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RESEARCH ARTICLE

Tree species abundance changes at the edges of their climatic distribution: An interplay between climate change, plant traits and forest management

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Abstract

1. Climate change is anticipated to have an increased impact on tree populations located at the edges of their climatic tolerances. However, there is still uncertainty about how the interaction between climate change and functional traits drives changes in tree species abundance at climate edges, especially in the context of the abandonment of the traditional forest activity.
2. We used data from ~445,000 monitored tree stems from 68 species in Spain to (1) quantify tree species abundance changes at the edges of their climatic distributions (cold and wet vs. warm and dry) over the last 25 years and (2) determine the impact of climate change, functional traits and forest densification (used here as an indicator of forest regrowth following anthropogenic disturbance) on these abundance changes. We developed a null model to test whether tree species abundance changes at the climate edges were higher or lower than expected, considering random stem gains and losses along the entire climate gradient.
3. Across the study area, we found an average increase in tree species abundance over time. Our findings also show a higher than random average increase in tree species abundance at the cold and wet edge, but a random increase at the warm and dry edge. Tree species abundance changes along the entire climate gradient and in the edges were primarily associated with forest densification. However, the interaction between climate change and plant traits impacted tree species abundance changes at the climate edges. Tree species that invested more in their root systems and adopted more acquisitive leaf strategies showed greater increases in abundance in response to climate change.
4. *Synthesis*: Our research emphasizes the crucial impact of historical forest management in shaping the current distribution of tree species. After controlling for the effect of forest management, climate change directly influenced tree demographics, favouring species based on their traits. As tree species regain their ecological niches after succession, climate change will determine their abundance by filtering for particular ecological strategies.

KEYWORDS
broadleaved forests, coniferous forests, forest ecology, functional traits, global change, Iberian Peninsula, species distribution, tree diversity

1 | INTRODUCTION

Anthropogenic climate change is reshuffling the geographic distributions of species globally (Pecl et al., 2017). Stationary and long-lived organisms such as tree species are particularly susceptible to suffer range changes given their unavoidable exposure to climate variation (Scheffer et al., 2001). The decline of tree populations can occur at the rear (warm and dry) edge of their climatic distribution when climate shifts exceed species' physiological and ecological tolerances. Consequently, tree populations located at the rear edge face a higher risk of local extinction compared to central populations (Ackerly et al., 2010; Brown, 1984). This increased risk can be attributed to their inhabitation of less favourable habitats with lower and fluctuating population densities (Lawton, 1993; Vucetich & Waite, 2003). In contrast, tree populations located at the leading (cold and wet) edge of their climatic distribution may increase and expand into previously inaccessible environments (Astigarraga et al., 2024; Matías & Jump, 2014). Nevertheless, there is inconsistent evidence regarding tree species abundance changes at the edges of their climatic distribution (Lenoir & Svenning, 2015; Vilà-Cabrera et al., 2019) and cases of population persistence in edges are well-documented (e.g. Granda et al., 2018; Hampe & Jump, 2011; Lázaro-Nogal et al., 2015). Understanding how tree species abundance and distribution respond to climate change at the limits of their climatic distribution is crucial for developing effective biodiversity conservation and natural resource management strategies.

Several factors can affect the accuracy of biogeographical predictions regarding how tree species respond to climate change at the rear and leading edges of their climatic distribution (Vilà-Cabrera et al., 2019). For example, population performance can be influenced by the interplay among different fine-scale ecological factors (e.g. micro-climate, soil quality, water availability), biotic interactions, confounding ontogenetic effects or the adaptability and genetic diversity within phenotypes (Anderegg & HilleRisLambers, 2019; Heiland et al., 2022; Jump et al., 2017; Valladares et al., 2015). Furthermore, other global change drivers can also alter species distributions. For example, recent socioeconomic changes have resulted in contrasting impacts on forest landscapes (Meyfroidt et al., 2010). In many developed countries of the Mediterranean Basin, the abandonment of forest management and agricultural practices has triggered large-scale afforestation, leading to forest densification (Astigarraga et al., 2020; McGrath et al., 2015). This transformation has been characterized by a widespread expansion of Fagaceae family trees at the expense of Pinaceae (Carnicer et al., 2014; Vadell et al., 2016; Vayreda et al., 2016). Broadleaved tree species have a superior ability to effectively respond to various disturbances and a higher competitive ability. As the forest canopy gradually closes, competition for sunlight increases, favouring the replacement of early-successional, light-sensitive conifers with late-successional, shade-tolerant broadleaved species, which are less impacted by light competition (Sánchez-Gómez et al., 2008; Zavala et al., 2011). Additionally, several broadleaved species possess an exclusive capacity to resprout, affording them a greater ability to rapidly recover following disturbances like wildfires or thinning. Therefore, land use changes and forest management practices are crucial drivers of tree species distribution, as they can potentially deviate climate-induced population declines at climate edges (Goring & Williams, 2017).

Climate change plays a direct role in influencing the demographic responses of trees by selectively favouring species based on their ecological strategies (Fernández-de-Uña et al., 2023; Keddy, 1992; Selwyn et al., 2024). Alterations in climate conditions can disrupt species performance, with the extent of disruption dependent on species' functional traits—indicators of their strategies for coping with stress (Adler et al., 2014; Mouillot et al., 2013). For example, in subtropical forests, tree species with more acquisitive leaf strategies have increased in abundance compared to species with conservative strategies in response to drought stress (Li et al., 2015). The growing availability of data on plant functional traits (Kattge et al., 2020) now enables us to quantitatively characterize the ecological strategies of species. By examining trait-climate interactions, we can identify which traits confer greater capacity to respond to changing conditions, allowing us to forecast species abundance changes over time.

