and control plots were observed, likely because of a common species pool at

the landscape-level. Furthermore, smaller seedlings are prone to die in both die-off plots and controls similarly as they have shallow and poorly developed root systems (Pratt et al., 2008); thus, being sensitive to climate stresses (Canham and Murphy, 2017; Dobrowski et al., 2015). In contrast, the mortality-induced competition release likely favoured larger recruits because of their relatively well-developed root systems compared to smaller recruits (Lloret et al., 2009). More specifically, resprouting and drought-resistant capacity of larger recruits of *Q. humilis*, and *Q. ilex* in affected sites with warmer Mediterranean climate (Appendix A, Figure A6), probably favoured these species, thus enhancing higher richness and evenness of largest recruits' category (Batllori et al., 2020). Conversely, *P. sylvestris* recruitment lowered in drier sites (Appendix A, Figure A6), also probably due to the reduction of seed cone production under this climatic condition (Clark et al., 2016).

The pattern of higher shrub richness, diversity, and evenness in drier die-off affected sites indicated that, similar to tree layer, several new shrub species occupy the vacant spaces. Specifically, shrub species such as *E. scoparia*, *L. vulgare*, and *Rosa spp.* with Mediterranean distribution tend to occupy the drier sites affected by die-off event. In turn, wetter sites provided favourable condition for *B. sempervirens* – a sub-Mediterranean shrub species that tends to become dominant in the study sites, lowering shrub richness, diversity, and evenness (Appendix A, Figure A7). Interestingly, our findings about the positive influence of temperature on tree diversity and evenness (i.e., tree species in both canopy and recruiting community) contrasted with the declining of shrub evenness across the temperature gradient, suggesting that warmer sites favour the growth of larger tree recruits into the tree layer, potentially outcompeting shrub species.

Intense drought episodes can drive plant community shifts in forest through the replacement of dead trees of dominant species by recruits of a different species, which eventually become adults (Martínez-Vilalta and Lloret, 2016). Interestingly, we observed higher similarity between tree layer and recruiting communities in die-off-affected plots. This could be explained by two co-existing successional processes. First, saplings of shade-tolerant tree species that remained suppressed under the tree layer prior to the drought event eventually incorporated into the canopy layer where the species was previously absent. Second, canopy trees belonging to species other than the dominant *P. sylvestris* got better opportunities for reproduction than in pre-die-off conditions becoming more abundant in the recruiting community. This is supported by

the fact that die-off plots exhibited low species turnover between tree layer and recruiting communities, resulting in higher similarity. Conversely, unaffected plots showed lower similarity potentially due to the establishment of shade-tolerant recruits of different species arriving from outside the sampled plots and thriving under a more closed canopy (Selwyn et al., 2024). Overall, these simultaneous processes initiate a new successional trajectory that promotes plant community shift in die-off-induced *P. sylvestris* forests, especially in tree layer. Concomitantly, the available resources and the favourable microclimate produced after tree mortality would assist the germination and growth of new recruits, increasing tree species richness in the understory layer. Specifically, seedlings or resprouts of the shade-tolerant *Q. ilex* and *Q. humilis* may persist in the understorey until canopy opening (Espelta, 2004), thanks to its resprouting and drought adaptive capacity (Zeppel et al., 2015). Furthermore, these features provide *Quercus spp.* some competitive advantages over *P. sylvestris* under drought stress conditions (Marañón et al., 2004; Zeppel et al., 2015) across the studied climatic range, especially in warmer sites (Figure 2.3, 2.6). Meanwhile, the successional process that we observed in this study is accompanied by a reduced recruitment of *P. sylvestris* in drier-warmer sites (Figure 2.3, 2.6). In these sites, when experiencing extreme drought, the final regeneration success of *P. sylvestris* is jeopardized by the environmental requirements of juveniles (Galiano et al., 2010), which are stricter than for adults (Jackson et al., 2009). The result is an increase in the dominance of *Quercus spp.* in the study sites, pinpointing the need of protecting recruiting communities (e.g., from potential grazing by livestock), especially in the forest stands where *P. sylvestris* recruitment is vulnerable to climate change.

However, these inferences are subjected to the inherent limitations, including geographical factors, past forest management practices, and soil characteristics, when assessing the complex dynamics of forest ecosystems. Thus, experiments associated to gaps opened after die-off and long-term forest monitoring will be necessary to better understand the consequences of extreme climate events and their associated disturbances on forest composition, and particularly the eventual existence of shifts. Overall, this study on forest stands dominated by *P. sylvestris* highlights the importance of recruiting communities on this successional process. Also, it shows that local climate conditions combined with structural changes in forest stands due to drought-induced tree mortality and die-off episodes appear to operate as a filter in plant community that

is leading to compositional shifting. These processes are expected to be exacerbated under climate change, thus accelerating forest adaption to the new conditions.

Chapter 3: Demographic Response

Canopy cover and species' climatic niche shape *Pinus sylvestris* regeneration after drought-induced die-off

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Abstract

Drought-induced die-off alters canopy structure and understory microclimatic conditions, but its consequences for tree regeneration remain unclear. We assessed how canopy-driven microclimate filtering and climatic suitability influenced *Pinus sylvestris* regeneration across developmental stages (seedlings, young saplings, and old saplings) following drought-induced die-off in forests across Catalonia (NE Spain). We analysed recruit densities with linear mixed models incorporating forest condition (die-off vs. control), canopy type (closed, defoliated, and open gaps), survey year (2013, 2017, and 2022), and climatic-niche metrics as fixed effects, while site and plot were considered as random effects. In closed habitats, die-off lowered both young and old saplings relative to controls. Defoliated habitats consistently failed to support regeneration across all stages, even in climatically favourable sites, likely due to impaired propagule supply. Open habitat enhanced seedling and sapling densities in die-off plots. Regarding the position in the climatic niche, old saplings persisted in closed habitats at climatically marginal sites, likely benefiting from canopy-mediated microclimate control. Canopy buffering also protected young saplings in closed habitats during the periods with strong interannual climate fluctuations. In open habitats, young and old saplings were sensitive to climatic position in species' niche, with their densities declining with increasing distance to the optimum, core niche. Overall, seedlings' density was higher near the climatic optimum in die-off plots than in controls. Also, nearly a decade after the drought, only young sapling densities increased in die-off plots, likely reflecting disturbance legacies and favourable climatic fluctuations. Our results highlight the silvicultural value of maintaining a mosaic of canopy structures, retaining open habitats in climatically optimal sites to enhance seedling establishment and progression, while preserving closed canopy refugia in marginal climatic sites to buffer climate extremes, thus, favouring saplings survival against increasing drought stress.

Keywords: Canopy buffering; drought legacy; species niche; regeneration density; tree mortality.

3.1. Introduction

Ongoing climate change is increasing the frequency and severity of droughts, triggering widespread tree mortality and forest die-off across various forest types and biomes (Allen et al., 2015; Anderegg et al., 2015). This phenomenon poses significant challenges to forest regeneration and potentially alter the forest succession process (Anderson et al., 2025; Xu et al., 2024). Water-limited Mediterranean forests are particularly vulnerable to large-scale drought-induced tree die-off, leading to shifts in dominant species, which might eventually initiate ecosystem collapse (Dorado-Liñán et al., 2019; Galiano et al., 2013; Lloret and Batllori, 2021). As a result, forests may experience an immediate and significant decline in biodiversity, ecosystem functions and services, thereby disrupting soil-atmosphere interactions (Anderegg et al., 2013). Paradoxically, such disturbances may also create opportunities for an ecological reset in the affected forest stands. Specifically, the opening of gaps and the accumulation and decay of deadwood promote forest heterogeneity, that, concomitant with reduced competition, may enhance stand biodiversity by allowing different species to establish and modify the community composition (Batllori et al., 2020; Chowdhury et al., 2025, 2024). This dual nature of drought-induced die-offs, involving both destructive and regenerative processes (i.e., disturbance paradox; see Thom and Seidl, 2016) can lead to less predictable successional trajectories. Yet, the long-term effects of drought-induced forest die-off on plant community dynamics remain difficult to anticipate due to the complexity of the different processes involving forest ecosystems functioning under climate change (Lloret and Batllori, 2021; Martínez-Vilalta and Lloret, 2016).

Successional trajectories after die-off are shaped, in addition to adult performance, by both the regeneration success and the pre-disturbance composition of advanced regeneration stages belonging to dominant and co-dominant canopy tree species (Gazol et al., 2018a). Canopy mortality often triggers competition release by increasing light, water, and nutrients availability, which in turn promotes the rapid growth of previously suppressed saplings (Chowdhury et al., 2025). Two short-term main successional pathways can be recognized afterwards: self-replacement (i.e., auto-succession), in which the dominant, affected species re-establishes and replacement, where a co-dominant or different species reaches dominance (Lloret et al., 2022; Margalef-Marrase et al., 2022). In Mediterranean-type forests, the resulting successional pathways tend to favour shade-tolerant species with drought-adaptive traits, such as efficient water-use

strategies (Lloret et al., 2012; Martínez-Vilalta and Lloret, 2016), in addition to those with the ability to resprout (Zeppel et al., 2015). Ultimately, the ability of dominant species to recover following drought-induced die-off may be outcompeted by more resilient co-dominant species, whose functional traits and regenerative strategies confer them a competitive advantage in the successional process (Lloret and Batllori, 2021; Martínez-Vilalta and Lloret, 2016). Also, other species may migrate from surrounding areas through seed or propagule dispersal (Selwyn et al., 2024), although competition, facilitation, and priority effects (i.e., the order in which species arrive) will determine which species ultimately establish successfully (Fukami, 2015; Maestre et al., 2009).

Climate conditions also shape regeneration based on the species-specific climatic niche requirements (Grubb, 1977; Pironon et al., 2018). The species' climatic niche can be quantified by constructing bioclimatic hypervolumes that capture the range of environmental conditions associated with known occurrences of the species. However, ongoing shifts in temperature and precipitation induced by climate change may narrow the extent of the historic suitable climatic ranges, pushing many species toward the limits of their climatic tolerance (Rehm et al., 2015). This pattern is described within the “core vs. edge” framework, i.e., species would tend to perform better at the core of their climatic niche, where environmental conditions align with their physiological and evolutionary optimum (Pérez Navarro et al., 2019; Pironon et al., 2018). Yet, populations in these locations may also suffer high mortality during drought episodes likely due to their acclimation to mild, favourable conditions (Elvira et al., 2021; Lloret and Kitzberger, 2018). In turn, populations placed close to the edges of their climatic niches are expected to perform worse and may be particularly vulnerable during drought episodes (Pérez Navarro et al., 2021, 2019). Otherwise, these edge populations may also be adapted to local conditions such as extreme weather, thereby experiencing reduced mortality during drought events (Margalef-Marrase et al., 2022). Also, tree regeneration is expected to decline after drought due to climatic stress, given that recruits (seedlings and saplings) typically have more restrictive niche requirements than adults (Elvira et al., 2021; Grubb, 1977; Jackson et al., 2009). Yet, regeneration success may recover once climate conditions become favourable again, provided that sufficient regenerative material remains in the system (Grubb, 1977; Jackson et al., 2009). Interestingly, regeneration even could be maintained if the climatic buffering provided by the canopy of surviving trees is sufficient to support and promote seedling

establishment. This facilitative process, named as canopy service, may help and sustain the regeneration event in populations located away from the species' climatic optimum (Margalef-Marrase et al., 2025). As a result, canopy cover can contribute to a mismatch between species climatic requirements and its actual distribution (Pérez Navarro et al., 2024).

Local climatic conditions are strongly influenced by canopy cover (De Frenne et al., 2019). Following drought-induced die-off, the degree of sunlight penetration governs microclimatic conditions beneath the canopy by influencing temperature and soil moisture conditions (Thom et al., 2020). In those situations, canopies of surviving trees can buffer climatic extremes and create localized refugia that support recruit's establishment (Pérez Navarro et al., 2024; Thom et al., 2023), particularly for shade-tolerant species. This canopy-driven facilitation may prolong the persistence of the regeneration of dominant species in the forest stand by extending local extinction lags under ongoing adverse microclimatic conditions (Alexander et al., 2018). Additionally, tree mortality increases deadwood accumulation, potentially contributing to favourable habitats for seedling establishment by providing shade, retaining moisture, and protecting them against desiccation and predation (Hagge et al., 2019). However, stands with extensive canopy loss could experience reduced structural buffering compared to the dense canopy cover, resulting in higher temperatures and lower relative humidity at the forest floor. These harsher conditions can hinder seedling establishment and survival (Schmidt et al., 2017; Thom et al., 2020), potentially leading to regeneration bottlenecks (Gazol et al., 2018a). Under these conditions, the trajectory of forest regeneration is likely to be shaped by the adaptive capacity of accompanying tree species, particularly those able to tolerate projected climatic extremes.

Pinus sylvestris L. (Scots pine) is a long-lived, shade-intolerant conifer with wind-dispersed seeds and is one of the most widely distributed conifer species across the Northern Hemisphere, especially in Europe (Figure 3.1A, Bose et al., 2024). While it has traditionally been considered as a relatively drought-tolerant species, it has shown increasing vulnerability to climate-induced die-off across its distribution range, including core and marginal climatic zones of temperate and Mediterranean regions (Bose et al., 2024; Margalef-Marrase et al., 2023). Although mortality and die-off events in *P. sylvestris* forests reduce stand biomass, they also contribute to higher structural complexity over time through deadwood accumulation and changes in woody

plant composition (Chowdhury et al., 2025, 2024). These changes may alter microclimatic conditions in habitats with variable canopy cover, from open sites to defoliated canopies and intact, closed canopies (Margalef-Marrase et al., 2022). Because *P. sylvestris* has high light requirements for seedling establishment and survival (Carlisle and Brown, 1968), its regeneration success is likely dependent on canopy openness. However, it is still poorly understood how the interaction of canopy openness and drought can affect the success of *P. sylvestris* regeneration following die-off events, and how this response varies depending on the population's position within the species' climatic niche. To address this knowledge gap, we have analyzed the density of recruits at different development stages in a paired plot design, including plots affected by drought-induced die-off and unaffected ones across Catalonia (NE Spain), a region covering a wide range of climatic conditions. Specifically, we hypothesize:

- i) *P. sylvestris* recruit density will be higher in die-off plots due to reduced competition following overstory mortality and favourable light conditions for this species.
- ii) *P. sylvestris* recruit density will vary under different canopy conditions, likely reflecting differences in regeneration success driven by varying microclimatic buffering provided by canopy cover.
- iii) Recruit density will decline with increasing distance from the species climatic niche optimum (i.e., centroid), consistent with the core vs. edge framework. However, this trend may be modulated by different canopy conditions.

3.2. Methods

3.2.1. Study Area

We studied forests dominated by *P. sylvestris* in Catalonia (NE Spain), as they have experienced drought-induced die-off and tree mortality in recent decades (Margalef-Marrase et al., 2023). These impacts were particularly severe following the 2012 drought, which was further exacerbated by bark beetle infestations (Jaime et al., 2019). *P. sylvestris* reaches its southernmost and driest distribution limit in the Iberian Peninsula, allowing to investigate its regeneration under bioclimatic limiting conditions. Accordingly, we surveyed twenty forest sites (Figure 3.1B; Appendix B, Table B1), with a mean distance of 52.4 km among them (range: 14.7 to 90.1 km) covering a wide elevation (range: 600 to 1650 m a.s.l.) and climate gradients (ranging from cold-wet

conditions in the Pyrenees to drier-warmer conditions in the Catalan Coastal Range; Appendix B, Figure B1, Table B1). Mean annual temperature was 10.3°C (ranging from 6.5 to 13.9°C), and annual precipitation was 774 mm (ranging from 341 to 1427 mm). During the drought-affected year (2012), mean annual precipitation dropped to 580 mm (ranging from 467 to 667 mm), while mean temperature remained similar (10.5°C; ranging from 8 to 13.3°C) across the studied area, indicating a severe precipitation deficit relative to the long-term mean. The composition of the sites, which was once dominated by pure *P. sylvestris* and mixed stands with *Quercus ilex* and *Q. humilis*, is transitioning into a more drought-tolerant and diverse Mediterranean woodland with an increasing presence in the canopy and the regeneration layer of *Quercus*, *Acer*, *Crataegus*, and *Prunus* species (Chowdhury et al., 2025).

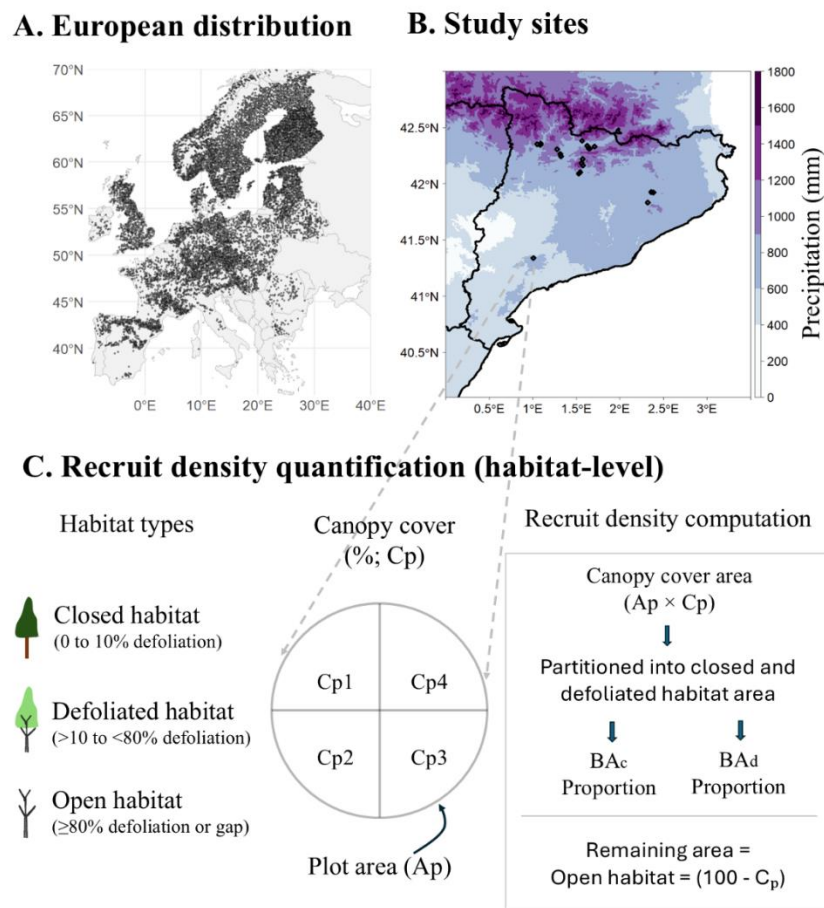


Figure 3.1: (A) European distribution of *P. sylvestris*, (B) Study sites across Catalonia (NE Spain) shown over a precipitation gradient (data source: Fick and Hijmans, 2017), and (C) Schematic representation of habitat-level recruit density quantification. Left:

three canopy-cover habitats were distinguished based on defoliation of overstorey trees: closed habitat (0-10% defoliation), defoliated habitat (>10-<80% defoliation), and open habitat ($\geq 80\%$ defoliation including dead tree or gaps). Middle: plot canopy cover (C_p) was visually estimated from four quadrants within each circular plot ($A_p = 314 \text{ m}^2$). Right: the canopy-covered area ($A_p \times C_p$) was then partitioned into closed and defoliated habitat areas according to the basal area proportion of trees in each defoliation class (BA_c and BA_d). The remaining area ($100 - C_p$) was considered open habitat. Recruit density in each habitat type was calculated using Equations i-iii in the Methods.

3.2.2. Sampling design and data collection

In 2013, two circular-paired plots with a 10-meter radius (314 m^2) were established in each of the twenty forest sites (Figure 3.1B; Appendix B, Table B1). One plot was located in a stand showing clear signs of drought-induced tree die-off and mortality, characterized by recently dead trees due to the 2012 drought (die-off plot), while the second plot was positioned 50 to 150 meters away in a visually unaffected stand (control plot; see plot characteristics in Chowdhury et al., 2024; Margalef-Marrase et al., 2023). This paired plot design allowed direct comparisons between affected and unaffected forest conditions, while minimizing variability in environmental, topographical, and soil properties. No salvage logging occurred at the affected sites following the die-off, enabling the observation of *P. sylvestris* forest succession in natural conditions.

All *P. sylvestris* recruits ($\leq 2.5 \text{ cm dbh}$, diameter at breast height) were identified and counted at the plot level in 2013 and categorized into three developmental stages: T1, corresponding to seedlings under two years old with height $\leq 30 \text{ cm}$; T2, corresponding to young saplings older than two years with height $> 30 \text{ cm}$ but $< 130 \text{ cm}$; and T3, corresponding to old saplings with height $\geq 130 \text{ cm}$ but with dbh $\leq 2.5 \text{ cm}$ (LIFE RedBosques, 2019). Resampling was conducted in all plots in 2017 and 2022 following the same procedure. Additionally, in each survey, we also visually identified the habitat where recruits grew, based on the overstorey over them. More precise methods to quantify canopy cover, for instance by hemispherical photography were discarded for operational purposes given that the presence of large number of recruits. Specifically, we recognized three canopy cover types based on the tree defoliation classes (Michel et

al., 2023): (i) closed habitat, which consisted of canopies of alive trees with 0-10% defoliation; (ii) defoliated habitat, which consisted of canopies of alive trees with more than 10% but less than 80% defoliation; and (iii) open habitat or gaps, which consisted of alive trees with 80% or more defoliation, standing dead trees or open spaces with no trees (Figure 3.1C; Appendix B, Figure B2, B3).

We also measured all alive trees with a dbh > 2.5 cm in 2013, 2017, and 2022 to estimate tree basal area in each canopy cover type (Appendix B, Figure B2). While measuring DBH, we also visually estimated the defoliation level of each tree to allocate them to the above-mentioned canopy cover types (Figure 3.1C; Appendix B, Figure B3). Tree defoliation was characterized as the loss of leaves in relation to pre-established healthy trees, ranging from 0% (fully green or closed canopy) to 100% (fully defoliated or dead tree). This procedure is widely employed in studies characterizing forest die-off (Gazol et al., 2018a; Sapes et al., 2017) and is supported by photographic records of given levels of defoliation for visual comparison. The reliability of the procedure was further underpinned by cross validation between different surveyors. During the 2017 and 2022 surveys, newly incorporated trees that had reached a dbh > 2.5 cm were identified by comparing data from previous surveys and we measured their dbh and defoliation level.

3.2.3. *Quantification of recruit density*

The estimation of recruit density in each habitat category required an estimation of the area of each canopy cover type, which was unsuitable to be directly obtained in the field due to the canopy overlapping of trees with different level of defoliation (Appendix B, Figure B3). Therefore, we used to approximate the area corresponding to each canopy cover type through a proxy based on the basal area and the defoliation level of alive trees, combined with the overall plot canopy cover (Figure 3.1C; Appendix B, Figure B3). First, in 2022, each plot was divided into four quadrants - to reduce errors relative to a single measurement -, where the percentage of canopy cover (0 to 100%) was visually estimated. The mean plot canopy cover of the four quadrants was used to estimate the overall canopy cover (%) of the plot (C_p ; Appendix B, Figure B3). Next, we calculated the approximate canopy-covered area of each plot by multiplying C_p with the actual plot area ($A_p = 314 \text{ m}^2$). Then we split the canopy-covered area of each plot into the two habitat categories -closed and defoliated-, considering the proportion of the

plot basal area of trees belonging to each canopy cover category. Specifically, the basal area of the closed habitat (BA_c) was calculated by summing the basal area of tree individuals with 0 to 10% defoliation, while the basal area of defoliated habitat (BA_d) was calculated by summing the basal area of individuals with more than 10% but less than 80% defoliation. Then, the proportion of closed canopy habitat was defined as the ratio of BA_c to total alive tree basal area ($BA_c + BA_d$), and this value was multiplied by the overall canopy area in the plot ($C_p \times A_p$) to estimate the area of closed habitat. Similarly, the area of the defoliated habitat was calculated as the ratio between BA_d and total alive tree basal area under canopy cover ($BA_c + BA_d$), which was then multiplied by the canopy area ($C_p \times A_p$). Finally, the area of the open habitat (C_o) was calculated as the proportion of open gaps (i.e., 100 minus canopy cover of plot, $100 - C_p$) and multiplied by plot area (A_p). We did not include the basal area of alive trees with 80% defoliation or more when estimating the area of the open canopy cover, as recruits under these trees received no partial canopy shedding like in the open spaces with no trees.

These habitat-specific areas were used to calculate recruit densities in each habitat by dividing the number of recruits observed in closed (N_c), defoliated (N_d) and open (N_o) habitat by the respective habitat area (equations i, ii and iii).

$$\text{Recruits' density in closed habitat (no./ha), } D_c = \frac{N_c \times 10000}{\left(\frac{A_p \times C_p}{100}\right) \times \left(\frac{BA_c}{BA_c + BA_d}\right)} \quad (\text{i})$$

$$\text{Recruits' density in defoliated habitat (no./ha), } D_d = \frac{N_d \times 10000}{\left(\frac{A_p \times C_p}{100}\right) \times \left(\frac{BA_d}{BA_c + BA_d}\right)} \quad (\text{ii})$$

$$\text{Recruits' density in open habitat (no./ha), } D_o = \frac{N_o \times 10000}{A_p \times \left(\frac{(100 - C_p)}{100}\right)} \quad (\text{iii})$$

Where, 10,000 converts the result from recruits per m² to recruits per hectare (ha), and the denominator of 100 converts canopy cover from percentage to proportion.

3.2.4. *Quantifying the historical climate niche and plot niche matrices of P. sylvestris*

We obtained 9351 unique occurrence records of *P. sylvestris* populations from the EU-Forest dataset (i.e., European tree species distribution) to construct the species historical climate niche (Mauri et al., 2017). For each of these locations, we extracted daily minimum temperature, daily maximum temperature, and daily precipitation by means of the *easyclimate* R package for 1980-2021 period (Cruz-Alonso et al., 2023).

From these daily data, we calculated monthly values to derive yearly bioclimatic variables, allowing us to characterize the interannual variability in the environmental conditions experienced by the species (Pérez Navarro et al., 2021). Specifically, we computed 19 standard yearly bioclimatic variables (i.e., BIO1 to BIO19; see Appendix B, Table B2) over the 42-year period using the R package *dismo* (Hijmans et al., 2024). Among the bioclimatic variables, 12 were used to construct an environmental climatic space through a principal component analysis (PCA) using the *ade4* R package (Dray and Dufour, 2007; Appendix B, Table B2), according to Pérez Navarro et al. (2021). The first principal component (PC1 / Dim1) accounted for 41.2% of the total variance, while the second principal component (PC2 / Dim2) explained an additional 32.1%, indicating an overall good fit of the PCA (Figure 3.2A). Variables like bio12, bio13, bio14, bio16, and bio17 (related to precipitation) showed a strong positive relationship with Dim1 and a moderate positive correlation with Dim2 (Figure 3.2A). Meanwhile, bio1, bio6, bio10, and bio11 (temperature-related) showed a negative relationship with Dim1 and Dim2 (Figure 3.2A). Furthermore, bio4 (temperature seasonality) showed a negative relationship with Dim1 but a positive one with Dim2 (Figure 3.2A).

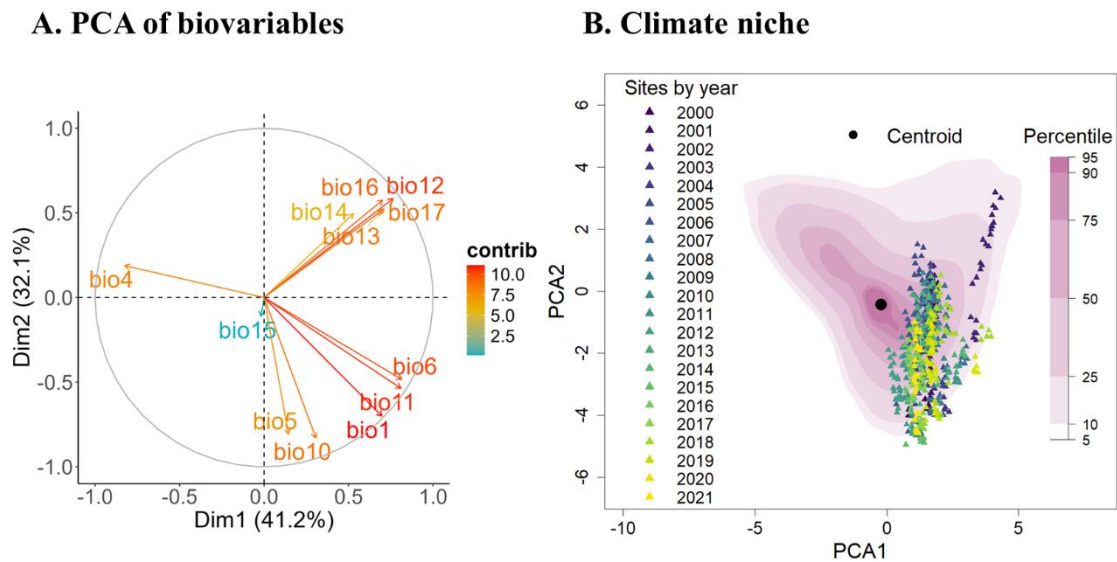


Figure 3.2: (A) Biplot of principal component analysis (PCA) with 12 bioclimatic variables indicating their relative contributions to the first two principal components (Dim1 and Dim2), and (B) climate niche of *P. sylvestris* in the PCA space (at 5 to 95% kernel density contours), indicating the centroid (black dot), and showing the study site

positions by year (2000 to 2021). Year-specific site distributions are detailed in Appendix B, Figure B4.

Subsequently, we applied kernel density estimation with *ks* R package (Chacón and Duong, 2018) to determine the density of *P. sylvestris* European occurrences within a two-dimensional environmental space. From this, we identified the *P. sylvestris* climatic niche using the 5% to 95% kernel density contours, representing the realized climatic niche of the species (Figure 3.2B). Within this climatic niche, we characterized the core (i.e., niche centroid) corresponding to the area of highest occurrence density in the climatic space, and the boundaries (i.e., niche edge) which reflects the species' tolerance limits (Figure 3.2B). Next, we determined the relative positions within the realized climatic niche of our study plots during the 2000-2021 period (Appendix B, Figure B4), accounting for the estimated period of recruitment occurrences (Appendix B, Table B3) and using 2021 as the last year to capture a full annual cycle, since the third survey was conducted in summer 2022. To do that, we translated the values of the 12 annual bioclimatic variables for that period (Appendix B, Table B2) to the above-mentioned environmental climatic space (i.e., the PCA; Figure 3.2A) by using the *subrow* function of *ade4* R package (Dray and Dufour, 2007). To characterize the position of each plot within the species' climatic niche in every year during 2000-2021, we calculated the Euclidean distance between each position and the niche centroid (core distance, hereafter; Figure 3.2B, Appendix B, Figure B4). We used this methodology instead of percentiles or other climate suitability metrics given that some locations of the study plots moved beyond the limits of the niche in several years of the period assessed (Pérez Navarro et al., 2021).

