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Unprecedented but understudied: A brief review of climate-induced forest decline in Central Chile

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ABSTRACT

Mediterranean-type ecosystems (MTEs) are among the most biodiverse and climate-vulnerable ecosystems globally. Rising temperatures, combined with more frequent and intense droughts, have driven widespread forest decline across all five MTE regions, accounting for 48% of globally documented forest mortality events. Among these, Central Chile has experienced the most severe climatic anomalies, including a persistent megadrought since 2010, two hyperdroughts in 2019 and 2021 with precipitation deficits exceeding 75%, and recurrent spring and summer heatwaves. These unprecedented conditions position Central Chile as a potential worst-case scenario for the future of MTEs worldwide. This review synthesises current knowledge on climate-induced forest decline in Central Chile, summarising recent research conducted across multiple spatial and ecological scales. Emerging evidence reveals a regional forest decline characterised by reduced productivity, radial growth declines, impaired seedling establishment, and widespread canopy browning. While these responses are comparable to those observed in other MTEs, the ecological implications of hyperdroughts and regional warming for forest resilience remain poorly understood. Despite growing research efforts, critical knowledge gaps persist regarding forest mortality rates, regeneration dynamics, and the physiological mechanisms underlying tree survival and mortality. We identify key research priorities, including the need for quantified mortality data, mechanistic understanding of decline processes, assessment of post-disturbance ecological dynamics, and integrative approaches that link plot-based observations with remote sensing and modelling. Addressing these gaps is essential to evaluate changes in productivity, species composition, and the long-term trajectory of Chilean MTEs, while contributing to a broader predictive understanding of forest resilience in Mediterranean-type ecosystems globally.

1. Introduction

Understanding the impacts of climate change on natural ecosystems is one of the most challenging issues for scientists and policymakers. Anthropogenic emissions of greenhouse gasses have constantly increased since the 19th Century (IPCC, 2023), leading to an overall increase in global temperature and causing planetary-scale effects on natural ecosystems, including reductions in snow-covered areas, sea level rise and increasingly intense, prolonged and frequent droughts (Cook et al., 2018; Hooijer and Vernimmen, 2021; Young, 2023). Coupled with changes in land use, more frequent heat waves, and wildfires, these conditions have driven a widespread forest decline in recent decades (Scheffer et al., 2001; Sato and Lindenmayer, 2018; Lloret and Batllori, 2021; Hartmann et al., 2022), defined as a progressive reduction of forest productivity and health (Auclair et al., 1997). Moreover, current climatic projections suggest that the observed climatic trends are likely to be maintained or accelerate during the rest of the 21st Century (Zappa et al., 2020), with serious implications for terrestrial ecosystems' carbon and hydrological dynamics (IPCC, 2023).

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Forests are among the most vulnerable ecosystems to climate change, especially in mid-latitudes and Mediterranean-type regions (Sala et al., 2000; Giorgi and Lionello, 2008; Giorgi et al., 2019). They cover one-third of the Earth's land surface and play a major role dominating the structural patterns and processes in their ecosystems, including regulating the water cycle and functioning as a carbon recycling mechanism (Pan et al., 2011; Choat et al., 2018). Since trees have adapted to local environmental conditions for thousands of years (Allen et al., 2010; Kijowska-Oberc et al., 2020), accelerated climate change, including rising temperatures, prolonged droughts, and extreme weather events, can affect their resilience, defined as the capacity to absorb disturbances, recover and reorganize while maintaining their structure, identity and functions (Folke et al., 2010), which can potentially lead to collapse (Greenwood et al., 2017; Anderegg et al., 2019; Hammond et al., 2022). Climate change, therefore, poses major risks to forests as it is leading to consequences such as a reduction in photosynthetic activity, radial growth, germination rates and tree mortality, observed at a global scale (Anderson-Teixeira et al., 2021; Italiano et al., 2024; González-Reyes et al., 2024; Vicente and Benito Garzón, 2024), all of which are indicators of forest decline. Within this context, MTEs appear as one of the most threatened by the current and future climatic conditions (Allen et al., 2015; Anderegg et al., 2016 & 2019; Greenwood et al., 2017), due to their high exposure to global change drivers, including climate warming, altered precipitation regimes, land-use change, and biological invasions (Underwood et al., 2009; Rundel et al., 2016; Peñuelas et al., 2017; Aurelle et al., 2022).

MTEs occur in five regions worldwide, namely the Mediterranean Basin, California, the Cape Region of South Africa, southwestern Australia, and Central Chile, and are characterized by a distinctive climate of cool, wet winters and hot, dry summers (Aschmann, 1973).