In the Iberian Peninsula, at the transition zone between the Mediterranean and Temperate biomes, several drought-sensitive Eurasian tree species, including *Fagus sylvatica* or *Quercus petraea*, extend to their southernmost geographical distribution. Population performance of these species responds negatively to drought, with expectations of further impacts (Camarero et al., 2015; Lindner et al., 2010). Conversely, several drought-tolerant Mediterranean tree species, such as *Quercus ilex* or *Pinus halepensis*, confront their cold thresholds in this area. Moreover, the geologic and orographic complexity of the Iberian Peninsula significantly amplifies the variety of environments, resulting in a rich array of tree assemblages that are compositionally unique within the European context (Mauri et al., 2017; Padullés Cubino, 2023). This topographic complexity also creates a broad altitudinal gradient, exposing numerous tree species to the boundaries of their climatic tolerances. Consequently, Iberian forests serve as a valuable model to comprehend the impacts of changing climatic conditions on tree populations, particularly at their rear and leading climate edges.

In this study, we analysed 25 years of changes in ~445,000 monitored tree stems belonging to 68 species in the Iberian Peninsula to assess long-term tree species abundance changes in their climate edges (cold and wet vs. warm and dry). To assess these changes, we used a null-model approach to determine whether changes in species-specific abundance at these climate edges exceeded or fell below expected levels, assuming random occurrences of abundance gains and losses along their climatic distribution. We then quantified the effect of forest densification as well as the individual and interactive effects of climate change and plant traits on tree species abundance changes. Specifically, we address the following questions: (1) Has the abundance of Iberian tree species changed over time in the edges of their climatic distribution? (2) Are these changes more influenced by forest densification or by the individual and interactive effects of climate change and species traits?

2 | MATERIALS AND METHODS

2.1 | Forest inventory data

The study area encompasses the entire climatic spectrum of peninsular Spain, spanning from 43°47′25″ N to 36°00′38″ N in latitude and from 3°19′20″ E to 9°18′05″ W in longitude (Appendix S1). We collected data from the second (2SFI; 1986–1996) and fourth (4SFI; 2008–2019) Spanish Forest Inventories (SFIs). These permanent forest inventory plots are distributed across a 1 km^2 grid that covers most of Spain's forested regions (Villaescusa & Díaz, 1998). Between 2SFI and 4SFI, tree stem density in the plots has increased an average of 96 stems per hectare (Appendix S2). Each inventory involved survey plots that consisted of four concentric subplots: one with a 5-m radius (used for measuring stems with a diameter at breast height—DBH—≥7.5 cm), one with a 10-m radius (for stems with a DBH ≥12.5 cm), one with a 15-m radius (for stems with a DBH ≥22.5 cm) and one with a 25-m radius (for stems with a DBH ≥42.5 cm). During each survey, species name, DBH, height, distance from the plot centre and tree condition (alive or dead), were recorded for each mature tree (DBH ≥7.5, Villaescusa & Díaz, 1998). To determine the total number of mature tree stems in each plot, we first selected stems with DBH ≥12.5 cm within a 10-m radius (~314 m^2). Subsequently, we multiplied the number of stems with DBH <7.5 cm in the 5-m radius by four to extrapolate this smaller diameter stem class to the larger 10-m radius.

In total, we analysed a subset of 21,717 plots taken from the larger pool of publicly available plots as of March 20, 2024. These plots were sampled during both 2SFI and 4SFI (Appendix S1). The average interval between 2SFI and 4SFI was 24.6 years. There were a total of 318,204 and 445,411 tree stems in 2SFI and 4SFI, respectively, from 68 species. Further details on plot-level data cleaning and processing are in Appendix S3.

2.2 | Tree species traits

We acquired data for the 68 species on six traits known to exhibit significant interspecific variation in response to the abiotic or biotic environments (Lavorel & Garnier, 2002). These traits were maximum tree height (TH), specific stem density (SSD), seed mass (SM), specific leaf area (SLA), root mass fraction (RMF) and xylem resistance to embolism (i.e. the water potential at which a plant loses 50% of xylem hydraulic conductivity; P50). These traits are related to various ecological functions, including dispersal, establishment, reproduction and resource acquisition (Díaz et al., 2016; Freschet et al., 2021; Moles, 2018; Reich, 2014; Appendix S4).

We obtained trait data for TH, SSD and SM from the TRY database (Kattge et al., 2020). Since TRY data typically includes multiple trait records for each species, we calculated the average values and removed original trait records that were >4 standard deviations from the species' mean to avoid potential outlier effects (Díaz et al., 2016). We acquired data on RMF from the Global Root Trait (GRooT) database (Guerrero-Ramírez et al., 2021) and on P50 from Pausas et al. (2016).

