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Cloud Forest Tree Growth Responses to Climate and Drought Vary by Island and Species in the Macaronesian Region

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ABSTRACT

Aim: Macaronesian cloud forests are insular ecosystems subjected to local environmental variability, but the responses of their tree species to climate variations have never been studied. Our aim was to assess how the variation in environmental conditions associated with the geographical location of several islands in three Macaronesian archipelagos affects the growth patterns and drought-resistance of the dominant cloud forests trees.

Location: Azores, Madeira and Canary archipelagos. Portugal and Spain.

Taxon: Lauraceae, Aquifoliaceae, Clethraceae, Oleaceae, Rosaceae and Cupressaceae.

Methods: We assessed variations in the radial growth response of 10 cloud forest tree species from 18 populations on 5 islands along a geographical gradient in Macaronesia. We quantified the influence of local climatic variables and North Atlantic Oscillation (NAO) and East Atlantic Pattern (EA) circulation patterns on tree growth and how drought events affected to the resistance, recovery and resilience indices estimated for these species.

Results: Trees from the same island showed similar growth patterns, particularly in islands with marked hydric stress. In Madeira and the Canary Islands, radial growth was mainly determined by water availability, winter NAO negatively affected

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growth and droughts caused abrupt narrow growth-ring width. In the Azores, the effect of the EA was positive, as it increased temperature and relative humidity and promoted growth. Trees from wetter environments demonstrated higher growth resistance to drought, while trees from drier sites showed faster growth recovery after drought events.

Main Conclusions: Homogeneous growth patterns among species from the same island suggested that the radial growth of trees in cloud forests is mostly determined by local environmental conditions, which are more important for their growth than phenotypic traits. The variability in water availability determined by a latitudinal geographical gradient throughout the Macaronesian region influenced both the climatic response of the trees and their resilience to drought.

1 | Introduction

The rise in global temperatures and the increasing frequency and intensity of droughts have been observed over the past few decades (IPCC 2023), leading to high environmental stress and increasing tree mortality rates in forest biomes worldwide (Yi et al. 2022; Miranda et al. 2023; Wang et al. 2023; Zhang et al. 2023). Changes in temperature and water availability directly impact physiological processes such as hydraulic transport, potentially leading to tree weakening and death (Barigah et al. 2013; Hartmann et al. 2022). These responses are species-specific and reflect structural and physiological differences that enable some tree species to withstand drought better than others (Eilmann and Rigling 2012; Rodríguez-Ramírez et al. 2024). Furthermore, a community-dependent variability of these responses has been found in regions that have suffered large-scale forest decay after severe drought events, which have occurred sooner than predicted by climatic models (Guzmán, Hamann, and Sánchez-Azofeifa 2024). This suggests that climate change could modify the community structure of forests in a shorter time than expected (Miranda et al. 2023). Therefore, understanding how different tree species respond to drought is essential to anticipate potential important shifts in terrestrial ecosystems driven by climate change.

Forests on oceanic islands exhibit variable local environmental conditions that are modulated by topography and exposure to climatic forces, which create marked environmental gradients (Vázquez-Garcia 1995; Whittaker and Fernández-Palacios 2007; Losos and Ricklefs 2009). The main insular area in the North East Atlantic Ocean is the Macaronesia, which includes the volcanic archipelagos of Azores, Madeira, Selvages, the Canary Islands, and Cabo Verde (Fernández-Palacios et al. 2024). This insular region is distributed along a broad latitudinal gradient, between 39° 45′N, 31° 17′W of the northernmost island (Corvo, Azores), and 14° 49′N, 13 ° 20′W of the southernmost one (Brava, Cabo Verde). The geographical distribution of these archipelagos leads to significant differences in the climate of the islands. Precipitation varies according to three geographic gradients in the region, with decreasing precipitation from north to south and from west to east, and increasing precipitation with elevation (de Nicolás et al. 1989; Fernández-Palacios 2011). Temperatures also increase from north to south, and decrease as altitude increase (Fernández-Palacios 2011). The Canary Islands exhibit a Mediterranean climate with cool winters and warm and dry summers, Madeira has both Mediterranean and temperate climates with dry and temperate summer, and the Azores have a temperate oceanic climate without dry season with temperate summer (del Arco Aguilar et al. 2010; Couto 2011).

The differences in latitude, altitude and degree of isolation among the islands result in exceptional biodiversity with a high proportion of endemic species (de Nicolás et al. 1989). Among the different vegetation types, the region of Macaronesia hosts cloud forests dominated by *Juniperus brevifolia* (Seub.) Antoine and *Laurus azorica* (Seub.) Franco in the Azores (Elias et al. 2016), by *Ocotea foetens* (Aiton) Baill in Madeira (Capelo et al. 2021), and by *Laurus novocanariensis* Rivas Mart., Lousã, Fern. Prieto, E. Días, J. C. Costa & C. Aguiar in the Canary Islands (del Arco Aguilar et al. 2010). In the Canary and Madeira Islands, these forests are distributed in the montane and submontane belts on the windward slopes of the islands, where trade winds are intercepted by mountains and grow under the influence of a cloud belt (Aboal, Saavedra, and Hernández Moreno 2015; Regalado and Ritter 2021). The Azores archipelago is under the influence of westerlies and cloud forests have a widespread potential range within the islands, potentially being able to cover a large part of the islands (Elias et al. 2016). The almost permanent influence of the cloud belt implies abundant horizontal precipitation and low incident radiation in the cloud (Ritter, Regalado, and Aschan 2009; Regalado and Ritter 2021).