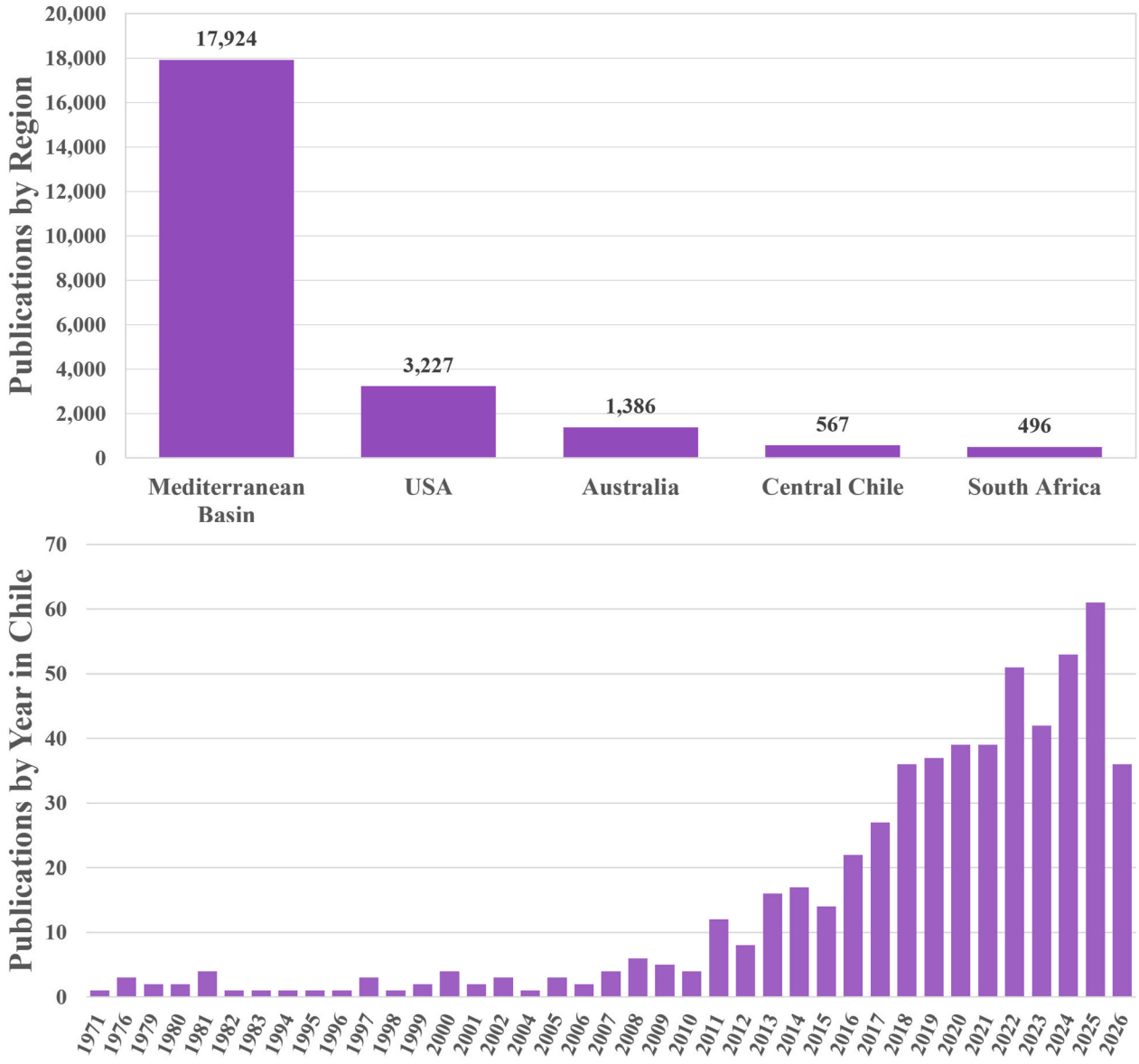


Fig. 1. Number of peer-reviewed publications related to MTEs across major global regions, based on the Web of Science database, and number of publications per year in Central Chile. The search was performed in September 2026 and included all publications available. For each region, we used a combination of Boolean operators and search strings structured around three thematic blocks: (i) climate-related terms (e.g., "climate change," drought, heatwave, "extreme heat," "heat-wave," hotter, and decline), (ii) MTE-related terms (e.g., Mediterranean, "Mediterranean-type," MTE, MTEs), and (iii) vegetation/ecosystem terms (e.g., forest, woodland, shrub, sclerophyll, chaparral, fynbos, matorral), combined with region-specific geographic terms (Chile; Mediterranean Basin countries; California/southwestern US; South Africa/Cape Region; Australia/southwestern Australia). The search was restricted to article titles, abstracts, and keywords. Only peer-reviewed journal articles and review articles were included, whereas book chapters, conference proceedings, and editorials were excluded.

Even though these ecosystems cover less than 5% of the Earth's land surface, these regions have exceptionally high levels of plant diversity, largely due to their climatic variability, and long-term evolutionary stability (Cowling et al., 1996; Myers et al., 2000; Rundel et al., 2016). They also contribute to carbon storage, water balance, and support high biodiversity in areas with high anthropogenic pressure (Carnicer et al., 2019; Klausmeyer and Shaw, 2009). However, despite these key functions, only 4% of the total coverage of MTEs is protected by law worldwide (Klausmeyer and Shaw, 2009).

Among all MTEs, the Mediterranean bioregion of Central Chile (32-36.5°S, 70.5-71.5°W) is one of the most affected by climate change, as it is the only one that is experiencing a drying process in all seasons (Seager et al., 2024). Moreover, the severity of droughts affecting this region since 2010 is unmatched in the recent history of all MTEs, with severe consequences on forest productivity and triggering a widespread canopy browning event (Miranda et al., 2023). This makes Central Chile an outstanding natural laboratory for studying the ecological consequences of unprecedented extreme droughts on Mediterranean-type forests (Arroyo et al., 1995; Schneider-Valenzuela et al., 2023; Delpiano et al., 2024). Hence, the combination of these conditions, coupled with the increased probability of future hyperdroughts (Garreaud et al., 2025), emphasises the urgency for studying unprecedented climatic stress on Mediterranean-type forests. However, despite the severity of droughts found in Central Chile and the increasing literature on the related subjects (Fig. 1), research in this region remains scarce (567 publications since the 1970s) compared to other Mediterranean-type regions such as the Mediterranean basin (17,924) and California (3,227). Consequently, studying drought-induced forest decline in Central Chile constitutes both an urgent scientific priority and a rare opportunity to anticipate the future trajectories of Mediterranean ecosystems under accelerating climate change.

Given this opportunity to study the effects of extreme droughts on Mediterranean-type forests, this non-systematic review aims to **(i)** contextualize the relevance of Central Chile within the broader framework of global MTEs vulnerability, by characterizing its climate, dominant forest types, and the unprecedented severity of recent drought conditions; **(ii)** summarize existing evidence of climate-induced forest decline across ecological scales, from individual trees to regional landscapes in Central Chile; and **(iii)** identify key knowledge gaps to propose a roadmap for future research.

As this review is non-systematic, we explicitly acknowledge its limitations regarding reproducibility. Our literature selection was guided by the following criteria: we included peer-reviewed journal articles published primarily since 2010 to capture research coincident with the Central Chile megadrought, and we excluded book chapters and grey literature to ensure methodological consistency across sources. While we endeavoured to survey the breadth of relevant literature through targeted searches in major ecological journals and citation tracking, we do not claim exhaustive coverage. These limitations should be considered when interpreting the knowledge gaps and priorities identified.

2. Climate change impacts on mediterranean-type ecosystems

2.1. Overview of mediterranean-type ecosystems

The World Meteorological Organization's (WMO, 2024) *"State of the Global Climate 2023"* report states that 2023 was 1.45 ± 0.12 °C above the 1850-1900 baseline, marking the first year whose uncertainty range overlaps the 1.5 °C threshold. The IPCC projects that this threshold will be crossed "in the near term" and state that every additional increment in temperature intensifies the risk of natural hazards like droughts and heatwaves (IPCC, 2023). In this global context, Mediterranean-type regions emerge as particularly vulnerable to climate change, largely driven by above-average warming rates and their heightened exposure to extreme events such as droughts and heatwaves (Vogel et al., 2021; Zhang et al., 2024). This vulnerability has already been observed across several Mediterranean-type regions worldwide. For instance, precipitation in south-west Australia has declined by 20% during the 21st century (Rauniyar et al., 2023), while northern Italy increasingly experiences the occurrence of simultaneous heatwaves and droughts (Lazoglou et al., 2024). These conditions have been directly linked to increased risks of forest fires, such as the events recorded in California (Swain et al., 2025) and Central Chile (Kolden et al., 2025) in the past years and pose a significant threat to the overall health of native forests. Moreover, significant reductions in forest productivity have been observed in all Mediterranean regions, with Chile exhibiting the strongest declines (Brouwers and Coops, 2016; Alexander et al., 2023; Miranda et al., 2023; Tijerín-Triviño et al., 2025; Dalmonech et al., 2026). Changes in forest distribution have also been reported in both xeric and sclerophyllous species, with xeric species colonising into humid areas due to higher rates of water stress, phenomenon associated with desertification, while sclerophyllous trees tend to migrate to higher elevations (Bussotti et al., 2014; Eldridge et al., 2011; Maestre et al., 2009). Furthermore, according to the International Tree Mortality Network's database (https://www.tree-mortality.net/globaltreemortalitydatabase/), 48% of all forest mortality events recorded between 1970 and 2018 occurred in Mediterranean-type regions like California (Mueller et al., 2005), South Africa (Rundel et al., 2016), the Mediterranean Basin (Senf et al., 2020) and western Australia (Godfree et al., 2019). Together, these cases evidence the IPCC's assessment of increasing risk of natural hazards and illustrate the consequences of the "business as usual" emissions pathway (IPCC, 2023).