We used different periods to account time windows relevant to each recruit stage: four years prior to sampling for T1, eight years prior to sampling for T2, and twelve years prior to sampling for T3 stage (Appendix B, Table B3). For each sampled year and developmental stage, we computed the sites' mean Euclidean distances to calculate distances to core for each time window for each survey. To capture temporal climatic variability, we also calculated the coefficient of variation (hereafter, core distance CV) of these distances for each stage across the three sampled years.

3.2.5. Statistical analyses

To investigate the combined effects of the die-off event (reflecting die-off and control plots) across time (2013, 2017, and 2022), canopy types (closed, defoliated, and open), and niche metrics, i.e., position in the species climatic niche, we constructed separate linear mixed models (LMMs) with recruits' density at each developmental stage (T1, T2, and T3) as the response variable. In these models, fixed effects were forest condition (die-off and control), survey year, canopy types, and niche metrics (core distance and core distance CV). Interaction terms up to the second order were incorporated in the full model. Both site and plot identity were treated as random effects to account for the paired plot design and repeated measures across survey years, respectively.

To further assess the impact of forest die-off on the recruitment in the specific survey year we constructed individual LMMs for each developmental stage at each survey year using recruits' density as the response variable. In these models, forest condition was included as fixed effect and site identity was incorporated as a random effect to account for the paired design of our sampling. Besides die-off, we also developed individual LMMs to evaluate the influence of canopy cover variations on the recruitment at each specific survey year. Recruits' density at each developmental stage was used as the response variable and canopy types was the fixed effect. Site and plot identity were included as random effects to account for the paired plot design and repeated measures across survey years, respectively. Finally, to assess the effect of forest condition within each canopy type and development stages, we performed separate Tukey HSD tests comparing die-off and control plots, for each canopy type and development stage by pooling data without considering the survey years.

The LMMs were implemented using the *lmer* function from the *lme4* R package (Bates et al., 2003; R Core Team, 2024). Continuous explanatory variables were scaled, and model selection was performed using the *dredge* function for fixed and random factors using the *MuMIn* package, based on AIC with a threshold of 2 (Bartoń, 2010).

Table 3.1: Estimates from linear mixed models (LMMs) assessing the effects of drought-induced die-off (compared to control), canopy cover types (closed, defoliated, open), and niche metrics (core distance and core distance coefficient of variance, CV) on *P. sylvestris* recruits at different development stages (T1, T2, and T3; see Methods)

across three survey years (2013, 2017, and 2022) in forests from Catalonia (NE Spain). Marginal and conditional R^2 values are also given. Detailed model specifications and additional results are provided in the Appendix B.

Predictors	Estimates		
	T1 stage	T2 stage	T3 stage
Die-off	-0.33	-66.71	-13.59
Closed habitat	17.74	156.03 ***	52.58 ***
Open habitat	18.89	70.06	6.77
2017		-6.47	0.13
2022		0.92	-3.97
Core distance	2.91	-0.01	-1.82
Core distance CV	-1.99	18.49	
Die-off: Closed habitat	-4.43	-75.26 *	-24.49 *
Die-off: Open habitat	39.04 *	107.75 **	38.20 ***
Die-off: 2017		56.18	8.10
Die-off: 2022		105.47 **	19.38
Closed habitat: 2017		-63.00	-27.43
Open habitat: 2017		-49.11	-6.18
Closed habitat: 2022		-117.54	-37.32 **
Open habitat: 2022		-79.62	4.30
Die-off: Core distance	-18.30 *		
Closed habitat: Core distance		-50.92 *	-9.63
Open habitat: Core distance		-84.66 ***	-17.13 **
Closed habitat: Core distance CV	-3.19	-23.42	
Open habitat: Core distance CV	-16.47	-68.80 *	
<i>Marginal R^2 / Conditional R^2</i>	<i>0.10 / 0.15</i>	<i>0.18 / 0.41</i>	<i>0.18 / 0.33</i>
* $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$			

3.3. Results

Seedling-stage (T1) density of *P. sylvestris* did not differ significantly between forest condition, either when data were pooled across years (Table 3.1; Appendix B, Table B4) or when assessed separately for 2013, 2017, and 2022 (Appendix B, Table B5). Moreover, no differences were observed between canopy habitats when data were

pooled across the studied period (Table 3.1; Appendix B, Table B4). However, across survey years, open habitats consistently supported higher T1 densities than defoliated ones (Table 3.2; Appendix B, Table B6). In 2013, T1 recruitment was also higher in closed habitats than in defoliated ones (Table 3.2; Appendix B, Table B6). T1 recruits were more abundant in die-off plots under open canopy (Figure 3.3A, Appendix B, Figure B5A), as reflected in the interaction between open canopy and die-off (Table 3.1; Appendix B, Table B4), but pair comparisons between die-off and control plots for T1 recruits in open canopy failed to obtain statistical significance (Appendix B, Figure B5A). Regarding niche determinants, the density of T1 recruits in die-off plots declined with increasing distance to the core (Figure 3.4; Table 3.1).

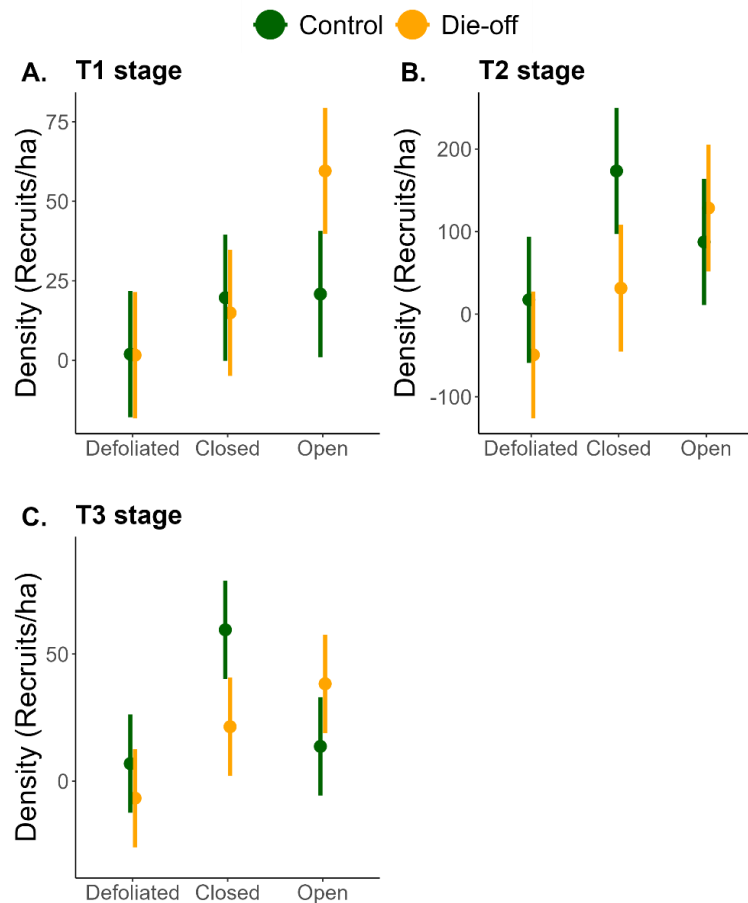


Figure 3.3: *Pinus sylvestris* density (recruits/ha) for the studied development stages (A) T1 (seedlings), (B) T2 (young saplings), and (C) T3 (old saplings) in the different canopy cover types (closed, defoliated, and open), based on data pooled across years. The figure reflects model predictions. The dots denote point estimates, while error bars

represent 95% confidence intervals. Model summary and statistical significance of the interaction effects are provided in Table 3.1.

Table 3.2: Estimates from linear mixed models (LMMs) assessing the effect of canopy cover types (closed, defoliated, open) on *P. sylvestris* recruits at different development stages (T1, T2, and T3; see Methods) across three survey years (2013, 2017, and 2022) in forests from Catalonia (NE Spain). Marginal and conditional R^2 values are also given. Detailed model specifications and additional results are provided in the Appendix B.

Development stage	Canopy cover type	Estimate		
		2013	2017	2022
T1	Closed	35.38 *	1.99	9.20
	Open	32.47 *	17.50 *	65.25 **
T2	Closed	108.26 **	56.99	9.39
	Open	81.25 *	79.55 *	82.27 **
T3	Closed	40.17 **	14.26	1.83
	Open	25.58 *	22.09 *	28.05 *
<i>Marginal R^2 / Conditional R^2</i>		0.06 / 0.11	0.04 / 0.04	0.08 / 0.08

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

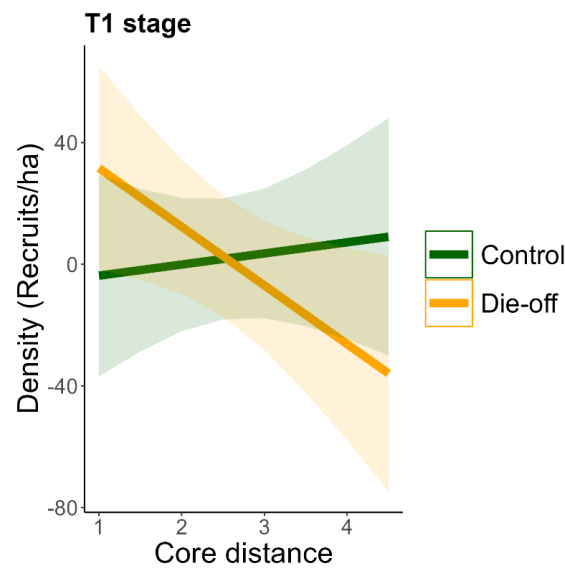


Figure 3.4. Interaction effects of forest condition (die-off vs. control) and core distance in the climatic niche (see methods) on density (recruits/ha) of *P. sylvestris* at T1

development stage (seedlings), based on data pooled across years. The envelopes around effect lines denote 95% confidence intervals. The figure reflects model predictions. Model summary and statistical significance of the interaction effects are provided in Table 3.1.

Young sapling recruits (T2) also showed no significant differences between forest condition when data were pooled without considering distinct years (Tables 3.1; Appendix B, Table B7) or the three survey years individually (Appendix B, Table B8). Regarding canopy type, closed habitats exhibited significantly higher T2 densities than defoliated ones when data were pooled across the surveys (Table 3.1, Appendix B, Table B7). Meanwhile, T2 density was significantly higher in open habitats compared to defoliated habitats in each survey year (Table 3.2; Appendix B, Table B9). Also, in 2013, T2 density was higher in closed habitats compared to defoliated ones (Table 3.2; Appendix B, Table B9). Open habitats in die-off plots (136 ± 32 saplings/ha) exhibited higher T2 density compared to control ones (44 ± 15 saplings/ha), whereas closed habitats in die-off plots (22 ± 8 saplings/ha) showed a lower density relative to control ones (112 ± 38 saplings/ha; Appendix B, Figure B5B), as reflected by the significant interactions between canopy habitats and forest condition (Figure 3B; Table 3.1; Appendix B, Table B7). Besides, T2 density increased in die-off plots by 2022, whereas T2 recruitment in control plots remained relatively stable across years (Figure 3.5A; Table 3.1). Climatic niche metrics determined T2 recruitment by their interactions with canopy habitat (Figure 3.6A, 3.6B; Table 3.1). T2 density declined with increasing core distance in both closed and open canopy habitats, whereas in defoliated habitats recruitment was not affected by increasing core distances in the climatic niche (Figure 3.6A; Table 3.1). Besides, T2 recruitment was higher in closed habitat when core distance CV was high (Figure 3.6B; Table 3.1).

Recruitment at the old sapling stage (T3) showed no significant differences between forest condition, whether analysed using pooled data (Tables 3.1; Appendix B, Table B10) or separately for 2013, 2017, and 2022 (Appendix B, Table B11). Regarding canopy habitat, only closed canopy habitats had higher older saplings compared to defoliated ones when data were pooled across surveys (Table 3.1; Appendix B, Table B11). However, open habitats consistently supported significantly higher T3 recruitment compared to the defoliated ones in 2013, 2017, and 2022 (Table 3.2, Appendix B, Table B12). Also, closed habitats exhibited higher T3 recruitment than

defoliated ones in 2013 (Table 3.2; Appendix B, Table B12). Open habitat in die-off plots showed higher T3 density (45 ± 12 saplings/ha) than in control ones (12 ± 4 saplings/ha), while closed habitat in die-off plots (8 ± 2 saplings/ha) had lower density compared to control ones (37 ± 8 saplings/ha; Appendix B, Figure B5C), as reflected by the interactions between canopy habitats and forest condition (Figure 3.3C; Table 3.1). Regarding temporal changes, T3 recruitment in closed habitats declined by 2022 (Figure 3.5B; Table 3.1). Finally, core distance was negatively associated with T3 density in open habitats compared to defoliated ones (Figure 3.6C; Table 3.1).

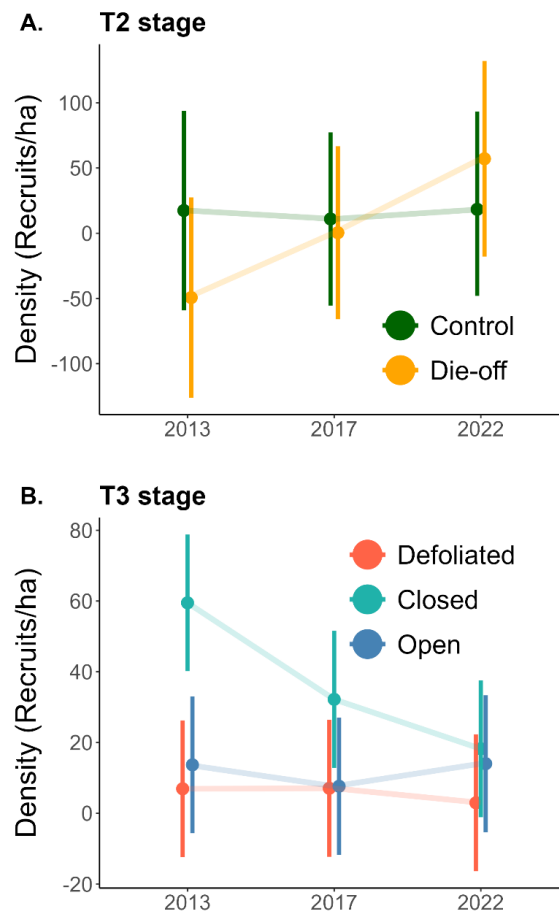


Figure 3.5: Density (recruits/ha) of *P. sylvestris* at (A) T2 stage (young saplings) modelled forest condition (die-off vs. control) for the three survey years (2013, 2017, 2022), and at (B) T3 stage (old saplings) modelled by canopy cover type (closed, defoliated, and open) for the three survey years. The figure reflects model predictions. The dots denote point estimates, while error bars represent 95% confidence intervals. Model summary and statistical significance of the related interaction effects are provided in Table 3.1.

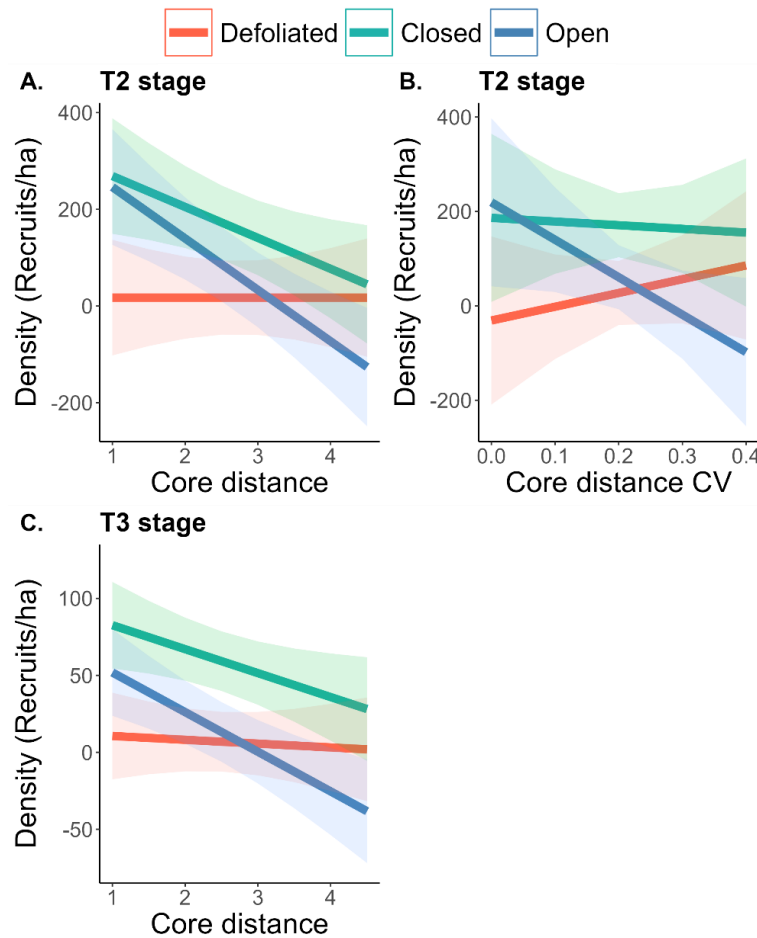


Figure 3.6: Interaction effects between canopy cover type (closed, defoliated, open) with (A) core distance and (B) core distance variability (coefficient of variation, CV) on T2 (young saplings) density (recruits/ha) of *P. sylvestris* recruits, and between (C) canopy habitat and core distance on T3 (old saplings) density (recruits/ha). The figure reflects model prediction, based on data pooled across years. The envelopes around effect lines denote 95% confidence intervals. Model summary and statistical significance of the interaction effects are provided in Table 3.1.

In general, the linear mixed models explained only a small part of the variability of the data when forest condition and canopy cover type were included as a single fixed factor, also considering the random effects in the model (Appendix B, Table B5, B6, B8, B9, B11, B12). However, despite low marginal R^2 values in models with multiple fixed factors, the conditional R^2 increased when the random factors (site and plot) were included.

3.4. Discussion

Drought-driven defoliated habitats consistently failed to support regeneration across all recruits' developmental stages throughout the nine-years study period, and this limitation persisted even at sites that were considered climatically suitable for *P. sylvestris*. The position of populations in the species climatic niche explains regeneration in open habitat, particularly in young and old saplings stages, as their density declined at sites located farther from the core of the species' climatic niche. Interestingly, old saplings persisted in marginal sites under closed canopies, pointing to the potential buffering role of canopy cover (Pérez Navarro et al., 2024).

3.4.1. Canopy cover type effect on regeneration success

The effect of die-off in *P. sylvestris* recruitment was strongly associated to its interaction with the microlocal modification of canopy-cover. The reduced recruitment in defoliated habitats was likely due to severely defoliated *P. sylvestris* trees that, although survived the drought, they experienced severe damage, and probably produced few viable cones or poor-quality seeds, limiting propagule availability (Galiano et al., 2013; Vilà-Cabrera et al., 2015).

In contrast, open habitat in die-off plots favoured the establishment of new seedlings and its successive development stages (i.e., young and old saplings; Figure 3.3), likely due to increased light availability associated with reduced competition. *P. sylvestris* reproduction is highly influenced by light availability, as cone opening and seed germination typically require favourable irradiance and thermal conditions (Carlisle and Brown, 1968). Therefore, competition release following die-off allowed light-demanding *P. sylvestris* seedlings to establish successfully and progress toward next developmental stages.

In turn, young and old saplings were more abundant in the closed habitats than in the defoliated ones (Table 3.1), particularly in control plots (Figure 3.3B, 3.3C; Appendix B, Figure B5B, B5C), where canopy cover was maintained (Appendix B, Figure B3). This likely strengthened canopy cover-mediated microclimatic buffering by reducing temperature extremes and maintaining higher soil moisture, which in turn favoured the survival of young saplings and their progression into old stage (Keppel et al., 2017). However, sapling densities declined in the closed habitats of die-off plots (Figure S5B,

S5C), suggesting that drought not only triggered the mortality of overstory adult *P. sylvestris* trees in these plots but also reduced the survival of understory saplings. In closed habitats of die-off plots, recruits also faced competition from both surviving *P. sylvestris* individuals and co-occurring drought-tolerant species. This competition likely limited the self-replacement potential of *P. sylvestris*. In turn, advanced regeneration belonging to more drought-resilient species (e.g. *Quercus spp.*, *Acer spp.*, *Crataegus monogyna*, *Prunus spp.*, and other broadleaf species) persisted and grew toward the canopy layer (Chowdhury et al., 2025). As a result of inter- and intraspecific competition, the ability of closed habitats to support *P. sylvestris* regeneration may shifted in favour of drought-tolerant taxa following the die-off event. This was also reflected in the temporal dynamics of regeneration decline under closed canopies (Figure 3.5B), reaching levels comparable to defoliated habitats when data were pooled without considering forest condition (Table 3.2).

However, there are methodological limitations in our study that should be considered when interpreting the results obtained for the estimation of recruits' density. Particularly, we applied a proxy-based approach to estimate recruit density by using canopy cover and tree basal area. While these proxies provide a reasonable approximation, we acknowledge that it cannot fully capture the fine-scale variability in microsite conditions experienced by recruits, although the inclusion of random variables improved the reliability of LMMs. Also, we used visual observations to estimate tree defoliation level and canopy cover in the field, which is subjected to some degree of errors in spite of cross validation between surveyors based on references from photographic records.

3.4.2. Interaction between climatic niche and canopy cover

Apart from the characteristics of canopy cover, the population's position in the species climatic niche determined recruitment patterns, particularly in die-off plots, where the density of seedlings declined with increasing core distance (Figure 3.4). This is consistent with previous studies showing lower performance in terms of species abundance associated to drought events in populations living far from the climatic niche optimum (Margalef-Marrase et al., 2022). Our study expands this pattern to the recruitment capacities of tree seedlings in drought-affected plots.

Sapling densities also declined with increasing distance from the climatic niche core, but the magnitude of this response differed between developmental stages and canopy conditions (Figure 3.6A, 3.6C; Table 3.1). Young saplings were consistently climate-sensitive across increasing core distance, showing strong declines in both closed and open habitats, which indicates that canopy cover did not improve their persistence under less suitable climatic conditions. In contrast, old saplings experienced this strong decline only in open habitats, while this effect was weaker beneath closed canopies, suggesting that canopy cover partially buffered them against climatic stress (Margalef-Marrase et al., 2025; Pérez Navarro et al., 2024). In climatically optimal sites, such buffering is expected to be less critical, as recruits generally experience favourable temperatures and lower water stress, allowing both young and old saplings to establish across closed and open habitats. However, toward harsher conditions near the niche edge, canopy cover would provide a degree of protection that enabled some persistence of old saplings. The deeper rooting of these saplings likely enhanced their persistence during drought stress, allowing them to take more benefit from canopy-moderated microclimates than younger saplings. Overall, this canopy-driven facilitation may delay local extinction for old saplings, creating extinction lags in regeneration trajectories (Alexander et al., 2018).

Nevertheless, defoliated habitats consistently failed to sustain regeneration across the species' climatic niche gradient. Over time, defoliation-induced regeneration failure could drive long-term ecosystem shifts (Bowd et al., 2023) across the climatic gradients in which *P. sylvestris* lives, gradually transforming forested areas into locally open woodlands or shrublands (Batllori et al., 2020; Lloret and Batllori, 2021).

3.4.3. Interaction between climatic niche variability and canopy cover

The negative consequences of interannual climate fluctuations (i.e., variability relative to the core distance) on *P. sylvestris* recruitment were more evident in open habitats, where increased irradiance combined with limited water availability may have contributed to young sapling decline during very dry or warm years. Such fluctuations were likely associated with unusually dry or warm years before and after the drought-driven die-off event (Appendix B, Figure B1). In contrast, closed canopies likely buffered young saplings during these years of high climatic fluctuation, helping to maintain their abundance (i.e., a non-significant decline compared to defoliated habitat;

Figure 3.6B; Table 3.1). Thus, temporal maintenance in climatic conditions appears relevant for recruitment success alongside historical climatic suitability.

Finally, the increase in young sapling density in die-off plots only became evident almost a decade after the drought (Figure 3.5A) and may reflect a recent shift from harsher to milder local climate conditions - particularly in terms of precipitation - in some sites (Appendix B, Figure B1). This is supported by the observed shift in the climatic niche position of certain *P. sylvestris* populations, which have transitioned from previously marginal locations into more climatically suitable conditions (Figure 3.2B; Appendix B, Figure B4). In addition, the accumulation of deadwood in die-off plots may enhanced microsite conditions for young saplings, gradually assisting the transition of seedlings into the young sapling stage (Thom et al., 2023). Thus, regeneration success appears to be shaped by both site-level disturbance legacies and broader meso-climatic trends (Batllori et al., 2020; Jackson et al., 2009; Pérez Navarro et al., 2024, 2021). Nonetheless, more fine-scale information is needed to explain this phenomenon more precisely.

3.5. Conclusion and management implications

Our findings show that *P. sylvestris* regeneration success following drought-induced die-off is shaped by canopy structure and the position of populations in the species' climate niche, with differences across recruitment development stages. Die-off reduced both young and old saplings in closed habitats, likely influenced by species turnover toward more drought-tolerant accompanying taxa. Regeneration consistently failed in defoliated habitats, regardless of climatic suitability or recruits' development stages. Open habitats in die-off plots promoted seedling emergence and progression to later sapling stages. In this habitat, higher sapling abundance appeared in sites near to species' climatic optimum. However, in climatically marginal sites, open conditions became limiting, and regeneration was restricted to only old saplings persisting under closed canopy refugia.

These results highlight the importance of maintaining canopy structural heterogeneity to support regeneration across varying climate contexts. Management strategies such as continuous cover silviculture are well-suited to promote this structural diversity (Gonçalves, 2023), particularly by conserving closed canopy refugia in marginal climatic sites to buffer extreme climatic stress, while maintaining open conditions in

optimal sites to promote seedling establishment and their progression to saplings. Deadwood retention likely acted as a key structural component, along with favourable climatic fluctuations, that gradually enhanced microsite conditions for young sapling survival. Accordingly, we found higher seedling densities in die-off plots near the species' climatic optimum and noted an increase in young sapling densities nearly a decade after the drought and subsequent die-off event. Thus, to support natural regeneration and the long-term resilience of *P. sylvestris* stands under climate stress, we recommend adaptive forest management following drought-induced die-off events. This should incorporate canopy structure management and deadwood retention, while explicitly considering the species' climate niche.

Chapter 4: Habitat Response

**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.

Keywords: Biodiversity; climate warming; deadwood decay; dendrohabitat; forest heterogeneity; tree mortality.

4.1. 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., 2014), often together with heatwaves, has prompted concerns about the vulnerability of forest ecosystems to potential shifts on species composition and structure, and even collapse (Lloret and Batllori, 2021), particularly in temperate and Mediterranean areas (Margalef-Marrase et al., 2023; Samaniego et al., 2018). 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 and Seidl, 2016), provided that disturbances are not too frequent (i.e., “intermediate disturbance hypothesis” in Connell, 1978; also see 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 (LIFE RedBosques, 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 (Asbeck et al., 2021; Großmann et al., 2018; Paillet et al., 2019,

2017). In turn, these TreMs have been observed to be closely related with the diversity of birds, bats, and invertebrates (Basile et al., 2020; Paillet et al., 2018). 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; Bouget et al., 2024; Sallé et al., 2020; Thom and Seidl, 2016). 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 (Batllori et al., 2020; García-Valdés et al., 2021; Lloret et al., 2012). 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 and Gonin, 2008; but see 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 (Hararuk et al., 2020; Přívětivý et al., 2016), 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.

4.2. Methods

4.2.1. Study area and sampling design

We surveyed twenty different forest sites in 2022 across Catalonia (NE Spain; Appendix C, Figure C1; Appendix C, Table C1) 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 to 90.1 km) and elevation approximately ranged from 600 to 1650 m asl. (Appendix C, Table C1). 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 13.7°C (mean: ~10.5°C) while the range of annual precipitation does from 550 to 800 mm (mean: ~730 mm, Appendix C, Table C1).

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 (Appendix C, Figure C2; see 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 (Appendix C, Table C2).

4.2.2. *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 LIFE RedBosques (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 Appendix C, Table C3A; Figure C3 for further details. Similarly to LIFE RedBosques (2019) and Bouget et al. (2024), 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 Appendix C, Table C3B. All these categories were defined based on the survey in 2022.

Following Bouget et al. (2024), 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 Appendix C, Table C4; Appendix C, Figure C4). 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 (Appendix C, Table C5). Although lying deadwood can be considered an indicator of biodiversity in itself, similarly to Bouget et al. (2024), 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 reclassified TreMs into saproxylic and epixylic categories, where saproxylic refers to those TreMs that contain deadwood, whereas epixylic does not (details in Appendix C, Table C4, see also Bouget et al. (2024)). 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.

4.2.3. 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; Hararuk 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 $\times$ 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 (Appendix C, Figure C5) was performed between these climatic variables, and we eventually selected mean annual temperature (hereafter, temperature) and annual precipitation (hereafter, precipitation) for further statistical analyses.

4.2.4. 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 $\times$ temperature, and plot condition $\times$ 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 $\times$ 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 $\times$ basal area in 2013, plot condition $\times$ temperature, and plot condition $\times$ 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.

4.3. Results

4.3.1. Drought affection

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 (Figure 4.1A), but it was not influenced by temperature and precipitation across the studied gradient (Appendix C, Table C6). 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 (Appendix C, Table C7).

4.3.2. 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 (Figure 4.1A; Table 1; Appendix C, Table C8), with a positive effect of the basal area in 2013 on the three metrics. The interaction effect between plot condition (die-off vs control) and temperature (Appendix C, Table C8) 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 (Figure 4.2A-4.2C).

Table 4.1: 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 (NE Spain). Details are presented in Appendix C.

Predictors	Estimates		
	Deadwood abundance (as basal area)	Unbroken snag proportion	Broken snag proportion
Die-off	22.55 ***	-0.28 **	0.38 ***
Basal area in 2013	4.63 ***		
Temperature	1.93		
Precipitation		0.16 *	-0.14 *
Die-off : Temperature	-5.01 *		
Die-off : Precipitation		-0.15	0.14
* $p < 0.05$ ** $p < 0.01$ *** $p < 0.0$			

Table 4.1: Continued

Predictors	Estimates			
	Hard log proportion	Soft log proportion	Deadwood richness	Deadwood diversity
Die-off	-0.12	0.17 *	1.64 **	0.26 *
Basal area in 2013				
Temperature			-1.23 ***	-0.32 **
Precipitation	-0.16 *	0.19 **	-0.97 *	-0.25 *
Die-off : Temperature				
Die-off : Precipitation	0.21 *	-0.23 **	1.36 *	0.20
* $p < 0.05$ ** $p < 0.01$ *** $p < 0.0$				

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 (Appendix C, Table C9). 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 4.1; Appendix C, C10). 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 4.1; Appendix C, C10). 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 4.1; Appendix C, Table C10). 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 increased (Figure 4.3A). The reverse situation was observed for soft logs (i.e., a decrease in die-off plots in wettest sites) (Figure 4.3B).