The proportion of missing trait values in the dataset ranged from 0% (TH) to 25% (RMF; Appendix S4). To fill in missing trait data, we used the R package “missForest” (Stekhoven, 2022). This approach utilizes a Random Forest technique and precise phylogenetic data to impute species trait values (Penone et al., 2014). Moreover, it offers the advantage of rapid computational processing. To incorporate the phylogenetic data, we employed phylogenetic eigenvectors (Debastiani et al., 2021), which were obtained from the R package “PVR” (Santos, 2018). The highest correlation between traits was between TH and P50 (Pearson's $r=0.54$; Appendix S4).

To impute missing trait data and visualize species-level results considering the evolutionary relationships between species, we built a phylogenetic tree by linking our tree species ($N=68$) to the mega-phylogeny implemented in the R package “V.PhyloMaker2” (Jin & Qian, 2022). This mega-phylogeny, originally compiled by Smith and Brown (2018), contains ~74,000 species. We added missing species from the tree (6 species; 9% of the total) using the “scenario 3” method (for details, see Jin & Qian, 2022).

2.3 | Climate variables

We obtained historical monthly climate data for total precipitation (mm) and average maximum temperature (°C) from the WorldClim database (Harris et al., 2020). These data cover the global terrestrial surface from 1960 to 2018 at 2.5 min (~21 km^2 at the equator) resolution. For total precipitation, we summed the monthly precipitation over the year. For average maximum temperature, we averaged monthly values for each year. We used principal component analyses (PCA) with Varimax rotation to synthetize climate variability, integrating both total annual precipitation and the average maximum temperature into a single axis of variation. We conducted a PCA annually between 1976 and 2018, resulting in a distinct PCA for each year. On average, across these years, the resulting principal component explained 77% ± 0.01 (mean ± standard deviation) of the total variation. This principal component defined a gradient spanning from cold and wet (leading edge) to warm and dry (rear edge) climate conditions (Appendix S1). Then, we calculated the long-term average values for this principal component by averaging the annual data for both the 10 years before 2SFI and 4SFI (Bernhardt-Römermann et al., 2015). This method considers the probable delays in the changes that occur in vegetation over time and how tree species adjust to enduring alterations in their environment (De Frenne et al., 2013; Li & Waller, 2017). We extracted long-term average climate data using the geographical coordinates of the plots and the R package "raster" (Hijmans, 2023). We then assigned plot-level climate values to individual tree stems in each plot. This allowed us to define the climate niche of each tree species across the study area.

2.4 | Statistical analyses

We conducted analyses with R v. 4.2.0 (R Core Team, 2023) and determined statistical significance at $\alpha = 0.05$.

2.4.1 | Calculation of the climate edges of tree species

Identifying edge populations along an environmental gradient can be challenging due to the lack of clear-cut boundaries. In this study, for each tree species in 2SFI, we defined the cold and wet (leading) edge as the 20th quantile of the principal component values assigned to the tree stems of that species. Similarly, we defined the warm and dry (rear) edge as the 80th quantile along this same gradient. Subsequently, we summed up the number of tree stems for each species occurring below and above these edge values in 2SFI. Using the edge values extracted from 2SFI, we then calculated the number of tree stems for each species that fell both below and above these thresholds in 4SFI. These values for 4SFI represent the number of tree stems of each species at the two climate edges relative to the baseline edge values identified in 2SFI. To evaluate the robustness of the edge definition, we repeated the analyses using a stricter edge threshold (10th and 90th quantiles; Appendix S5). Furthermore, we present the proportion of plots situated at the climate edges for each tree species in 2SFI and 4SFI as an estimation of the spatial amplitude of climate edges per species (Appendix S6), thereby complementing the findings detailed in the main text.

2.4.2 | Calculation of changes in tree species abundance

For each tree species in 2SFI and 4SFI, we calculated the proportional change in tree species' abundance as the logarithm of the ratio between the number of tree stems of each species in 4SFI and 2SFI across the entire climate gradient and within the two edges of the climate gradient. Consequently, this metric provides a quantitative assessment of the average proportional change in tree species abundance across all plots from 2SFI to 4SF. We used *t*-tests to assess if the average changes in abundance across species differed from zero.

2.4.3 | Null model

Changes in tree species abundances at the climate edges and along the entire climate gradient can be highly correlated. For example, for a particular species, an increased number of tree stems in the warm and dry edge could be correlated with an overall increase in tree stems throughout the study area. To investigate this, we developed a null model to assess for each species whether the increases and decreases in the number of tree stems at the two climate edges (cold and wet vs. warm and dry) exceeded or fell below the expected levels if tree stems gains and losses were distributed randomly across the climate gradient. To achieve this, for each species, we performed 1000 permutations of the observed tree stems gains and losses between 2SFI and 4SFI along the entire climate gradient. Subsequently, we recalculated the changes in abundance at each climate edge to establish a null distribution of expected values. To accurately report the extent to which abundance changes at the climate edges deviated from the null model, we retained the difference between the observed change in abundance and the mean expected change derived from randomizations (i.e. unstandardized effect sizes; Observed – Expected). We determined two-tailed *p*-values by comparing the observed change in abundance with the distributions of randomly generated values. In cases where a species demonstrated an absolute increase in either climate edge, positive values with $p > 0.975$ indicated a greater gain in trees than expected under random conditions, whereas negative values with $p > 0.025$ indicated a lesser gain than expected. Conversely, for species with an absolute decrease in either climate edge, positive values with $p > 0.975$ indicated fewer tree losses than randomly expected under random conditions, while negative values with $p > 0.025$ indicated more tree losses than expected. We used *t*-tests to assess if the average unstandardized effect sizes of the changes in abundance across tree species differed from zero.