2.2. Overview of Chilean Mediterranean bioregion

MTEs in South America can only be found in Central Chile, where they span a geographical transition across the Coastal and Andean mountain ranges. The climate in this region is primarily determined by the interaction between the Southeast Pacific Subtropical Anticyclone and the seasonal migration of the mid-latitude westerly winds. During the austral winter, the westerlies shift equatorward, bringing frontal precipitation to the region; conversely, during the austral summer, the subtropical anticyclone intensifies and shifts poleward, suppressing rainfall and creating the characteristic hot, dry summers of Mediterranean-type climates (Garreaud et al., 2010; Sarricolea et al., 2017). Superimposed on this seasonal cycle, the region's climate is also modulated by large-scale modes of variability, including the El Niño-Southern Oscillation and the Southern Annular Mode, which influence interannual precipitation variability inducing sporadic drought years (Garreaud et al., 2017).

This region is recognised as a biodiversity hotspot due to its high proportion of endemic species (Myers et al., 2000) and hosts a wide variety of ecosystems and forest types due to its geographical and environmental heterogeneity (Payne et al., 2017). Forest ecosystems in Central Chile stand out for their high biodiversity, productivity, and soil fertility that, in places like Santiago de Chile, generally exceeds or even double the global average (Pantoja et al., 2025), and are primarily composed of xeric and shrubland ecosystems alongside sclerophyllous and deciduous forests (Fig. 2) (Bannister et al., 2012). Xeric and shrubland ecosystems are characterized by open forests of evergreen xerophytic species, growing up to 1500 m.a.s.l. most usually found in northern-exposure slopes, and dominated by shrubs and thorny species, seasonal herbs, succulents and cacti (Donoso, 1982). The sclerophyllous forests are mainly classified into three community types: hygrophilous and riparian forest, sclerophyllous moist forest and sclerophyllous dry forest (https://simbio.mma.gob.cl/). The first type corresponds to ecosystems associated with permanent or seasonal water availability along rivers, streams, and groundwater-dependent environments. These conditions support taller, large-stature tree species and higher biomass, including *Beilschmiedia miersii*, *Myrceugenia exsucca, Persea lingue*, and *Crinodendron patagua*. Moist sclerophyllous forests represent the low-elevation ravines and south-facing slopes, where the reduced

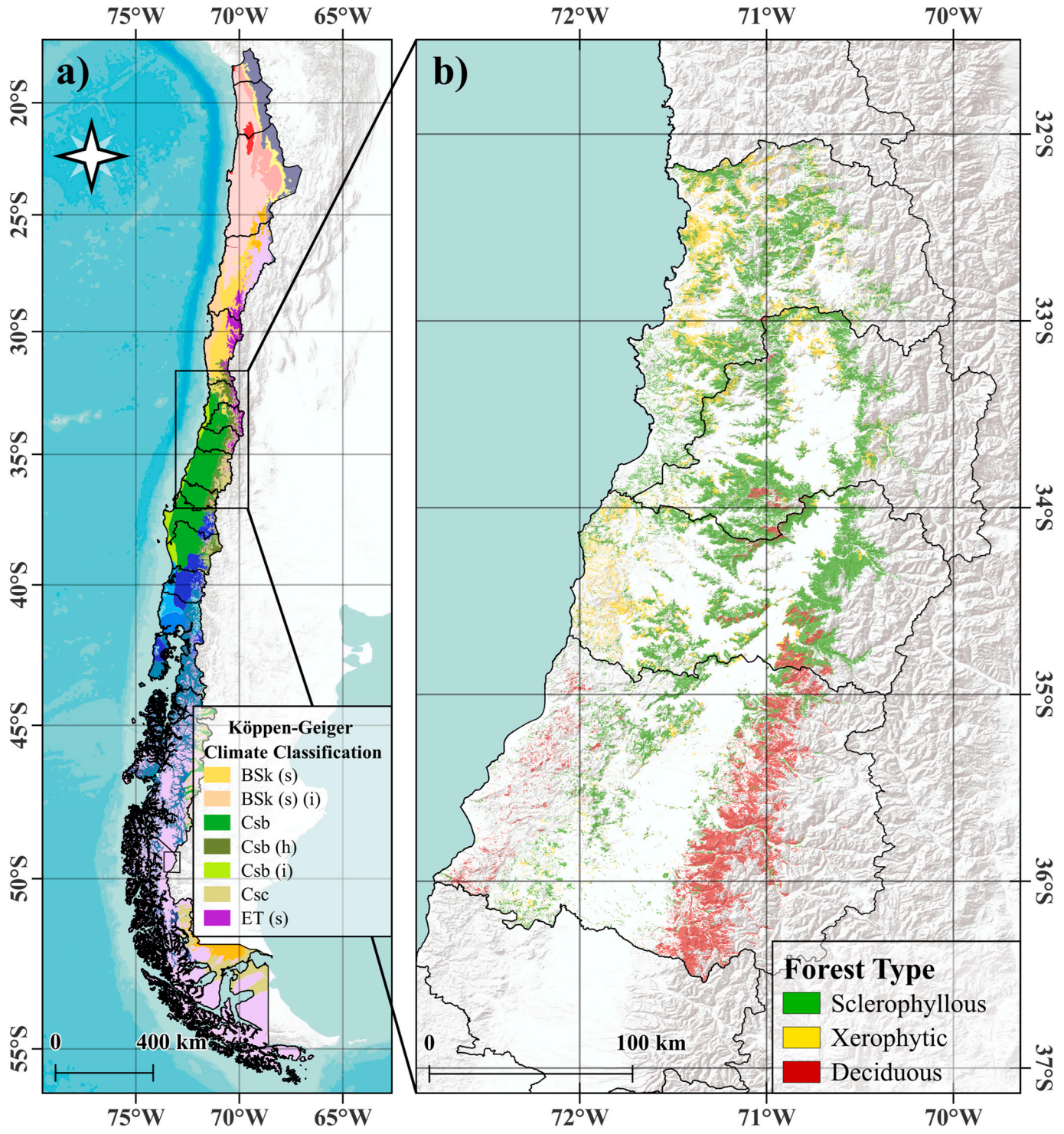


Fig. 2. Distribution of Mediterranean-type forests in Central Chile. The figure illustrates **a)** the spatial extent of the Mediterranean-type climate region in Central Chile from the updated version of the Köppen-Geiger climate classification (Kottek et al., 2006) elaborated by (Sarricolea et al., 2017). The classification is represented using the following legend: **BSK (s)** Cold Semi-arid climate with dry summer, **BSk (s) (i)** Cold Semi-arid climate with dry summer and oceanic influence, **Csb** Mediterranean climate (warm summer), **Csb (h)** Mediterranean climate (warm summer) with mountain influence, **Csb (i)** Mediterranean climate (warm summer) with oceanic influence, **Csc** Mediterranean climate (mild summer), **ET (s)** Tundra climate with dry summer. The map **b) s**hows the distribution of native forests derived from the National Forest Cadastre from the Valparaíso to Maule administrative regions.

sunlight preserves humidity and set microclimatic conditions suitable for drought-sensitive species, like the *Cryptocarya alba, Peumus boldus,* and *Schinus latifolius*. Dry-sclerophyllous forests are mainly located in low to mid-elevation northern exposure slopes, where direct solar radiation increases temperature and atmospheric water demand (vapour pressure deficit - VPD), making it more suitable for drought-resistant tree species like *Quillaja saponaria, L. caustica, Vachellia caven and Kageneckia oblonga*. Finally, deciduous forests are dominated by *Nothofagus* spp, distributed in discontinuous populations at medium (300-1000 m a.s.l.: *Nothofagus glauca* and *N. obliqua*) and high elevations

(*N. macrocarpa* 1300–2000 m.a.s.l.) (Donoso, 1982). These forests are relicts from the last glacial period (Villagrán, 1995) and are smaller in extent, more isolated and potentially at greater risk of habitat loss and mortality than other forests in this MTE (Mathiasen et al., 2020; Venegas-González et al., 2018a).