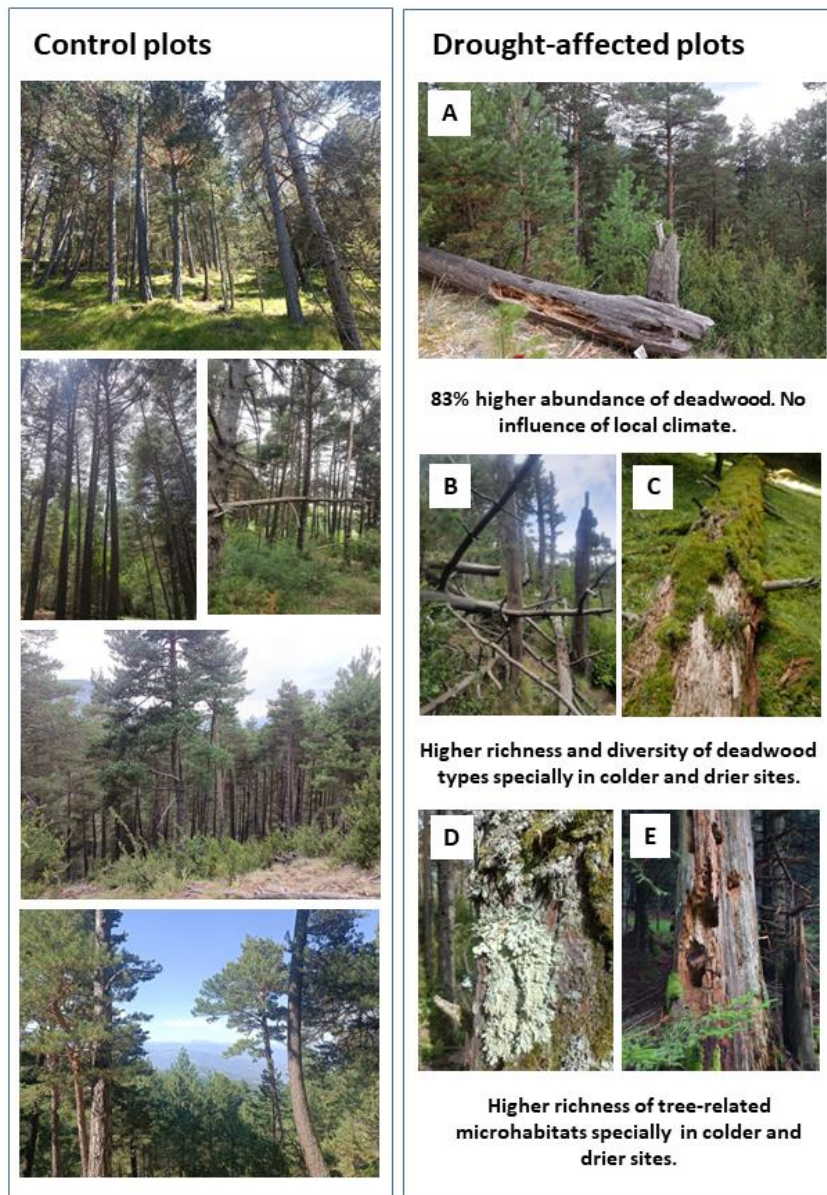


Figure 4.1: Infography depicting a general view and the main differences between control and drought-affected die-off plots dominated by Scots Pine (*Pinus sylvestris*) regarding the presence of deadwood and Tree-related Microhabitat (TreM). The left panel shows some general views of Scots pine forests 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 interaction with local climate (i.e. precipitation and temperature).

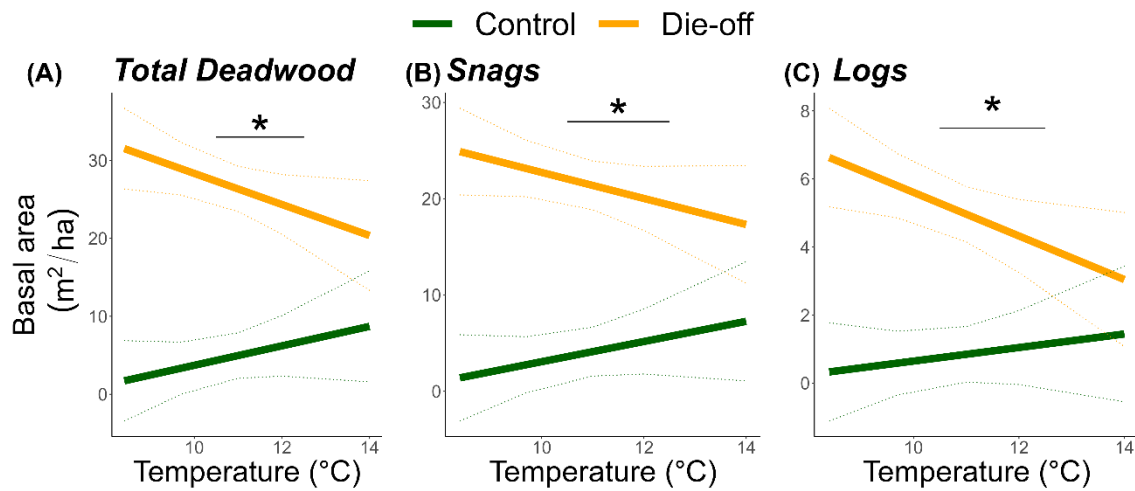


Figure 4.2: Interaction effect of forest condition (die-off vs control plots) and local mean temperature on (A) total deadwood basal area in 2022, (B) snags basal area in 2022, and (C) logs basal area in 2022. Asterisk signs indicate the significance level of p-values (* : $p < 0.05$, ** : $p < 0.01$, *** $p < 0.001$). The envelopes around effect lines denote 95% confidence interval.

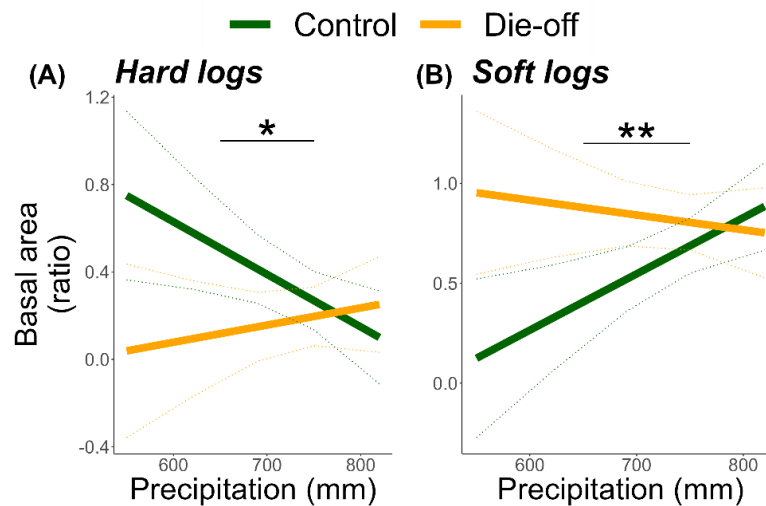


Figure 4.3: Interaction effect of forest condition (die-off vs control plots) and local mean precipitation on the proportion of (A) hard logs or (B) soft logs over the total amount of deadwood (basal area ratio). The meaning of asterisk signs and envelopes around effect lines are given at Figure 4.2.

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 (Figure 4.1B-4.1C; Table 4.1), while there was no significant difference observed in evenness (Appendix C, Table C11). Regarding climatic conditions, both temperature and precipitation had a negative effect on the diversity and evenness of deadwood types (Table 4.1; Appendix C, Table C11), 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 (Appendix C, Figure C6).

4.3.3. 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 (Figure 4.1D, E; Table 4.2; Appendix C, Table C12, C13). The abundance of total and saproxylic TreM was positively influenced by the basal area in 2013 (Table 4.2; Appendix C, Table C12, S13) while several significant interactions existed with climatic conditions (Table 4.2; Appendix C, Table C12, 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 (Figure 4.4A-4.4D). In turn, the interaction effects between plot condition and temperature pointed out to a higher increase in TreM with temperature in die-off plots (Figure 4.5A). 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 (Appendix C, Figure C7). 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 4.2; Appendix C, Table C14). Besides, we did not observe any effects of climate factors on epixylic TreM (Table 4.2; Appendix C, C14).

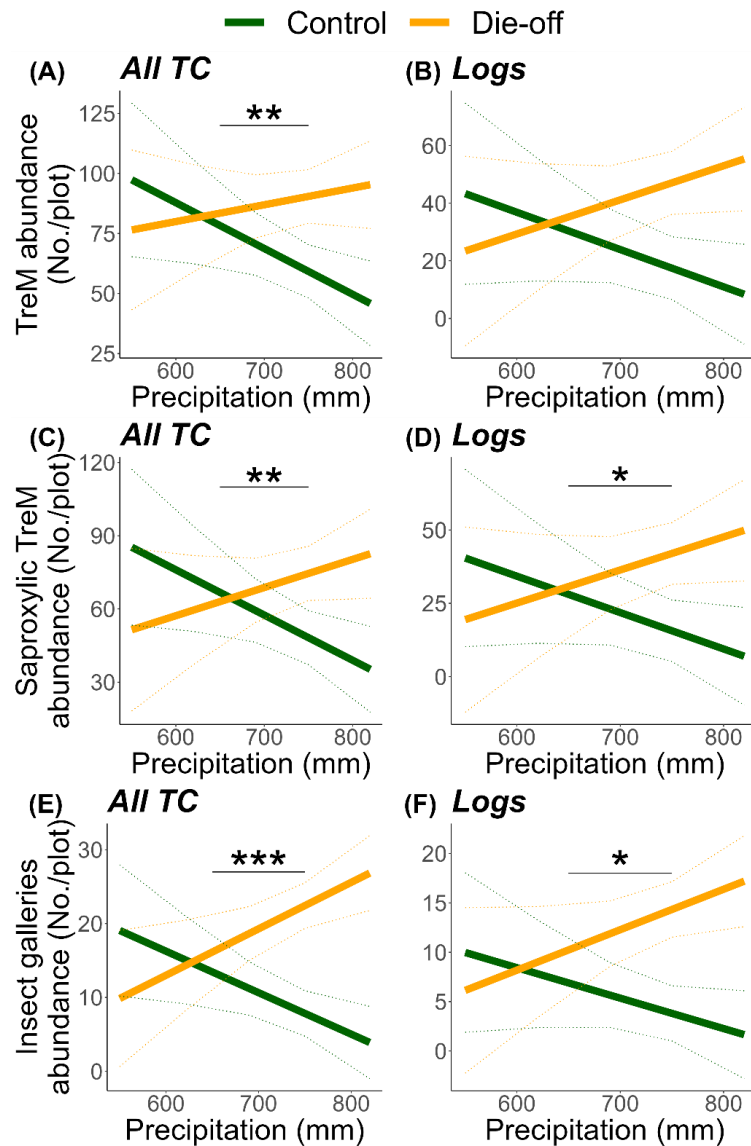


Figure 4.4: Interaction effect of forest condition (die-off vs control plots) and local mean precipitation on the abundance (number per plot) of TreM in (A) all tree conditions (TC) and (B) logs, saproxylic TreM abundance in (C) all TC and (D) logs, and insect galleries in (E) all TC and (F) logs. The meaning of asterisk signs and envelopes around effect lines are given at Figure 4.2.

Table 4.2: 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 (NE Spain) in all Tree

Condition (TC), alive tree, snag, and log. Details co-efficient tables are presented in Appendix C.

TreM parameter	Predictors	Estimates			
		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 galleries (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 :			-2.68	
	Temperature				
	Die-off :	7.84	0.78		4.73 **
	Precipitation	***			
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 :	-2.57		-1.44 *	
	Temperature	**			
* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$					

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 (Figure 4.1D, 4.1E; Table 4.2; Appendix C,

C15, C16). 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 4.2; Appendix C, Table C15, C16). Furthermore, increasing temperature and precipitation had a negative effect on both TreM richness and diversity in snags (Table 4.2; Appendix C, Table C15, C16). We only found higher TreM evenness in alive trees in die-off plots than in controls (Appendix C, Table C17).

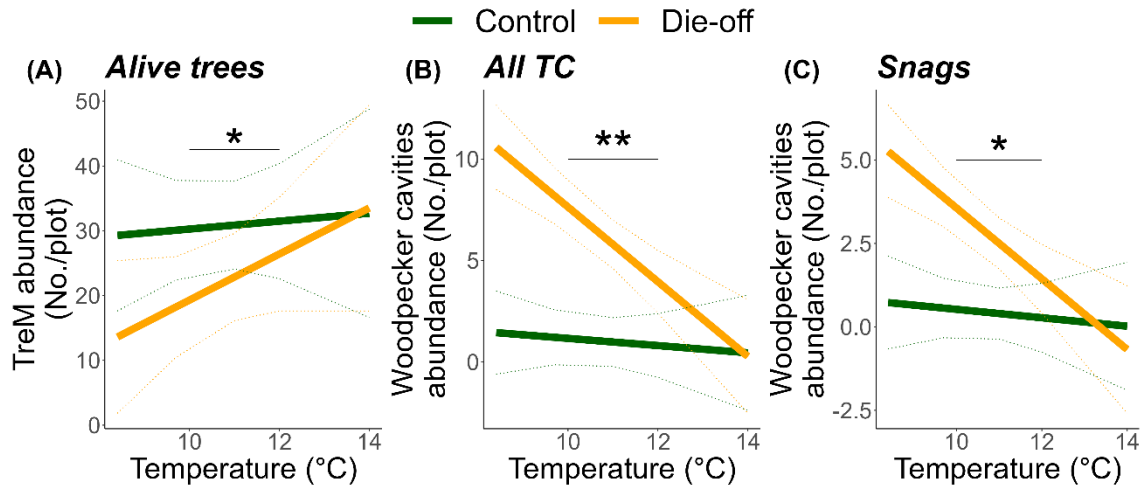


Figure 4.5: Interaction effect of forest condition (die-off vs control plots) and local mean temperature on the abundance (number per plot) of TreM in (A) alive trees and abundance of woodpecker cavities in (C) all tree conditions (TC) and (D) snags. The meaning of asterisk signs and envelopes around effect lines are given at Figure 4.2.

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 (Appendix C, Table C18, C19). Like TreM abundance, the 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 (Figure 4.4E, 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 (Figure 4.5B, 4.5C). 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 (Appendix C, Figure C8).

4.4. 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 (Chagnon et al., 2022; Hararuk et al., 2020).

4.4.1. *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. (2024), 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 (Gough et al., 2022; Turner, 2010). Such heterogeneity could potentially enhance habitat provisioning for biodiversity through different deadwood types and TreMs (Basile et al., 2020; Paillet et al., 2018; 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., 2024).

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.

4.4.2. 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). 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., 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 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.

4.5. 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.

Chapter 5: General Discussion

Drought die-off driven forest reorganization enhances biodiversity potential



5.1. From die-off to forest reorganization

In Chapter 1, we introduce how global climate change is altering disturbance dynamics in forest ecosystems, specifically focusing on drought-induced die-off events at the southernmost xeric limits of *Pinus sylvestris* L. populations. The chapter also highlights the uncertainty surrounding how those ecosystems respond to die-offs, primarily focusing on the knowledge gaps in post-die-off composition, demographic processes, and habitat (e.g., deadwood and Tree-related Microhabitats or TreMs) responses.

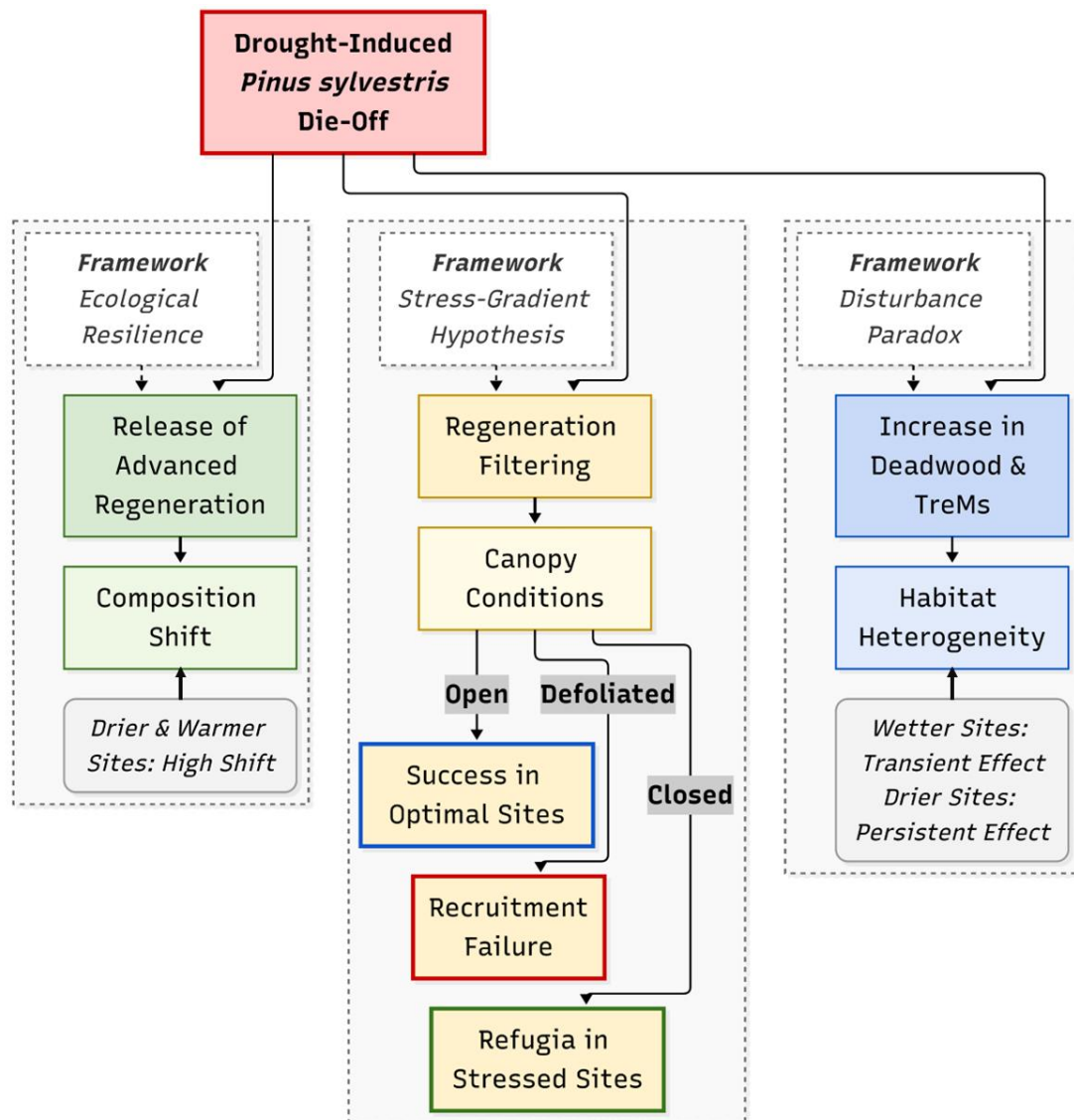


Figure 5.1: Responses of three ecosystem components following drought-induced die-off in *P. sylvestris* forests: (i) compositional shifts driven by advanced regeneration (Chapter 2), (i) regeneration filtering of dominant *P. sylvestris* recruits (Chapter 3), and

(iii) increase of habitat heterogeneity through deadwood and Tree-related Microhabitats (TreMs; Chapter 4).

Accordingly, we identified that die-off is not an endpoint of forest degradation but an active catalyst that drive changes in three ecosystem components (Figure 5.1), i.e., (i) promote species composition shift (Chapter 2, see Chowdhury et al., 2025), (ii) direct regeneration filtering (Chapter 3, see Chowdhury et al., 2026), and (iii) increase habitat heterogeneity (Chapter 4, see Chowdhury et al., 2024), resulting in overall process of forest reorganization.

5.2. Compositional response: resilience through species replacement

A major concern regarding drought-induced forest die-off is its potential for ecosystem collapse, a scenario where the mortality of a dominant species (e.g., *P. sylvestris*) forces a transition into alternative states like shrublands or open woodlands (Batllori et al., 2020; Lloret and Batllori, 2021). However, we found that the drought die-off event in the *P. sylvestris* forests of Catalonia ultimately promotes a compositional reorganization driven by enhanced tree diversity with broadleaf species (Figure 5.1, 5.2; Chapter 2).

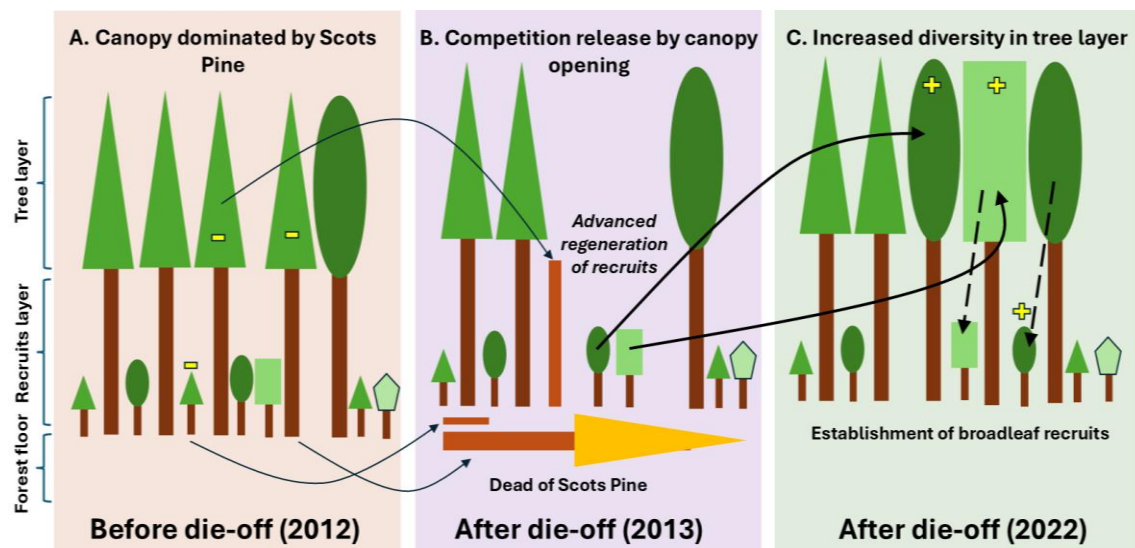


Figure 5.2: Conceptual diagram of species composition shift through the *Pinus sylvestris* replacement, showing the release of advanced regeneration (Chapter 2). (A) Pre-die-off forest where *P. sylvestris* suppresses understory broadleaves recruits. (B) Drought-induced mortality promotes canopy opening. (C) Broadleaves recruits reach the canopy layer, where established broadleaves provide propagules for new recruitments.

5.2.1. From *P. sylvestris* dominance to mixed forests

The mortality of the overstory *P. sylvestris* caused a competitive release, removing the suppression of light and water resources (Gazol et al., 2018b), allowing the ascent of drought-tolerant broadleaf species that were previously suppressed in the understory as advanced regeneration (Figure 5.1, 5.2), ultimately increasing species diversity in the tree layer of the affected forests (Chapter 2). In this way, the affected forest stands do not revert to their pre-die-off canopy cover with *P. sylvestris* dominance. While this implies of failure of resilience (*sensu* Holling, 1996; also see Lloret et al., 2024, 2012), in terms of species composition, the expected trajectory of replacement by broadleaf could allow the resilience of forest cover in the mid- to long-term (Holling, 1973; Walker et al., 2004).

Specifically, Mediterranean broadleaves such as *Quercus ilex*, *Quercus humilis*, *Acer monspessulanum*, and *Sorbus aria* benefited from a priority effect (Fukami, 2015). As these saplings were already established, they could pre-emptively monopolize the newly available resources (Chang and HilleRisLambers, 2016; Fukami, 2015), outcompeting new *P. sylvestris* seedlings or other colonizing trees. This functional turnover, i.e., from Gymnosperm-dominated forest stands to Angiosperm-dominated mixed ones equipped with diverse hydraulic strategies (e.g., resprouting capacity and higher water use efficiency; Niinemets and Valladares, 2006; Zeppel et al., 2015), thereby potentially enhances the ecosystem's resilience to future climatic stresses (Martínez-Vilalta and Lloret, 2016).

This compositional reorganization is specifically regulated by the local climatic gradient, as the replacement of *P. sylvestris* by broadleaves is most pronounced at the warmer and drier edge of the distribution (Figure 5.2; Chapter 2). Here, climatic pressure likely exceeds the physiological tolerance of *P. sylvestris* (Bose et al., 2024; Dorado-Liñán et al., 2019), preventing self-replacement, transitioning affected stand into mixed *P. sylvestris*-broadleaves forests (Batllori et al., 2020; Galiano et al., 2010). Conversely, at the colder and wetter edge, where precipitation remains sufficient after the drought episode, self-replacement of *P. sylvestris* maintains lower stand diversity and preserves *P. sylvestris* dominance (Bose et al., 2024; Chowdhury et al., 2026).

5.2.2. *Larger broadleaf recruits nourish successional trajectory*

Indeed, post-disturbance recruitment dynamics drives the tree species composition shift in affected forest (Chapter 2; also see Martínez-Vilalta and Lloret, 2016). The critical question, however, is whether this post-disturbance composition represents a transient effect or will result in a species-rich successional trajectory, likely to be sustained along time. The response of the post-die-off recruitment layer provides evidence for the latter, as die-off affected forests exhibited higher richness and evenness of larger recruits (T3 saplings; see Methods in Chapter 2) compared to unaffected forests (Table 2.2).

Crucially, the post-die-off succession appears to have restored (or maintained) the compositional coupling between canopy tree and understory tree recruits (i.e., 29% higher Sørensen similarity index in die-off plots compared to controls; see Figure 2.5). Unlike the pre-die-off stands, where the canopy (*P. sylvestris*-dominated) and understory (mixed *P. sylvestris*-broadleaves) were mismatched, following the die-off event these layers have become similar in terms of tree species identity. Previous co-dominant trees are now reproducing and recruiting successfully, making the system capable of recovery with broadleaves (Lloret et al., 2012; Martínez-Vilalta and Lloret, 2016; see also Chapter 2). Thus, larger recruits (T3 stage) secure the future trajectory of this compositional shift (Holling, 1973; Lloret et al., 2012). The water-use traits of some of these broadleaf species (such as *Quercus ilex*) grant them a distinct advantage over *P. sylvestris* in water-limited environments (Niinemets and Valladares, 2006; Zeppel et al., 2015), while the well-developed root systems of advanced regeneration ensure higher survival rates compared to smaller recruits (T1 and T2 stages; see Methods in Chapter 2).

The shrub community also respond to this successional process (Chapter 2), with higher shrub richness and diversity at the drier edge of the climatic gradient (Figure 2.4), where these water-limited sites may favour shrub dominance (Batllori et al., 2020). If established, these dense shrub layers can exert an inhibitory effect, trapping tree recruits and arresting succession (Holmgren et al., 1997; Maestre et al., 2005). Indeed, if the drought-tolerant broadleaf species at the advanced regeneration stage were absent under pre-die-off conditions, this inhibitory mechanism might have triggered a collapse of the tree-dominated forest into a shrub-dominated state (Batllori et al., 2020; Koderó et al., 2024), likely pushing the stands toward a critical tipping point (Martínez-Vilalta and Lloret, 2016; Scheffer et al., 2001). However, broadleaf community's recruitment

dynamics (i.e., growth of advanced regeneration and the subsequent establishment of larger saplings; Figure 5.2) safeguarded the tree-dominance forest structure, averting this collapse and ensuring that the system retains its forest structure rather than degrading into shrubland.

5.3. Demographic response: canopy cover and climate-filtered regeneration

As die-off-affected stands undergo reorganization of species composition, the self-replacement capacity of *P. sylvestris* is restricted by recruits' developmental stages (seedling, young and old saplings; Chapter 3), particularly when considering the interaction between post-die-off canopy cover conditions and the population's position within the species' climatic niche (Figure 5.1, 5.3).

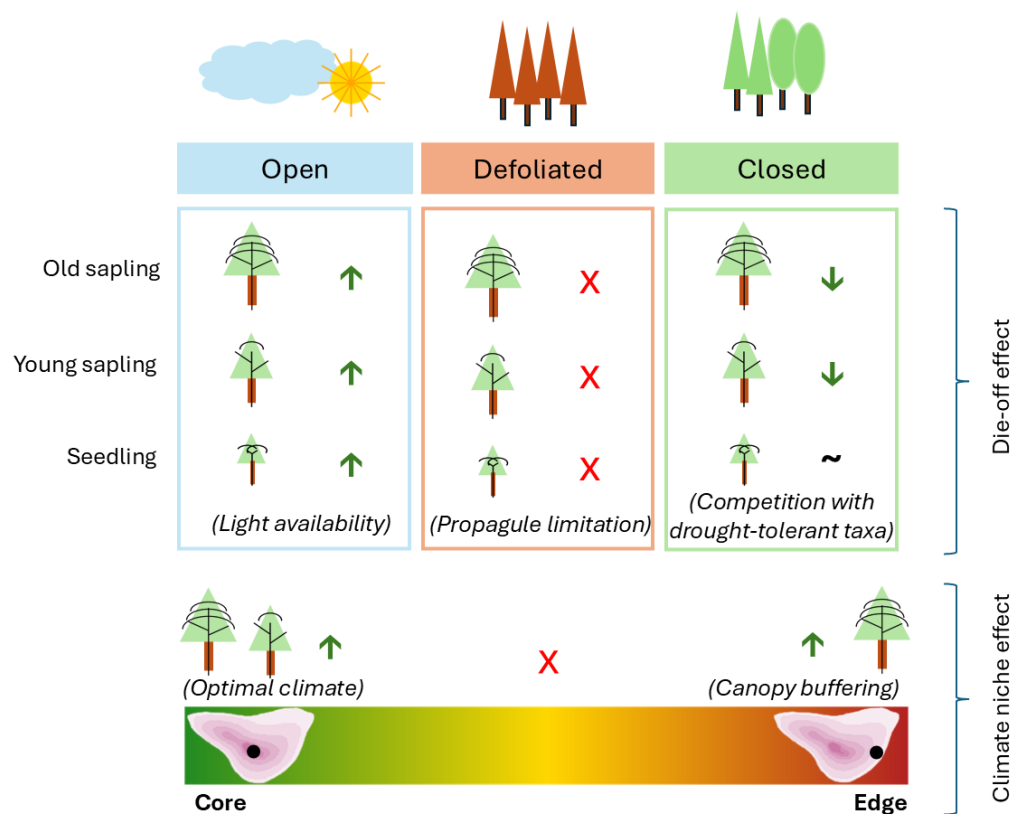


Figure 5.3: The interaction between canopy cover condition (closed canopy, defoliated canopy, and open gaps) and the climatic gradient (core vs. edge) in determining *P. sylvestris* recruitment success (Chapter 3). Top panel showing how die-off affects regeneration across recruits' development stages (seedling, young and old sapling) under each canopy condition. Bottom panel showing stage-dependent recruitment outcomes and how it shifted from competition-driven to facilitation-driven along the climatic niche gradient in line with Stress-Gradient Hypothesis. Upward and downward

arrow indicate the increase and decline, respectively. Meanwhile, the red X and curly dash denote regeneration failure and no effect, respectively (figure adopted from the graphical abstract of Chowdhury et al., 2026).