2.4.4 | Calculation of the change in tree stem density

In the Iberian Peninsula, forest densification predominantly results from the abandonment of forest management activities, such as thinning and logging, and agricultural practices (Astigarraga et al., 2020; McGrath et al., 2015; Selwyn et al., 2024; Vayreda et al., 2016). As such, in our models, we utilized the change in tree stem density in the plots as a proxy for the temporal change in forest management, given that this specific variable was unavailable from the inventories. However, we acknowledge that changes in forest density can also result from natural disturbances such as wildfires. Moreover, the phenomenon wherein tree species become more abundant, coinciding with forest densification, can be interpreted in two ways: either these species become more abundant because the forests are denser or their increase in abundance is what actually makes the forests denser. We address this dual interpretation in our interpretation of the results.

To obtain a measure of the change in tree stem density (Δ Tree density) associated with each tree species, we averaged the change in tree density between 4SFI and 2SFI in the plots where each species was present.

2.4.5 | Calculation of climate change

For each species, we calculated the difference in average climate conditions where trees occurred between 4SFI and 2SFI. Essentially, these variables indicate alterations in the mean climate conditions across the entire climate gradient spanning the two time periods. We employed this metric as a predictor for the change in tree species abundance across the entire climate gradient. Then, we calculated the difference in average climate conditions for trees situated at the climate edges between 4SFI and 2SFI. Consequently, these differences reflect changes in mean climate conditions at the climate edges, alluding to the initial 2SFI conditions. We used this second set of metrics as predictors for the observed and unstandardized values of the proportional changes in abundance at the climate edges. For simplicity, we jointly refer to these variables as Δ Climate in the Results.

2.4.6 | Modelling changes in tree species abundance

We conducted ordinary least squares (OLS) regression to assess the relationship between the response variables (i.e. the observed and unstandardized [Observed − Expected] changes in tree species abundance) and focal predictors: Δ Tree density, Δ Climate, plant traits (TH, SM, SLA, SSD, RMF and P50) and the interaction between Δ Climate and plant traits (Δ Climate × trait). We conducted separate OLS regressions for each trait to prevent over-parametrization of the models ($N = 68$). We computed the average estimates and standard errors (SE) for Δ Tree density and Δ Climate across all models. This allowed us to determine the mean effect size of these parameters. We $\log_e$-transformed SM to improve normality and reduce dispersion in model residuals. Additionally, we included the initial number of trees in 2SFI and the average initial tree density in the plots where each species occurred as covariates in all models to consider differences in initial stand development and composition. Prior to model fitting, we standardized and centred all explanatory variables to ensure comparable coefficients (Zuur et al., 2007). Finally, we used diagnostic plots to verify model assumptions (i.e. normally distributed errors with constant variance, absence of correlation in the residuals, homogeneity of variance and residual independence; Zuur et al., 2007).

One of the fundamental assumptions of OLS regression is that data points are independent of each other. However, species that share a common evolutionary history are not independent because they share traits inherited from their common ancestors. Therefore, we repeated our models using phylogenetic generalized least squares (PGLS) regression. The PGLS approach offers flexibility in evolutionary assumptions and incorporates generalized least squares to account for the predicted covariance among species in the model (Ives & Zhu, 2006). Because we find virtually identical results between OLS and PGLS, we only report results for OLS in the main text.

3 | RESULTS

3.1 | Changes in tree species abundance

On average, tree species experienced a significant proportional increase across the study area (Figure 1a) and at the climate edges (Figure 1b). However, only the average proportional change in tree species abundance in the cold and wet edge was higher than expected considering random gains and losses of tree stems along the entire climate gradient (Figure 1c). We found similar patterns when considering a more restrictive threshold for climate edges (Appendix S5).

Tree species that exhibited higher proportional increases in abundance across the entire climate gradient were generally

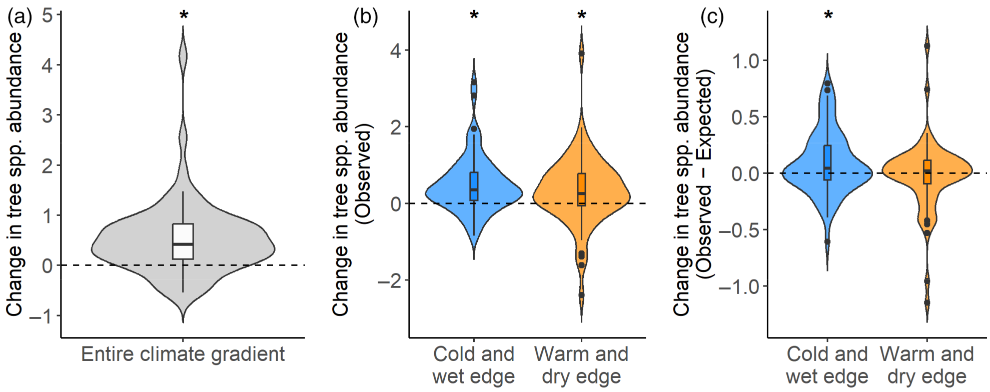

FIGURE 1 Violin and boxplots showing the proportional change in tree species (spp.) abundance over time across the entire climate gradient (a) and at the climate edges (observed [b] and unstandardized [Observed − Expected] values [c]) ($N = 68$). Asterisks (*) indicate significant differences in average values when compared to zero according to t-tests.

cultivated (e.g. *Acacia melanoxylon*, *Prunus avium* and *Laurus nobilis*). Additionally, common widespread broadleaved species, notably those from the Fagaceae family, also saw high increases in abundance (Figure 2). Conversely, species from the Pinaceae family predominantly experienced higher proportional declines in abundance.