Forests in Central Chile are increasingly threatened by the combined pressures of climate change and human activity. The Chilean Mediterranean bioregion overlaps with approximately 65% of the country's total population, substantially increasing the risk of anthropogenic impacts (Delpiano et al., 2024). Forests in this region have been proven to be particularly vulnerable to prolonged droughts, heatwaves, and habitat degradation driven by anthropic activities (Schulz et al., 2010; Garreaud et al., 2017; Miranda et al., 2017; Garreaud et al., 2020; Barría et al., 2021a), experiencing extensive surface losses due to land-use change, including conversion to urban areas, vineyards, and water-demanding timber plantations (Van de Wouw et al., 2011; Viers et al., 2013; Miranda et al., 2017).

Consistent with broader trends observed in MTEs, the current condition of Chilean Mediterranean-type forests has been further exacerbated by severe climate anomalies, particularly during the 2010-2022 period, the driest and warmest decade in the region since the 14th century (Garreaud et al., 2017 & 2020). Since 2010, Central Chile has experienced an extreme and prolonged drought, with precipitation deficits of 25-45%, culminating with two hyperdroughts in 2019 and 2021 that exceeded 75% of precipitation deficit (Alvarez-Garreton et al., 2021; Garreaud et al., 2025), an unprecedented event in the recent history of all Mediterranean regions (Miranda et al., 2023). Additionally, under ongoing drought conditions, heatwaves have become more frequent during spring and summer (González-Reyes et al., 2023). This has contributed to declines in lake levels (Fuentealba et al., 2021), snow cover (Dietz et al., 2025), and glacier surface area in the Andes mountain range, thereby reducing water availability for both forests and people (McCarthy et al., 2022). This long-term decline in water availability suggests that Chile could be going through an aridification process, transitioning from episodic droughts towards a more arid climate (Zambrano et al., 2025). Under this scenario of rapid environmental change, the risk of ecosystem-level collapse has emerged as a critical and pressing challenge.

3. Climate-induced forest decline in mediterranean Chile

Climate induced forest decline has been increasingly reported across all MTEs, and Central Chile represents a particularly illustrative case. Research addressing this issue in this region has increased in recent years, addressing how rising temperatures, together with more frequent, prolonged and severe droughts, have been associated with reduced forest productivity (Miranda et al., 2023), diminished tree growth (Venegas-González et al., 2018a), lowered forest resilience (Venegas-González et al., 2018b), and the emergence of widespread canopy browning events (Fuentes et al., 2025). Thus, consequences of climate-induced forest decline have been observed at all ecological levels. Throughout this review, we use the term 'forest decline' to encompass the full spectrum of drought-induced responses, from reduced germination, growth, and productivity to canopy browning and tree mortality. Where the referenced studies use specific terminology, we retain their original phrasing for accuracy.

3.1. Growth decline

Long-term dendroecological studies consistently reveal a strong sensitivity of tree-ring width to local and regional climate variability across the Chilean Mediterranean bioregion (e.g. Le Quesne et al. (2006), Venegas-González et al. (2018a), Gipoulou-Zúñiga et al. (2025)). Recent studies have provided regional evidence of growth decline in relict *Nothofagus* forests, associated with current drought conditions, showing strong growth-precipitation correlations, and suggesting that future warmer and drier conditions will likely mean growth reductions in *Nothofagus* forests in the future (Venegas-González et al., 2018a, 2018b, & 2019; Matskovsky et al., 2021; Urrutia-Jalabert et al., 2021). In a similar context, studies focused on hygrophilous species such as *C. alba* and *B. miersii* show a marked and persistent decline in radial growth since 2002, strongly correlated with increased climatic water deficit and reduced winter-spring precipitation (Venegas-González et al., 2023). Gibson-Carpintero et al. (2024) also reported how radial growth and biomass accumulation have experienced a substantial decrease during the 2010-2019 period. Furthermore, this phenomenon was observed in xeric, hygrophilous, sclerophyllous and deciduous communities, regardless of their elevation, and with increasing impacts in ecotonal communities. These pieces of evidence are particularly alarming, since even drought-tolerant species are experiencing growth limitations under prolonged water stress (Venegas-González et al., 2023).

Modelling approaches further indicate that soil moisture driven by winter and spring precipitation, and modulated by evaporative demand, closely related to VPD, during spring and summer, is the main limiting factor for radial growth of dominant tree species such as *Austrocedrus chilensis* and *N. macrocarpa*, with projections suggesting further growth declines under future climate scenarios, particularly under high-emission pathways (Matskovsky et al., 2021). Thus, species such as *C. alba*, *P. boldus*, *B. miersii*, *N. macrocarpa* and *A. chilensis* exhibit particularly strong growth-drought response, emphasizing the effects of climate change on tree growth among different types of forests.

Growth sensitivity is strongly age-dependent, with younger trees showing higher responsiveness to climatic variability, particularly winter-spring precipitation and spring-early summer temperatures (Venegas-González et al., 2019). Despite these differences, all age classes display a generalized decline in growth since ~1980, coinciding with regional warming and reduced precipitation. Although rising atmospheric CO_2 may have temporarily enhanced growth in younger trees, this effect has not compensated for the negative impacts of recent drought conditions (Venegas-González et al., 2019). In parallel, resilience to extreme drought events, in terms of tree growth responses as defined by Lloret and Batllori (2021), is modulated by site conditions, with mesic populations exhibiting higher resistance for *N. macrocarpa* populations, whereas xeric populations display faster recovery, reflecting contrasting adaptive strategies (Venegas-González et al., 2022). These patterns suggest that both phenotypic plasticity, genetic differentiation and local environmental conditions play dominant roles in shaping drought responses (Urrutia-Jalabert et al., 2025). At the species level, forest responses are further differentiated by leaf habit and habitats; evergreen sclerophyllous species such as *C. alba* show greater resistance to drought, while more mesic or deciduous species like *N. macrocarpa* and *P. lingue* experience stronger growth declines under sustained water limitation (Gipoulou-Zúñiga et al., 2025). Overall, these findings highlight that drought resilience in central Chilean forests emerges from trade-offs between resistance and recovery, with important implications for forest vulnerability under increasing drought frequency and intensity.