5.3.1. Canopy-induced barriers to recruitment

The primary demographic constraint in *P. sylvestris* regeneration is the consistent failure of recruitment beneath defoliated trees, even in climatically suitable sites (Figure 5.3). The surviving but severely damaged trees likely allocate resources toward survival rather than reproductive effort, leading to propagule limitation (Adams et al., 2017; Gazol et al., 2018a). Besides, recruitment is also governed by shifting competition dynamics that respond differently between open and closed canopy conditions (Figure 5.3). In open habitats, increased irradiance allows the re-colonization of shade-intolerant *P. sylvestris* (Carlisle and Brown, 1968; Gazol et al., 2018a), resulting in higher seedling and sapling densities compared to unaffected controls. Conversely, sapling density declines beneath closed canopies in affected stands, as the drought triggers concurrent mortality among recruits and adults, while broadleaf species intensify interspecific competition for light and water (see Section 5.2), reducing *P. sylvestris* self-replacement potential.

5.3.2. Climatic and competitive constraints to canopy facilitation

The interaction between forest canopy cover and the species' climatic niche governs *P. sylvestris* regeneration, providing support to the Stress-Gradient Hypothesis (SGH; Figure 5.3), which posits a shift from competition to facilitation as environmental stress increases (Maestre et al., 2009). In climatically optimum sites (near the niche core), our findings indicate a diminished reliance on facilitation (De Frenne et al., 2019; Grubb, 1977; Pérez Navarro et al., 2024). So, near the niche core, where abiotic stress is negligible, the regeneration niche of *P. sylvestris* is structurally broad, allowing the species to maintain statistically similar sapling densities across the heterogeneous mosaic of canopy conditions, specifically in open gaps and beneath closed canopies (De Frenne et al., 2019; Finocchiaro et al., 2023; Grubb, 1977; Lembrechts et al., 2015).

However, as sites transition toward the edge of the climatic niche, abiotic stress becomes the dominant environmental filter, modifying these interactions. In these marginal sites, open gaps become inhospitable due to radiation and soil desiccation that exceed physiological tolerances of recruits, leading to a decline in sapling densities

(Elvira et al., 2021). Instead, canopy-mediated facilitation becomes a critical driver of persistence, particularly for old saplings with developed root systems, which survive in closed habitats whereas they disappear in open gaps (Margalef-Marrase et al., 2025; Pérez Navarro et al., 2024). By buffering microclimatic extremes, the closed canopy expands the realized regeneration niche of *P. sylvestris* under suboptimum conditions (Grubb, 1977), providing refuge that extends the species' survival boundary beyond the limits imposed in open environments.

Furthermore, while the disturbance-induced resource release successfully enhances early recruitment near the niche core, deadwood facilitation and milder conditions probably allow a rise in young sapling density almost a decade later (Figure 3.5; also see Chowdhury et al., 2024). However, any long-term recruitment success of *P. sylvestris* would likely be suppressed by the priority effects of broadleaf recruits (Section 5.2). Specifically, *Quercus spp.* and other broadleaves pre-emptively occupy the understory, thereby they monopolize die-off affected stands by utilizing light and soil resources before the new *P. sylvestris* cohort can establish (Fukami, 2015; see section 5.2). This prevents self-replacement, leading the ecosystem into a directional successional trajectory toward a mixed forest in which *P. sylvestris* assumes a subordinate successional role.

5.4. Habitat response: deadwood-driven heterogeneity

Apart from the compositional shift and regeneration filtering (see sections 5.2 and 5.3, respectively), the deadwood dynamics following a drought-induced die-off also enhance habitat heterogeneity (Figure 5.1, 5.4). The accumulation and decay of deadwood and diversity of Tree-related Microhabitat (TreM) provide compensatory habitat in die-off-affected forests. This enhances the biodiversity potential during the transitional phase when the living canopy remains fragmented, supporting the disturbance paradox concept (Thom and Seidl, 2016; Figure 5.1, 5.4).

5.4.1. Habitat enrichment by deadwood and TreM

After ten years following the die-off event, the increased deadwood abundance and higher richness and diversity of deadwood types alters forest structure and promotes structural complexity in the affected stands (Table 4.1; Harmon et al., 2004, 1986). This deadwood legacy also hosts higher abundances of functionally distinct Tree-related Microhabitats (TreMs; Table 4.2), ranging from saproxylic types (e.g., rot holes, insect

galleries) to epixylic features (e.g., mosses). Together, the various deadwood decaying stages and TreMs (both wood- and surface-dependent) potentially support multitaxon diversity (Asbeck et al., 2021; Seibold et al., 2015), including xylophagous insects, cavity-nesting vertebrates, birds and epiphytic fungi and bryophytes (Basile et al., 2020; Paillet et al., 2018).

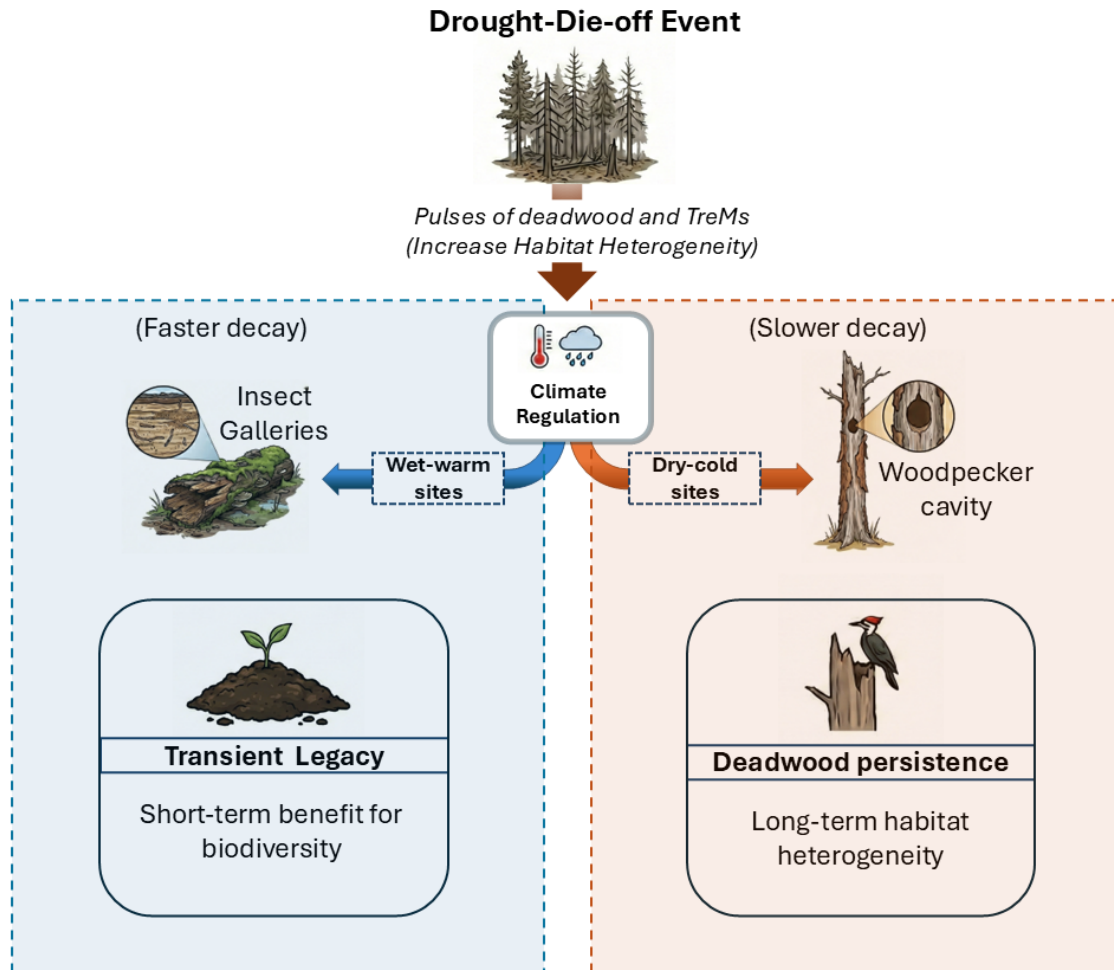


Figure 5.4: Conceptual diagram showing how drought-induced die-off generates habitat heterogeneity through the accumulation of deadwood and Tree-related Microhabitats (TreMs; Chapter 4) and how their temporal dynamics is regulated by local climatic conditions. Transient legacy (left path, blue zone): In wetter or warmer sites, moisture availability accelerates decomposition, potentially leading to a temporary increase of biodiversity. Persistent legacy (right path, red zone): In drier or colder sites, climatic constraints (aridity or low temperature) limit biological decomposition, resulting in long-term persistence of deadwood, which maintains habitat provision for a longer period.

Furthermore, the specific distribution of TreMs across different deadwood decaying stages indicates a distinct shift in ecosystem structure and habitat utilization. For instance, saproxylic activity (e.g., insect galleries) is particularly abundant in logs, while vertebrate features (e.g., woodpecker cavities) proliferate in standing snags (Figure 4.4, 4.5). In this way, the die-off event re-routes the ecosystem's energy flow toward saproxylic communities and saprotrophic pathways that depend on specific deadwood positions and decay stages (Bouget et al., 2024). Accordingly, this transitions the forest's habitat provisioning from living trees to the deadwood compartment that create new breeding sites and provide refuges to multitaxon organisms (Stokland et al., 2012). This living, dying, and dead components configuration ultimately expands available ecological niches, thereby increasing the overall biodiversity potential of the forest (Asbeck et al., 2021; Basile et al., 2020; Seibold et al., 2015; Stokland et al., 2012).

5.4.2. Climate-mediated trade-offs in habitat quality and persistence

Functional quality and longevity of deadwood were strongly modulated by local climatic conditions, determining how long this structural legacy persisted in the system, likely driven by differences in deadwood decomposition rates (Figure 5.4; Chapter 4). High moisture availability in wetter sites promotes higher richness of deadwood types and TreM abundance (e.g., saproxylic features and insect galleries), reflecting rapid colonization by decomposer communities following the deadwood-induced pulse of resources (Bouget et al., 2024; Bouget and Cours, 2025; Chagnon et al., 2022; Oettel et al., 2023). However, this high-quality habitat is likely transient, as the same rapid decaying process in these mesic environments makes these structural legacies relatively short-lived, providing only temporary support for elevated biodiversity (Bouget et al., 2024; Stokland et al., 2012).

At the same time, higher temperatures accelerate decomposer activity, resulting in lower deadwood abundance in warmer sites (Chagnon et al., 2022; Stokland et al., 2012). This rapid decay directly limits the abundance of woodpecker cavity in warmer die-off affected sites (Figure 4.5), for example, as deadwood decomposes too quickly to maintain the density and structural integrity required for excavation (Jackson and Jackson, 2004; Oettel et al., 2023). It is also possible that any transient structural benefits in these warmer sites was too short to be detected by our survey.

Conversely, at the drier and colder edges of the climatic gradient, decomposition is slower due to moisture and temperature limitations (Chagnon et al., 2022; Hararuk et al., 2020). As a result, these sites maintain a higher overall deadwood abundance (particularly logs; see Figure 4.2, 4.3) because climatic constraints limit decomposer activity and allow the deadwood to persist for longer periods without mineralizing (Stokland et al., 2012). This persistent structural refuge provides critical shelter for deadwood-dependent organisms and contributes to ecosystem functioning by maintaining physical cover and habitat provision over extended periods, thereby supporting high biodiversity potential under stressful climatic conditions (Bouget and Cours, 2025; Seibold et al., 2015).

5.5. Synthesis: The “successional accelerator” model

Overall, drought-induced die-off represents a climate-driven event that shapes the successional trajectory in affected forests. Specifically, the combination of species enrichment (Section 5.2), regeneration filtering (Section 5.3), and deadwood substrate dynamics (Section 5.4) speed up the succession and reorganize the die-off affected forests compared to unaffected ones. We therefore conceptualize this drought-driven mortality pulse as a “successional accelerator”. This acceleration represents a significant divergence from the slow, gradual background mortality and gap-phase replacement that typically would characterize forest dynamics under incremental climate change (Allen et al., 2010; Batllori et al., 2020; McDowell et al., 2008; Van Mantgem et al., 2009). The die-off event triggers the transition from a climate-sensitive *P. sylvestris*-dominated stand to a climate-change resilient broadleaf forest that capable of supporting multitaxon diversity by driving three distinct ecological responses.

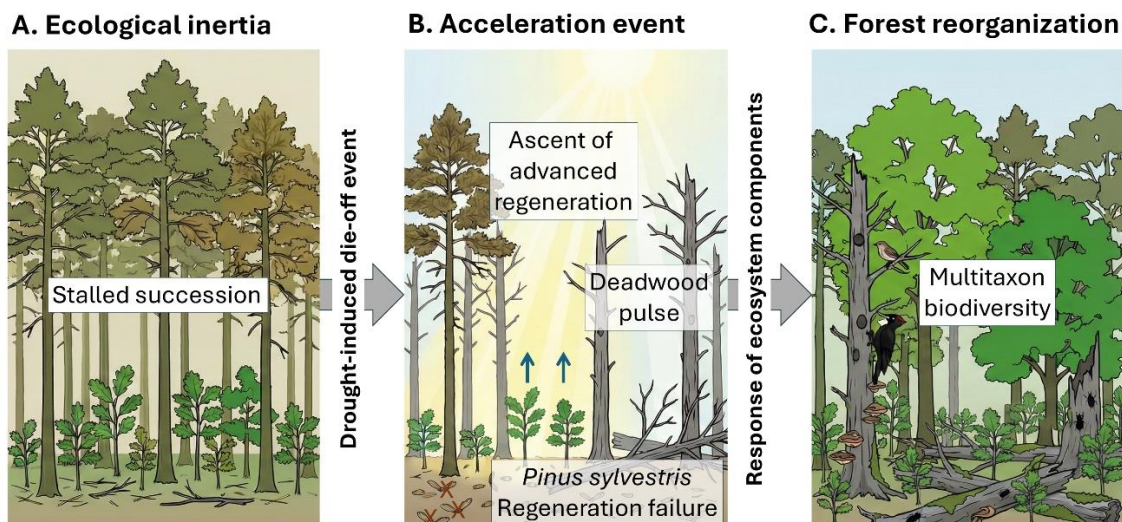


Figure 5.5: The “successional accelerator” model illustrating its three-stage transition. (A) Community inertia: Prior to the die-off, the forest is occupied by stressed *P. sylvestris* canopy that suppresses drought-tolerant broadleaf in advanced regeneration, stalling the succession process. (B) Acceleration event: Drought-induced die-off breaks this inertia through responses of three ecosystem components: (i) the ascent of advanced regeneration following the mortality of climate-sensitive *P. sylvestris* (compositional response); (ii) regeneration filtering that drives *P. sylvestris* recruitment failure (demographic response); and (iii) tree mortality that increase deadwood and TreM (habitat response). (C) Forest reorganization: The response of these ecosystem components drives a shift toward a resilient, mixed *P. sylvestris*-broadleaf forest that enhance diversity of broadleaf recruits, while the persistent deadwood legacy provides enriched habitat that potentially support multitaxon biodiversity.

Firstly, the die-off breaks community inertia (Lloret et al., 2012; Martínez-Vilalta and Lloret, 2016), thus driving the compositional shift. Prior to the disturbance, a physiologically stressed *P. sylvestris* canopy maintained its dominance despite a progressively less favourable climate, keeping the forest ecologically stalled (Holmgren et al., 1997; Lloret and Batllori, 2021; Martínez-Vilalta and Piñol, 2002). The die-off pulse breaks this inertia by removing climate-sensitive *P. sylvestris* adults (Bose et al., 2024; Hereş et al., 2012; Martínez-Vilalta and Piñol, 2002) and simultaneously releasing previously suppressed, drought-tolerant broadleaf recruits, redirecting successional trajectories toward a more resilient mixed canopy and understorey recruits (Section 5.2). Secondly, the post-die-off local climate imposes an environmental filter that triggers the regeneration failure of *P. sylvestris* (Gazol et al., 2018a; Martínez-Vilalta and Lloret, 2016; see Section 5.3). This filter prevents *P. sylvestris* regeneration across open gaps in marginal sites, under defoliated trees, and beneath closed canopies, restricting the affected forests from reverting to their prior climate-vulnerable state (Section 5.2). Finally, the mortality pulse increases habitat provisioning through a pronounced deadwood legacy and functionally distinct TreMs. This maintains a crucial habitat structure for enhancing multitaxon biodiversity throughout the compositional changes (Section 5.4). Ultimately, this forest reorganization process combines elevated woody plant diversity and enhanced recruits diversity with the enrichment of deadwood legacies, increasing niche availability for different organisms and transforming

structurally simplified stands into complex natural systems that exhibit characteristics of unmanaged old-growth forests (Asbeck et al., 2021, 2019).

However, the persistence and ecological significance of this increased biodiversity potential are strongly modulated by the local climate. In mesic (colder-wetter) sites, where the climate remains favourable, the “successional accelerator” is suppressed, as *P. sylvestris* retains its self-replacement capacity (Section 5.3; also see Bose et al., 2024) and rapid deadwood decomposition constrains the long-term availability of structural habitat (Section 5.3; also see Bouget et al., 2024; Paillet et al., 2019). Conversely, in climatically marginal, drier sites, where *P. sylvestris* regeneration mostly fails (but see Section 5.4.2 about the canopy facilitation for old *P. sylvestris* saplings at suboptimal sites), the canopy composition shifts toward broadleaves and the deadwood legacy persists for the longer period (Section 5.2, 5.3, 5.4; also see Batllori et al., 2020; Hararuk et al., 2020; Seibold et al., 2015). This retained structure provides a critical, long-lasting buffer that maintains habitat heterogeneity while the dominant canopy species are being replaced. So, contrary to expectations of ecosystem collapse, dry-edge forests reorganize into structurally complex, multi-layered stands that likely support enriched biodiversity potential under increasingly arid conditions.

5.6. Limitations and directions for future research

While the “successional accelerator” model explains ecosystem responses that reorganize the die-off affected forests, its applicability is limited by some constraints, which also highlight opportunities for future research.

Compositionally, the proposed model requires pre-established advanced regeneration of drought-tolerant species. Without these saplings, affected stands would likely transition toward a shrub-dominated state (Section 5.2). Furthermore, the observed regeneration failure of *P. sylvestris* was focuses on the xeric edge of the species’ southernmost distribution limit (Section 5.3), which may not be universal across its broader climatic niche. Also, from a temporal perspective, the decadal scope of our study captures only mid-term forest reorganization, but it remains a relatively short time span on a broader successional scale (Chang and HilleRisLambers, 2016). Currently, we cannot definitively determine the fate of *P. sylvestris* saplings (e.g., those under canopy refugia) nor the mature state of the broadleaf community (Sections 5.2, 5.3). Therefore, long-term monitoring in these plots will confirm whether the broadleaf community

undergoes a resilient, mature mixed-forest, or will suffer further successional shifts over time.

Environmentally, our results were obtained across a relatively reduced, regional climatic gradient, introducing a degree of stochastic uncertainty. To overcome these limitations and test the “successional accelerator” model across wider climatic gradients, future research may use remote sensing technologies (e.g., LiDAR) with in situ microclimatic monitoring considering gap dynamics (De Frenne et al., 2019; Finocchiaro et al., 2023; Zellweger et al., 2019). Scaling up these methodologies across the broader distribution range of *P. sylvestris* will allow for precise modelling of canopy gap dynamics, microrefugia, and deadwood decay dynamics.

Methodologically, our inferences are subject to inherent limitations associated with unmeasured geographic factors, soil characteristics, and past forest management practices. Future studies may investigate the below-ground ecological dynamics associated with the transition from a gymnosperm-dominated to an angiosperm-enriched canopy and understory recruits. Analysing shifts in the soil microbiome (e.g., alterations in mycorrhizal fungal networks; see Gehring et al., 2014) and investigating fine-root competition for water resources will provide a holistic understanding of how functional traits drive post-die-off resilience. Also, estimating recruit densities of *P. sylvestris* here relied on proxy-based approaches (utilizing canopy cover and tree basal area; see Chapter 4), which cannot fully capture fine-scale microsite variability. Moreover, visual field estimations are inherently subject to observer error. These limitations imply a note of caution when interpreting the results.

Finally, care must be taken when inferring realized biodiversity from structural proxies, such as deadwood and TreMs. While these proxies are robust bio-indicators for habitat provisioning (Asbeck et al., 2021), the realized biodiversity in extreme dry-edge sites may remain constrained by the physiological limits of organisms (see Section 5.4). Severe thermal or aridity stress may restrict fauna from utilizing these structures despite the physical abundance of habitat. Consequently, future work must transition from assessing biodiversity potential to quantifying realized biodiversity by incorporating comprehensive multitaxon field or eDNA surveys. Empirical validation likely detects the colonization success of saproxylic insects, cavity-nesting vertebrates, and epiphytic communities at the climatic edge (Basile et al., 2020; Seibold et al., 2015). Furthermore, given the persistent deadwood at this xeric edge, investigation on the compounding

effects of subsequent disturbances, specifically wildfires are important. It is vital to evaluate whether a fire event in these newly reorganized, deadwood-rich stands would safeguard the broadleaf trajectory through resprouting mechanisms or push the system toward a tipping point leading to degraded shrubland state (Batllori et al., 2020; Zeppel et al., 2015).

5.7. Management implications

As drought-induced die-off accelerates forest transitions, forest management also need to shift from traditional, uniform interventions to adaptive close-to-nature (CTN) forestry principles (O'Hara, 2016). Because CTN practices aim to mimic natural forest dynamics, they are suitable for guiding post-die-off forest reorganization (Brang et al., 2014). Based on our findings, CTN can be implemented through the following three management strategies:

First, safeguard advanced regeneration from secondary stressors (based on Chapter 2). As pre-existing broadleaf understory saplings are the primary drivers of the plant composition shift that prevents the ecosystem from degrading into a shrubland, they should be conserved (Batllori et al., 2020; Chowdhury et al., 2025). Management interventions need to be focused to limit secondary stressors (e.g., browsing, mechanical damage during silvicultural operations, etc.) before, during, and after a die-off event (Lindenmayer et al., 2004; Thom et al., 2023).

Second, implement climate-adaptive continuous cover silviculture interventions (based on Chapter 3). While general CTN forestry often relies on continuous cover to maintain heterogeneous microclimates (Gonçalves, 2023), our results emphasize that canopy cover management needs to account for the species' position within its climatic niche. In climatically optimal sites, managers can allow open gaps to promote the establishment of light-demanding seedlings. However, in marginal, drier sites, management should focus on conserving some closed-canopy patches that can provide microclimatic refugia to buffer saplings from extreme abiotic stress.

Third, apply context-dependent retention of deadwood and tree-related microhabitats (TreMs; based on Chapter 4). Retaining snags and downed logs provides critical physical microsites that aid sapling survival and host saproxylic biodiversity (Chowdhury et al., 2024; Harmon et al., 1986; Motta et al., 2006; Thom et al., 2023), but retention strategies need to account for deadwood decomposition rates. In wetter

and warmer sites, rapid decomposition requires a continuous input of structures generating new habitat. So, weakened, defoliated trees should be preserved at some extent to provide future deadwood. In contrast, colder and drier sites allow deadwood to persist much longer. Here, management should maximize the retention of the pulse of deadwood generated by the die-off to secure long-term habitat heterogeneity. In both cases, conserving large TreM-bearing habitat trees is also essential to support long-term multitaxon biodiversity (Asbeck et al., 2021; Basile et al., 2020).

Chapter 6: General Conclusions



6.1. Conclusions

Following ten years of drought-induced die-off in *Pinus sylvestris* L. dominated forests in Catalonia (NE Spain), the affected forest reorganized, reflecting changes in three ecosystem components: plant compositional shifts, regeneration filtering, and enhanced habitat heterogeneity.

6.2. Composition shift (Chapter 2)

- Forest affected by drought-induced die-off exhibit a reduction in basal area, with broadleaf tree species (e.g., *Quercus spp.*, *Acer spp.*, *Prunus spp.*) growing into the tree canopy. As a result, die-off plots show higher species richness, diversity, and evenness in the tree layer compared to unaffected ones, with these increases being more pronounced in the drier and warmer sites of the climatic gradient.
- The species richness and evenness of established recruits are higher in die-off plots relative to control plots.
- Species composition between the tree canopy layer and the tree recruiting community shows higher similarity (Sørensen index) in die-off plots relative to controls, which is primarily driven by species turnover.

6.3. Regeneration filtering (Chapter 3)

- The regeneration success of *P. sylvestris* following drought-induced die-off is shaped by the interaction between forest canopy cover conditions (defoliated and closed canopies, and open gaps) and the population's position within the species' climatic niche.
- Severely defoliated canopy habitats consistently fail to support *P. sylvestris* regeneration across all developmental stages, regardless of climatic suitability.
- Open canopy habitats within die-off plots exhibit increased densities of seedlings and saplings compared to control plots, while sapling density is lowered in closed habitats.
- Open habitats in die-off affected plots show higher densities of seedlings compared to unaffected ones, especially in optimal sites of the species' climatic niche.

- In climatically marginal sites of the species' niche, young and old sapling densities of *P. sylvestris* are lowered in open habitats, whereas closed canopy habitats support the persistence of old, established saplings.

6.4. Habitat response (Chapter 4)

- Ten years following the post-drought-induced die-off event, the affected forests exhibit a higher abundance, richness, and diversity of deadwood across different decay stages compared to control plots, which subsequently host higher abundance, richness, and diversity of tree-related microhabitats (TreMs).
- The standing snags and downed logs in die-off plots contain a higher abundance, richness, and diversity of TreMs, including an increased abundance of both saproxylic and epixylic TreM categories.
- Wetter sites exhibit a higher proportion of recent deadwood (unbroken snags) and higher overall TreM abundance in die-off plots compared to unaffected ones. Meanwhile, colder sites show higher standing snags, downed logs, and overall deadwood abundance compared to warmer sites.

Overall, drought-induced tree mortality in *P. sylvestris*-dominated stands drives compositional and habitat reorganization. The reduction in the dominant *P. sylvestris* canopy provides opportunity for mixed broadleaf establishment, while the filtering of *P. sylvestris* regeneration is restricted by canopy conditions and climatic constraints. Furthermore, the increase in deadwood and TreMs enhances the habitat complexity. These ecosystem responses are especially pronounced at the drier edge of the climatic gradient, resulting in a transition from *P. sylvestris*-dominated stands to structurally complex and more Mediterranean mixed forests.

Appendix

Appendix A

Based on chapter 2

Table A1 List of tree components (tree and tree recruits) and shrub species in the twenty sites of *Pinus sylvestris* forest in Catalonia (NE Spain)

Tree species	Recruit tree species	Shrub species
<i>Acer monspessulanum</i>	<i>Acer campestre</i>	<i>Amelanchier ovalis</i>
<i>Arbutus unedo</i>	<i>Acer monspessulanum</i>	<i>Buxus sempervirens</i>
<i>Crataegus monogyna</i>	<i>Acer opalus</i>	<i>Calluna vulgaris</i>
<i>Erica arborea</i>	<i>Acer pseudoplatanus</i>	<i>Cistus salviifolius</i>
<i>Fraxinus excelsior</i>	<i>Arbutus unedo</i>	<i>Cornus sanguinea</i>
<i>Juniperus communis</i>	<i>Betula pendula</i>	<i>Erica scoparia</i>
<i>Phillyrea latifolia</i>	<i>Celtis australis</i>	<i>Genista scorpius</i>
<i>Pinus nigra</i>	<i>Corylus avellana</i>	<i>Ligustrum vulgare</i>
<i>Pinus sylvestris</i>	<i>Crataegus monogyna</i>	<i>Lonicera xylosteum</i>
<i>Pinus uncinata</i>	<i>Fraxinus excelsior</i>	<i>Prunus spinosa</i>
<i>Prunus avium</i>	<i>Ilex aquifolium</i>	<i>Rhamnus alaternus</i>
<i>Prunus mahaleb</i>	<i>Juglans regia</i>	<i>Rhamnus saxatilis</i>
<i>Quercus humilis</i>	<i>Prunus avium</i>	<i>Rosa spp.</i>
<i>Quercus ilex</i>	<i>Prunus domestica</i>	<i>Rubus ulmifolius</i>
<i>Sorbus aria</i>	<i>Prunus mahaleb</i>	
<i>Sorbus domestica</i>	<i>Pinus nigra</i>	
	<i>Pinus sylvestris</i>	
	<i>Pistacia terebinthus</i>	
	<i>Phillyrea latifolia</i>	
	<i>Pyrus communis</i>	
	<i>Quercus humilis</i>	
	<i>Quercus ilex</i>	
	<i>Sorbus aria</i>	
	<i>Sorbus aucuparia</i>	
	<i>Sorbus domestica</i>	
	<i>Salix caprea</i>	

Table A2 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) since the die-off episode in 2012 on plot basal area in tree layer on (A) 2022, (B) 2017, and (C) 2013 in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00_{\text{sites}}}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

	A. Basal area (2022)			B. Basal area (2017)			C. Basal area (2013)		
Predictors	Estimates	CI	<i>p</i>	Estimates	CI	<i>p</i>	Estimates	CI	<i>p</i>
(Intercept)	39.72	33.73 – 45.70	<0.001	37.59	32.29 – 42.88	<0.001	34.75	29.55 – 39.95	<0.001
Die-off	-19.63	-26.87 – -12.39	<0.001	-19.73	-26.14 – -13.32	<0.001	-18.65	-25.04 – -12.27	<0.001
Random Effects									
σ^2	127.55			99.88			99.12		
τ_{00}	46.68			36.44			32.41		
ICC	0.27			0.27			0.25		
N	20			20			20		
Observations	40			40			40		
Marginal R^2 / Conditional R^2	0.36 / 0.53			0.42 / 0.58			0.41 / 0.55		

Table A3 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) since the die-off episode in 2013 on plot basal area in tree layer in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00_{\text{sites}}}$ and plot, $\tau_{00_{\text{plots}}}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

Basal area (tree layer)			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	34.79	29.48 – 40.10	<0.001
Year [2017]	2.00	-0.59 – 4.58	0.129
Year [2022]	4.40	1.14 – 7.65	0.009
Die-off	-18.49	-25.08 – -11.91	<0.001
Temperature	-4.01	-7.73 – -0.29	0.035
Precipitation	0.51	-1.28 – 2.31	0.573
Year [2017] : Die-off	-1.03	-2.50 – 0.43	0.166
Year [2022] : Die-off	-0.92	-2.38 – 0.55	0.217
Temperature : Precipitation	-0.77	-1.16 – -0.37	<0.001
Random Effects			
σ^2	2.73		
$\tau_{00_{\text{plots}}}$	107.55		
$\tau_{00_{\text{sites}}}$	15.85		
ICC	0.98		
N_{plot}	40		
N_{sites}	20		
Observations	120		
Marginal R^2 / Conditional R^2	0.48 / 0.98		

Table A4 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) since the die-off episode in 2012 on species richness in tree layer on (A) 2022, (B) 2017, and (C) 2013 in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

	A. Richness (tree layer 2022)			B. Richness (tree layer 2017)			C. Richness (tree layer 2013)		
Predictors	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
(Intercept)	2.55	1.89 – 3.21	<0.001	2.20	1.62 – 2.78	<0.001	2.10	1.54 – 2.66	<0.001
Die-off	0.60	-0.06 – 1.26	0.075	0.50	-0.08 – 1.08	0.089	0.35	-0.31 – 1.01	0.291
Random Effects									
σ^2	1.07			0.82			1.07		
τ_{00}	1.07			0.80			0.48		
ICC	0.50			0.50			0.31		
N	20			20			20		
Observations	40			40			40		
Marginal R^2 / Conditional R^2	0.04 / 0.52			0.04 / 0.52			0.02 / 0.32		