Tree-ring studies provide important information about the climate sensitivity of tree species and the effects of climate change and drought events on annual variation in secondary tree growth (Brienen, Schöngart, and Zuidema 2016; Correa-Díaz et al. 2023). Previous studies on Macaronesian cloud forests have shown that several tree species are suitable for conducting dendrochronological assessments of environmental and anthropogenic impacts on tree growth (Pupo-Correia 2016; Matos et al. 2019; Pavão et al. 2022, Pavão, Jevšenak, Engblom, et al. 2023, Pavão, Jevšenak, Silva, et al. 2023; Rozas et al. 2023). Several studies have analysed tree growth resilience strategies to drought in the Mediterranean region, finding that trees from wetter forests have greater resistance to these events, whereas trees from drier forests tend to recover more quickly after drought (Gazol and Camarero 2016; Gazol et al. 2018; Sánchez-Salguero et al. 2018; Marcotti et al. 2021). Although we can assume that almost permanent vapour plume exposure of cloud forests will alleviate water stress caused by droughts (Rodríguez-Ramírez et al. 2023), pronounced negative effects of drought on tree growth have been observed worldwide, even in areas without water restrictions (Huang et al. 2021; Su et al. 2021; Yang et al. 2022). In fact, a recent study has found abrupt declines in the annual growth of cloud forest trees that coincided with severe drought events on Tenerife, the Canary Islands (García-López et al. 2022). Nonetheless, there is limited information on the drought resilience strategies of cloud forest trees, and a comprehensive analysis of the growth response of tree species to climate at the scale of the Macaronesian region is still missing.

In this work, we conducted a dendrochronological study of 10 cloud forest tree species from 15 populations along the Macaronesian region in the archipelagos of the Azores, Madeira and the Canary Islands. We established robust tree-ring chronologies and quantified the relationship between Macaronesian cloud forest tree growth and climate records to determine their responses to climate variability and drought events. We hypothesize that there is a latitudinal gradient in water availability, and that the growth of different species depends on local climate variables modulated by circulation patterns. We also expect that cloud forest trees further north will show a less pronounced impact of drought on growth and should be more resistant to drought events than trees in the south, while individuals further south will be more frequently affected by drought and will have a greater ability to recover growth after drought events. Our aims were to: (i) identify common growth patterns among tree species and islands along the geographical gradients of cloud forests in Macaronesia, (ii) quantify the relationship between tree growth and local climatic variables, (iii) evaluate the influence of the NAO and EA circulation patterns on tree growth and (iv) assess the resilience capacity of secondary growth of cloud forest tree species in the face of extreme drought events.

2 | Materials and Methods

2.1 | Macaronesian Cloud Forests

Macaronesian cloud forests in the Canary Islands and Madeira are young secondary forests dominated by *Laurus novocanariensis* and *Ocotea foetens*, respectively, along with other evergreen trees with lauroid leaves, and have a canopy that can reach up to 30 m high. These forests represent relict stands of a thermophilic forest type that dominated Europe and North Africa for more than 50 million years in the Tertiary (Mai 1991; Nogué et al. 2013; Fernández-Palacios et al. 2017). These forests occur between 300 and 1500 m a.s.l depending on the island, and usually are immersed in a cloud belt formed by vapour plumes that arise when the trade winds are intercepted by the inselbergs (Prada et al. 2009; Figueira et al. 2013; Regalado and Ritter 2021). In the Azores, primary low-canopy montane forests dominate, with tree heights ranging from 3 to 5 m, which were established on solidified lava flows. This forest type includes *Juniperus brevifolia*, *Ilex azorica* (Loes.) Tutin, and *Laurus azorica*, and is found at elevations between 600 and 1000 m a.s.l. (Elias et al. 2016). The three archipelagos share genera such as *Picconia, Laurus, Ilex, Erica*, *Morella* and *Prunus*. The genera *Apollonias, Persea*, *Ocotea*, *Heberdenia* and *Visnea* are shared by Madeira and the Canary Islands, and there are also local endemics such as *J. brevifolia* in Azores, *Clethra arborea* Aiton in Madeira or *Arbutus canariensis* Weill. and *Pleiomeris canariensis* (Willd.) A. DC. in the Canaries (Capelo et al. 2007; Dias et al. 2007). The Cape Verde archipelago was excluded from this study because it lacked the necessary climatic conditions for the existence of cloud forests.

2.2 | Study Taxa

This study includes a total of 10 species from eight genera and six families (Table S1). These species are *Laurus azorica*, *L. novocanariensis*, *Ocotea foetens* and *Persea indica* (L.) C.K. Spreng (Lauraceae), *Picconia excelsa* (Aiton) DC. (Oleaceae), *Ilex azorica* and *I. perado* Aiton subsp. *platyphylla* (Webb & Berthel.) Tutin (Aquifoliaceae), *Clethra arborea* (Clethraceae), *Prunus lusitanica* L. subsp. *hixa* (Willd.) Franco (Rosaceae) and *Juniperus brevifolia* (Cupressaceae). All studied species from the cloud forest exhibit distinct tree-ring boundaries, enabling to obtain complete annual growth series in the majority of studied individuals (Pupo-Correia 2016; Matos et al. 2019; García-López et al. 2022; Pavão et al. 2022, Pavão, Jevšenak, Engblom, et al. 2023, Pavão, Jevšenak, Silva, et al. 2023). The families, sampling sites and distribution range of each study species are summarised in Table S1.

2.3 | Field and Laboratory Work

We studied forest plots in the islands of Terceira in the Azores archipelago, Madeira in the Madeira archipelago and Tenerife, La Palma and La Gomera in the Canary archipelago (Figure 1a). Sampling was conducted between September 2019 and March 2022. We established a total of 18 plots with a radius of 20–25 m across the islands. Three plots were delineated on each island, with the exception of Tenerife, where six plots were established, three in the western tip and three in the eastern tip of the island (Figure 1e–i). In each plot, we identified the trees at species level, measured their diameter at breast height (DBH), and cored those with a DBH greater than 10 cm. On Terceira, Madeira, and Tenerife, we cored 80 individuals per plot including all the species present, while in La Gomera and La Palma, only 20 individuals of *Laurus novocanariensis* and 20 of *Persea indica* per plot were cored (Table 1). We obtained two wood cores per tree using 5.2-mm diameter increment borers (Haglöf, Sweden).