3.2. Productivity decline and forest browning

Remote sensing-based studies in this region reveal how native forests have experienced substantial declines in net primary productivity and vegetation vigour, with the most severe decreases concentrated in the northern distribution of Chilean Mediterranean-type forests (Cueto et al., 2025). These reductions have been directly linked to the persistent drought conditions since 2010, with particularly intense declines after the 2019 and 2021 hyperdroughts (Zambrano et al., 2020; Chávez et al., 2022; Miranda et al., 2023). The unprecedented length and severity of these droughts have also triggered a widespread forest browning event, observed across nearly one-third of the forests in Central Chile after 2019, which occurred in synchronicity along the

region within 100 days (Miranda et al., 2020 & 2023). Browning intensity varied with topography and forest type, with mesic microsites such as ravine bottoms acting as refugia from drought, while semi-arid sclerophyllous forests and north-facing slopes experienced the strongest canopy stress (Miranda et al., 2023). When comparing this case to the global context of MTEs the results confirmed that the magnitude and synchronicity of the browning observed in Central Chile were unmatched elsewhere, with abrupt annual NDVI declines exceeding regional variability for multiple consecutive years and affecting over 90% of forested areas in late 2019 (Miranda et al., 2023). Even though vegetation recovery has been observed (expressed in positive changes of vegetation indices after the extreme droughts), it has been slow and incomplete, with less than 20% of the total area returning to pre-drought conditions after four years (Fuentes et al., 2025). This is consistent with other studies carried out in this region where recovery patterns have been observed in shrublands, although with high heterogeneity over short distances, likely explained by varying soil conditions and species composition (Vega-Briones et al., 2023; Abel et al., 2024). However, despite the growing evidence of recovery, the underlying mechanisms behind this recovery are still unknown, raising serious concerns about the ecological consequences of extreme droughts.

3.3. Reduced regeneration capacity

The observed canopy damage across Chilean Mediterranean-type forests can have negative implications for ecosystem resilience. A lower canopy cover can generate increasing direct solar radiation on the understories, as well as a higher rate of reflected radiation from the soil, increased evaporation, and decreased soil protection from eroding factors like wind or water drops (Magliano et al., 2017; Davis et al., 2019; Suhardi et al., 2020; Zellweger et al., 2020; De Frenne et al., 2021; Webb et al., 2021). Current evidence indicates that water availability is the primary driver of plant survival, growth and ecosystem functioning across Central Chile. Researchers have addressed how soil water availability and shading conditions can determine plant survival. For instance, Acevedo et al. (2024) showed that survival of *N. glauca* seedlings in field conditions was controlled mainly by soil water content, followed by air relative humidity. Experimental field studies have shown that shading can outweigh the benefits of supplemental watering for seedling establishment in sclerophyllous species (Yáñez et al., 2024), highlighting the importance of reduced irradiance and evaporative demand under drought conditions (Davis et al., 2019). Similarly, Magni et al. (2022) found that seedling survival was restricted to dense forest cover, where 55.2% of individuals persisted, while survival was null in more open habitat types, underscoring the role of canopy cover as a critical drought refuge.

Complementing these findings, species selection and intraspecific variability can be relevant for regeneration success, as Espinoza et al. (2026) reported marked interspecific differences in post-transplant survival linked to drought response strategies, while Santelices-Moya et al., 2017 highlighted the role of genetic diversity and phenotypic plasticity in driving variation between and within populations. Moreover, Ocampo-Zuleta et al. (2022) found that increased wildfire frequency in the future may erode the genetic diversity of the native flora, as seed persistence to fire can be a less common trait than previously reported among woody plants from the Chilean Mediterranean region. Resprouting also plays a central role as a regeneration response following extreme events like fires and droughts, enabling post-disturbance recovery (Gómez-González et al., 2017). At broader temporal scales, regeneration dynamics are also tightly coupled to climatic variability, as wet years have been shown to trigger pulses of *N. macrocarpa* establishment, emphasizing the strong dependence of recruitment on favourable moisture conditions (Venegas-González et al., 2018b). Together, these findings highlight the importance of soil water availability, shading, and interannual climatic variability for plant germination and establishment, underscoring how canopy-driven microclimatic buffering mediates plant responses to drought and heat stress (De Frenne et al., 2021).

3.4. Mechanisms of forest decline and tree mortality

Long-term droughts can affect tree survival through multiple interacting physiological pathways involving water transport, carbon assimilation, non-structural carbohydrate (NSC) dynamics, and tissue-level adjustments (McDowell et al., 2022). Rather than acting as mutually exclusive mechanisms, hydraulic dysfunction, carbon limitation and impaired recovery may interact depending on drought duration, atmospheric demand, species traits and local site conditions (McDowell et al., 2008; Hajek et al., 2022). This framework is particularly relevant to Central Chile, where prolonged drought has been accompanied by increasing aridity, recurrent heat extremes and high atmospheric evaporative demand. Recent evidence from mature sclerophyllous forests indicates that drought-related crown decline is associated with limitations in carbon assimilation and stomatal regulation, but not necessarily with generalized depletion of NSC pools (Piper and Paula, 2026). Thus, forest decline appears to reflect a progressive disruption of the coordination between carbon gain, water conservation and hydraulic functioning rather than a single physiological mechanism.

Stable isotopes provide an important integrative approach for examining these processes over longer timescales. Carbon isotope discrimination ($\Delta^{13}C$) and oxygen isotope composition ($\delta^{18}O$) in tree rings can provide complementary information on intrinsic water-use efficiency, stomatal regulation and changes in the balance between carbon gain and water loss. Along a Mediterranean-temperate gradient in south-central Chile, *N. obliqua* showed increasing intrinsic water-use efficiency during recent decades, together with changes in $\delta^{18}O$ patterns at the driest site that were interpreted as consistent with increasing reliance on deeper or more isotopically depleted water sources (Urrutia-Jalabert et al., 2023). Importantly, these adjustments were not accompanied by a concurrent reduction in growth at the driest site, suggesting that some populations can maintain growth through coordinated regulation of water use and water acquisition. Conversely, recent work in Chilean sclerophyllous forests indicates that trees experiencing greater crown decline may be characterized by stronger biochemical limitations to carbon assimilation, highlighting that increased water-use efficiency does not necessarily indicate greater physiological performance under drought (Piper and Paula, 2026).

Anatomical plasticity in leaves can contribute to water conservation and maintenance of leaf function under declining soil moisture (Peñuelas et al., 2017). demonstrated drought-induced anatomical changes in *Q. saponaria* and *C. alba* under controlled water restriction, including changes in leaf thickness and tissue structure associated with water conservation and photosynthetic function. These responses complement field evidence showing strong interspecific differences in the capacity of Central Chilean sclerophyllous species to maintain physiological performance under water limitation. For example, Espinoza et al. (2026) found marked differences among six sclerophyllous species in physiological responses and performance under restricted soil water availability. Together, these findings indicate that drought resistance involves coordinated adjustments in leaf structure, stomatal regulation and hydraulic function, with responses varying substantially among species.

Hydraulic and anatomical adjustments provide a complementary mechanism through which trees may buffer drought stress, although these responses can involve trade-offs between hydraulic safety, transport efficiency and growth (von Arx et al., 2016). Drought-induced changes in vessel diameter, vessel density and pit characteristics can reduce vulnerability to embolism but may also constrain hydraulic conductivity and carbon uptake. Evidence from Central Chile supports such adjustments across different taxa: *Kageneckia angustifolia* showed smaller and more numerous vessels and changes in pit characteristics during extreme drought, accompanied by increased intrinsic water-use

efficiency and reduced growth (Santini et al., 2024), while *Nothofagus dombeyi* populations from drier sites exhibited higher vessel density and smaller hydraulic diameters, with stronger growth sensitivity to drought and temperature (Guzmán-Marín et al., 2024). Recent evidence from a centennial *N. obliqua* population further suggests high sensitivity of vessel size to climatic variability and declining potential hydraulic conductivity under recent drying (Legue et al., 2026).