Table A5 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) since the die-off episode in 2012 on species diversity in tree layer (Shannon index) on (A) 2022, (B) 2017, and (C) 2013 in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00_{\text{sites}}}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

	A. Shannon index (tree layer 2022)			B. Shannon index (tree layer 2017)			C. Shannon index (tree layer 2013)		
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.26	0.08 – 0.44	0.005	0.22	0.05 – 0.40	0.011	0.22	0.05 – 0.38	0.013
Die-off	0.24	0.07 – 0.41	0.006	0.24	0.08 – 0.41	0.005	0.17	0.02 – 0.33	0.029
Random Effects									
σ^2	0.07			0.07			0.06		
τ_{00}	0.09			0.08			0.08		
ICC	0.57			0.53			0.56		
N	20			20			20		
Observations	40			40			40		
Marginal R^2 / Conditional R^2	0.09 / 0.61			0.10 / 0.58			0.06 / 0.59		

Table A6 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) since the die-off episode in 2013 on species richness in tree layer in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00_{\text{sites}}}$ and plot, $\tau_{00_{\text{plots}}}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

<i>Predictors</i>	Tree species richness (tree layer)		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	2.24	1.44 – 3.04	<0.001
Year [2017]	-0.06	-0.92 – 0.81	0.900
Year [2022]	0.20	-0.88 – 1.28	0.710
Die-off	-0.49	-1.38 – 0.40	0.275
Temperature	0.46	-0.01 – 0.92	0.053
Precipitation	0.12	-0.48 – 0.72	0.691
Year [2017] : Die-off	1.24	0.23 – 2.26	0.017
Year [2022] : Die-off	1.62	0.41 – 2.84	0.009
Die-off : Precipitation	-0.82	-1.48 – -0.16	0.015
Random Effects			
σ^2	0.32		
$\tau_{00_{\text{plots}}}$	0.57		
$\tau_{00_{\text{sites}}}$	0.49		
ICC	0.77		
N _{plots}	40		
N _{sites}	20		
Observations	120		
Marginal R^2 / Conditional R^2	0.29 / 0.83		

Table A7 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) since the die-off episode in 2013 on species diversity in tree layer (Shannon index) in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00_{\text{sites}}}$ and plot, $\tau_{00_{\text{plots}}}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

<i>Predictors</i>	Shannon index (tree layer)		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.29	0.11 – 0.47	0.002
Year [2017]	-0.08	-0.25 – 0.10	0.387
Year [2022]	-0.08	-0.30 – 0.14	0.468
Die-off	-0.06	-0.26 – 0.14	0.559
Temperature	0.18	0.06 – 0.30	0.004
Precipitation	0.07	-0.06 – 0.19	0.287
Year [2017] : Die-off	0.37	0.16 – 0.58	0.001
Year [2022] : Die-off	0.45	0.19 – 0.70	0.001
Die-off : Precipitation	-0.23	-0.37 – -0.08	0.002
Random Effects			
σ^2	0.01		
$\tau_{00_{\text{plots}}}$	0.04		
$\tau_{00_{\text{sites}}}$	0.04		
ICC	0.89		
N _{plots}	40		
N _{sites}	20		
Observations	120		
Marginal R^2 / Conditional R^2	0.39 / 0.93		

Table A8 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) since the die-off episode in 2012 on species diversity in tree layer (Shannon index) on (A) 2022, (B) 2017, and (C) 2013 in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00_{\text{sites}}}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

	A. Pielou index (tree layer 2022)			B. Pielou index (tree layer 2017)			C. Pielou index (tree layer 2013)		
Predictors	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
(Intercept)	0.30	0.16 – 0.44	<0.001	0.32	0.19 – 0.46	<0.001	0.34	0.20 – 0.48	<0.001
Die-off	0.16	0.02 – 0.30	0.028	0.17	0.05 – 0.30	0.009	0.12	-0.03 – 0.28	0.113
Random Effects									
σ^2	0.03			0.02			0.03		
τ_{00}	0.04			0.04			0.03		
ICC	0.54			0.59			0.47		
N	18			17			17		
Observations	31			29			27		
Marginal R^2 / Conditional R^2	0.09 / 0.58			0.12 / 0.64			0.06 / 0.50		

Table A9 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) since the die-off episode in 2013 on species evenness in tree layer (Pielou index) in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00_{\text{sites}}}$ and plot, $\tau_{00_{\text{plots}}}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

<i>Predictors</i>	Pielou index (tree layer)		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.28	0.14 – 0.43	<0.001
Year [2017]	0.01	-0.08 – 0.11	0.776
Year [2022]	0.04	-0.08 – 0.16	0.515
Die-off	0.10	-0.02 – 0.22	0.110
Temperature	0.03	-0.08 – 0.15	0.590
Precipitation	-0.02	-0.09 – 0.04	0.437
Year [2017] : Die-off	0.06	0.00 – 0.11	0.046
Year [2022] : Die-off	0.01	-0.04 – 0.07	0.646
Die-off : MAT	0.12	0.01 – 0.23	0.038
Random Effects			
σ^2	0.00		
$\tau_{00_{\text{plots}}}$	0.02		
$\tau_{00_{\text{sites}}}$	0.03		
ICC	0.95		
N _{plots}	32		
N _{sites}	18		
Observations	87		
Marginal R^2 / Conditional R^2	0.27 / 0.97		

Table A10 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) since the die-off episode in 2013 on the on all tree recruits (T1, T2 and T3 stages combinedly; see Methods) (A) richness, (B) diversity (Shannon index), and (C) evenness (Pielou index) in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

	A. Species richness (all tree recruits) (log transformed)			B. Shannon index (all tree recruits)			C. Pielou index (all tree recruit)		
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	1.42	1.14 – 1.70	<0.001	1.00	0.77 – 1.24	<0.001	0.64	0.53 – 0.76	<0.001
Die-off	0.03	-0.15 – 0.21	0.745	-0.04	-0.23 – 0.14	0.631	-0.01	-0.09 – 0.08	0.875
Precipitation	-0.24	-0.62 – 0.15	0.214	-0.17	-0.50 – 0.16	0.295	-0.03	-0.13 – 0.08	0.637
Temperature	-0.17	-0.56 – 0.23	0.403	-0.13	-0.46 – 0.20	0.435			
Die-off : Precipitation	0.09	-0.16 – 0.34	0.452	-0.02	-0.28 – 0.23	0.864	-0.07	-0.16 – 0.02	0.117
Die-off : Temperature	0.05	-0.20 – 0.30	0.707	0.11	-0.15 – 0.36	0.405			
Random Effects									
σ^2	0.08			0.08			0.02		
τ_{00}	0.30			0.18			0.04		
ICC	0.80			0.69			0.71		
N	20			20			20		
Observations	40			40			40		
Marginal R^2 / Conditional R^2	0.05 / 0.81			0.08 / 0.72			0.07 / 0.73		

Table A11 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) since the die-off episode in 2013 on the T1 stage tree recruits (see Methods) (A) richness, (B) diversity (Shannon index), and (C) evenness (Pielou index) in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

	A. Species richness (T1 stage tree recruits) (log transformed)			B. Shannon index (T1 stage tree recruits)			C. Pielou index (T1 stage tree recruits)		
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	1.48	1.20 – 1.76	<0.001	0.82	0.57 – 1.08	<0.001	0.63	0.49 – 0.76	<0.001
Die-off	-0.11	-0.31 – 0.10	0.295	-0.03	-0.26 – 0.20	0.769	0.09	-0.05 – 0.24	0.208
Temperature	-0.11	-0.52 – 0.29	0.568	-0.11	-0.43 – 0.21	0.484	-0.00	-0.16 – 0.15	0.955
Precipitation	-0.18	-0.57 – 0.21	0.363	-0.21	-0.53 – 0.10	0.182	-0.08	-0.23 – 0.08	0.309
Die-off : Temperature	0.08	-0.21 – 0.36	0.574						
Die-off : Precipitation	0.06	-0.22 – 0.35	0.649						
Random Effects									
σ^2	0.10			0.13			0.04		
τ_{00}	0.28			0.20			0.04		
ICC	0.74			0.61			0.48		
N	20			20			20		
Observations	40			40			35		
Marginal R^2 / Conditional R^2	0.04 / 0.75			0.07 / 0.64			0.10 / 0.53		

Table A12 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) since the die-off episode in 2013 on the T2 stage tree recruits (see Methods) (A) richness, (B) diversity (Shannon index), and (C) evenness (Pielou index) in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

	A. Species richness (T2 stage tree recruits)			B. Shannon index (T2 stage tree recruits)			C. Pielou index (T2 stage tree recruits)		
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	3.80	2.72 – 4.88	<0.001	0.84	0.61 – 1.08	<0.001	0.74	0.64 – 0.84	<0.001
Die-off	0.25	-0.57 – 1.08	0.534	0.03	-0.17 – 0.23	0.774	-0.03	-0.16 – 0.09	0.587
Temperature	-0.65	-2.02 – 0.71	0.340	-0.11	-0.43 – 0.21	0.480	0.06	-0.07 – 0.20	0.367
Precipitation	-0.87	-2.21 – 0.48	0.200	-0.16	-0.46 – 0.13	0.270	-0.01	-0.17 – 0.16	0.950
Die-off : Temperature				0.06	-0.14 – 0.27	0.521	-0.05	-0.22 – 0.12	0.549
Die-off : Precipitation							-0.03	-0.22 – 0.16	0.768
Random Effects									
σ^2	1.64			0.09			0.03		
τ_{00}	3.98			0.18			0.01		
ICC	0.71			0.65			0.17		
N	20			20			19		
Observations	40			40			36		
Marginal R^2 / Conditional R^2	0.07 / 0.73			0.06 / 0.67			0.07 / 0.23		

Table A13 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) since the die-off episode in 2013 on the T3 stage tree recruits (see Methods) (A) richness, (B) diversity (Shannon index), and (C) evenness (Pielou index) in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00_{\text{sites}}}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

	A. Species richness (T3 stage tree recruits)			B. Shannon index (T3 stage tree recruits)			C. Pielou index (T3 stage tree recruits)		
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	1.26	0.69 – 1.83	<0.001	0.24	0.05 – 0.43	0.016	0.39	0.18 – 0.61	0.001
Die-off	0.68	0.01 – 1.35	0.046	0.18	-0.07 – 0.43	0.147	0.35	0.06 – 0.65	0.022
Temperature	0.50	0.03 – 0.97	0.037	0.20	0.05 – 0.35	0.010	0.25	0.02 – 0.49	0.033
Die-off : Temperature							-0.16	-0.46 – 0.13	0.254
Random Effects									
σ^2	1.09			0.15			0.09		
τ_{00}	0.50			0.03			0.03		
ICC	0.32			0.16			0.27		
N	20			20			16		
Observations	40			40			23		
Marginal R^2 / Conditional R^2	0.19 / 0.45			0.22 / 0.35			0.33 / 0.51		

Table A14 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) since the die-off episode in 2013 on the shrub species (A) richness, (B) diversity, and (C) evenness in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

<i>Predictors</i>	A. Shrub richness			B. Shrub diversity			C. Shrub evenness		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	1.94	1.30 – 2.59	<0.001	0.38	0.23 – 0.53	<0.001	0.51	0.37 – 0.65	<0.001
Die-off	0.36	-0.23 – 0.94	0.223	0.02	-0.13 – 0.18	0.755	-0.04	-0.22 – 0.14	0.629
Precipitation	-0.22	-1.05 – 0.62	0.601	-0.03	-0.22 – 0.16	0.774	0.01	-0.16 – 0.18	0.886
Temperature	-0.47	-1.26 – 0.32	0.231	-0.18	-0.36 – 0.00	0.051	-0.19	-0.33 – -0.04	0.015
Die-off : Precipitation	-0.62	-1.21 – -0.02	0.043	-0.18	-0.34 – -0.02	0.026	-0.17	-0.35 – -0.00	0.047
Random Effects									
σ^2	0.82			0.06			0.06		
τ_{00}	1.18			0.05			0.01		
ICC	0.59			0.47			0.16		
N	20			20			19		
Observations	40			40			33		
Marginal R^2 / Conditional R^2	0.13 / 0.64			0.19 / 0.58			0.30 / 0.41		

Table A15 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) on the (A) similarity (Sørensen index), (B) nestedness, and (C) turnover of tree layer between 2013 and 2017 in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00_{\text{sites}}}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

<i>Predictors</i>	A. Similarity 2013 vs. 2017			B. Nestedness 2013 vs. 2017			C. Turnover 2013 vs. 2017		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.98	0.92 – 1.04	<0.001	0.02	-0.04 – 0.08	0.482	0.00	-0.01 – 0.01	0.992
Die-off	-0.04	-0.12 – 0.04	0.332	0.03	-0.05 – 0.11	0.461	0.01	-0.01 – 0.03	0.322
Temperature	-0.01	-0.06 – 0.05	0.846	0.00	-0.05 – 0.06	0.895	0.00	-0.01 – 0.01	0.796
Precipitation	0.01	-0.04 – 0.07	0.617	-0.00	-0.06 – 0.05	0.850	-0.01	-0.02 – 0.00	0.204
Random Effects									
σ^2	0.02			0.02			0.00		
τ_{00}	0.00			0.00			0.00		
N	20			20			20		
Observations	40			40			40		
Marginal R^2 / Conditional R^2	0.04			0.02			0.11		

Table A16 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) on the (A) similarity (Sørensen index), (B) nestedness, and (C) turnover of tree layer between 2013 and 2022 in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00 \text{ sites}}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

	A. Similarity 2013 vs. 2022			B. Nestedness 2013 vs. 2022			C. Turnover 2013 vs. 2022		
Predictors	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
(Intercept)	0.92	0.84 – 0.99	<0.001	0.08	0.01 – 0.16	0.038	0.00	-0.02 – 0.02	0.978
Die-off	-0.07	-0.17 – 0.03	0.161	0.05	-0.05 – 0.16	0.337	0.02	-0.01 – 0.04	0.154
Temperature	-0.01	-0.09 – 0.08	0.856	-0.01	-0.09 – 0.08	0.893	0.01	-0.00 – 0.03	0.122
Precipitation	0.02	-0.07 – 0.11	0.655	-0.02	-0.10 – 0.06	0.629	-0.00	-0.02 – 0.02	0.998
Random Effects									
σ^2	0.02			0.03			0.00		
$\tau_{00 \text{ sites}}$	0.01			0.00			0.00		
ICC	0.25			0.10					
N _{sites}	20			20			20		
Observations	40			40			40		
Marginal R^2 / Conditional R^2	0.06 / 0.29			0.03 / 0.13			0.15		

Table A17 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) on the (A) similarity (Sørensen index), (B) nestedness, and (C) turnover of tree layer between 2017 and 2022 in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00 \text{ sites}}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

	A. Similarity 2017 vs. 2022			B. Nestedness 2017 vs. 2022			C. Turnover 2017 vs. 2022		
Predictors	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
(Intercept)	0.94	0.86 – 1.01	<0.001	0.06	-0.00 – 0.13	0.054	0.00	-0.04 – 0.04	0.999
Die-off	-0.06	-0.15 – 0.03	0.220	0.02	-0.06 – 0.10	0.565	0.03	-0.02 – 0.09	0.208
Temperature	0.00	-0.08 – 0.08	0.995	-0.01	-0.08 – 0.06	0.772	0.01	-0.03 – 0.05	0.594
Precipitation	0.00	-0.07 – 0.08	0.943	-0.02	-0.09 – 0.05	0.610	0.02	-0.02 – 0.05	0.413
Random Effects									
σ^2	0.02			0.01			0.01		
$\tau_{00 \text{ sites}}$	0.00			0.01			0.00		
ICC	0.19			0.27			0.04		
N _{sites}	20			20			20		
Observations	40			40			40		
Marginal R^2 / Conditional R^2	0.03 / 0.22			0.02 / 0.28			0.06 / 0.09		

Table A18 Results of LMMs determining the effect of drought-induced die-off and climate (temperature and precipitation) on the (A) similarity (Sørensen index), (B) nestedness, and (C) turnover of tree layer and recruits community on 2022 in *P. sylvestris* forests of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00 \text{ sites}}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

<i>Predictors</i>	A. Similarity (tree layer vs. recruits)			B. Nestedness (tree layer vs. recruits)			C. Turnover (tree layer vs. recruits)		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.40	0.30 – 0.51	<0.001	0.20	0.10 – 0.30	<0.001	0.94	0.24 – 1.64	0.010
Die-off	0.16	0.03 – 0.28	0.016	0.05	-0.08 – 0.17	0.431	-0.19	-0.38 – 0.01	0.058
Temperature	0.12	0.02 – 0.23	0.021	-0.06	-0.14 – 0.02	0.139	-0.05	-0.12 – 0.01	0.117
Die-off : Temperature	0.01	-0.11 – 0.14	0.813						
Random Effects									
σ^2	0.04			0.04			0.09		
$\tau_{00 \text{ sites}}$	0.01			0.01			0.00		
ICC	0.29			0.21					
N _{sites}	20			20			20		
Observations	40			40			40		
Marginal R^2 / Conditional R^2	0.32 / 0.51			0.08 / 0.27			0.14		

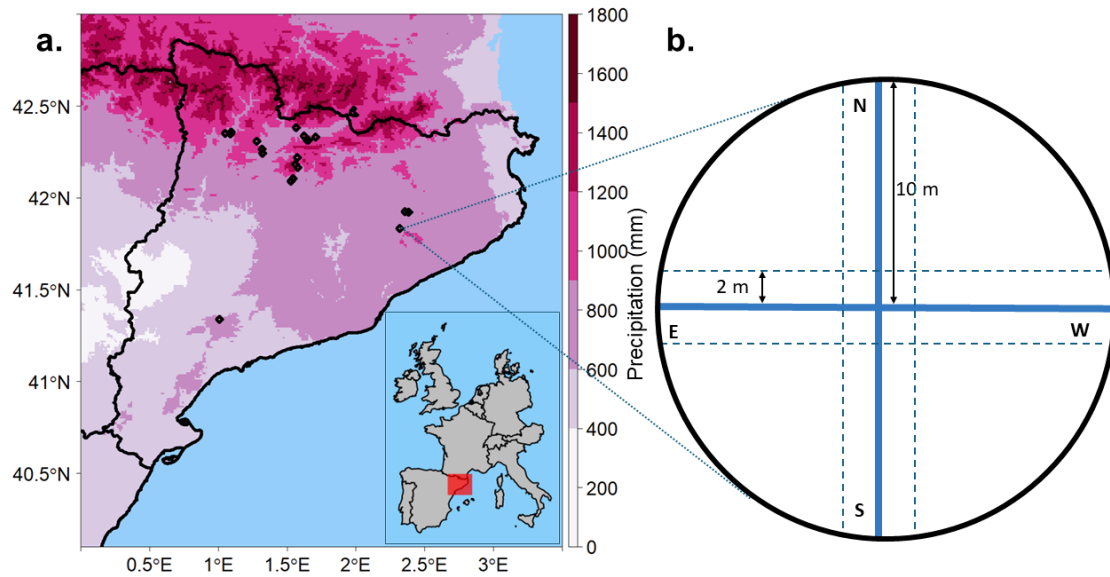


Figure A1 Study area with locations across precipitation (mean annual precipitation in mm) gradient (a) and plot layout (b). Two paired circular plots (i.e., drought-induced die-off and non-affected plots) with a 10-meter radius was established in twenty forest sites dominated by *P. silvestris*. Trees having >2.5 cm dbh were measured. Meanwhile, recruits and shrubs information were collected in transect belts (2 m wide in each side) and transect lines, respectively, which were oriented in a North (N) – South (S) and East (E) – West (W) direction, intersecting at the centre of the plot (see Methods for details). The precipitation raster layer was obtained from Fick and Hijmans, 2017) to draw the map.

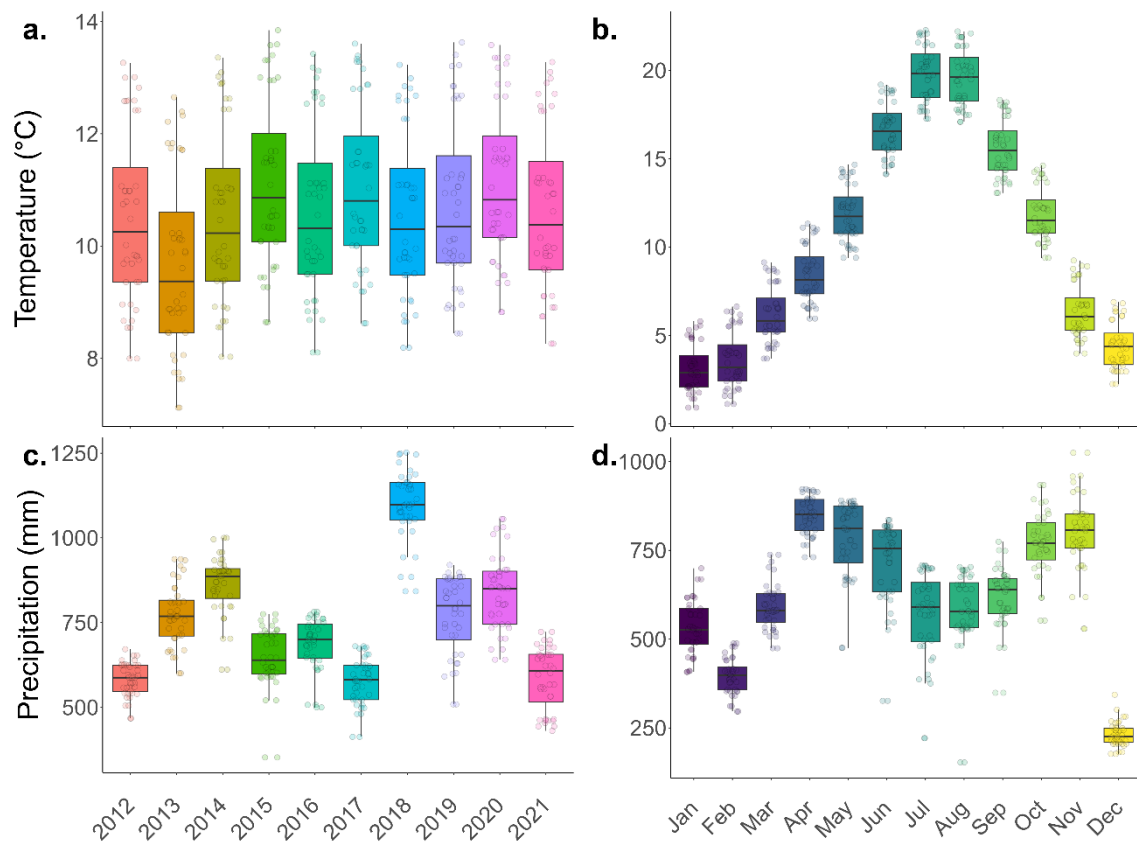


Figure A2 Boxplots of mean annual temperature (°C; a, b), and mean annual precipitation (mm; c, d) in the twenty study sites from 2012 to 2021 (data source: Cruz-Alonso et al., 2023).

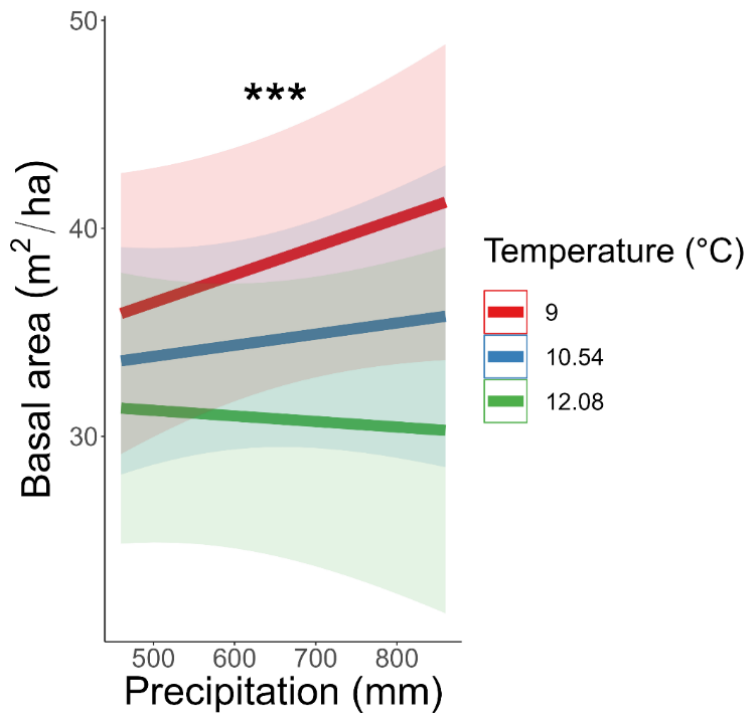


Figure A3 interaction effect of plot basal area (m^2/ha) of tree species with mean annual temperature ($^{\circ}\text{C}$) and mean annual precipitation (mm) across the survey years (2013, 2017, and 2022). Asterisk signs indicate the significance level of p-values (*: $p < 0.05$, **: $p < 0.01$, *** $p < 0.001$). The envelopes around effect lines denote 95% confidence interval.

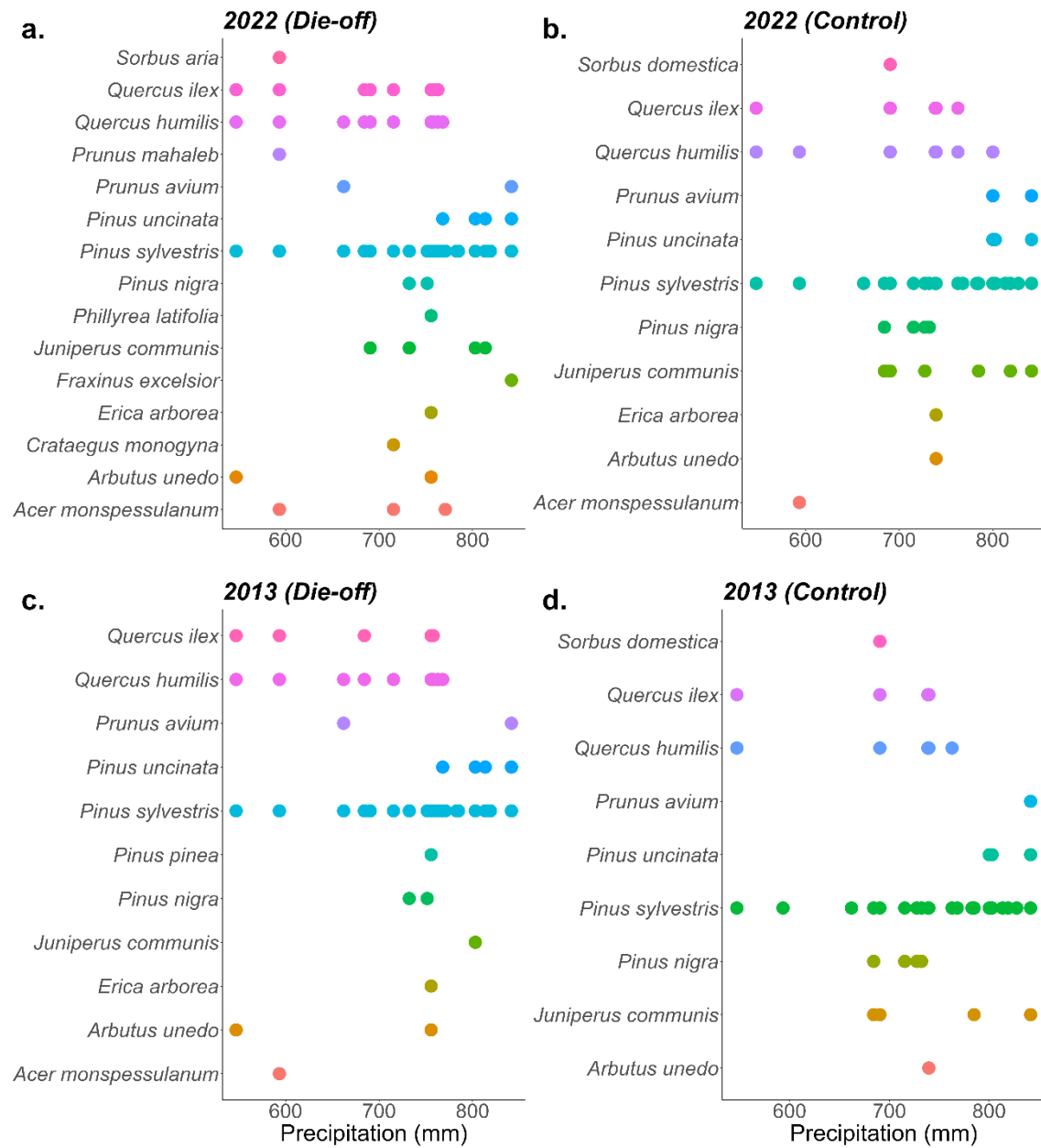


Figure A4 Presence of species in tree layer across the precipitation (mm) gradients in the die-off (a, c) and control (b, d) plots for 2022 (a, b) and 2013 (c, d) in the study sites.