Wood cores were air-dried, glued to wooden mounts and polished in the transverse plane with increasingly finer grit sandpaper, according to Speer (2010). The cores were then digitised using the CaptuRING device, which automatically captures multiple images (García-Hidalgo et al. 2022) at a resolution of 5931 dpi, and the resulting images were merged using PTGUI v8.3.10 Pro (New House Internet Services B.V., Rotterdam, the Netherlands). We used the CooRecorder software to date the annual tree rings and to measure their widths (Maxwell and Larsson 2021). Cross-dating and measurement errors were checked using the COFECHA software (Holmes 1983). Series with potential dating errors were either corrected when feasible or discarded otherwise.

2.4 | Tree-Ring Chronologies Development

We standardised the ring-width time series for each species and island using a two-step procedure to obtain dimensionless ring-width indices. First, we removed long term trends in annual ring width associated with increasing tree age and/or size

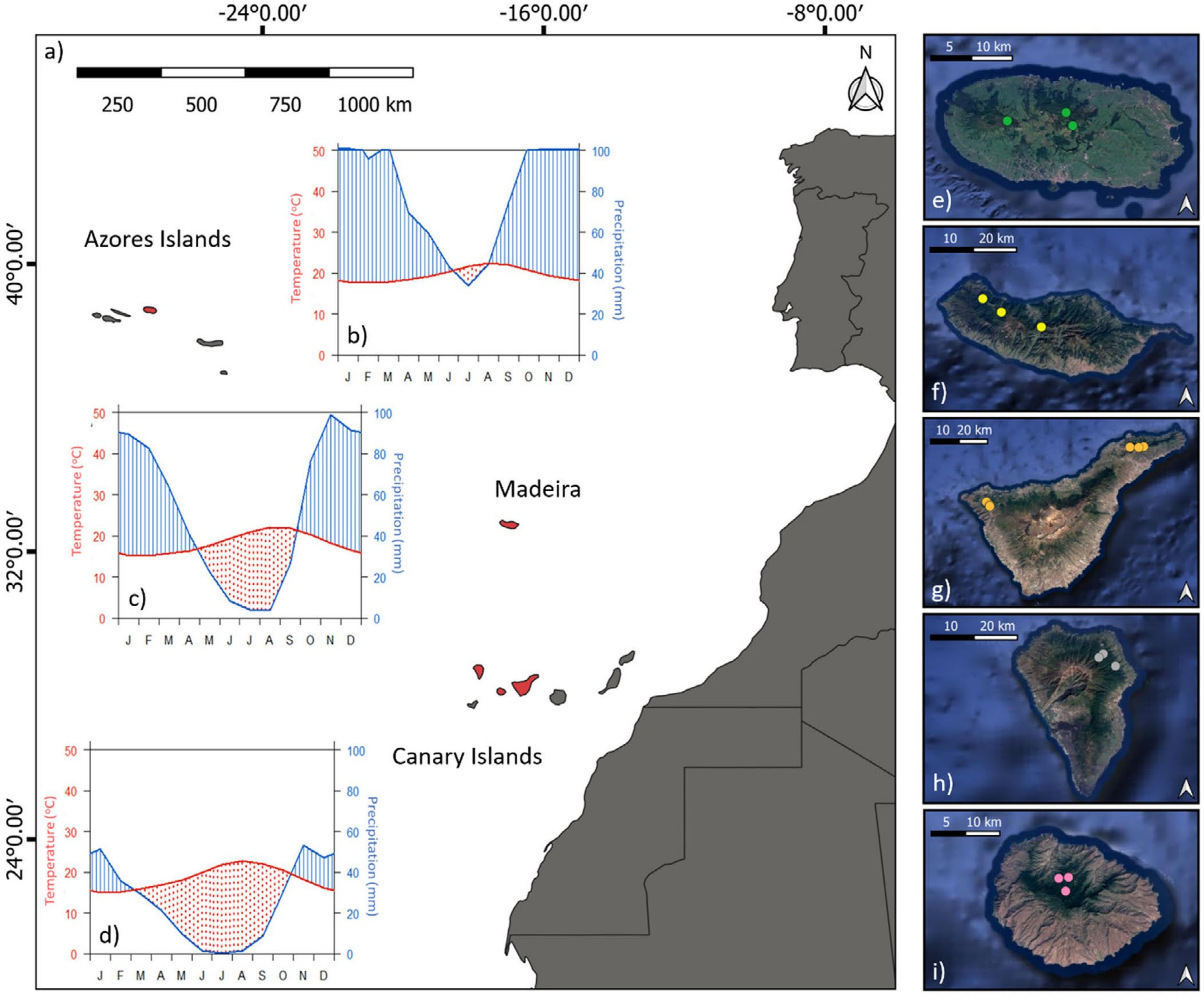

FIGURE 1 | Location (a, in red) of the study islands of Terceira (Azores Islands), Madeira, and Tenerife, La Gomera and La Palma (Canary Islands, from east to west) and climate diagrams of study archipelagos (b-d). Precipitation (mm): Accumulated monthly vertical precipitation. Temperature (°C): Mean monthly temperature. Location of the study plots in Terceira (e), Madeira (f), Tenerife (g), La Palma (h) and La Gomera (i). Data for climatic diagrams were obtained from http://climexp.knmi.nl/ and the period of the data used corresponds to the length of the chronologies for each island.