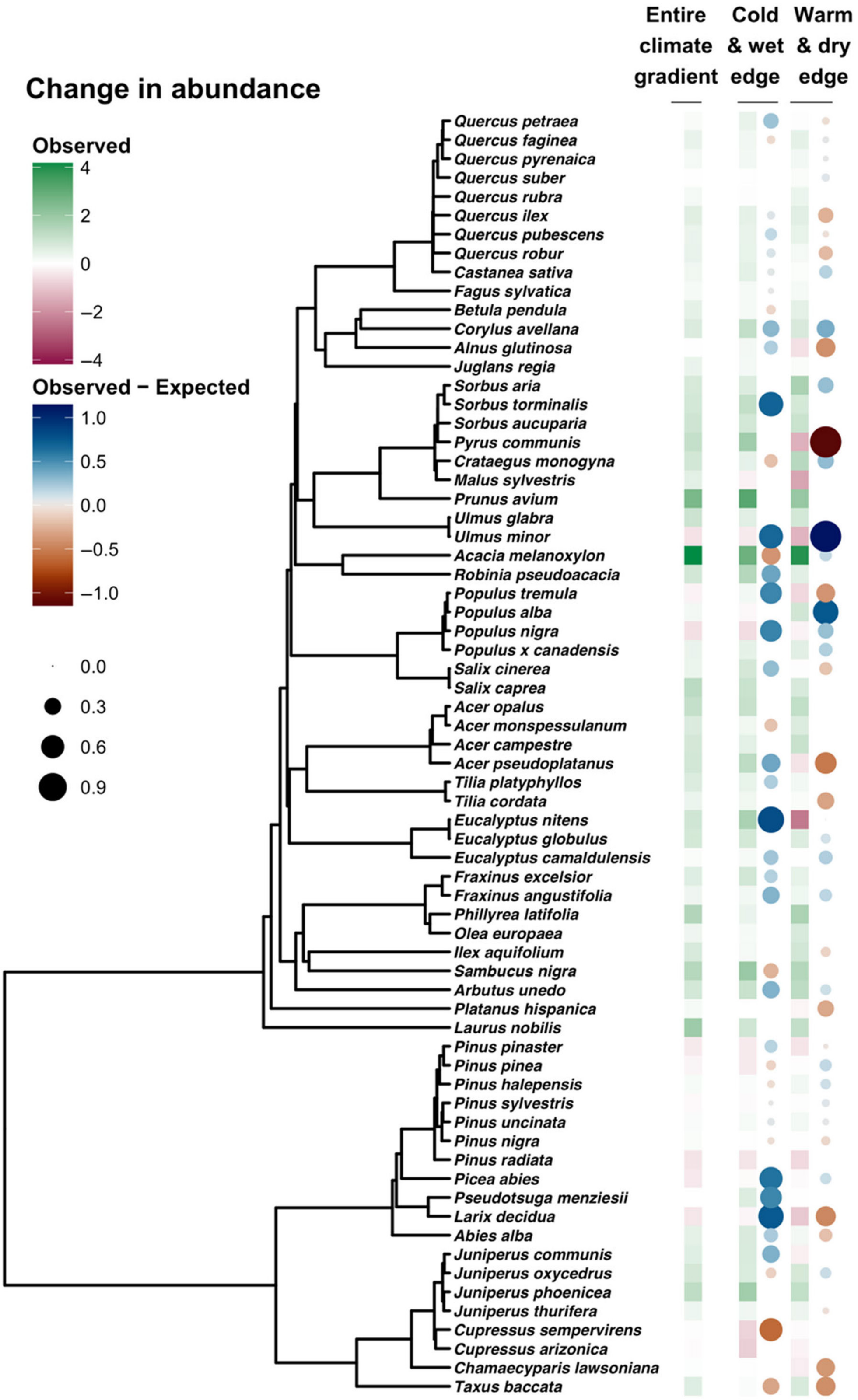

FIGURE 2 Phylogeny of Iberian tree species showing their proportional change in abundance over time across the entire climate gradient and at the climate edges (observed and unstandardized [Observed – Expected values) ($N=68$). Rectangles and circles represent observed and unstandardized values, respectively. The size of the circles is proportional to the unstandardized values.

In the cold and wet edge, tree species that experienced more gains than randomly expected included, for example, native Fagaceae species, such as *Quercus pubescens*, *Q. petraea* and *Fagus sylvatica* (Figure 2; Appendix S7). Conversely, tree species that experienced more losses than randomly expected included *Pinus pinea* and *Cupressus sempervirens*. In the warm and dry edge, common native tree species that experienced more gains than randomly expected included, for example, *Pinus halepensis*, *Quercus faginea* and *Q. suber*. In contrast, native species such as *Pinus pinaster*, *Alnus glutinosa* or *Salix cinerea* experienced more losses than randomly expected.