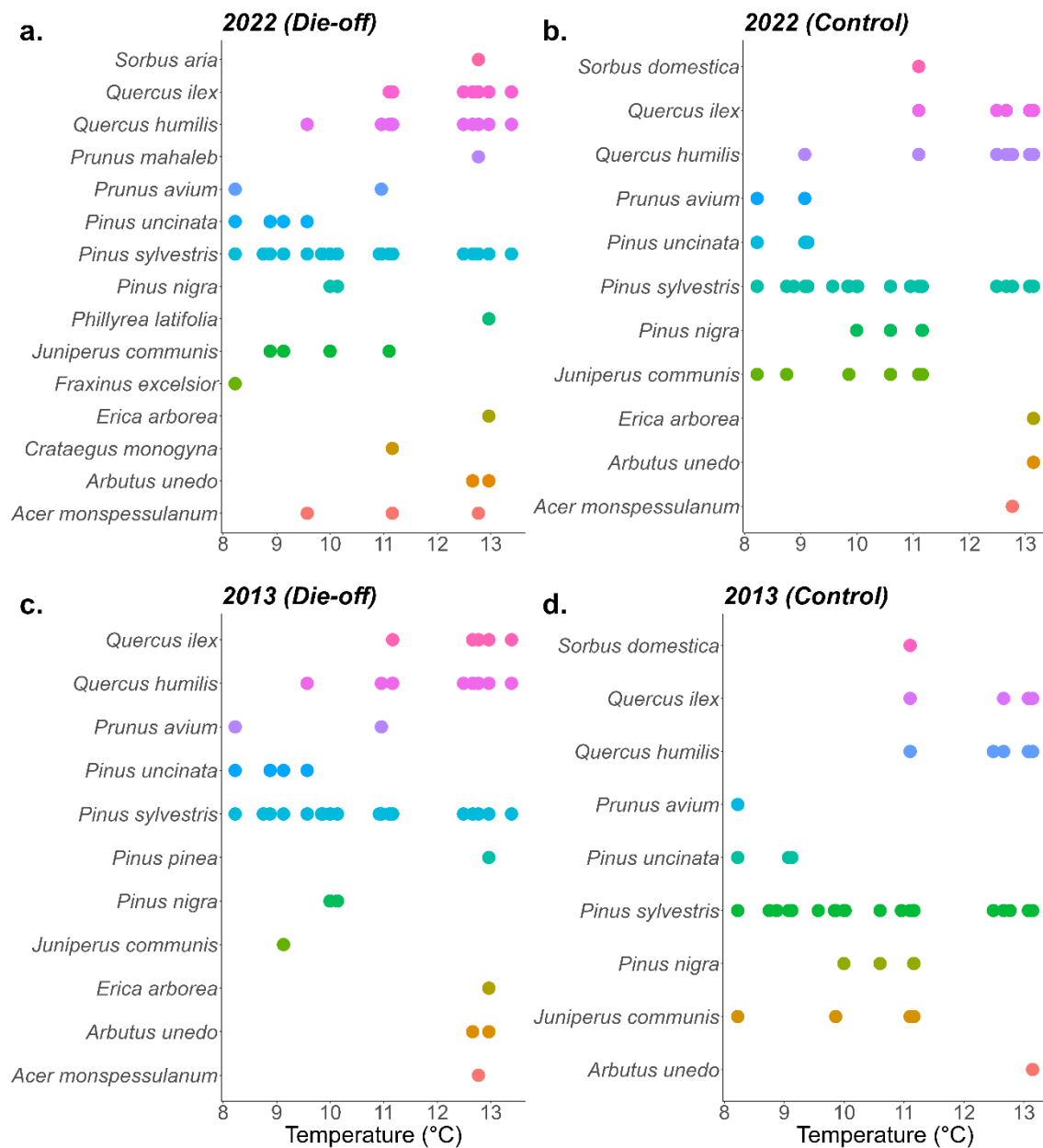


Figure A5 Presence of species in tree layer across the temperature (°C) gradients in the die-off (a, c) and control (b, d) plots for 2022 (a, b) and 2013 (c, d) in the study sites.

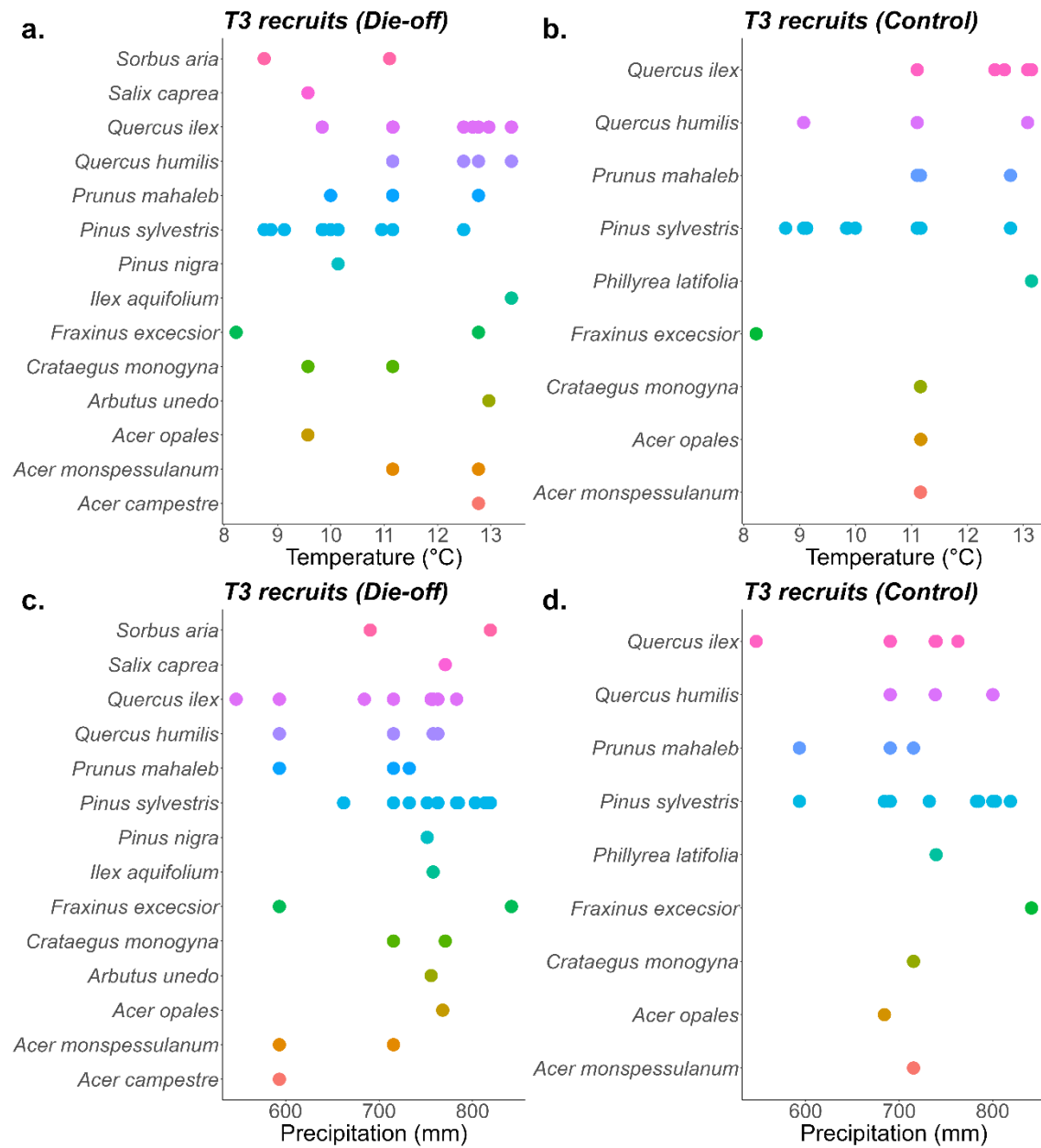


Figure A6 Presence of tree recruits at T3 stage (see Methods for details) across the temperature (°C; a, b) and precipitation (mm; c, d) gradient gradients in the die-off (a, c) and control (b, d) plots for 2022 in the study sites.

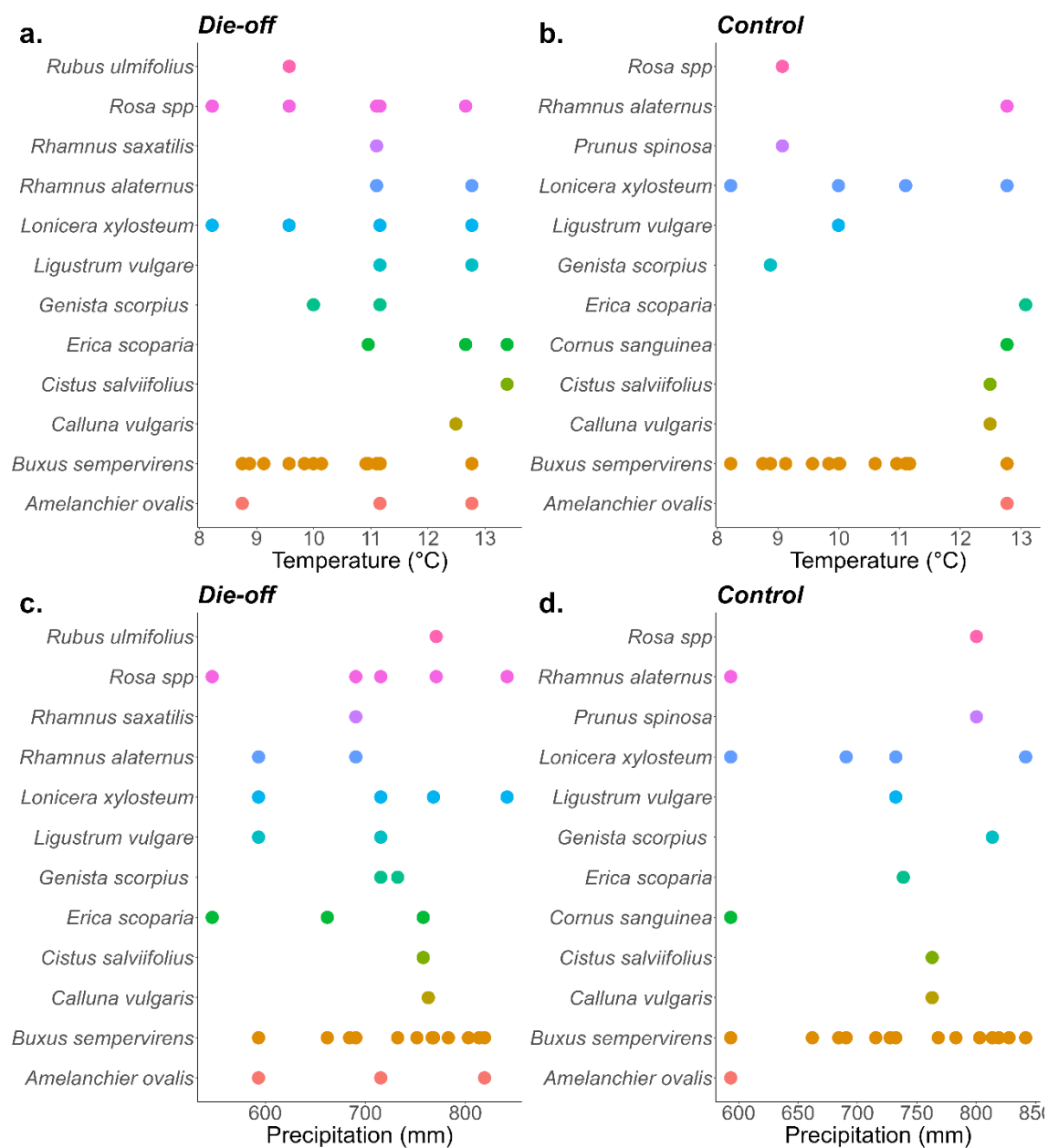


Figure A7 Presence of shrub species across the temperature (°C; a, b) and precipitation (mm; c, d) gradient gradients in the die-off (a, c) and control (b, d) plots for 2022 in the study sites.

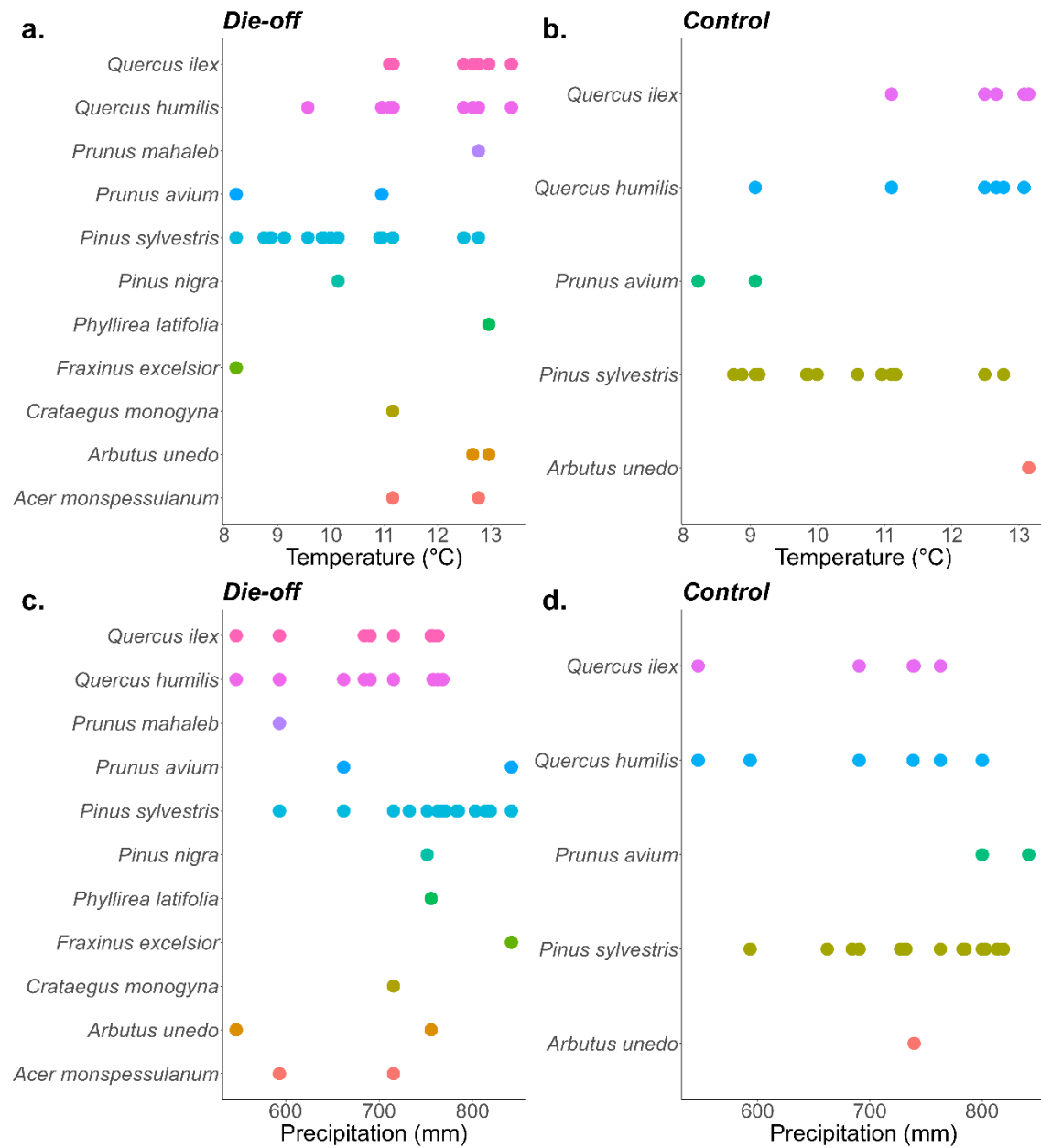


Figure A8 Presence of major tree species that share the tree and recruiting communities (see Methods for details) across the temperature (°C; a, b) and precipitation (mm; c, d) gradient gradients in the die-off (a, c) and control (b, d) plots in 2022 in the study sites.

Appendix B

Based on chapter 3

Table B1: Different locations of *Pinus sylvestris* stands in Catalonia (NE Spain) considered in this study.

Location id.	Longitude	Latitude	Counties in Catalonia	Geographical region
1	1.577	42.1644	Solsonès	Pre-Pyrenees
2	1.5433	42.1046	Solsonès	Pre-Pyrenees
3	1.5736	42.2202	Alt Urgell	Pre-Pyrenees
4	1.6424	42.3175	Alt Urgell	Pre-Pyrenees
5	1.6532	42.3137	Alt Urgell	Pre-Pyrenees
6	1.6252	42.337	Alt Urgell	Pre-Pyrenees
7	1.5672	42.3839	Alt Urgell	Pyrenees
8	1.7094	42.3324	Baixa Cerdanya	Pre-Pyrenees
9	1.3231	42.2437	Alt Urgell	Pre-Pyrenees
10	1.3162	42.2649	Alt Urgell	Pre-Pyrenees
11	1.2812	42.3084	Alt Urgell	Pyrenees
12	1.5296	42.0911	Solsonès	Pre-Pyrenees
13	1.5596	42.1843	Solsonès	Pre-Pyrenees
14	2.3841	41.9218	Osona	Pre-Coastal Range
15	2.3182	41.8338	Osona	Pre-Coastal Range
16	2.3584	41.926	Osona	Pre-Coastal Range
17	1.0887	42.3479	Pallars Sobirà	Pre-Pyrenees
18	1.0912	42.359	Pallars Sobirà	Pre-Pyrenees
19	1.0506	42.3529	Pallars Sobirà	Pre-Pyrenees
20	1.0086	41.3388	Conca de Barberà	Pre-Coastal Range

Table B2: Description of bioclimatic variables (bio) with their definitions (Hijmans et al., 2024), and indication of variables used in the climate niche modelling of *Pinus sylvestris*. “✓” indicates that the variable was finally used in building the climatic niche model, while “×” indicates that it was not.

Code	Definitions	Used/not used
bio1	Annual Mean Temperature	✓
bio2	Mean Diurnal Range (Mean of monthly (maximum temp – minimum temp))	×
bio3	Isothermality (bio2/ bio7) (× 100)	×
bio4	Temperature Seasonality (standard deviation × 100)	✓
bio5	Maximum Temperature of Warmest Month	✓
bio6	Minimum Temperature of Coldest Month	✓
bio7	Temperature Annual Range (bio5- bio6)	×
bio8	Mean Temperature of Wettest Quarter	×
bio9	Mean Temperature of Driest Quarter	×
bio10	Mean Temperature of Warmest Quarter	✓
bio11	Mean Temperature of Coldest Quarter	✓
bio12	Annual Precipitation	✓
bio13	Precipitation of Wettest Month	✓
bio14	Precipitation of Driest Month	✓
bio15	Precipitation Seasonality (Coefficient of Variation)	✓
bio16	Precipitation of Wettest Quarter	✓
bio17	Precipitation of Driest Quarter	✓
bio18	Precipitation of Warmest Quarter	×
bio19	Precipitation of Coldest Quarter	×

Table B3: Years for which climate variables were considered for the analyses of the different development stages of recruits (see details in Methods).

Development stages of <i>P. sylvestris</i> recruits	Survey years		
	2013	2017	2022
T1 (seedlings under two years old with height < 30 cm)	2009-2012	2013-2016	2018-2021
T2 (young saplings older than two years with height > 30 cm but < 130 cm)	2005-2012	2009-2016	2014-2021
T3 (advanced saplings with height $\geq$ 130 cm and dbh $\leq$ 2.5 cm)	2001-2012	2005-2016	2010-2021

Table B4: Results of Linear Mixed Models (LMMs) determining the effect of drought-induced die-off (compared to control), canopy habitat (defoliated, closed, and open), and climate niche metrics on *P. sylvestris* recruits at T1 development stage (seedlings) across the three-survey year (i.e., 2013, 2017, and 2022) in forests of Catalonia. Significant *p-values* are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00} sites and plot, τ_{00} plots), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

<i>Predictors</i>	T1 stage		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	1.94	-17.90 – 21.77	0.848
Die-off	-0.33	-27.34 – 26.68	0.981
Closed canopy	17.74	-7.95 – 43.42	0.175
Open canopy	18.89	-6.80 – 44.58	0.149
Core distance	2.91	-10.78 – 16.61	0.676
Core distance CV	-1.99	-15.55 – 11.56	0.773
Die-off: Closed canopy	-4.43	-40.76 – 31.90	0.811
Die-off: Open canopy	39.04	2.71 – 75.37	0.035
Die-off : Core distance	-18.30	-35.30 – -1.31	0.035
Closed canopy : Core distance CV	-3.19	-21.38 – 15.00	0.731
Open canopy : Core distance CV	-16.47	-34.66 – 1.72	0.076
Random Effects			
σ^2	5116.65		
τ_{00} plots	180.25		
τ_{00} sites	147.54		
ICC	0.06		
N_{plots}	40		
N_{sites}	20		
Observations	360		
Marginal R^2 / Conditional R^2	0.095 / 0.150		

Table B5: Results of Linear Mixed Models (LMMs) determining the effect of drought-induced die-off (compared to control) on *P. sylvestris* recruits at T1 development stage (seedlings) at (A) 2013, (B) 2017, and (C) 2022 in forests of Catalonia. Significant *p-values* are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column. The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00}\text{sites}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

	A. T1 stage (2013)			B. T1 stage (2017)			C. T1 stage (2022)		
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	18.21	-0.66 – 37.09	0.058	3.64	-7.51 – 14.80	0.512	20.73	-7.87 – 49.34	0.150
Die-off	9.18	-16.15 – 34.51	0.467	10.13	-5.65 – 25.90	0.201	13.41	-27.05 – 53.87	0.506
Random Effects									
σ^2	1559.89			605.01			3979.59		
$\tau_{00}\text{ sites}$	172.48			0.00			0.00		
ICC	0.10								
N	20			20			20		
Observations	40			40			40		
Marginal R^2 / Conditional R^2	0.012 / 0.111			0.042 / NA			0.011 / NA		

Table B6: Results of Linear Mixed Models (LMMs) determining the effect of canopy habitat (defoliated, closed, and open) on *P. sylvestris* at T1 development stage (seedlings) at (A) 2013, (B) 2017, and (C) 2022 in forests of Catalonia. Significant *p-values* are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column. The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00}\text{sites}$ and plot, $\tau_{00}\text{plots}$) the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

	A. T1 stage (2013)			B. T1 stage (2017)			C. T1 stage (2022)		
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.19	-21.43 – 21.81	0.986	2.21	-10.27 – 14.68	0.727	2.62	-29.40 – 34.65	0.871
Closed	35.38	6.37 – 64.39	0.017	1.99	-14.91 – 18.90	0.816	9.20	-34.65 – 53.04	0.679
Open	32.47	3.46 – 61.48	0.029	17.50	0.60 – 34.41	0.043	65.25	21.41 – 109.09	0.004
Random Effects									
σ^2	4289.33			1456.51			9795.78		
$\tau_{00}\text{ plots}$	94.26			130.29			658.39		
$\tau_{00}\text{ sites}$	190.40			0.00			0.00		
ICC	0.06								
N_{sites}	20			20			20		
N_{plots}	40			40			40		
Observations	120			120			120		
Marginal R^2 / Conditional R^2	0.054 / 0.113			0.041 / NA			0.079 / NA		

Table B7: Results of Linear Mixed Models (LMMs) determining the effect of drought-induced die-off (compared to control), canopy habitat (defoliated, closed, and open), and climate niche metrics on *P. sylvestris* recruits at T2 development stage (young saplings) across the three-survey year (i.e., 2013, 2017, and 2022) in forests of Catalonia. Significant *p*-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case plot, τ_{00} plots), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

<i>Predictors</i>	T2 stage		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	17.40	-59.07 – 93.87	0.655
Die-off	-66.71	-151.01 – 17.59	0.121
Closed canopy	156.03	71.26 – 240.79	<0.001
Open canopy	70.06	-14.70 – 154.83	0.105
2017	-6.47	-89.01 – 76.07	0.878
2022	0.92	-101.16 – 103.01	0.986
Core distance	-0.01	-42.89 – 42.87	1.000
Variability in core distance	18.49	-30.14 – 67.11	0.455
Die-off: Closed canopy	-75.26	-146.05 – -4.48	0.037
Die-off: Open canopy	107.75	36.96 – 178.53	0.003
Die-off: 2017	56.18	-14.61 – 126.98	0.119
Die-off: 2022	105.47	34.70 – 176.24	0.004
Closed canopy : 2017	-63.00	-163.75 – 37.76	0.220
Open canopy : 2017	-49.11	-149.87 – 51.64	0.338
Closed canopy : 2022	-117.54	-242.77 – 7.69	0.066
Open canopy : 2022	-79.62	-204.85 – 45.61	0.212
Closed canopy : Core distance	-50.92	-95.48 – -6.37	0.025
Open canopy : Core distance	-84.66	-129.22 – -40.11	<0.001
Closed canopy : Core distance CV	-23.42	-83.46 – 36.61	0.443
Open canopy : Core distance CV	-68.80	-128.83 – -8.76	0.025
Random Effects			
σ^2	19416.75		
τ_{00} plots	7577.15		
ICC	0.28		
N _{plots}	40		

Appendix

Observations	360
Marginal R^2 / Conditional R^2	0.177 / 0.408

Table B8: Results of Linear Mixed Models (LMMs) determining the effect of drought-induced die-off (compared to control) on *P. sylvestris* recruits at T2 development stage (young saplings) at (A) 2013, (B) 2017, and (C) 2022 in forests of Catalonia. Significant *p-values* are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column. The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00}\text{sites}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

	A. T2 stage (2013)			B. T2 stage (2017)			C. T2 stage (2022)		
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	91.51	24.80 – 158.22	0.009	50.52	3.31 – 97.73	0.037	29.25	-18.49 – 76.99	0.222
Die-off	-56.58	-150.92 – 37.76	0.232	-1.26	-68.03 – 65.50	0.970	48.59	-13.23 – 110.41	0.120
Random Effects									
σ^2	21636.29			10837.97			9290.45		
$\tau_{00}\text{ sites}$	0.00			0.00			1792.57		
ICC							0.16		
N_{sites}	20			20			20		
Observations	40			40			40		
Marginal R^2 / Conditional R^2	0.037 / NA			0.000 / NA			0.052 / 0.205		

Table B9: Results of Linear Mixed Models (LMMs) determining the effect of canopy habitat (defoliated, closed, and open) on *P. sylvestris* at T2 development stage (young saplings) at (A) 2013, (B) 2017, and (C) 2022 in forests of Catalonia. Significant *p-values* are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column. The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00} sites and plot, τ_{00} plots) the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

	A. T2 stage (2013)			B. T2 stage (2017)			C. T2 stage (2022)		
Predictors	Estimates	CI	<i>p</i>	Estimates	CI	<i>p</i>	Estimates	CI	<i>p</i>
(Intercept)	0.05	-65.06 – 65.15	0.999	4.38	-44.57 – 53.32	0.860	22.99	-27.11 – 73.09	0.365
Closed	108.26	29.09 – 187.44	0.008	56.99	-6.86 – 120.85	0.080	9.39	-51.77 – 70.55	0.762
Open	81.25	2.07 – 160.43	0.044	79.55	15.69 – 143.40	0.015	82.27	21.11 – 143.43	0.009
Random Effects									
σ^2	31950.03			20780.38			19062.01		
τ_{00} plots	11252.39			3633.69			3652.40		
τ_{00} sites	0.00			0.00			1434.60		
ICC							0.21		
N _{sites}	20			20			20		
N _{plots}	40			40			40		
Observations	120			120			120		
Marginal R^2 / Conditional R^2	0.063 / NA			0.052 / NA			0.053 / 0.253		

Table B10: Results of Linear Mixed Models (LMMs) determining the effect of drought-induced die-off (compared to control), canopy habitat (defoliated, closed, and open), and climate niche metrics on *P. sylvestris* recruits at T3 development stage (old saplings) across the three-survey year (i.e., 2013, 2017, and 2022) in forests of Catalonia. Significant *p*-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column, which is reduced from the full model (see Methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00} sites and plot, τ_{00} plots), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

<i>Predictors</i>	T3 stage		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	6.92	-12.40 – 26.24	0.482
Die-off	-13.59	-37.64 – 10.46	0.267
Closed canopy	52.58	30.15 – 75.02	<0.001
Open canopy	6.77	-15.67 – 29.20	0.553
2017	0.13	-22.36 – 22.63	0.991
2022	-3.97	-26.42 – 18.49	0.729
Core distance	-1.82	-11.89 – 8.25	0.722
Die-off: Closed canopy	-24.49	-46.93 – -2.06	0.032
Die-off: Open canopy	38.20	15.77 – 60.64	0.001
Die-off: 2017	8.10	-14.33 – 30.54	0.478
Die-off: 2022	19.38	-3.06 – 41.81	0.090
Closed canopy : 2017	-27.43	-54.96 – 0.10	0.051
Open canopy : 2017	-6.18	-33.72 – 21.35	0.659
Closed canopy : 2022	-37.32	-64.82 – -9.82	0.008
Open canopy : 2022	4.30	-23.20 – 31.80	0.759
Closed canopy : Core distance	-9.63	-20.93 – 1.67	0.095
Open canopy : Core distance	-17.13	-28.43 – -5.83	0.003
Random Effects			
σ^2	1951.11		
τ_{00} plots	411.39		
τ_{00} sites	0.45		
ICC	0.17		
N _{plots}	40		
N _{sites}	20		
Observations	360		

Marginal R^2 / Conditional R^2

0.182 / 0.325

Table B11: Results of Linear Mixed Models (LMMs) determining the effect of drought-induced die-off (compared to control) on *P. sylvestris* recruits at T3 development stage (old saplings) at (A) 2013, (B) 2017, and (C) 2022 in forests of Catalonia. Significant *p-values* are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column. The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00\text{sites}}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given.

	A. T3 stage (2013)			B. T3 stage (2017)			C. T3 stage (2022)		
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	26.58	11.17 – 41.99	0.001	17.24	4.81 – 29.67	0.008	10.55	-4.42 – 25.52	0.162
Die-off	-9.14	-26.07 – 7.79	0.281	-1.11	-18.55 – 16.33	0.898	10.06	-11.11 – 31.23	0.341
Random Effects									
σ^2	697.05			739.54			1089.45		
$\tau_{00\text{ sites}}$	457.64			11.73			0.00		
ICC	0.40			0.02					
N _{sites}	20			20			20		
Observations	40			40			40		
Marginal R^2 / Conditional R^2	0.018 / 0.407			0.000 / 0.016			0.023 / NA		

Table B12: Results of Linear Mixed Models (LMMs) determining the effect of canopy habitat (defoliated, closed, and open) on *P. sylvestris* at T3 development stage (old saplings) at (A) 2013, (B) 2017, and (C) 2022 in forests of Catalonia. Significant *p-values* are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor column. The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, $\tau_{00}\text{sites}$ and plot, $\tau_{00}\text{plots}$), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and marginal and conditional R^2 values are also given

	A. T3 stage (2013)			B. T3 stage (2017)			C. T3 stage (2022)		
Predictors	Estimates	CI	<i>p</i>	Estimates	CI	<i>p</i>	Estimates	CI	<i>p</i>
(Intercept)	0.09	-18.54 – 18.73	0.992	4.57	-8.79 – 17.92	0.499	5.62	-11.33 – 22.57	0.512
Closed	40.17	16.35 – 63.99	0.001	14.26	-3.36 – 31.87	0.112	1.83	-21.45 – 25.11	0.877
Open	25.58	1.76 – 49.40	0.036	22.09	4.47 – 39.71	0.014	28.05	4.77 – 51.33	0.019
Random Effects									
σ^2	2891.70			1581.87			2761.78		
$\tau_{00}\text{ plots}$	0.00			175.90			166.88		
$\tau_{00}\text{ sites}$	324.22			29.90			0.00		
ICC				0.12					
N_{sites}	20			20			20		
N_{plots}	40			40			40		
Observations	120			120			120		
Marginal R^2 / Conditional R^2	0.088 / NA			0.045 / 0.155			0.057 / NA		

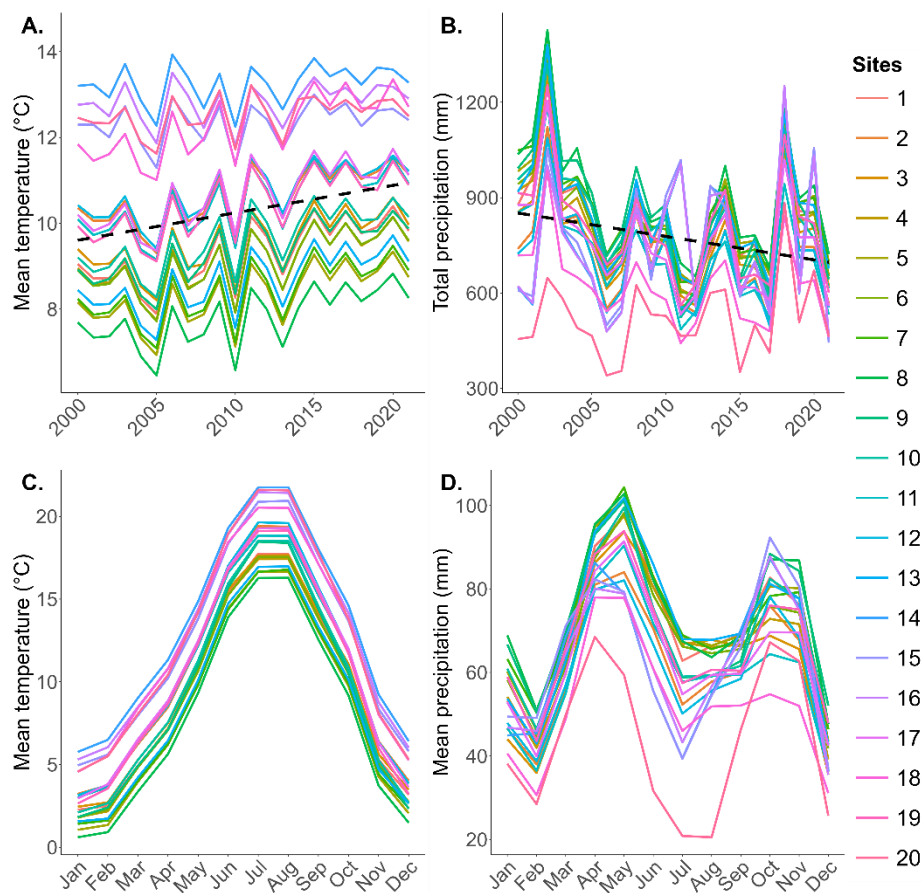


Figure B1: Mean annual temperature (°C; A), annual precipitation (mm; B), mean monthly temperature (°C; C) and mean monthly precipitation (mm; D) across the twenty study sites (see Table S1 for site description). Overall trend line across sites is represented by black dashed line. Daily temperature and precipitation variables are obtained from Cruz-Alonso et al., 2023), and details are given at Methods.