using a linear or negative exponential function. Second, we applied a cubic smoothing spline with a 50% frequency response cut-off of 0.67 of series length years to reduce any non-climatic variance in the chronology (Cook and Peters 1981). Finally, we calculated the standardised ring width index (RWI) chronologies as a biweight robust mean of all individual series of previously obtained growth indices (Cook et al. 1990). To verify the quality of the dating and the common signal of the tree-ring series used to calculate each chronology, we obtained three descriptive chronology statistics for the optimal period per species and island (Table 1). Mean sensitivity (MS) quantifies the year-to-year variability in tree-ring width ranging from 0 to 1. Complacent tree-ring series showing low variability have MS values close to 0, whereas MS values around 0.2 and larger are generally accepted for series which are sensitive enough for climate reconstruction (Speer 2010). Series intercorrelation (r_{xy}), or the mean of all possible correlations between individual series, was computed as the average of the correlations between each series (x) and the master dating chronology (y), which in our case represents the common signal recorded per species and island. Finally, expressed population signal (EPS) is a measure of shared variability in a chronology that depends on sampling depth (Speer 2010). If the EPS is higher than 0.85, the chronology is considered to have a sufficiently high level of replication and dating quality, whereas if the EPS value is <0.85, the chronology is considered to be well dated, but may lead to large confidence limits in a climate reconstruction (Wigley, Briffa, and Jones 1984; Buras 2017). Chronologies and their quality statistics were obtained using the package *detrendeR* (Campelo, García-González, and Nabais 2012) in *R* environment (R Core Team 2023).

2.5 | Climate Data

Gridded climate time series for the two 0.5° longitude ×0.5° latitude sectors in which each of the study islands was located were downloaded. Monthly average temperatures

TABLE 1 | Name of the study island, archipelago, and tree species, number of dated tree-ring width series and trees included in the chronology, maximum tree age, optimal interval analysis in years for each chronology ($n > 12$), statistics obtained for the optimum period for each chronology (MS, r_{xy}, EPS), mean tree-ring width (MRW) and mean diameter at breast height (DBH) for each species. MS: Mean sensitivity; r_{xy}: Series intercorrelation; EPS: Expressed population signal; MRW: Mean ring width (mm ± SD): DBH: Diameter at breast height (cm ± SD).

Island	Species	Series/ trees in chronology	Min/mean/ max tree age (years)	Optimal interval analysis	MS	r_{xy}	EPS	MRW	DBH
Terceira	*Laurus azorica*	24/15	30/41/61	1992–2017	0.358	0.499	0.894	1.1 ± 0.6	11.03 ± 2.83
	Ilex azorica	28/20	26/56/126	1980–2020	0.428	0.503	0.837	1.4 ± 0.8	20.12 ± 8.46
	Juniperus brevifolia	40/32	32/45/63	1989–2021	0.307	0.572	0.929	1.4 ± 0.8	17.39 ± 5.00
Madeira	*Laurus novocanariensis*	48/31	16/56/90	1977–2019	0.346	0.398	0.888	1.8 ± 0.9	23.45 ± 5.51
	Ocotea foetens	25/15	21/43/62	1989–2020	0.346	0.468	0.775	2.4 ± 1.2	29.63 ± 11.33
	Clethra arborea	38/25	20/31/44	1996–2015	0.235	0.703	0.964	2.8 ± 1.3	20.75 ± 3.54
Tenerife	*Laurus novocanariesis*	163/118	35/60/87	1974–2018	0.410	0.413	0.976	2.2 ± 1.3	31.16 ± 8.16
	Persea indica	21/14	43/68/84	1965–2019	0.396	0.627	0.942	2.9 ± 2	33.03 ± 11.32
	Picconia excelsa	40/25	22/50/92	1982–2015	0.558	0.397	0.862	2.3 ± 1.7	30.23 ± 14.02
	Prunus lusitanica	26/17	35/62/82	1967–2017	0.529	0.455	0.739	1.7 ± 1.2	26.76 ± 5.84
	Ilex perado	22/14	45/63/81	1969–2014	0.550	0.433	0.789	1.9 ± 1.2	32.89 ± 8.79
La Palma	*Laurus novocanariesis*	45/33	32/52/86	1972–2016	0.350	0.271	0.791	2.6 ± 1.4	32.86 ± 8.00
	Persea indica	30/19	20/49/87	1973–2019	0.369	0.524	0.893	3.2 ± 1.6	41.71 ± 15.59
La Gomera	*Laurus novocanariesis*	58/36	32/52/85	1990–2017	0.414	0.444	0.965	3.3 ± 1,6	40.37 ± 9.29
	Persea indica	26/16	28/49/67	1980–2018	0.396	0.677	0.949	3.9 ± 1.8	48.04 ± 8.71

(T), total precipitation (P) and standardised precipitation-evapotranspiration index (SPEI; Vicente-Serrano, Beguería, and López-Moreno 2010) time series were obtained from the CRU TS 4.01 data set (Harris et al. 2014). We used the SPEI1, SPEI3 and SPEI12 databases to obtain annual, seasonal, and hydrological year SPEI values, respectively. We also obtained monthly gridded time series for the two most influential climate indices in the study area (Barnston and Livezey 1987), the North Atlantic Oscillation (NAO) and the East Atlantic Pattern (EA). Monthly climate time series covered the periods 1901–2019 (T, P and SPEI) and 1950–2023 (NAO and EA). Access to the data was provided from the Climate Explorer of the Royal Netherlands Meteorological Institute (http://climexp.knmi.nl/; Trouet and Van Oldenborgh 2013).

According to these data, the Azores archipelago has a temperate oceanic climate with high relative humidity and a short dry period in July (Figure 1b). Climate in the Madeira archipelago (Figure 1c) is temperate with a dry season from May to September and mild temperatures in summer and winter. The Canary Islands (Figure 1d) display a Mediterranean climate with most rainfall occurring in autumn and winter, and summer being the dry season.