3.2 | Models for temporal changes in tree species abundance

After adjusting for the species' initial number of trees and average tree density in the plots (i.e. initial stand development), the change in tree species abundance was significantly positively related to forest densification (Δ Tree density) across the entire climate gradient (averaged estimate ± SE = 0.56 ± 0.11; Figure 3a), at the cold and wet edge (0.50 ± 0.12; Figures 3b), and at the warm and dry edge (0.80 ± 0.08; Figure 3d). This effect increased when considering a more restrictive threshold for the climate edges (Appendix S5). Additionally, the change in tree species abundance was significantly related to climate change (Δ Climate) at the climate edges. Specifically, in the cold and wet edge, tree species that experienced higher abundance increases tended to shift their distribution towards colder and wetter conditions (−0.26 ± 0.11; Figure 3b). Conversely, at the warm and dry edge, species showing increased abundance tended to shift towards warmer and drier conditions (0.29 ± 0.09; Figure 3d).

At the cold and wet edge, our analysis revealed a significant negative relationship between abundance changes and the interaction between climate change and root mass fraction (RMF; −0.31 ± 0.11), specific leaf area (SLA; −0.25 ± 0.08) and, marginally, seed mass (SM; −0.27 ± 0.13; Figure 3b). These interactions indicate that species that became more abundant towards colder and wetter areas also had higher RMF, SLA and SM (Appendix S8). Greater increases in tree species abundance than expected if stem gains and losses occurred randomly across the climate gradient were positively related to forest densification when controlling for tree height (TH; 0.34 ± 0.14) and specific stem density (SSD, 0.41 ± 0.15; Figure 3c). Greater increases than random were also positively related to TH (0.33 ± 0.13) and negatively related to SSD (−0.27 ± 0.13) and its interaction with climate change (−0.28 ± 0.11).

At the warm and dry edge, the significant interaction between Δ Climate and RMF (0.27 ± 0.07) indicates that species that became more abundant towards warmer and drier areas also had higher RMF (Figure 3d; Appendix S8). Greater increases than random were significantly positively related to forest densification when adjusting for TH, SSD, RMF and the xylem resistance to embolism (P50), albeit with an overall weak effect size (0.27 ± 0.13; Figure 3e).

4 | DISCUSSION

Climate change is expected to exert a pronounced impact on tree populations inhabiting the edges of their climatic distribution,

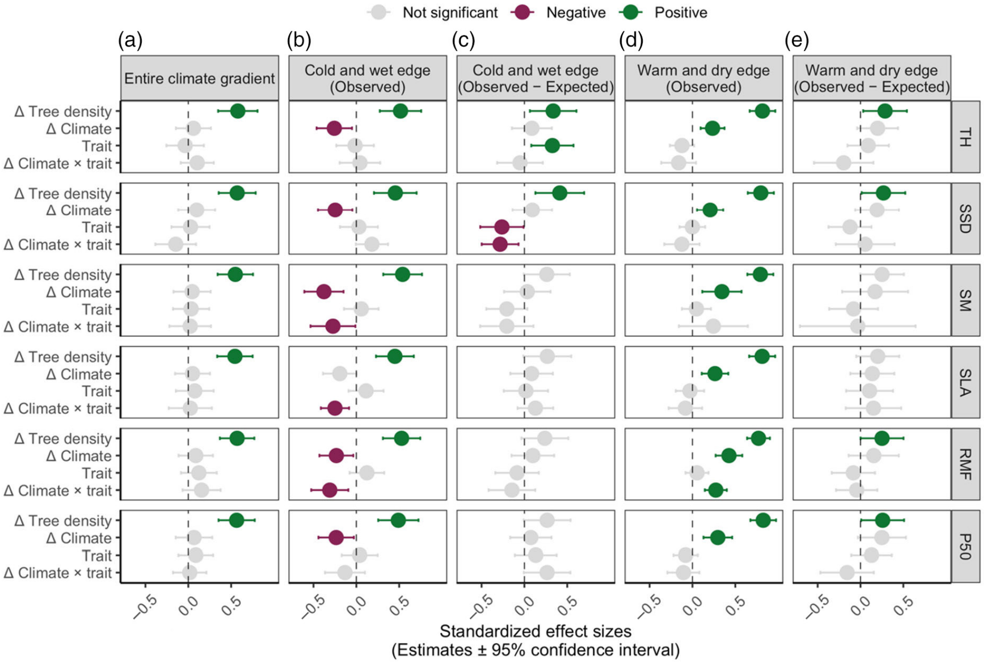

FIGURE 3 Results from ordinary least square (OLS) regressions predicting the proportional change in tree species abundance over time across the entire climate gradient and at the climate edges (observed and unstandardized [Observed − Expected] values) ($N = 68$). For each model, the standardized effect sizes (estimated coefficients ± 95% confidence intervals) of the variables are shown. P50, xylem resistance to embolism; RMF, root mass fraction; SLA, specific leaf area; SM, seed mass; SSD, specific stem density; TH, tree height.

given their proximity to ecological thresholds. Our analysis of over 445,000 monitored trees spanning 68 species across a 25-year period in Spain revealed a limited influence of macro-climate change on tree species abundance changes at the climate edges. Instead, we observed a stronger positive association between changes in tree species abundance at the climate edges and forest densification—a phenomenon stemming from the abandonment of traditional forest management practices (Astigarraga et al., 2020; Vayreda et al., 2016; Vilà-Cabrera et al., 2023). This underscores the pivotal role of historical forest management in shaping species distribution and moderating the effects of climate change. Nevertheless, our study uncovered the relationship between changes in tree species abundance and the interplay of climate change with species traits. We report species-specific temporal trends in abundance, highlighting species that experienced greater gains or losses at the climate edges than randomly expected.