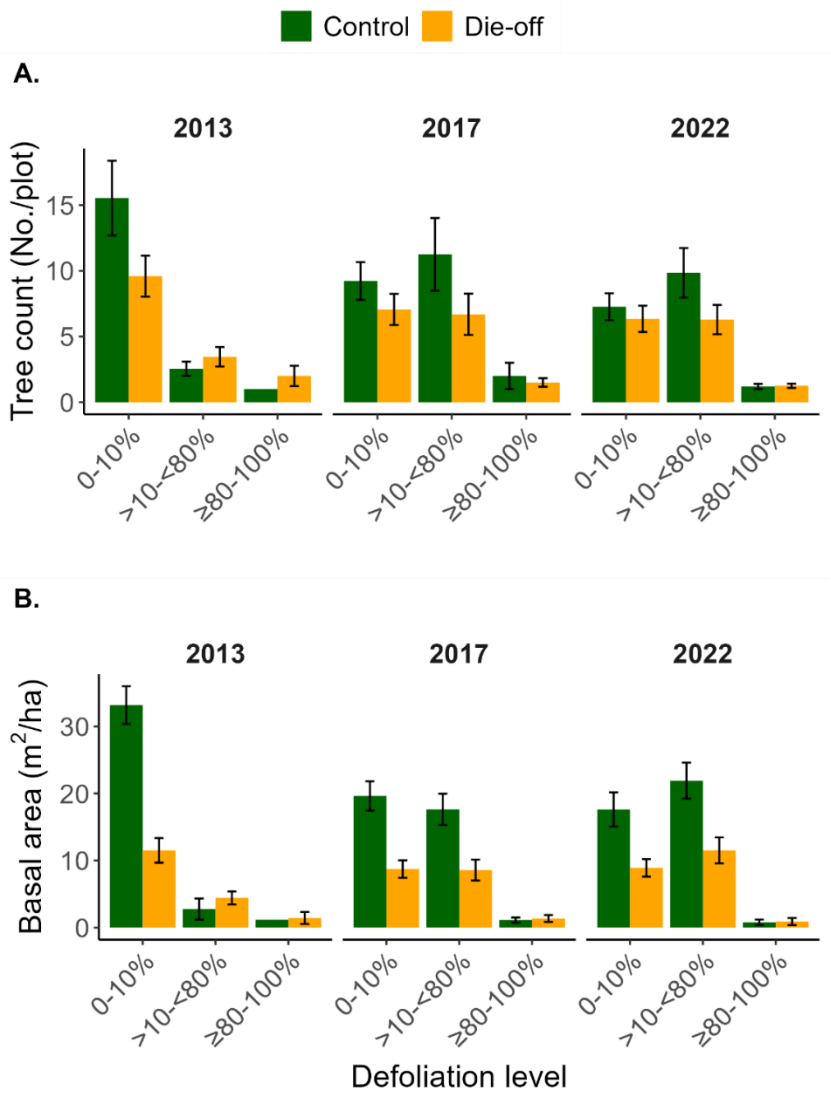


Figure B2: Alive tree count (A) and basal area (B) in control and die-off plots in 2013, 2017, and 2022, shown across defoliation-level classes. Defoliation categories follow those defined in the Methods: 0-10%, >10-<80%, and ≥80-100% defoliation.

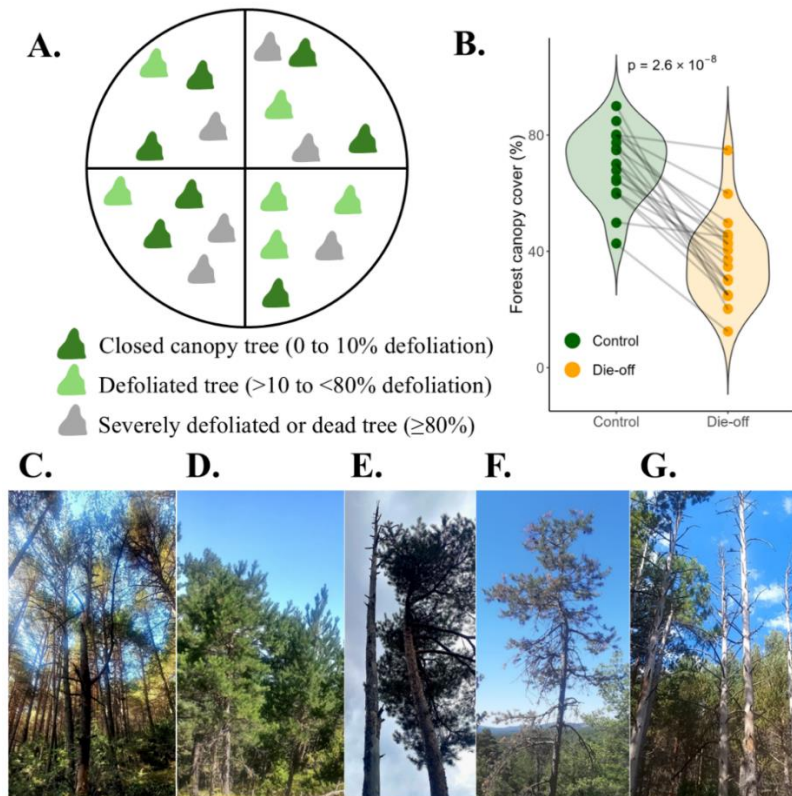


Figure B3: (A) Schematic of study plot illustrating spatial variation in canopy-cover conditions. Individual trees are represented using three defoliation-based categories: healthy (0 to 10% defoliation; dark green), defoliated (>10 to <80% defoliation; light green), and severely defoliated or dead tree (≥80% defoliation; grey). The white areas of the plot represent canopy gaps in the plot. These categories correspond to the canopy-cover habitats used to quantify habitat-level recruit densities (see Methods). (B) Violin plots of forest canopy cover according to forest condition (die-off vs. control) in 2022. P-value of the paired t-test between die-off and control plots is also shown. Connecting lines indicate plots belonging to the same site. (C-G) Field photographs illustrating the visual criteria used to assign canopy cover types in the field. (C) Example of overall forest canopy structure corresponding to the schematic in panel A. (D) Closed-canopy trees (0-10 % defoliation). (E) Mixed canopy containing defoliated trees (crown thinned) and dead trees (complete foliage loss). (F) Individual defoliated trees (>10-<80 % defoliation). (G) Dead or severely defoliated trees (complete crown collapse and missing foliage).

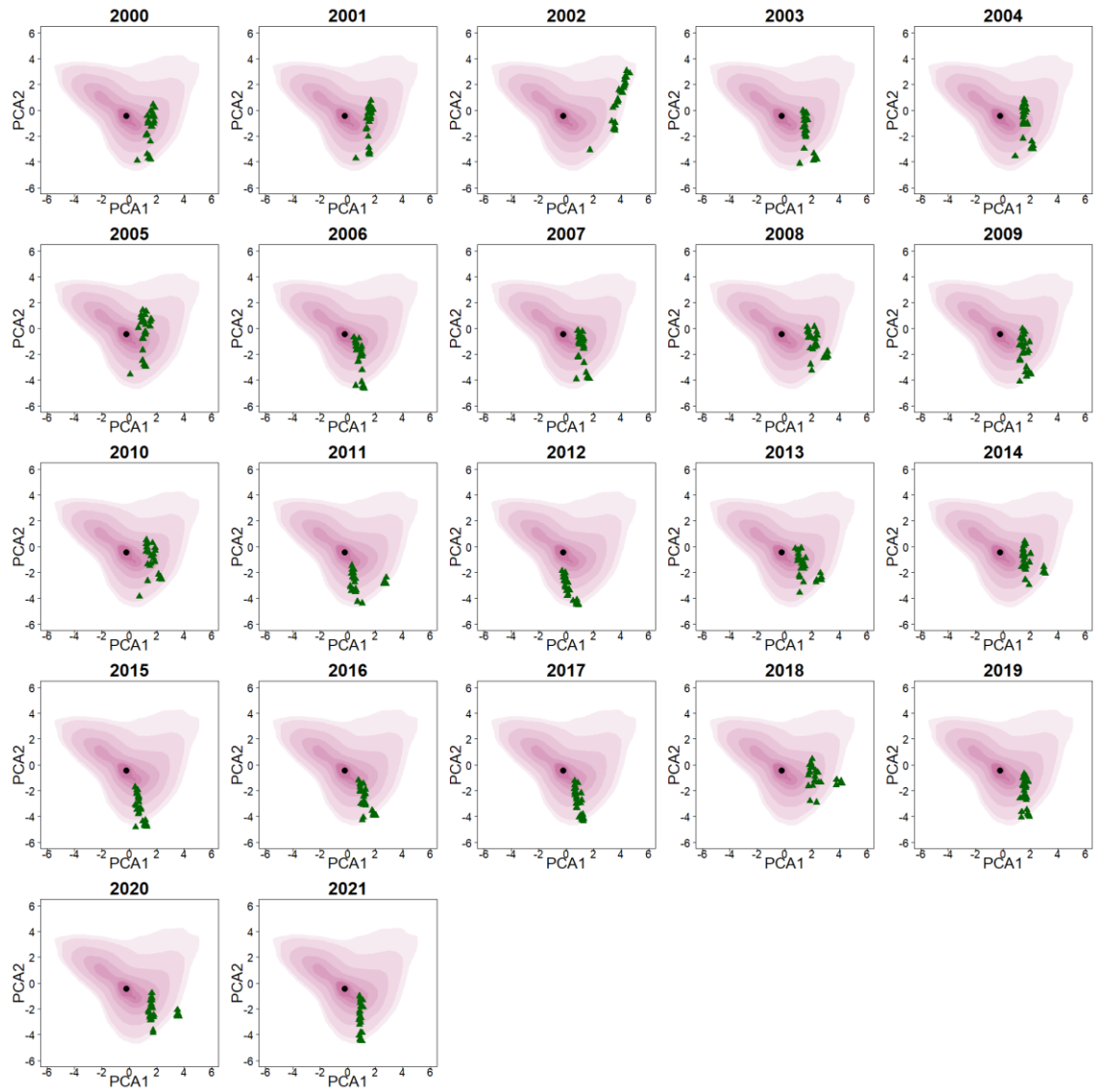


Figure B4: Realized climate niche of *P. sylvestris*, showing the position of study sites (green triangles) for each year (2000-2021) within the PCA-defined climate space. The black dot represents the centroid of the niche (see methods).

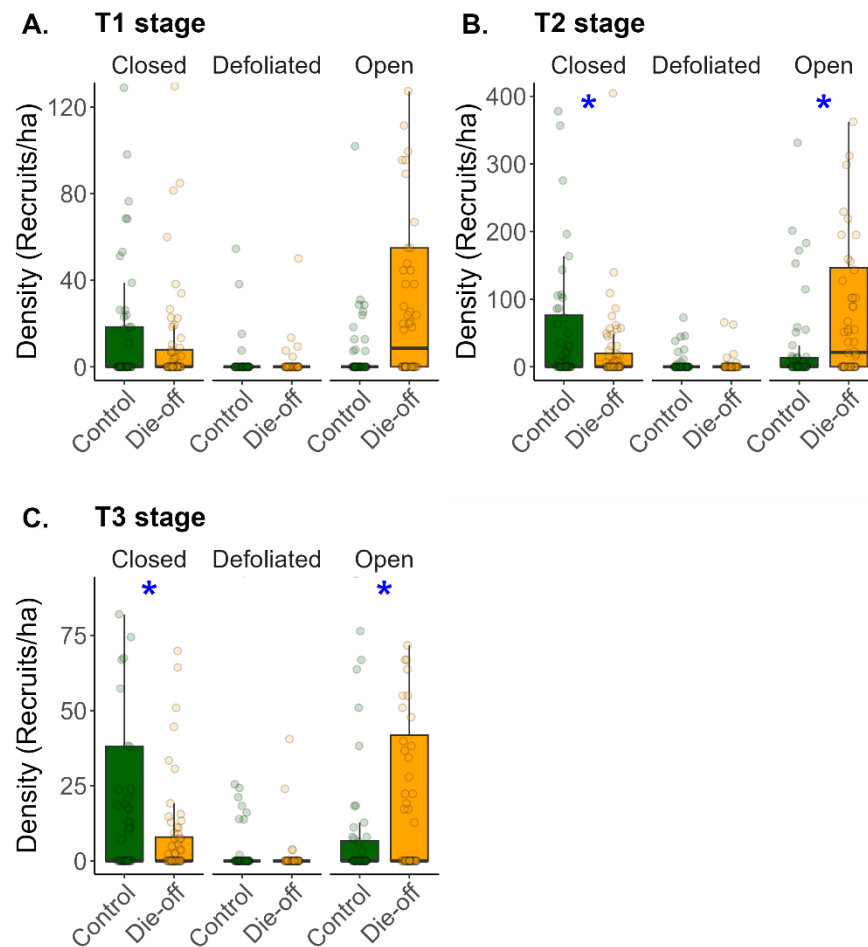


Figure B5: Boxplot of *P. sylvestris* recruit density (recruits/ha) in the different forest conditions (die-off and control) across canopy cover types (closed, defoliated, and open) at different recruits' development stages: (A) T1, (B) T2, and (C) T3. Asterisks (*) indicate statistically significant differences ($p < 0.05$) between forest conditions based on Tukey's HSD test.

Appendix C

Based on chapter 4

Table C1: Geographic, topographic and climate status (mean temperature and precipitation data) in the of 20 studied locations surveyed across Catalonia (NE, Spain)

Plot id	Longitude	Latitude	Country	Elevation	Temperature (°C)	Precipitation (mm)
1	1.577039	42.16438	Solsonès	1560	9.54	796.95
2	1.543319	42.10459	Solsonès	1321	10.72	715.35
3	1.573577	42.22022	Alt Urgell	1304	10.17	718.46
4	1.642382	42.31753	Alt Urgell	1489	9.96	717.40
5	1.65324	42.31369	Alt Urgell	1488	9.12	766.21
6	1.625174	42.33704	Alt Urgell	1456	10.01	722.16
7	1.567203	42.38395	Alt Urgell	1550	9.23	792.72
			Baixa	1434		
8	1.709379	42.33236	Cerdanya		8.46	798.44
9	1.323108	42.24369	Alt Urgell	1554	9.39	800.92
10	1.316169	42.26488	Alt Urgell	1448	9.64	775.41
11	1.28122	42.30836	Alt Urgell	1274	10.41	708.64
12	1.529583	42.09107	Solsonès	1326	10.83	702.92
13	1.559636	42.18425	Solsonès	1659	9.01	811.96
14	2.384135	41.92182	Osona	685	13.75	737.21
15	2.318187	41.8338	Osona	925	12.79	735.46
16	2.358357	41.92602	Osona	767	13.34	745.51
17	1.088749	42.34788	Pallars Sobirà	968	11.12	717.75
18	1.091157	42.35895	Pallars Sobirà	609	12.68	593.92
19	1.05057	42.3529	Pallars Sobirà	1217	10.64	762.27
			Conca de	912		
20	1.008624	41.33876	Barberà		12.59	552.01

Table C2: Structural features (mean $\pm$ SE) of forest plots on the 20 sites experiencing drought (die-off vs control) surveyed across Catalonia (NE Spain) immediately after the drought event (2013) and ten years later (2022)

Basal area considered in the study	Unit	Die-off	Control
Total basal area (alive trees and deadwood) in 2013	m ² /ha	36.44 $\pm$ 3.18	37.77 $\pm$ 3.32
Alive tree basal area in 2013	m ² /ha	16.10 $\pm$ 2.08	34.76 $\pm$ 2.97
Total deadwood basal area (snags only) in 2013	m ² /ha	20.35 $\pm$ 2.22	3.01 $\pm$ 0.65
Total basal area (alive trees and deadwood) in 2022	m ² /ha	46.85 $\pm$ 3.56	44.22 $\pm$ 3.85
Alive tree basal area in 2022	m ² /ha	20.06 $\pm$ 2.14	39.53 $\pm$ 3.58
Total deadwood basal area (snags and logs) in 2022	m ² /ha	26.79 $\pm$ 2.45	4.69 $\pm$ 0.78
Alive tree density in 2022	No./ha	1092.35 $\pm$ 126.79	1235.67 $\pm$ 158.85

Table C3: Types of tree conditions considered in the study, according to their structural features, from alive trees to the two types of dead trees (snags and logs) according to LIFE RedBosques (2019) and different decaying stages for snags and logs according to Bouget et al. (2024): (A) Complete expanded Table and (B) Table with the simplified decaying stages.

Sl. No.	Variables	Description
A	<i>Alive tree</i>	i = Healthy, living trees, having all leaves and branches in good health.
	<i>(tree aspect i-ii)</i>	ii = Defoliated, living trees, having visible symptoms of decay (browning or defoliation > 50% but <100%), or broken canopy by abiotic or biotic agent.
	<i>Snag</i>	iii = Dead tree without leaves and in which less than the 50% of the twigs are dropped, but the main branches are present.
	<i>(tree aspect iii-ix)</i>	iv = Dead trees without leaves or twigs, in which more than 50% of branches are lost, and the tips part of the remaining branches are usually broken. v = Dead tree in which most of the branches, and some bases of the branches remain empty, and the top is broken. vi = Dead trees without any branches, some at the base of the trunk are present but rotten, and approximately 2/3 of the tree is still standing. vii = Dead trees without branches, minimal remnants of rotten branches at the base of the trunk, and approximately 1/2 of the trunk remains. viii = Dead trees without branches or remains of rotten branches and approximately 1/3 of the trunk remains. ix = Dead trees with woody stump and accumulations of debris.
	<i>Log</i>	x = Downed deadwood that just fell, with bark, branches, and twigs. Intact and hard wood texture.
	<i>(tree aspect x-xiv)</i>	xi = Downed deadwood that is intact and hard, no evidence of decomposition. Branches are present. Missing bark in chunks. xii = Downed deadwood with the evidence of decomposition. Parts of the wood remained hard but other can be totally rotten. No branches are present. There may be traces of bark. xiii = Downed deadwood that has partially decomposed trunk. Mainly soft wood. Trunk completely laid on the ground. There may be traces of hard wood. xiv = Downed deadwood with decomposed trunk extremely soft texture. Trunk completely laid on the ground. Partially covered by organic soil or epiphytes.
B	<i>Simplified decaying stages</i>	Two decaying phases were considered for each tree conditions: • <i>alive tree: healthy</i> (tree aspect i) and <i>defoliated</i> (tree aspect ii) <i>trees</i>, • <i>snag: unbroken</i> (aspect iii – v) and <i>broken snag</i> (aspect vi – ix), • <i>log: hard</i> (aspect x – xi) and <i>soft log</i> (aspect xii – xiv).

Table C4: Tree-related Microhabitat (TreM) types and characteristics.

Variables	Description
TreM types	(i) Insect galleries, (ii) woodpecker cavities, (iii) other cavities, (iv) injuries and wounds, (v) bark complexity, (vi) crown deadwood, (vii) deformation/growth form, (viii) fruiting bodies of fungi, (ix) epiphytes, (x) nest, and (xi) others (resin/sap residues, micro-soil, etc.).
Diversity of TreM	Richness, diversity (Shannon index), and evenness (Pielou index) of TreM in all tree conditions, as well as in alive trees, snags, and logs.
Saproxyllic/Epixylic type TreM	i) Saproxyllic type TreM consist of woodpecker cavities, insect galleries, other cavities, damage signs, bark complexity, crown deadwood, stem deformation, nests, and sap residues. ii) Epixylic type TreM consist of fruiting bodies of fungi and epiphytes.

Table C5: Abundance (mean $\pm$ SE) of TreM types surveyed in 2022 in twenty pairs of *P. sylvestris*-dominated plots in sites of Catalonia where drought-induced die-off was observed. TreM abundance across all tree conditions (TC), alive trees, snags, and logs. *NA* denotes that this TreM was not available

TreM types	Drought impact	All TC	Alive tree	Snag	Log
Insect galleries	Die-off	21.25 $\pm$ 2.1	1.1 $\pm$ 0.33	6.6 $\pm$ 1.29	13.55 $\pm$ 1.76
	Control	8.85 $\pm$ 1.61	1.55 $\pm$ 0.53	2.9 $\pm$ 0.54	4.4 $\pm$ 1.24
Woodpecker cavity	Die-off	6.4 $\pm$ 0.96	0.15 $\pm$ 0.11	2.8 $\pm$ 0.71	3.45 $\pm$ 0.71
	Control	1.05 $\pm$ 0.34	0.25 $\pm$ 0.16	0.45 $\pm$ 0.15	0.35 $\pm$ 0.13
Other cavities	Die-off	11.15 $\pm$ 1.46	0.55 $\pm$ 0.23	2.00 $\pm$ 0.51	8.60 $\pm$ 1.52
	Control	4.30 $\pm$ 0.85	0.80 $\pm$ 0.33	0.75 $\pm$ 0.26	2.75 $\pm$ 0.77
Injuries and wounds	Die-off	15.55 $\pm$ 2.24	5.20 $\pm$ 1.51	2.15 $\pm$ 0.53	8.20 $\pm$ 1.96
	Control	10.10 $\pm$ 2.08	4.30 $\pm$ 0.96	1.65 $\pm$ 0.53	4.15 $\pm$ 1.44
Bark complexity	Die-off	8.85 $\pm$ 1.06	0.60 $\pm$ 0.28	4.05 $\pm$ 0.96	4.20 $\pm$ 0.77
	Control	8.50 $\pm$ 2.02	1.15 $\pm$ 0.52	4.05 $\pm$ 1.28	3.30 $\pm$ 1.11
Crown deadwood	Die-off	5.70 $\pm$ 1.24	5.70 $\pm$ 1.24	<i>NA</i>	<i>NA</i>
	Control	13.40 $\pm$ 2.39	13.40 $\pm$ 2.39	<i>NA</i>	<i>NA</i>
Deformation/growth form	Die-off	0.60 $\pm$ 0.41	0.55 $\pm$ 0.36	0.00 $\pm$ 0.00	0.05 $\pm$ 0.05
	Control	1.75 $\pm$ 0.95	1.65 $\pm$ 0.95	0.00 $\pm$ 0.00	0.10 $\pm$ 0.10
Fruiting bodies of fungi	Die-off	1.75 $\pm$ 0.49	0.15 $\pm$ 0.08	0.55 $\pm$ 0.22	1.05 $\pm$ 0.40
	Control	0.65 $\pm$ 0.24	0.30 $\pm$ 0.18	0.15 $\pm$ 0.11	0.20 $\pm$ 0.12
Epiphytes	Die-off	12.55 $\pm$ 1.91	5.55 $\pm$ 1.26	3.10 $\pm$ 0.63	3.90 $\pm$ 0.85
	Control	8.15 $\pm$ 1.38	4.70 $\pm$ 1.03	1.75 $\pm$ 0.42	1.70 $\pm$ 0.35
Nests	Die-off	0.20 $\pm$ 0.16	0.05 $\pm$ 0.05	0.15 $\pm$ 0.15	0.00 $\pm$ 0.00
	Control	0.35 $\pm$ 0.22	0.35 $\pm$ 0.22	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
Others (<i>Sap, resin, micro-soil. etc</i>)	Die-off	2.30 $\pm$ 0.44	1.60 $\pm$ 0.37	0.50 $\pm$ 0.15	0.20 $\pm$ 0.12
	Control	2.40 $\pm$ 0.60	1.90 $\pm$ 0.46	0.25 $\pm$ 0.12	0.25 $\pm$ 0.20

Table C6: Results of LMMs to determine the effect of drought-induced die-off and climate since the die-off episode (e.g., temperature and precipitation) on mortality extent, based on dead wood basal area, in *P. sylvestris* forest of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor's column, which is reduced from the full model (see methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and Marginal and conditional R^2 values are also shown.

<i>Predictors</i>	Mortality extent		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.13	0.05 – 0.20	0.002
Die-off	0.63	0.52 – 0.73	<0.001
Temperature	-0.02	-0.09 – 0.05	0.572
Precipitation	-0.01	-0.08 – 0.05	0.672
Random effect statistics			
σ^2	0.03		
τ_{00}	0.00		
N	20		
Observations	40		
Marginal R^2 / Conditional R^2	0.793 / 0.793		

Table C7: Results of LMMs to determine the effect of drought-induced die-off and climate since die-off (e.g., temperature and precipitation) on tree decay (proportion of partly defoliated trees out of alive trees) in *P. sylvestris* forest of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor's column, which is reduced from the full model (see methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and Marginal and conditional R^2 values are also shown.

Tree decay			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.04	0.00 – 0.08	0.045
Die-off	0.05	0.01 – 0.09	0.019
Random effect statistics			
σ^2	0.00		
τ_{00}	0.00		
ICC	0.54		
N	20		
Observations	40		
Marginal R^2 / Conditional R^2	0.067 / 0.568		

Table C8: Results of LMMs to determine the effect of drought-induced die-off and climate since die-off (e.g., temperature and precipitation) on (A) total deadwood, (B) snags, and (C) logs basal area in 2022 in *P. sylvestris* forest of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor's column, which is reduced from the full model (see methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and Marginal and conditional R^2 values are also shown.

<i>Predictors</i>	A. Total deadwood basal area in 2022			B. Snag basal area in 2022			C. Log basal area in 2022		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	4.51	1.68 – 7.35	0.003	3.74	1.28 – 6.20	0.004	0.78	-0.02 – 1.57	0.055
Die-off	22.55	18.54 – 26.56	<0.001	18.13	14.64 – 21.61	<0.001	4.42	3.30 – 5.54	<0.001
Basal area in 2013	4.63	2.45 – 6.81	<0.001	3.83	1.93 – 5.73	<0.001	0.80	0.19 – 1.41	0.012
Temperature	1.93	-1.06 – 4.91	0.198	1.62	-0.98 – 4.22	0.213	0.31	-0.53 – 1.14	0.459
Die-off : Temperature	-5.01	-9.06 – -0.95	0.017	-3.71	-7.24 – -0.18	0.040	-1.30	-2.43 – -0.16	0.026
Random effect statistics									
σ^2	38.72			29.26			3.03		
τ_{00}	0.00			0.00			0.00		
N	20			20			20		
Observations	40			40			40		
Marginal R^2 / Conditional R^2	0.800 / 0.800			0.773 / 0.773			0.671 / 0.671		

Table C9: Results of LMMs to determine the effect of drought-induced die-off and climate since die-off (e.g., temperature and precipitation) on (A) snags and (B) logs proportion in *P. sylvestris* forest of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor's column, which is reduced from the full model (see methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and Marginal and conditional R^2 values are also shown.

<i>Predictors</i>	A. Snag proportion			B. Log proportion		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.73	0.63 – 0.83	<0.001	0.27	0.17 – 0.37	<0.001
Die-off	0.08	-0.07 – 0.22	0.297	-0.08	-0.22 – 0.07	0.296
Temperature	-0.02	-0.09 – 0.06	0.643			
Precipitation				-0.03	-0.10 – 0.04	0.427
Random effect statistics						
σ^2	0.05			0.05		
τ_{00}	0.00			0.00		
N	20			20		
Observations	40			40		
Marginal R^2 / Conditional R^2	0.033 / 0.033			0.043 / 0.043		

Table C10: Results of LMMs to determine the effect of drought-induced die-off and climate since die-off (e.g., temperature and precipitation) on deadwood decaying stages namely, (A) unbroken proportion, (B) broken snags proportion, (C) hard logs, and (D) soft logs proportion in *P. sylvestris* forest of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor's column, which is reduced from the full model (see methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and Marginal and conditional R^2 values are also shown.

<i>Predictors</i>	A. Unbroken snag proportion			B. Broken snag proportion			C. Hard log proportion			D. Soft log proportion		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	0.43	0.31 – 0.56	<0.001	0.47	0.33 – 0.60	<0.001	0.31	0.18 – 0.44	<0.001	0.64	0.51 – 0.78	<0.001
Die-off	-0.28	-0.46 – -0.11	0.002	0.38	0.21 – 0.56	<0.001	-0.12	-0.29 – 0.04	0.138	0.17	0.02 – 0.33	0.029
Precipitation	0.16	0.03 – 0.28	0.017	-0.14	-0.27 – -0.01	0.033	-0.16	-0.29 – -0.03	0.018	0.19	0.05 – 0.32	0.008
Die-off : Precipitation	-0.15	-0.33 – 0.03	0.098	0.14	-0.04 – 0.31	0.131	0.21	0.04 – 0.38	0.015	-0.23	-0.39 – -0.08	0.005
Random effect statistics												
σ^2	0.07			0.07			0.07			0.06		
τ_{00}	0.01			0.01			0.02			0.03		
ICC	0.07			0.11			0.20			0.33		
N	20			20			20			20		
Observations	40			40			40			40		
Marginal R^2 / Conditional R^2	0.296 / 0.342			0.367 / 0.434			0.181 / 0.344			0.234 / 0.489		

Table C11: Results of LMMs to determine the effect of drought-induced die-off and climate since die-off (e.g., temperature and precipitation) on (A) richness, (B) diversity (Shannon index), (C) evenness (Pielou index) of deadwood types in *P. sylvestris* forest of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor's column, which is reduced from the full model (see methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and Marginal and conditional R^2 values are also shown.