2.6 | NAO And EA Circulation Patterns

In the North Atlantic and Western Europe regions, the main drivers of atmospheric variability are the North Atlantic Oscillation (NAO) and the East Atlantic pattern (EA) (Georg, Neves, and Relvas 2023). NAO manifests itself as a meridional dipole of sea-level pressure between two centres of action, Iceland and the Azores, and occurs in two phases, a positive phase associated with mild and rainy winters in northern Europe, and a negative phase associated with increased precipitation in southern Europe (Hurrell 1995; Trigo, Osborn, and Corte-Real 2002). The EA pattern consists of a monopole of mean sea-level pressure to the south of Iceland and west of the United Kingdom, near 52.5°N, 22.5°W (Barnston and Livezey 1987; Zubiate et al. 2017). The EA pattern is known to influence the climate variability of Western Europe (Murphy and Washington 2001) and plays an important role in the strength and location of the NAO (Moore, Pickart, and Renfrew 2011; Moore and Renfrew 2012). In the Macaronesia region, a positive phase of the NAO is associated with drier conditions and a weakening of the trade winds (Georg, Neves, and Relvas 2023). Some studies document the effects of these circulation patterns on the secondary growth of pine species in Macaronesia (Rozas et al. 2013; Vieira, Campelo, and Nabais 2017), where radial growth is negatively correlated with the NAO.

2.7 | Statistical Analyses

We used principal component analysis (PCA) to explore the common patterns of growth behaviour within our chronologies and to illustrate the main responses to climate of every set of chronologies per island. First, we performed a PCA using all tree-ring chronologies to identify common and unique grouping patterns between islands. We then conducted five separate PCAs, one per island, considering the tree-ring chronologies, climate variables, and circulation patterns for each island to identify patterns among species. PCAs were built using the package *factoextra* (Kassambara and Mundt 2020). We calculated Pearson's correlations between RWI chronologies per species and island as dependent variable, and the climate time series averaged per season (spring, March–May; summer, June–August; autumn, September–November; winter, December–February), per year (annual, January–December), and for the hydrological year (October–September) for every island as predictors. Predictor variables were selected by a stepwise selection approach using the package *olsrr* (Hebbali 2020), which provides collinearity diagnosis and selects the best regression model using a stepwise procedure based on *p*-values. All the statistical analyses were performed in R environment (R Core Team 2023).

We identified the negative pointer years, or years with remarkable stand-level growth decrease, in each chronology per species and island to evaluate the association between severe radial growth decreases and drought occurrence. A pointer year occurs when the majority of trees in a stand shows unusual growth responses, like very narrow or very wide ring widths (Jetschke, van der Maaten, and van der Maaten-Theunissen 2019). To identify negative pointer years, we used the moving window normalisation method introduced by Cropper (1979) with the package *pointRes* (van der Maaten-Theunissen, van der Maaten, and Bouriaud 2015). This method produces time series of so-called Cropper values (Cropper 1979), which are calculated for each year and reflect deviations in the form of standard deviations (SD) from the local mean of a moving window with a width of 13 years, as recommended by Jetschke, van der Maaten, and van der Maaten-Theunissen (2019). We considered negative pointer years only those in which more than 50% of the tree-ring series showed a growth reduction of at least 50% of the standard deviation from the local mean. We graphically examined the annual variation of climate variables related to drought (SPEI minimum values) and circulation patterns (EA and NAO minimum and maximum values) to check the association between negative pointer years and extreme events.

In the negative pointer years for each species and island, we used the *pointRes* R package (van der Maaten-Theunissen, van der Maaten, and Bouriaud 2015) to quantify tree growth responses to severe droughts using three indices proposed by Lloret, Keeling, and Sala (2011): *resistance* (R_t), *recovery* (R_c) and *resilience* (R_s). R_t quantifies the ability of trees to grow during a drought event, R_c describes the ability to continue growing 3 years after a drought event, and R_s measures the capacity to recover pre-drought growth rates 3 years before a drought event (Lloret, Keeling, and Sala 2011). The R_t, R_c and R_s values derived from each pointer year per tree were graphically displayed by species and island, fitting lineal and power models to describe the relationships between R_t and R_c indices.

Finally, we used the *lme4* package (Bates et al. 2015) to build general linear mixed-effects models (GLMM, Gamma family) and to assess whether R_t, R_c and R_s indices varied among species and islands. We performed two models for each response variable (R_t, R_c and R_s). In the first model we included island as an explanatory variable and species, year and individual as random factors. In the second model we included species as an explanatory variable and island, year and individual as random factors. We also performed two linear mixed-effects models for the tree indices of both *Laurus* species and *Persea indica* (response variable) and included island as an explanatory variable and year and individual as a random factor.

3 | Results

3.1 | Characteristics of the Tree-Ring Chronologies

We built 15 tree-ring chronologies with variable replication level. The most and least replicated chronologies were *Laurus novocanariensis* and *Persea indica* from Tenerife, with 163 series of 118 individuals and 21 series of 14 individuals, respectively (Figure 2). The length of chronologies varied between 44 years for *Clethra arborea* at Madeira, and 126 years for *Ilex azorica* at Terceira, with the average length of the chronologies being around 80 years (Table 1).

The mean sensitivity (MS) for the optimal interval for each species and island was above 0.2 in all cases, so that all tree species showed high year-to-year variability in tree-ring width, with a maximum MS value of 0.558 for *Picconia excelsa* in Tenerife Island. The inter-series correlation (r_{xy}) was the highest for *C. arborea* in Madeira with 0.703, and the EPS values in most cases exceeded the threshold of 0.85 at the optimal interval of each chronology. Mean ring widths varied between 1.1 ± 0.6 mm and 3.9 ± 1.8 mm per year (mean ± SD), and tree sizes ranged from 11.03 ± 2.83 cm to 48.04 ± 8.71 cm DBH. The lowest and highest mean values of both ring width and DBH were obtained for *Laurus azorica* in Terceira and *Persea indica* in La Gomera, respectively.

3.2 | Geographical Variation of Growth Responses to Climate

The PCA built with the 15 chronologies showed an explained variance of 68.6% (50% PC1 and 18% PC2). The growth patterns of the studied species tended to group according to their geographical origin, forming three groups that corresponded to the islands of Azores, Madeira and the Canary archipelago, whereas the species from La Gomera, La Palma, and Tenerife had more similar growth patterns (Figure 2).