At the same time, drought responses are not uniform among species or populations. Variation in drought tolerance traits within *N. obliqua* indicates an important role for phenotypic plasticity and population-level differences in hydraulic and growth responses (Urrutia-Jalabert et al., 2025). Together with evidence that declining sclerophyllous trees do not necessarily show generalized NSC depletion (Piper and Paula, 2026), these findings suggest that mortality risk may depend less on the absolute size of carbon reserves than on the capacity to maintain carbon assimilation, hydraulic function and recovery over prolonged drought. Finally, root traits may also contribute to drought resistance by influencing water acquisition and resource allocation, but their role in drought and heat tolerance remains poorly characterized for central Chilean forest species.

4. Knowledge gaps and research priorities for central Chile

Despite the growing body of evidence documenting climate-induced stress resulting in growth and productivity decline, canopy browning and compromised germination and establishment, across Central Chile, major uncertainties remain regarding ecosystem resilience, and long-term adaptive capacity under ongoing climate change. While similar patterns have been reported in other Mediterranean regions, the underlying mechanisms governing vulnerability, mortality, and post-disturbance recovery in Chilean Mediterranean-type forests remain poorly understood. Addressing these gaps is therefore essential to anticipate ecosystem trajectories under increasingly extreme drought and heatwave regimes.

4.1. Forest mortality: the missing data

One of the most critical gaps in the Chilean MTEs is the lack of quantified and spatially explicit data on drought-induced tree mortality. While physiological stress indicators, growth decline, reduced productivity, and canopy browning have been consistently reported since 2010, tree mortality rates have not yet been formally documented at local or regional scales. The lack of observations of forest mortality in Central Chile contrasts sharply with the disproportionate number of forest mortality events in MTEs, especially considering Chile's record-breaking drought conditions in 2019 and 2021. This raises fundamental questions regarding interspecific and intraspecific mortality thresholds and rates, canopy cover loss, forest structural changes, stress-to-mortality time lags, and the role of resprouting as a survival strategy, which adds an extra layer of complexity when defining tree mortality in an ecosystem where resprouting is a widespread trait (Gómez-González et al., 2017). Carrying out monitoring programs for assessing tree mortality rates over space and time, identifying vulnerable species and size classes, time lags between drought and forest responses (although advances have been made by Miranda et al. (2023) in this matter), evaluating changes in vegetation structure, germination patterns, and forest recovery capacity constitute urgent priorities for conservation, validating remote sensing data, and climate change mitigation (International Tree Mortality Network, 2025). Without this information, it is not possible to assess the nature and magnitude of ecosystem impacts, forecast future forest and forest carbon losses or design effective conservation and management strategies. In this context, there is a clear opportunity to expand the use of remote sensing records to better quantify spatiotemporal changes in canopy cover, vegetation structure, and regeneration dynamics at broader scales. Such data could provide critical insights into the extent and persistence of regeneration limitations, as well as improve the monitoring of ecosystem resilience under ongoing climatic change.

4.2. Disentangling the mechanisms underlying forest decline and tree mortality

Understanding why some trees survive extreme drought while others experience chronic decline, or mortality remains a major research gap in Central Chile. Although hydraulic dysfunction, carbon limitation and their interactions provide a useful conceptual framework (McDowell et al., 2008; Hajek et al., 2022), the relative contribution and temporal sequence of these mechanisms remain poorly resolved for mature Mediterranean forests. In particular, it remains unclear how soil-water depletion, high vapour pressure deficit and heat extremes interact with species-specific resistance thresholds and recovery capacity. Addressing this gap requires moving beyond single measurements of drought stress towards integrated, longitudinal assessments linking tree growth, physiology, hydraulic function and mortality.

Stable isotopes offer an important opportunity to reconstruct physiological responses over longer timescales, but their interpretation requires greater integration with direct measurements (Cherubini et al., 2021). Combining tree-ring and stable isotopes ($\delta^{13}C$, $\delta^{18}O$ and $\delta^{2}H$), soil- and xylem-water profiles, gas exchange and water potential could help distinguish whether increasing intrinsic water-use efficiency reflects effective stomatal regulation, changes in water sources, or declining carbon assimilation. This is particularly important because *N. obliqua* populations have shown increased iWUE and possible shifts in water sourcing during recent drought, whereas declining sclerophyllous trees may show stronger biochemical limitations (Urrutia-Jalabert et al., 2023; Piper and Paula, 2026).

Similarly, wood and leaf anatomical traits should be integrated with hydraulic measurements to determine whether anatomical adjustments provide effective long-term protection or represent responses that ultimately constrain hydraulic efficiency and growth (Fonti et al., 2009; Lens et al., 2022). Recent evidence of smaller and more numerous vessels, changes in pit characteristics and declining potential hydraulic conductivity suggests that hydraulic safety may be gained at the expense of transport efficiency under persistent drought (Guzmán-Marín et al., 2024; Santini et al., 2024; Legue et al., 2026). Future studies should therefore combine xylem vulnerability and embolism measurements with wood anatomy, growth and carbon-assimilation data across multiple years and drought intensities.

Carbon dynamics also require a more nuanced approach. The absence of generalized NSC depletion in declining Chilean sclerophyllous trees does not exclude carbon limitation, as changes in carbon assimilation, NSC turnover and the age of stored carbon may precede changes in total concentrations (Piper and Paula, 2026). Long-term experimental evidence from other seasonally dry forests shows that prolonged drought can progressively consume older carbon reserves even when short-term NSC concentrations remain relatively stable (Peltier et al., 2023). Consequently, future research should quantify not only NSC concentrations but also seasonal dynamics, carbon turnover and the contribution of stored carbon to maintenance and recovery.

Finally, drought vulnerability should be assessed across populations, life stages and environmental contexts. Evidence of substantial intraspecific variation in drought-related traits in *N. obliqua* and *K. angustifolia* indicates that species-average traits may obscure important differences in resistance and recovery (Urrutia-Jalabert et al., 2025). Integrating these physiological and anatomical measurements with root traits, regeneration, microclimatic exposure and long-term demographic monitoring would allow identification of the conditions under which physiological acclimation is sufficient to maintain forest persistence versus those leading to demographic decline. Such an interdisciplinary framework is needed to identify early warning signals of irreversible change and improve predictions of drought-induced

mortality in Central Chile.

4.3. Ecological consequences and post-mortality dynamics

While forest mortality could be conceptualised as an end point, it is more accurately viewed as a transition that initiates profound ecological reorganization. Across forested biomes, mortality events have been shown to trigger cascading changes in canopy structure, microclimate, species composition, and ecosystem functioning (Allen et al., 2010; Choat et al., 2018; Batllori et al., 2020). These transitions often begin with canopy loss through defoliation and stem collapse, disproportionately affecting large, dominant trees that regulate understory microclimates (McDowell and Allen, 2015). Loss of canopy cover can increase incoming solar radiation, soil evaporation, and atmospheric evaporative demand, potentially intensifying heat and water stress near the forest floor (De Frenne et al., 2019 & 2021). Such feedbacks may constrain regeneration and favour species or functional strategies better adapted to warmer and drier conditions, potentially leading to changes in community composition and forest structure (Allen et al., 2010; Greenwood et al., 2017).

Studies in Central Chile indicate strong effects of shading, soil moisture, and species-specific traits on early establishment. Yáñez et al. (2024) found that early growth and physiological acclimation of seven sclerophyllous species were strongly influenced by shade and water restriction, highlighting the importance of microclimatic buffering during establishment. Similarly, a three-year field experiment with the shade-intolerant *N. glauca* showed that soil water availability was the main determinant of seedling survival, whereas higher irradiance promoted biomass accumulation and growth, indicating that survival and growth may respond independently to different environmental constraints during establishment (Acevedo et al., 2024). Recruitment of *C. alba* was also influenced by seed source and forest cover (Magni et al., 2022), while *N. glauca* showed substantial variation in germination and seedling growth among provenances (Santelices-Moya et al., 2017).