<i>Predictors</i>	A. Richness			B. Diversity			C. Evenness		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	5.48	4.78 – 6.19	<0.001	1.02	0.85 – 1.19	<0.001	0.60	0.51 – 0.68	<0.001
Die-off	1.64	0.64 – 2.64	0.002	0.26	0.06 – 0.47	0.013	0.06	-0.03 – 0.15	0.199
Temperature	-1.23	-1.90 – -0.57	0.001	-0.32	-0.51 – -0.14	0.001	-0.17	-0.28 – -0.05	0.005
Precipitation	-0.97	-1.80 – -0.14	0.023	-0.25	-0.46 – -0.04	0.021	-0.12	-0.24 – -0.01	0.031
Die-off : Precipitation	1.36	0.34 – 2.37	0.010	0.20	-0.00 – 0.41	0.055	0.07	-0.05 – 0.19	0.234
Die-off : Temperature							0.06	-0.06 – 0.18	0.288
Random effect statistics									
σ^2	2.42			0.10			0.02		
τ_{00}	0.00			0.05			0.01		
ICC				0.32			0.44		
N	20			20			20		
Observations	40			40			40		
Marginal R^2 / Conditional R^2	0.476 / 0.476			0.376 / 0.574			0.267 / 0.586		

Table C12: Results of LMMs to determine the effect of drought-induced die-off and climate since die-off (e.g., temperature and precipitation) on TreM abundance in (A) all tree conditions (TC), (B) alive trees, (C) snags, and (D) logs in *P. sylvestris* forest of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor's column, which is reduced from the full model (see methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and Marginal and conditional R^2 values are also shown.

	A. All TC				B. Alive trees				C. Snags				D. Logs			
Predictors	Estimates CI		p		Estimates CI		p		Estimates CI		p		Estimates CI		p	
(Intercept)	62.25	51.42 73.07	–	<0.001	30.65	24.06 – 37.23	<0.001		12.13	5.95 – 18.31	<0.001		19.51	8.88 – 30.15	0.001	
Die-off	27.08	15.20 38.96	–	<0.001	-9.08	-13.00 – 5.16	<0.001		10.39	1.65 – 19.13	0.021		25.68	13.01 38.36	–	<0.001
Basal area in 2013	13.99	5.43 – 22.55		0.002	4.78	0.49 – 9.07	0.030		-1.28	-7.65 – 5.09	0.685		7.53	-2.80 – 17.87		0.147
Precipitation	-12.56	-23.3 – -1.86		0.023									-8.52	-19.06 – 2.02		0.109
Die-off : precipitation	17.15	4.91 – 29.40		0.007									16.32	3.26 – 29.38		0.016
Temperature					0.94	-5.66 – 7.55	0.774		-4.03	-8.79 – 0.73	0.094					
Die-off : Temperature					4.55	0.59 – 8.51	0.026									
Die-off : Basal area in 2013									8.80	-0.06 17.66	– 0.052		-6.61	-19.95 – 6.72		0.320
Random effect statistics																
σ^2	339.47				36.62				184.20				385.84			
τ_{00}	225.68				172.73				0.00				157.94			
ICC	0.40				0.83								0.29			

	A. All TC	B. Alive trees	C. Snags	D. Logs
N	20	20	20	20
Observations	40	40	40	40
Marginal R^2 / Conditional R^2	0.457 / 0.674	0.193 / 0.859	0.298 / 0.298	0.327 / 0.523

Table C13: Results of LMMs to determine the effect of drought-induced die-off and climate since die-off (e.g., temperature and precipitation) on abundance of saproxylic TreM in (A) all tree conditions (TC), (B) alive trees, (C) snags, and (D) logs in *P. sylvestris* forest of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor's column, which is reduced from the full model (see methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and Marginal and conditional R^2 values are also shown.

	A. All TC			B. Alive trees			C. Snags			D. Logs		
Predictors	Estimates CI		p	Estimates CI		p	Estimates CI		p	Estimates CI		p
(Intercept)	51.19	40.40 – 61.98	<0.001	23.56	17.81 – 29.31	<0.001	10.01	4.47 – 15.55	0.001	17.62	7.41 – 27.84	0.001
Die-off	21.51	9.33 – 33.69	0.001	-9.38	-14.40 – -4.36	0.001	8.30	0.61 – 15.99	0.035	22.57	11.12 – 34.03	<0.001
Basal area in 2013	10.84	0.48 – 21.20	0.041	5.59	0.30 – 10.89	0.039	-0.25	-5.73 – 5.24	0.928	6.23	-3.57 – 16.02	0.205
Precipitation	-12.20	-22.87 – -1.53	0.026							-8.16	-18.27 – 1.94	0.110
Die-off : Basal area in 2013	2.05	-10.83 – 14.93	0.748	-0.34	-6.18 – 5.51	0.908	8.03	0.20 – 15.87	0.045	-4.19	-16.31 – 7.94	0.487
Die-off : Precipitation	19.80	7.21 – 32.38	0.003							15.58	3.74 – 27.43	0.012
Temperature				3.75	-2.34 – 9.85	0.219						
Die-off : Temperature				2.16	-3.37 – 7.70	0.431						
Random effect statistics												
σ^2	356.09			60.38			142.80			315.13		
τ_{00}	203.76			98.68			5.48			186.93		
ICC	0.36			0.62			0.04			0.37		
N	20			20			20			20		
Observations	40			40			40			40		

	A. All TC	B. Alive trees	C. Snags	D. Logs
Marginal R^2 / Conditional R^2	0.400 / 0.618	0.271 / 0.723	0.233 / 0.262	0.299 / 0.560

Table C14: Results of LMMs to determine the effect of drought-induced die-off and climate since die-off (e.g., temperature and precipitation) on abundance of epixylic TreM in (A) all tree conditions (TC), (B) alive trees, (C) snags, and (D) logs in *P. sylvestris* forest of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor's column, which is reduced from the full model (see methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and Marginal and conditional R^2 values are also shown.

	A. All TC			B. Alive trees			C. Snags			D. Logs		
Predictors	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
(Intercept)	11.21	7.06 – 15.36	<0.001	6.85	4.16 – 9.55	<0.001	2.11	0.82 – 3.40	0.002	2.15	0.48 – 3.81	0.013
Die-off	5.38	0.93 – 9.82	0.019	0.49	-2.71 – 3.70	0.756	2.08	0.55 – 3.61	0.009	3.01	0.80 – 5.22	0.009
Precipitation	-1.56	-5.06 – 1.94	0.372							0.15	-1.12 – 1.41	0.817
Basal area in 2013				0.93	-1.28 – 3.14	0.399	0.84	-0.15 – 1.84	0.093	0.08	-1.17 – 1.33	0.896
Temperature				-0.23	-2.55 – 2.10	0.845						
Random effect statistics												
σ^2	47.99			24.84			5.65			11.78		
τ_{00}	35.52			10.26			2.37			1.69		
ICC	0.43			0.29			0.30			0.13		
N	20			20			20			20		
Observations	40			40			40			40		
Marginal R^2 / Conditional R^2	0.106 / 0.486			0.031 / 0.314			0.178 / 0.421			0.148 / 0.255		

Table C15: Results of LMMs to determine the effect of drought-induced die-off and climate since die-off (e.g., temperature and precipitation) on TreM richness in (A) all tree conditions (TC), (B) alive trees, (C) snags, and (D) logs in *P. sylvestris* forest of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor's column, which is reduced from the full model (see methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and Marginal and conditional R^2 values are also shown.

	A. All TC			B. Alive trees			C. Snags			D. Logs		
Predictors	Estimates CI		p	Estimates CI		p	Estimates CI		p	Estimates CI		p
(Intercept)	8.58	8.09 – 9.07	<0.001	5.79	4.80 – 6.77	<0.001	4.18	3.39 – 4.97	<0.001	4.72	3.87 – 5.57	<0.001
Die-off	0.60	0.04 – 1.16	0.038	-0.57	-1.56 – 0.41	0.245	1.53	0.42 – 2.65	0.009	1.67	0.59 – 2.75	0.003
Basal area in 2013	0.57	0.16 – 0.97	0.007	0.34	-0.48 – 1.16	0.406				0.84	0.15 – 1.53	0.018
Temperature	0.17	-0.26 – 0.60	0.425	-0.00	-1.21 – 1.20	0.997	-1.19	-1.93 – -0.46	0.002	0.28	-0.43 – 1.00	0.423
Precipitation				-0.40	-1.53 – 0.73	0.474	-0.78	-1.52 – -0.04	0.039			
Random effect statistics												
σ^2	0.76			2.34			3.02			2.81		
τ_{00}	0.41			2.34			0.00			0.69		
ICC	0.35			0.50						0.20		
N	20			20			20			20		
Observations	40			40			40			40		
Marginal R^2 / Conditional R^2	0.234 / 0.502			0.070 / 0.535			0.319 / 0.319			0.266 / 0.411		

Table C16: Results of LMMs to determine the effect of drought-induced die-off and climate since die-off (e.g., temperature and precipitation) on TreM diversity (Shannon index) in (A) all tree conditions (TC), (B) alive trees, (C) snags, and (D) logs in *P. sylvestris* forest of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor's column, which is reduced from the full model (see methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and Marginal and conditional R^2 values are also shown.

	A. All TC			B. Alive trees			C. Snags			D. Logs		
Predictors	Estimates CI		p	Estimates CI		p	Estimates CI		p	Estimates CI		p
(Intercept)	1.78	1.69 – 1.87	<0.001	1.29	1.09 – 1.49	<0.001	1.22	1.03 – 1.41	<0.001	1.29	1.11 – 1.47	<0.001
Die-off	0.12	0.00 – 0.23	0.045	-0.03	-0.28 – 0.21	0.792	0.28	0.01 – 0.54	0.040	0.29	0.05 – 0.53	0.020
Basal area in 2013	0.07	0.00 – 0.14	0.045	0.09	-0.08 – 0.26	0.289				0.10	-0.04 – 0.25	0.164
Temperature	0.04	-0.03 – 0.11	0.287	0.06	-0.17 – 0.29	0.590	-0.31	-0.48 – -0.13	0.001	0.11	-0.04 – 0.26	0.149
Precipitation				-0.03	-0.24 – 0.19	0.792	-0.18	-0.36 – -0.01	0.041			
Random effect statistics												
σ^2	0.03			0.14			0.17			0.14		
τ_{00}	0.00			0.05			0.00			0.02		
ICC	0.09			0.26						0.13		
N	20			20			20			20		
Observations	40			40			40			40		
Marginal R^2 / Conditional R^2	0.176 / 0.248			0.052 / 0.294			0.305 / 0.305			0.177 / 0.284		

Table C17: Results of LMMs to determine the effect of drought-induced die-off and climate since die-off (e.g., temperature and precipitation) on TreM evenness (Pielou index) in (A) all tree conditions (TC), (B) alive trees, (C) snags, and (D) logs in *P. sylvestris* forest of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor's column, which is reduced from the full model (see methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and Marginal and conditional R^2 values are also shown.

	A. All TC			B. Alive trees			C. Snags			D. Logs		
Predictors	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
(Intercept)	0.83	0.81 – 0.86	< 0.001	0.76	0.71 – 0.82	< 0.001	0.83	0.73 – 0.93	< 0.001	0.82	0.73 – 0.92	< 0.001
Die-off	0.03	-0.01 – 0.06	0.168	0.05	0.00 – 0.11	0.044	0.06	-0.08 – 0.20	0.353	0.04	-0.09 – 0.18	0.511
Basal area in 2013	0.01	-0.01 – 0.03	0.430							-0.02	-0.09 – 0.05	0.585
Temperature	0.01	-0.01 – 0.03	0.274	0.02	-0.03 – 0.06	0.474	-0.06	-0.13 – 0.02	0.127			
Random effect statistics												
σ^2	0.00			0.01			0.05			0.04		
τ_{00}	0.00			0.01			0.00			0.00		
ICC				0.53								
N	20			20			20			20		
Observations	40			39			39			40		
Marginal R^2 / Conditional R^2	0.079 / 0.079			0.072 / 0.565			0.082 / 0.082			0.020 / 0.020		

Table C18: Results of LMMs to determine the effect of drought-induced die-off and climate since die-off (e.g., temperature and precipitation) on abundance of insect galleries in (A) all tree conditions (TC), (B) alive trees, (C) snags, and (D) logs in *P. sylvestris* forest of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor's column, which is reduced from the full model (see methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and Marginal and conditional R^2 values are also shown.

	A. All TC			B. Alive trees			C. Snags			D. Logs		
Predictors	Estimates CI		p	Estimates CI		p	Estimates CI		p	Estimates CI		p
(Intercept)	8.72	5.72 – 11.72	<0.001	1.56	0.74 – 2.38	<0.001	2.90	1.01 – 4.79	0.004	4.31	1.58 – 7.03	0.003
Die-off	12.71	8.85 – 16.57	<0.001	-0.46	-1.40 – 0.47	0.323	3.74	1.07 – 6.42	0.007	9.37	5.96 – 12.78	<0.001
Basal area in 2013	3.35	1.07 – 5.64	0.005							2.36	0.26 – 4.46	0.029
Precipitation	-3.70	-6.68 – -0.72	0.016	-1.20	-2.01 – -0.39	0.005				-2.03	-4.73 – 0.68	0.137
Die-off : Precipitation	7.84	3.90 – 11.79	<0.001	0.78	-0.17 – 1.73	0.106				4.73	1.23 – 8.22	0.010
Temperature							0.20	-1.71 – 2.12	0.830			
Die-off : Temperature							-2.68	-5.38 – 0.03	0.053			
Random effect statistics												
σ^2	35.85			2.12			17.30			27.99		
τ_{00}	7.51			1.12			0.00			7.82		
ICC	0.17			0.35						0.22		
N	20			20			20			20		
Observations	40			40			40			40		
Marginal R^2 / Conditional R^2	0.613 / 0.680			0.215 / 0.486			0.276 / 0.276			0.486 / 0.598		

Table C19: Results of LMMs to determine the effect of drought-induced die-off and climate since die-off (e.g., temperature and precipitation) on abundance woodpecker cavities in (A) all tree conditions (TC), (B) snags, and (C) logs in *P. sylvestris* forest of Catalonia. Significant p-values are highlighted in bold. CI corresponds to the confidence interval at 95%. The fixed effect variables of the best models are given in the predictor's column, which is reduced from the full model (see methods for details). The random effects show the variance explained by the fixed factors (σ^2), the random factors (in our case site, τ_{00}), the Interclass Correlation Coefficient (ICC), and the number of plot locations (N). The number of observations and Marginal and conditional R^2 values are also shown.

	A. All TC			B. Snags			C. Logs		
Predictors	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
(Intercept)	1.04	-0.12 – 2.21	0.077	0.45	-0.30 – 1.19	0.230	0.34	-0.68 – 1.36	0.503
Die-off	5.41	3.76 – 7.05	<0.001	2.44	1.39 – 3.49	<0.001	3.12	1.74 – 4.50	<0.001
Temperature	-0.27	-1.45 – 0.91	0.640	-0.20	-1.01 – 0.61	0.626	-0.53	-1.29 – 0.23	0.165
Die-off : Temperature	-2.57	-4.24 – -0.90	0.004	-1.44	-2.59 – -0.30	0.015			
Basal area in 2013				0.02	-0.78 – 0.81	0.966			
Die-off : Basal area in 2013				1.20	0.06 – 2.34	0.040			
Random effect statistics									
σ^2	6.55			2.65			4.64		
τ_{00}	0.02			0.00			0.41		
ICC	0.00						0.08		
N	20			20			20		
Observations	40			40			40		
Marginal R^2 / Conditional R^2	0.635 / 0.636			0.613 / 0.613			0.352 / 0.405		

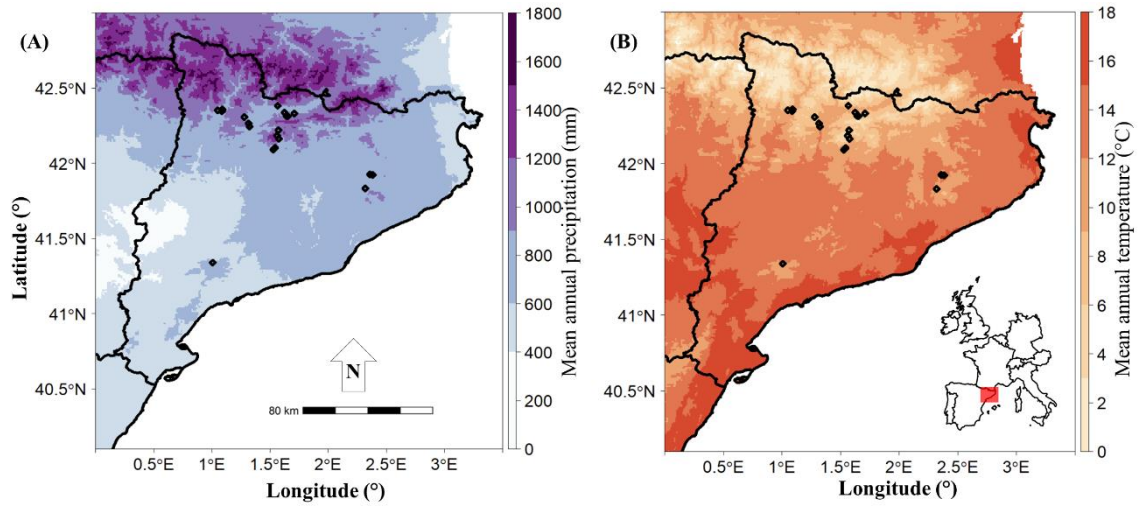


Figure C1: Map of the study area, showing the locations of the twenty surveyed plot pairs. The precipitation raster layer for making the map was obtained from Fick and Hijmans (2017).

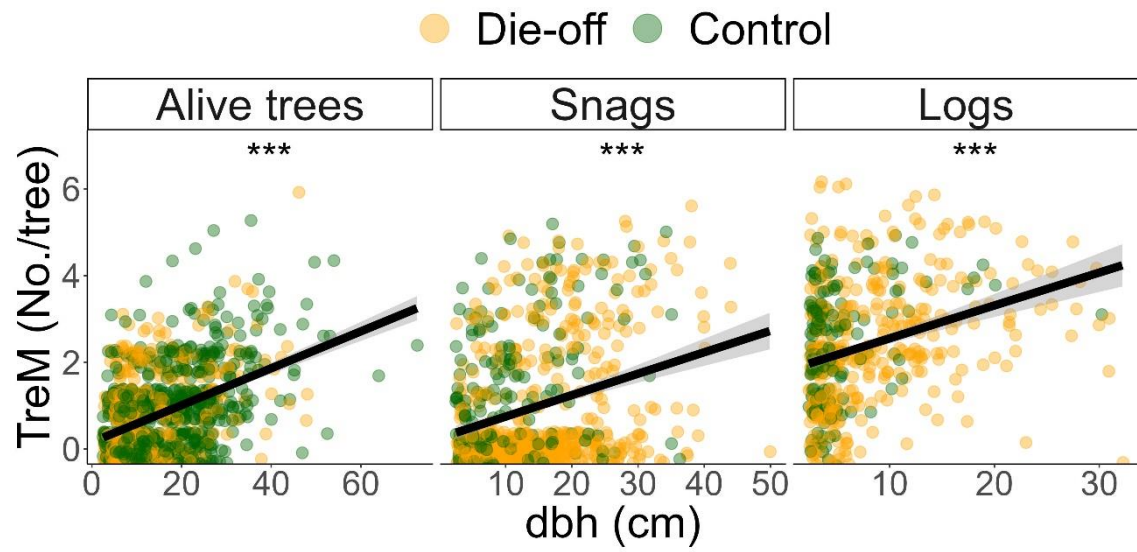


Figure C2: Relationship between dbh (diameter at breast height) and richness of TreM at tree level. Asterisk signs indicate significance level of p-values (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

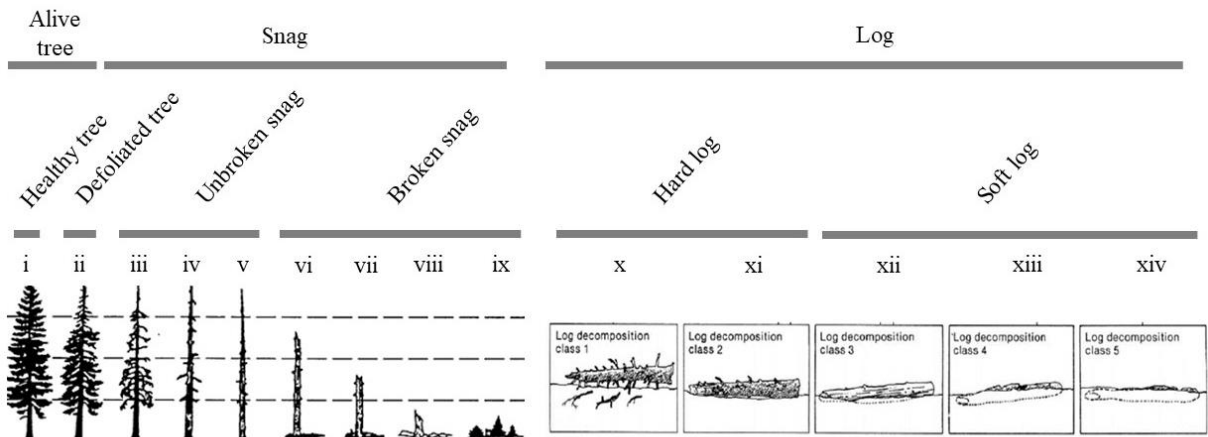


Figure C3: Different tree decaying stages considered in this study (adopted from Kraus et al., 2016; Larrieu et al., 2018).

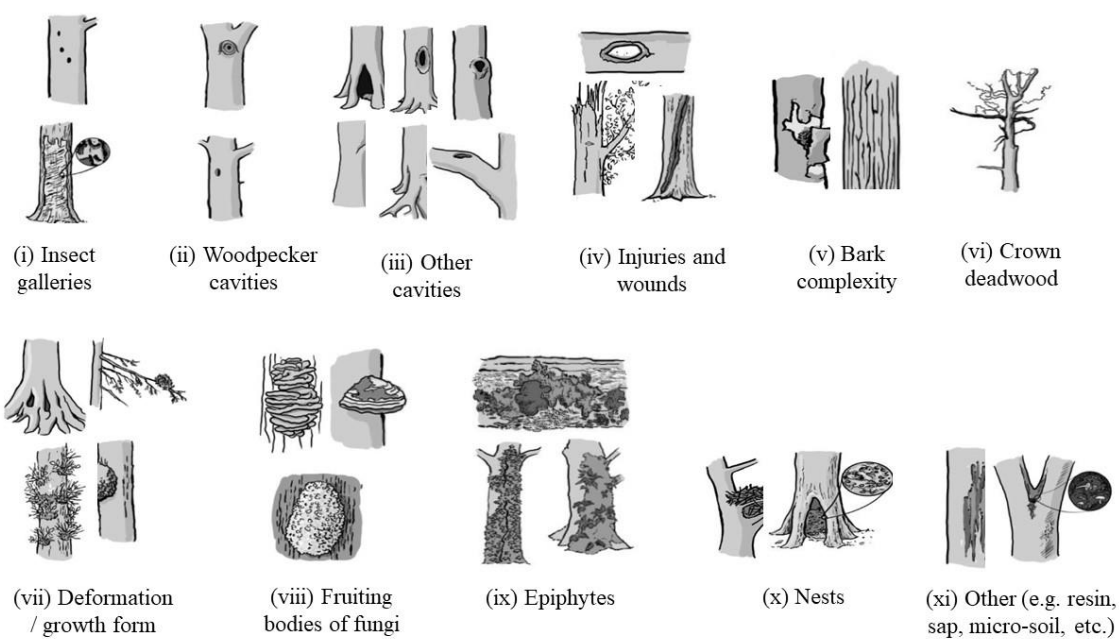


Figure C4: Different TreM types considered in this study (adopted from Larrieu et al., 2018).

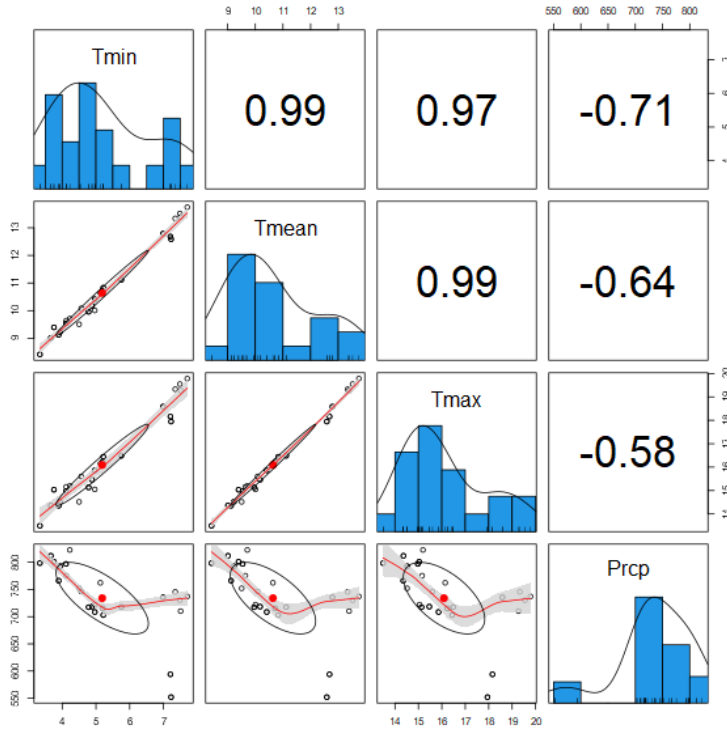


Figure C5: Correlation between the different climate variables obtained from *easyclimate* dataset (Cruz-Alonso et al., 2023) in the twenty studied sites after the drought-induced die-off event in 2012 (see more in methods). Tmin, Tmean, Tmax, and Prcp indicate mean annual minimum temperature, mean annual temperature, mean annual maximum temperature, and yearly precipitation.

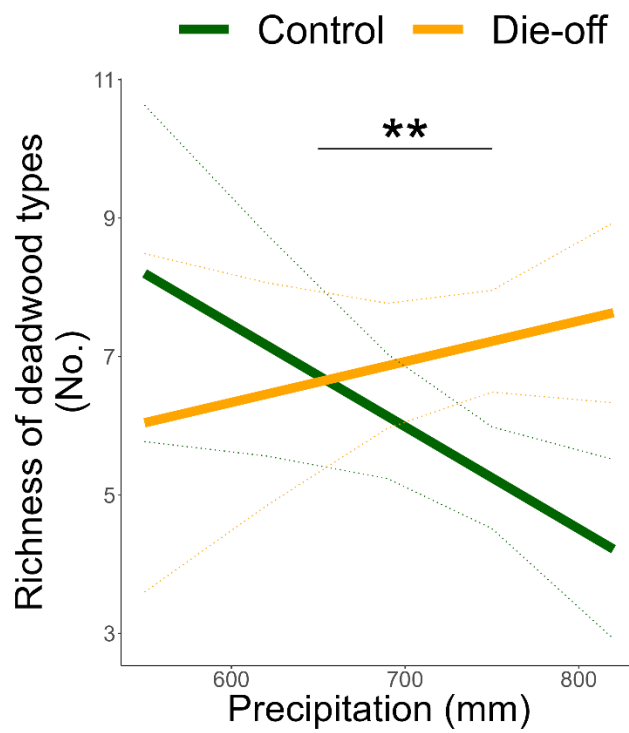


Figure C6: Interaction effect of forest condition (drought induced die-off plots vs control plots) and total basal area in 2013 on the richness of deadwood types. Asterisk signs indicate the significance level of p-values (* : $p < 0.05$, ** : $p < 0.01$, *** $p < 0.001$). The envelop around the effect lines denotes to confidence interval.

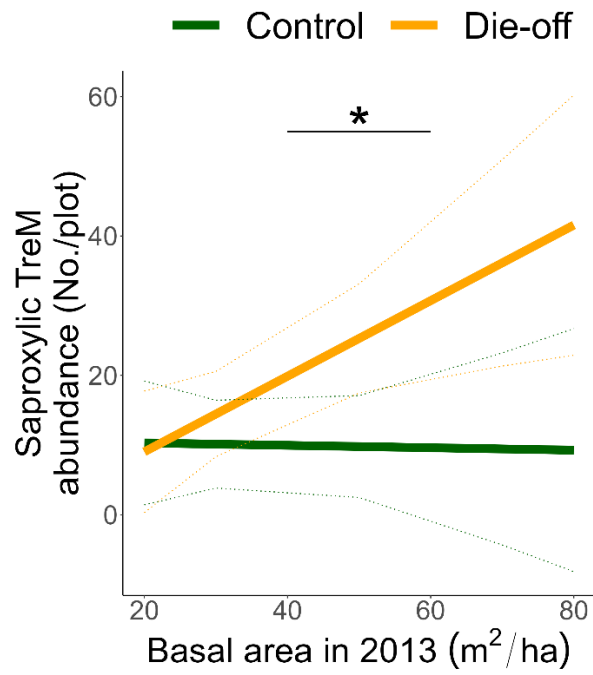


Figure C7: Interaction effect of forest condition (drought induced die-off plots vs control plots) and total basal area in 2013 on the abundance (number per plot) of saproxylic Tree-related Microhabitat (TreM). Asterisk signs indicate the significance level of p-values (* : $p < 0.05$, ** : $p < 0.01$, *** $p < 0.001$). The envelop around the effect lines denotes confidence interval.

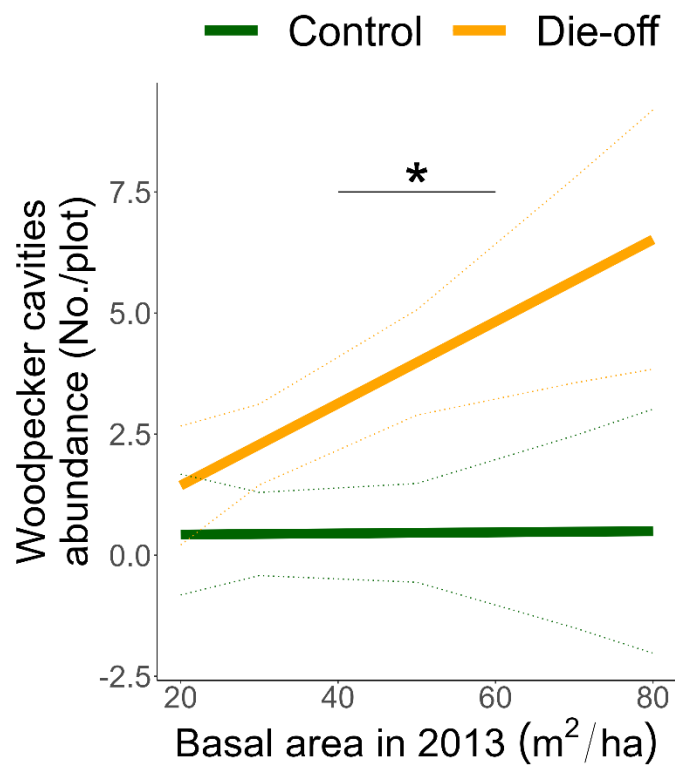


Figure C8: Interaction effect of forest condition (drought induced die-off plots vs control plots) and total basal area in 2013 on the abundance (number per plot) of woodpecker cavities. Asterisk signs indicate the significance level of p-values (* : $p < 0.05$, ** : $p < 0.01$, *** $p < 0.001$). The envelop around the effect lines denotes confidence interval.

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