The PCA generated for Terceira Island (Figure 3a) explained 65% of the total variance and the growth patterns of the three tree species were independent of each other. The growth of *I.*

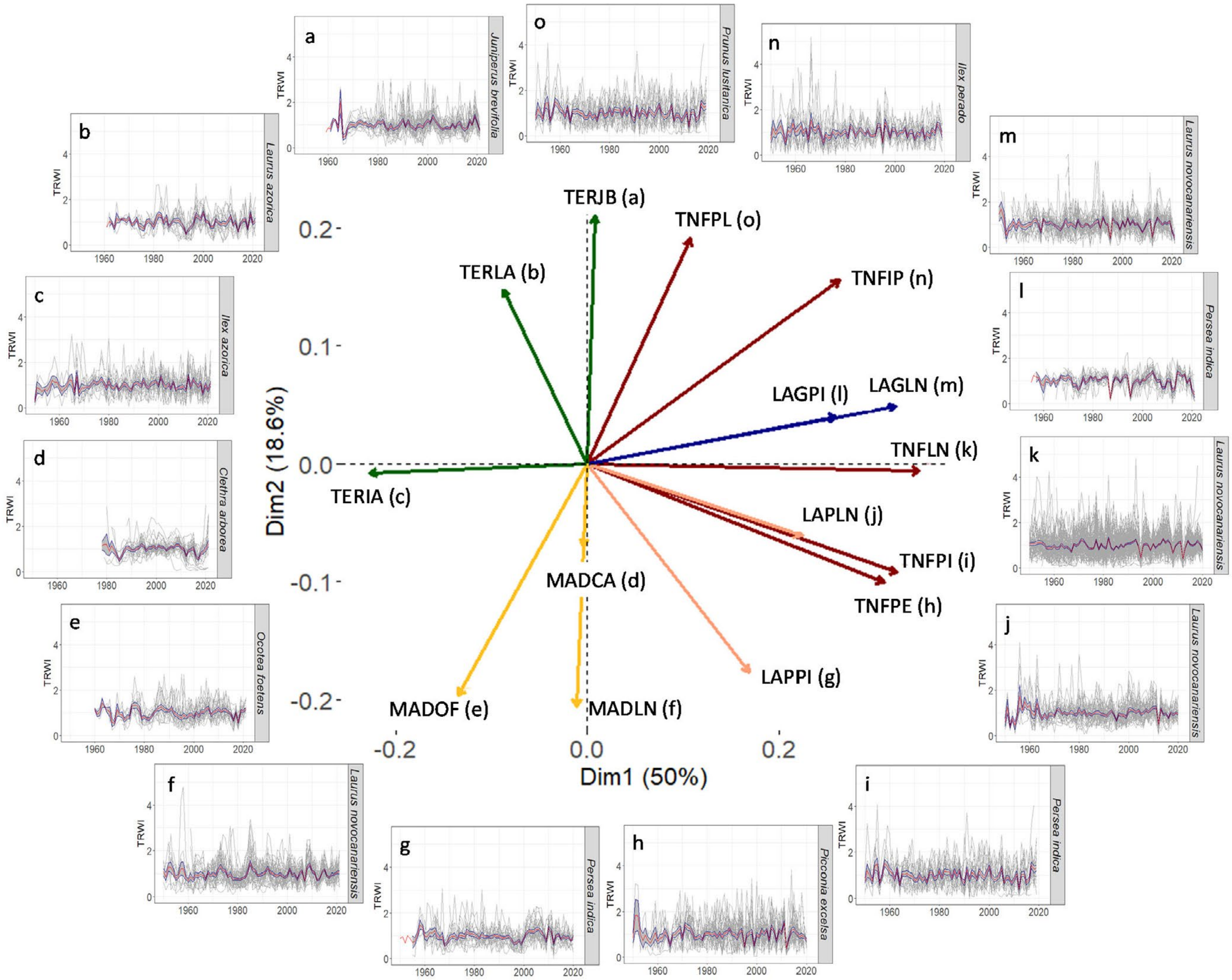

FIGURE 2 | Standardised tree-ring series (grey lines), mean chronologies (red lines) with their corresponding ±1 SE intervals (blue lines) of *Laurus azorica* (a), *Ilex azorica* (b) and *Juniperus brevifolia* (c) from Terceira Island (green arrows), *Laurus novocanariensis* (d), *Ocotea foetens* (e) and *Clethra arborea* (f) from Madeira (yellow arrows), *Laurus novocanariensis* (g), *Ilex perado* (h), *Persea indica* (i), *Picconia excelsa* (j) and *Prunus lusitanica* from Tenerife (red arrows), and *Persea indica* and *Laurus novocanariensis* from La Gomera (l and m; blue arrows) and La Palma (n and o; orange arrows), and Principal Components Analysis biplot including all chronologies. TRWI: Tree ring width index. The percentage of variance explained by the PC axes is shown. Abbreviations of the islands: TER (Terceira, green arrows), MAD (Madeira, yellow arrows), TNF (Tenerife, red arrows), LAG (La Gomera, blue arrows), LAP (La Palma, orange arrows). Abbreviations of the study species: IA (*Ilex azorica*), JB (*Juniperus brevifolia*), LA (*Laurus azorica*), LN (*Laurus novocanariensis*), OF (*Ocotea foetens*), CA (*Clethra arborea*), PE (*Picconia excelsa*), PI (*Persea indica*), IP (*Ilex perado*) and PL (*Prunus lusitanica*).

azorica was positively linked to summer precipitation, while the growth of *J. brevifolia* and *L. azorica* showed a negative influence of winter EA and annual NAO, respectively. In Madeira (Figure 3b), the total explained variance was 67.2%. *Laurus novocanariensis* and *O. foetens* exhibited similar growth patterns, with growth favoured by autumn and hydrological year precipitation and winter SPEI. Regarding *C. arborea*, it showed a growth pattern opposite to the other two species, showing negative relationships with winter SPEI and precipitation in autumn, spring and in the hydrological year.