4.1 | Tree species abundance changes along the entire climate gradient

Consistent with the expectations of the secondary successional trajectory in Mediterranean forests (Carnicer et al., 2014; Vayreda et al., 2016; Zavala & Zea, 2004), we found a proportional increase in the abundance of common broadleaved late-successional species, including *Quercus* species, as well as tree species associated with domestic human activities, such as the invasive Australian blackwood (*Acacia melanoxylon*) or the wild cherry (*Prunus avium*). In contrast, we found a decrease in early successional conifers, particularly *Pinus* species, across the study area. In the early twentieth century, conifer trees, particularly pines, were commonly used in Spain's forest restoration and afforestation efforts (Vadell et al., 2016). This preference for pine trees was largely influenced by the ecological facilitation idea, advocating for extensive use of single-species pine forests due to their ability to pioneer and thrive in various environments. This facilitated the later growth of broadleaved tree species (Valbuena-Carabaña et al., 2010). Therefore, our findings further support the trend towards an increase in slower-growing, longer-lived trees. These species rely on competitive strategies, exhibiting greater shade tolerance and a slower growth rate, crucial for their persistence in established ecosystems.

The proportional increase of most tree species in Spain primarily results from tree densification in the plots due to reduced forest management and anthropogenic disturbances (Ameztegui et al., 2016; Urbieta et al., 2008), rather than factors directly related to climate change. Recent forest densification in Spain can be interpreted as a consequence of the abandonment of forest management and agricultural practices, supported by a substantial body of literature (e.g. Astigarraga et al., 2020; McGrath et al., 2015; Selwyn et al., 2024; Vayreda et al., 2016). Although natural increases in tree abundance may contribute to this densification, they do not undermine the primary drivers identified in our analyses. While climate change does not appear to affect overall abundance changes across the study area, extreme episodes of warm and dry conditions and the spread of pathogens and insect outbreaks may have impacted local tree populations. Previous studies have shown this is particularly true for species at the southern limit of their distribution in the Iberian Peninsula, such as *Abies alba* (e.g. Hernández et al., 2019; Oliva & Colinas, 2007), *Fagus sylvatica* (e.g. Dorado-Liñán et al., 2022; Peñuelas & Boada, 2003) and *Pinus sylvestris* (e.g. Jaime et al., 2019; Martínez-Vilalta & Piñol, 2002). Additionally, the decline in traditional cultivated plantations could explain the general decrease in abundance of various other conifers, such as *Larix decidua* or *Picea abies*, or broadleaved trees with high water needs, such as *Populus nigra* or *P. tremula* (Vadell et al., 2016).

4.2 | Tree species abundance changes at the climate edges

Our study marks a pioneering use of the Spanish Forest Inventories (SFIs) to analyse species-specific abundance trends across the majority of Iberian tree species. Our approach allowed us to identify tree species undergoing higher changes in abundance at the climate edges than expected through random gains and losses across the entire climate gradient. We revealed contrasting temporal dynamics among tree species. Notably, *Fagus sylvatica*, *Abies alba* or *Quercus petraea*, species nearing their southernmost distribution in the Iberian Peninsula, exhibited greater increases at the cold and wet edge than randomly expected, but not at the warm and dry edge. In contrast, *Quercus ilex*, a common sclerophyllous tree in the Mediterranean basin, expanded at the warm and dry edge, albeit at a lower rate than randomly expected. Drought-adapted Mediterranean species, such as *Pinus halepensis*, *Quercus faginea* and *Q. suber*, showed increases exceeding random expectations in the warm and dry edge, corroborating findings from previous studies with shorter time spans (Vayreda et al., 2016). Their ability to resprout might give them a greater capacity for rapid recovery after wildfires or thinning at the warm and dry edge (Retana et al., 2002), although this effect could not be tested in our study. Conversely, native riparian species like *Alnus glutinosa* or *Salix cinerea* experienced high proportional declines at the warm and dry edge, surpassing those expected based on random patterns. This finding reinforces the idea that riparian forests are among the most endangered ecosystems, particularly in semi-arid Mediterranean regions (Bruno et al., 2014). It is important to note that our study focused exclusively on vegetation stands that were already forests during the initial survey. Investigating vegetation stands that have since been colonized by trees and evolved into forests could provide further valuable insights into the expansion patterns of Iberian tree species.