Post-mortality dynamics may ultimately determine whether drought-induced canopy loss leads to forest recovery, persistent decline, or longer-term ecological reorganization. Reduced canopy cover and altered regeneration conditions may favour smaller trees, shrubs, or species with greater drought and heat tolerance, with potential consequences for nutrient and water cycling and ecosystem functioning (Cook et al., 2018; Hooijer and Vernimmen, 2021; Young, 2023). Species replacement and thermophilization have been documented following drought-induced dieback in other Mediterranean-type and seasonally dry ecosystems (Christopher and Reyer, 2020; Cuni-Sanchez et al., 2024), but the extent to which similar processes are occurring in Central Chile remains poorly understood. In particular, it is unclear whether current canopy browning and decline following the 2019 and 2021 hyperdroughts represent transient responses, persistent reductions in forest function, or the early stages of sustained community reorganization (Miranda et al., 2020 & 2023,Vega-Briones et al., 2023; Abel et al., 2024; Fuentes et al., 2025). The long-term viability of resprouting, the capacity of recruitment to compensate for adult mortality, and the potential shift toward more drought- or heat-tolerant communities therefore represent key uncertainties for assessing the resilience and future trajectories of Central Chilean Mediterranean-type forests.

4.4. Identifying environmental and topographic controls

The marked seasonality and topographic complexity found in the Mediterranean bioregion of Central Chile are factors that modulate the ecohydrological processes and vegetation functioning (Garrido-Leiva et al., 2026). In the context of the ongoing megadrought since 2010, current research indicates that mesic microsites, such as ravine bottoms and south-facing slopes, may act as climate refugia (Miranda et al., 2023; Garrido-Leiva et al., 2026), yet their capacity to sustain populations under prolonged or repeated extreme droughts is uncertain. Moreover, the relative roles of microclimatic drivers, like canopy cover (Davis et al., 2019), soil hydraulic and biochemical characteristics (Morales et al., 2025), slope orientation, solar insolation, and terrain curvature (Dobrowski, 2011), in buffering or amplifying drought stress remain insufficiently quantified. Hence, future research should focus on identifying the role of environmental gradients in modulating microclimatic conditions, forests resistance and recovery following drought stress, and where thresholds of irreversible change are more likely to be crossed.

4.5. Scaling from populations to landscapes

The scaling up of field observations to regional patterns of forest decline also remains a substantial challenge due to the difficulty of integrating processes across biological and spatial scales (Newman et al., 2019). Existing studies in Central Chile are predominantly either plot-based, focusing on dendrochronological and physiological responses at the tree or stand level (e.g. Venegas-González et al., 2018a; Matskovsky et al., 2021) or regionally aggregated through climate-growth reconstructions (e.g. Le Quesne et al., 2006; González-Reyes et al., 2024) and regional forest productivity monitoring (Fuentes et al., 2025), that capture broad-scale variability but lack fine-scale ecological resolution. This methodological separation, and the lack of a mechanistic approach that connects the different manifestations of forest decline (e.g. macro- and micro-climate, recruitment, establishment, growth, productivity, browning and defoliation), limits the ability to directly link individual-level physiological responses with landscape-scale patterns of decline and mortality. Plot-based and dendrochronology studies provide detailed physiological and demographic data at fine spatial scales (individual trees to population), yet they are inherently limited in their capacity to capture spatial heterogeneity and regional patterns. In contrast, remote sensing approaches offer broad spatial coverage and repeated observations over time, but they lack the detail (e.g. community composition, species abundance, and forest structure) required to diagnose underlying physiological drivers and therefore need field validation. Thus, neither approach in isolation provides a complete picture of forest decline dynamics. Bridging this gap would require coordinated and integrative approaches that combine long-term field observations, experimental studies, high-resolution remote sensing, and climate modelling, to establish mechanistic links between individual-level physiological responses and landscape-scale patterns of forest decline and mortality.

Integrative approaches have been successfully applied elsewhere. For example, studies in Iberian forests have linked tree-level physiological responses derived from dendrochronology with regional mortality patterns, demonstrating that growth sensitivity to drought and resilience indices derived from tree rings can predict mortality risk at regional scales across large environmental gradients (Gazol and Camarero, 2022). Likewise, in the southwestern United States, tree-ring data and satellite vegetation indices have been combined to upscale drought responses from individual trees to landscape-level patterns, revealing that physiological thresholds observed at the tree level are detectable at broader scales through spectral indicators of canopy decline (Xu et al., 2019). Other studies have integrated multi-scale remote sensing (airborne and satellite) to map regional die-off dynamics, providing key evidence on drought-induced mortality across multiple forest types and that remote sensing can capture the spatial extent and temporal progression of these events when calibrated with high resolution imagery (Byer and Jin, 2017). Moreover, the combination of dendrochronology, isotopic analysis, and satellite vegetation indices has been used to detect early warning signals of pest-induced decline, identifying critical tipping points preceding tree mortality and unveiling the eco-physiological dynamics of forest decline (Niccoli et al., 2024).

Such multi-scale approaches are crucial as they enable the integration of processes operating at different biological and spatial scales,

allowing the identification of early warning signals of forest decline, the attribution of observed changes to specific climatic drivers, and the projection of future ecosystem trajectories under different emission scenarios. Central Chile, with its exceptional climatic extremes and environmental heterogeneity, offers a unique opportunity to advance this integrative framework and to improve global understanding of forest resilience in MTEs. Nevertheless, scaling the analysis from populations to landscapes remains a challenge in the absence of more detailed population-level evidence.

4.6. Broader implications for MTEs globally

Addressing these major knowledge gaps identified in Central Chile is not only critical for the regional understanding but also for advancing international research on MTEs under climate change. Central Chile is currently experiencing the most severe drought conditions documented among global MTEs, placing the region at the extreme end of the climatic stress spectrum, offering a unique opportunity to study ecosystem responses under conditions likely to become more widespread in the future.

From a global perspective, Central Chile also offers a valuable context for examining how environmental heterogeneity modulates forest vulnerability. The region's strong gradients in topography and microclimatic conditions allow assessment of resistance thresholds, refugial dynamics, and early warning signals of irreversible change, with insights that are transferable to other Mediterranean landscapes worldwide. Given the disproportionate contribution of MTEs to biodiversity, carbon storage, and ecosystem services, understanding how such forests respond to extreme drought has implications that extend beyond regional ecology. Intensifying research efforts in this system is therefore essential to improve international assessments of forest resilience, refine projections of ecosystem change, and most importantly, anticipate the future trajectories of MTEs under continued warming and aridification.

To translate these priorities into actionable research, we have synthesized the knowledge gaps, key challenges, and proposed approaches in Table 1. This framework is structured around six thematic areas, forest mortality monitoring, physiological mechanisms, ecological feedbacks, environmental controls, cross-scale scaling, and global relevance, and is intended to guide coordinated, interdisciplinary research efforts. In particular, we emphasize that meaningful progress in an integrative vegetation modelling will depend on first addressing the specific empirical and mechanistic gaps outlined in the table, as predictive models are only as robust as the data and process understanding that underpin them. Once these foundational gaps are filled, the integration of empirical data into process-based vegetation models will enable more accurate projections of forest trajectories under future climate scenarios.