In the Canary Islands, the PCAs generated for Tenerife, La Gomera and La Palma explained 66.3%, 83.3% and 83.1% of the variance, respectively. In Tenerife (Figure 3c), the growth patterns of *L. novocanariensis*, *P. excelsa*, *P. indica*, and *Prunus lusitanica* were very similar. Growth of these species showed positive relationships with winter SPEI and in the hydrological year and negative relationships with the average summer temperature and with annual and autumn EA, highlighting their dependence on water availability. The growth of *I. perado* showed a positive relationship with annual and spring NAO. In La Gomera (Figure 3d), the growth of *L. novocanariensis* and *P. indica* showed a similar pattern, with positive correlations with the hydrological year precipitation and negative correlations with the average summer and spring temperatures. In La Palma (Figure 3e), the growth of *L. novocanariensis* and *P. indica* was negatively associated to annual and winter NAO. Most studied species in the Canary Islands showed positive correlations of growth with precipitation and SPEI and negative correlations with temperatures, which would indicate that precipitation is the main driver of growth.

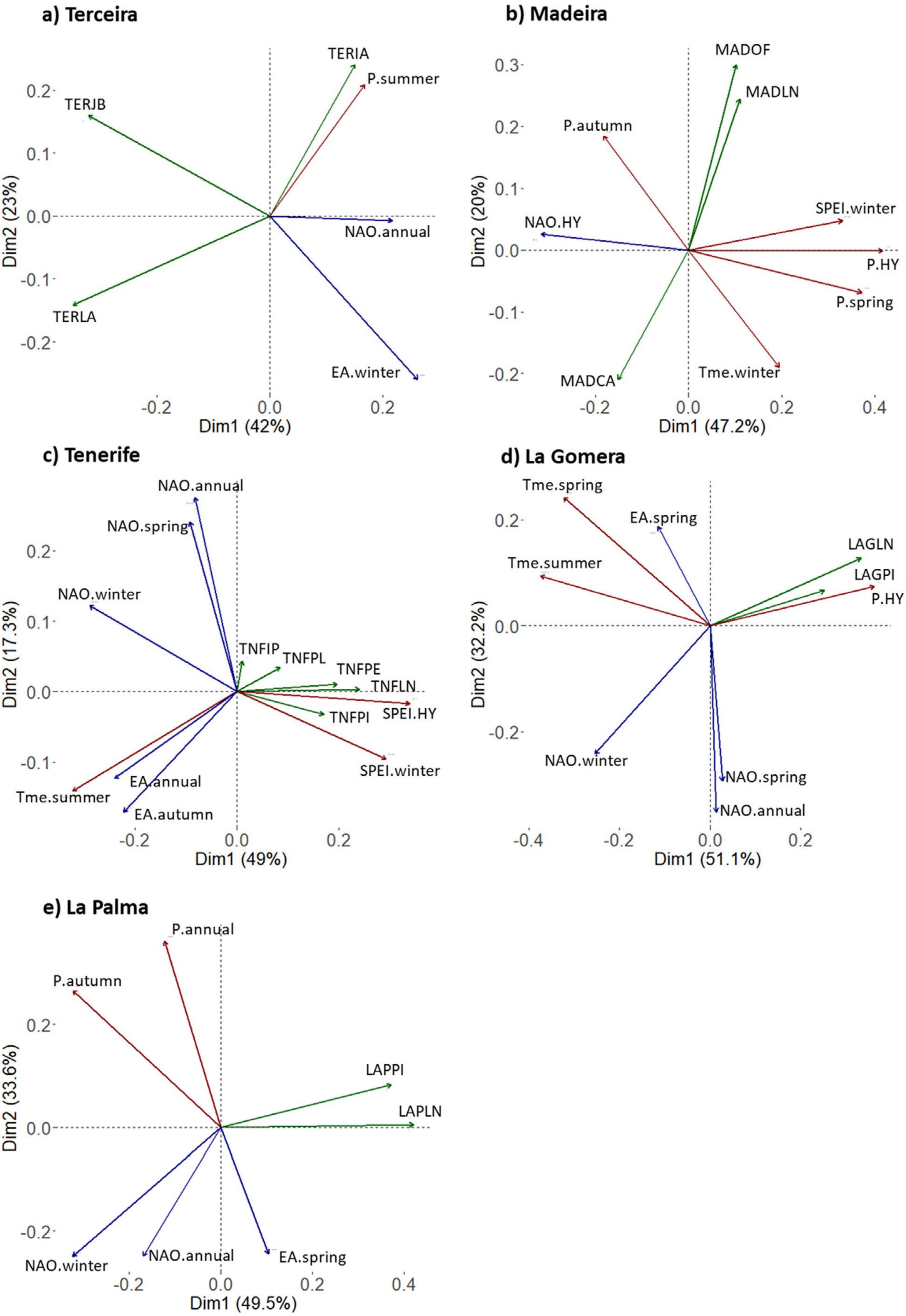

FIGURE 3 | Legend on next page.

FIGURE 3 | Principal components biplots including the chronologies of the studied species (green arrows) and the climate variables (red arrows) and circulation patterns (blue arrows). The percentage of variance explained by the PC axes is shown. Abbreviations of the climate variables and circulation patterns: SPEI (standardised precipitation-evapotranspiration index), P (total precipitation), T (mean temperature), NAO (North-Atlantic Oscillation), EA (East-Atlantic pattern), HY (hydrological year). See Figure 2 caption for abbreviations of the islands and study species.