Under global warming, tree populations existing at the rear edge of their climatic distributions, particularly in warmer and drier regions, are at greater risk of extinction due to reduced habitat favorability and population sizes (Ackerly et al., 2010; Brown, 1984). However, our study area did not conform to these expectations as we found consistent proportional increases in tree species abundance both at warm and dry (rear) and cold and wet (leading) edges. In both climate edges, these changes in tree species abundance were associated with a displacement of species towards more extreme climatic conditions. This observation suggests a plausible scenario where these species could be reclaiming their original ecological niche along the successional gradient (Carnicer et al., 2014; Vayreda et al., 2016). Once their ecological niche is re-established, the impact of climate change on species distribution may become more pronounced. Furthermore, we observed a higher average increase in tree species abundance at the cold and wet edge than would be expected through random gains and losses of stems across the entire climate gradient. In contrast, the increase at the warm and dry edge followed a random pattern. This observation is consistent with a recent study in North American and European forests, which reported similar increases in species abundance towards the colder and wetter regions of their climatic niches (Astigarraga et al., 2024). Notably, historical human interventions and land use changes have been more pronounced in Iberian forests situated in flatter and warmer areas than in remote, rugged high-altitude mountain areas (Grove & Rackham, 2001; Valbuena-Carabaña et al., 2010). This finding is also supported by our observation of a stronger association between abundance changes and forest densification at the warm and dry edge than at the cold and wet edge of the species distribution. As previously noted, forest densification in Spain is likely attributed to the abandonment of traditional management practices (Astigarraga et al., 2020; McGrath et al., 2015).

At the cold and wet edge, proportional increases in tree species abundance were associated with the interaction between climate change and species leaf traits. Specifically, we found that species that more significantly changed their distribution towards colder and wetter conditions also had a higher specific leaf area (SLA). SLA is known to correlate with other leaf traits, reflecting trade-offs between leaf construction and maintenance costs, and the duration of photosynthetic returns from these investments (Reich, 2014; Appendix S4). Plants with high SLA might prioritize capturing resources like light, water and nutrients quickly, which can be advantageous in environments with ample resources or during advanced recruitment (Díaz et al., 2016; Reich, 2014). Our study confirms the role of leaf economics in interaction with climate change in explaining tree species abundance changes at the cold and wet edge. We build upon prior studies highlighting the role of SLA in explaining the distribution of tree species across an aridity gradient in Spain (Costa-Saura et al., 2016; De la Riva et al., 2016). Additionally, SLA holds significance in various aspects of drought resistance. Lower SLA values mainly arise due to high leaf density, achieved through increased concentrations of lignin and structural carbohydrates in leaves (Poorter et al., 2009). Other traits, such as tree height (TH) and specific stem density (SSD), only showed significant effects on tree species abundance when comparing the observed to the expected values. This finding suggests that taller and faster-growing species may have a competitive advantage at the cold and wet edge, allowing them to increase in abundance more than would be expected if tree stem gains and losses occurred randomly.

Among tree species that changed towards more extreme climate conditions in both climate edges (cold and wet vs. warm and dry), those that increased more in abundance also invested more in their root system (i.e. had a higher RMF). This observed trend, particularly at the warm and dry edge, aligns with existing literature indicating that tree species confronting drought stress tend to exhibit a higher RMF. This high investment in underground biomass facilitates improved water uptake from deeper soil layers due to the proliferation of root systems (Eziz et al., 2017; Poorter et al., 2012). The deviation of observed values for proportional changes in abundance from the random expectation at the warm and dry edge did not respond to climate change, plant traits or their interaction. This suggests species-specific and stochastic dynamics are driving the non-random gains and losses of tree stems.

5 | CONCLUSIONS

The discourse surrounding the impact of climate change on tree populations at climate edges often assumes a direct correlation. However, our comprehensive analysis of Iberian tree species challenges this notion. While macro-climate change demonstrated limited influence on tree species abundance changes at climate edges, our findings highlight the intertwined relationship between a decreasing level of direct human pressure and these changes. The abandonment of traditional practices significantly contributed to forest densification, altering species abundance. This nuanced understanding emphasizes the pivotal role of historical forest management practices in moderating climate change effects. Moreover, our study elucidates the links between species traits and environmental factors in driving abundance changes, offering species-specific insights into the direction and strength of these changes. The intricate interplay of species traits like leaf economics and root system investment emerged as crucial factors in explaining these changes. Incorporating historical data on forest management and broadening research into areas that have become forested are crucial for understanding the complex dynamics influencing tree populations in the face of global environmental change.

AUTHOR CONTRIBUTIONS

Josep Padullés Cubino conceived the study with input from Albert Vilà-Cabrera and Javier Retana. Josep Padullés Cubino performed the analyses and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Secondary data and the code used for the analyses are available at https://doi.org/10.5281/zenodo.12619871 (Padullés Cubino, 2024). The primary data for the Spanish Forest Inventory were obtained from the Spanish Ministry for Ecological Transition and the Demographic Challenge. Specifically, data for the 2SFI were obtained from https://www.miteco.gob.es/en/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn2_descargas.html. Data for the 4SFI were obtained from https://www.miteco.gob.es/en/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional/cuarto_inventario.html. Climate data were obtained from the WorldClim database (https://www.worldclim.org).

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SUPPORTING INFORMATION

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

Appendix S1. Location of permanent forest plots.

Appendix S2. Changes in plot tree density between 2SFI and 4SFI.

Appendix S3. Plot-level data cleaning and processing.

Appendix S4. Plant traits and their correlations.

Appendix S5. Results considering a more restrictive edge threshold.

Appendix S7. Tree species experiencing greater variations in the number of trees in their rear and front edges than randomly expected.

Appendix S8. Interactive effect of climate change and plant traits on tree species abundance changes.

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