5. Conclusion

Mediterranean-type forests are among the most vulnerable ecosystems to climate change, and evidence from Central Chile highlights the urgency and scientific novelty of studying their responses under unprecedented drought conditions. The coincidence of a long-lasting megadrought (2010-present), record-breaking hyperdroughts (2019 and 2021), and rising temperatures has generated sustained and spatially extensive stress across Chilean Mediterranean-type forests, making this region one of the most climate-vulnerable MTEs globally. While anthropogenic land-use change and fire have historically contributed to forest loss in this region (Schulz et al., 2010; Miranda et al., 2017), the recent widespread decline observed in undisturbed forests since 2010 can be primarily attributed to the unprecedented severity and persistence of climatic anomalies. However, despite growing evidence of physiological stress, productivity decline, and widespread canopy browning, fundamental uncertainties remain

Table 1
Research Priorities and Knowledge Gaps in Chilean Mediterranean-Type Forests. Synthesis of critical data and research gaps in understanding drought-induced forest decline in Central Chile, and the region's relevance as a natural laboratory for studying ecosystem responses to extreme drought across global Mediterranean-type ecosystems. Throughout this review, 'forest decline' is used as the overarching term for drought-induced degradation, encompassing growth reduction, productivity loss, canopy browning, impaired regeneration, and tree mortality.

Knowledge Gaps	Key Challenge	Proposed Approach
1. Forest Mortality Data	No formal documentation of mortality rates at local or regional scales. Unknown species-specific mortality thresholds and time lags between stress and death.	Establish long-term monitoring research to assess tree mortality rates over space and time, identification of vulnerable species and size classes, mortality thresholds, time lags between stress and mortality, germination patterns, and forest recovery capacity.
	Limited spatial data on canopy cover loss and structural changes.	Expand the use of remote sensing to quantify spatiotemporal changes in canopy cover, vegetation structure, and recovery dynamics, and to validate satellite observations.
2. Mechanisms of Decline & Mortality	Limited evidence on hydraulic failure, carbon starvation, and biotic interactions as drivers of mortality. Lack of integration of physiological, anatomical, wood trait, and NSC dynamics data. Unclear relative importance and interaction of abiotic stressors in driving decline. Unknown species-level resistance thresholds and recovery capacities.	Develop integrated approaches combining dendrochronology, ecophysiology, wood anatomy, and NSC dynamics to assess species-specific vulnerability, including key traits such as leaf and wood anatomy, and growth resilience, disentangle the individual and interactive effects of soil moisture, VPD, and heat extremes on tree physiology, account for species interactions that may modulate drought responses, and study their resilience.
3. Post-Mortality Ecological Dynamics	Unknown impacts of canopy loss on understory microclimate, soil conditions, and ecosystem functioning. Unclear long-term viability of regeneration and resprouting strategies following extreme drought. Potential for sustained shifts toward more drought- or heat-tolerant species not assessed.	Study the cascading effects of canopy loss on understory microclimate, soil conditions, nutrient and water cycling, and ecosystem functioning. Under the long-term monitoring programmes, study regeneration and resprouting success over multiple seasons, monitor shifts in species composition and community structure, identify early signs of community reorganization, and evaluate feedbacks that may reinforce drought- or heat-tolerant states.
4. Environmental & Topographic Controls	Uncertain capacity of mesic microsites to act as long-term climate refugia under repeated extreme droughts. Relative roles of canopy cover, slope orientation, solar insolation, and terrain curvature in buffering or amplifying drought stress are poorly quantified.	Identify and monitor potential refugia to assess their capacity to sustain populations under prolonged or repeated drought stress. Quantify the relative importance of microclimatic drivers (canopy cover, insolation, slope, curvature) in modulating forest resistance and recovery.

(*continued on next page*)

Table 1 (*continued*)

Knowledge Gaps	Key Challenge	Proposed Approach
	Unknown where forests are more vulnerable to climate change across the landscape.	Map environmental gradients (e.g. terrain and soil characteristics) to identify areas where thresholds of irreversible change are most likely to be crossed.
5. Scaling from Populations to Landscapes	Disconnection between plot-based studies and remote sensing observations.	Develop multi-scale approaches that combine long-term field observations, experimental studies, high-resolution remote sensing, and climate modelling.
	Lack of mechanistic links between individual-level physiological responses and landscape-scale patterns of decline and mortality.	Establish statistical and process-based models that link tree-ring, physiological, and spectral data to detect early warning signals of forest decline, attribute observed changes to specific climatic drivers, and project future trajectories under different emission scenarios.
	Difficulty integrating processes operating at different biological and spatial scales (from tree to region).	Develop integrative frameworks connecting recruitment, growth, productivity, browning, and defoliation across scales.
6. Global Relevance for MTEs	Uncertainty whether observed responses in Chile are unique or representative of future trajectories for other MTEs.	Use Chile's extreme drought conditions as a natural laboratory to test hypotheses on forest decline and recovery applicable to other water-limited regions.
	Limited integration of Chilean data into global mortality databases and climate vulnerability models.	Integrate Chilean data into global databases and refine global vegetation models and strengthen current international collaborative networks to assess drought responses across all five MTE regions.

regarding tree mortality thresholds, spatiotemporal patterns of forest decline and mortality, recovery capacity, and long-term ecosystem reorganization and resilience.

Within this context, Central Chile emerges as a critical case study for understanding forest resilience, and potential tipping points in MTEs worldwide. The severity and persistence of recent droughts place Chilean forests at the forefront of climatic change impacts, offering a unique opportunity to examine ecosystem responses that may anticipate future trajectories in other Mediterranean regions. Insights gained from this system are therefore essential to test existing conceptual frameworks, refine predictions of drought-induced forest decline and assess the role of environmental heterogeneity in buffering or amplifying extreme climatic stress.

Addressing these knowledge gaps will require progress across multiple fronts: establishing long-term mortality monitoring, elucidating physiological mechanisms, tracking post-mortality ecological dynamics, quantifying environmental and topographic controls, and developing robust approaches to scale from individuals to landscapes. Each of these areas represents a substantial research agenda, with distinct methodological demands and analytical complexities. Nonetheless, their interconnected nature means that isolated lines of evidence, however robust, cannot fully capture the feedbacks and interactions that shape ecosystem-level changes. A truly comprehensive understanding will therefore depend on interdisciplinary synthesis that integrates long-term field observations, ecophysiological measurements, dendroecology, remote sensing, and modelling across spatial and temporal scales. Strengthening international collaboration and positioning the Chilean Mediterranean bioregion within the global MTEs context is therefore essential for understanding the future of Mediterranean ecosystems under climate change and for informing conservation and management strategies in a rapidly warming and increasingly arid ecosystem.

CRediT authorship contribution statement

Pablo T. Paredes-Berríos: Writing – original draft, Supervision, Project administration, Conceptualization. **Alistair S. Jump:** Writing – review & editing, Conceptualization. **Sarah Greenwood:** Writing – review & editing, Conceptualization. **Daniel Donoghue:** Writing – review & editing, Conceptualization. **Alejandro Venegas-González:** Writing – review & editing, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the main author used Copilot, and Grammarly to assist with grammar refinement and correction of spelling errors. After using this tool/service, the author thoroughly reviewed and edited the content as needed and takes full responsibility for the accuracy, integrity, and originality of the published article.

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