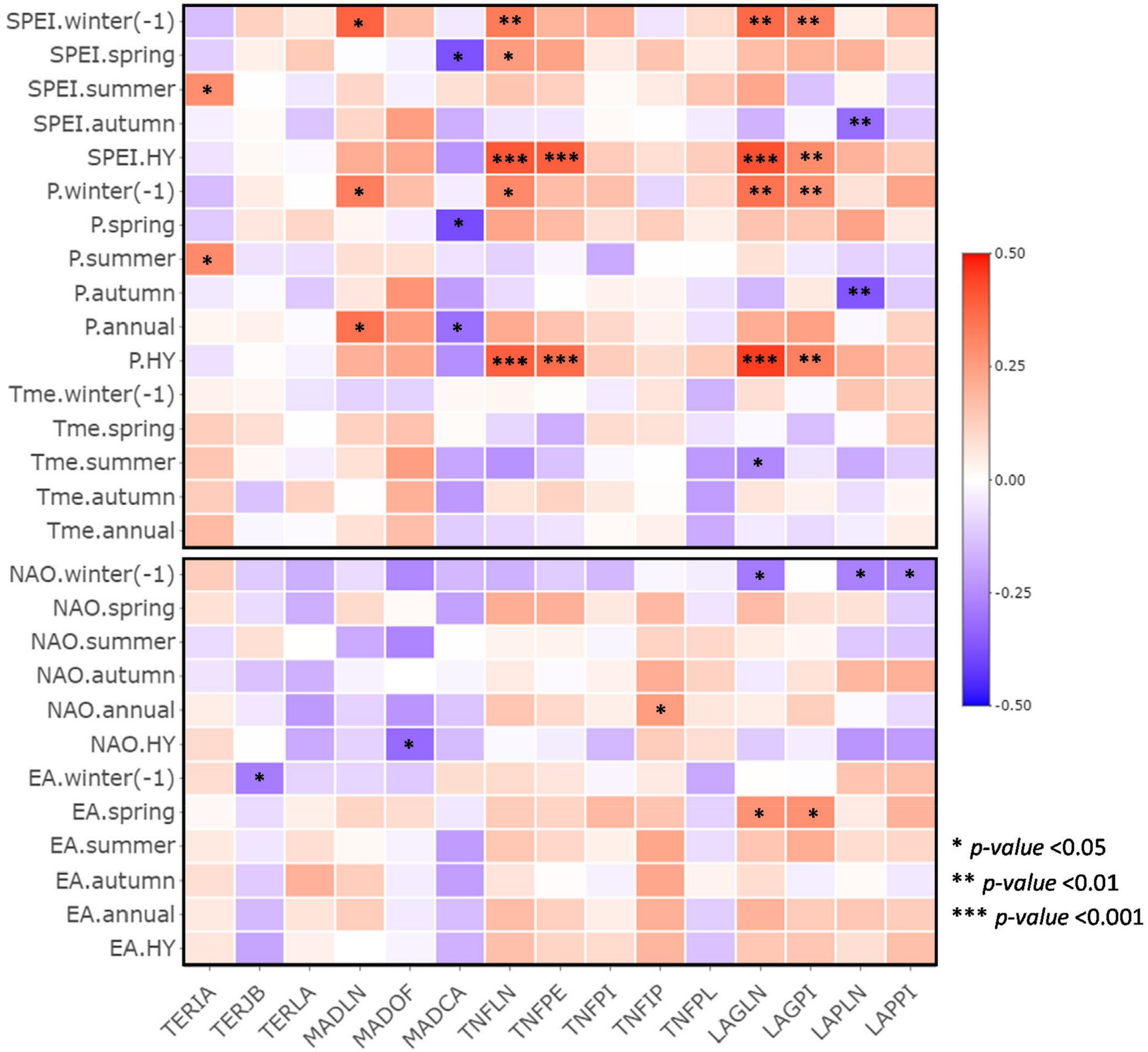

FIGURE 4 | Correlations between the tree-ring chronologies of the different study species and islands (horizontal) the local climatic variables (SPEI, P, T) and circulation patterns (NAO, EA). In red are shown the positive correlations and in blue the negative correlations. The size of the asterisks shows the significance value of each correlation. See the abbreviations of the studied species and islands in Figure 2, and of the climate variables and circulation patterns in Figure 3.

3.3 | Effects of Climate Variables and Circulation Patterns on Tree Growth

The most influential climate variables on tree growth in the Canary Islands were precipitation and SPEI, showing a positive effect on all species except *L. novocanariensis* in La Palma (Figure 4). The most notable positive correlations of tree-ring chronologies with SPEI and P occurred in winter and for the hydrological year, being significant for *Laurus novocanariensis* and *Picconia excelsa* in Tenerife and for *L. novocanariensis* and *Persea indica* in La Gomera. Positive correlations with SPEI and P in winter were also found for the growth of *L. novocanariensis* in Madeira. However, the growth of *Ilex azorica* in Terceira showed positive correlations with SPEI and P in summer. In contrast, the growth of *L. novocanariensis* in La Palma showed significant negative correlations with SPEI and P in autumn. Negative correlations were also observed for *Clethra arborea* growth with the annual and spring SPEI and P in Madeira. The only significant correlation with mean T was negative, indicating that high summer temperatures had detrimental effects on *L. novocanariensis* growth in La Gomera.

Only a few correlations between growth and circulation patterns were significant (Figure 4). In the Canary Islands, winter NAO generally showed a negative influence on tree growth, which was significant for *L. novocanariensis* in La Gomera and La Palma, and also for *P. indica* in La Palma. In the particular case of *Ilex perado* subsp. *platyphylla* in Tenerife, tree growth showed a positive correlation with the annual NAO. The growth of *L. novocanariensis* and *P. indica* in La Gomera showed significant positive correlations with spring EA. In the case of Azores and Madeira, NAO showed negative influence on species growth on both islands (Figure 4). The correlation between the NAO of the hydrological year and the growth of *Ocotea foetens* was significant in Madeira. In Azores, only *Juniperus brevifolia* showed a significant negative correlation with winter EA.

3.4 | Pointer Years and Growth Responses to Punctual Events

Negative pointer years were found in all the tree-ring chronologies except for *O. foetens* in Madeira (Figure 5). In Madeira and the Canary Islands, the pointer years corresponded to years with minimum SPEI values during the hydrological year (October to September). In Terceira, the three negative pointer years found coincided with a combination of high winter EA values and low summer EA values. We found common pointer years between species and islands and also pointer years that were unique to a single species or island.

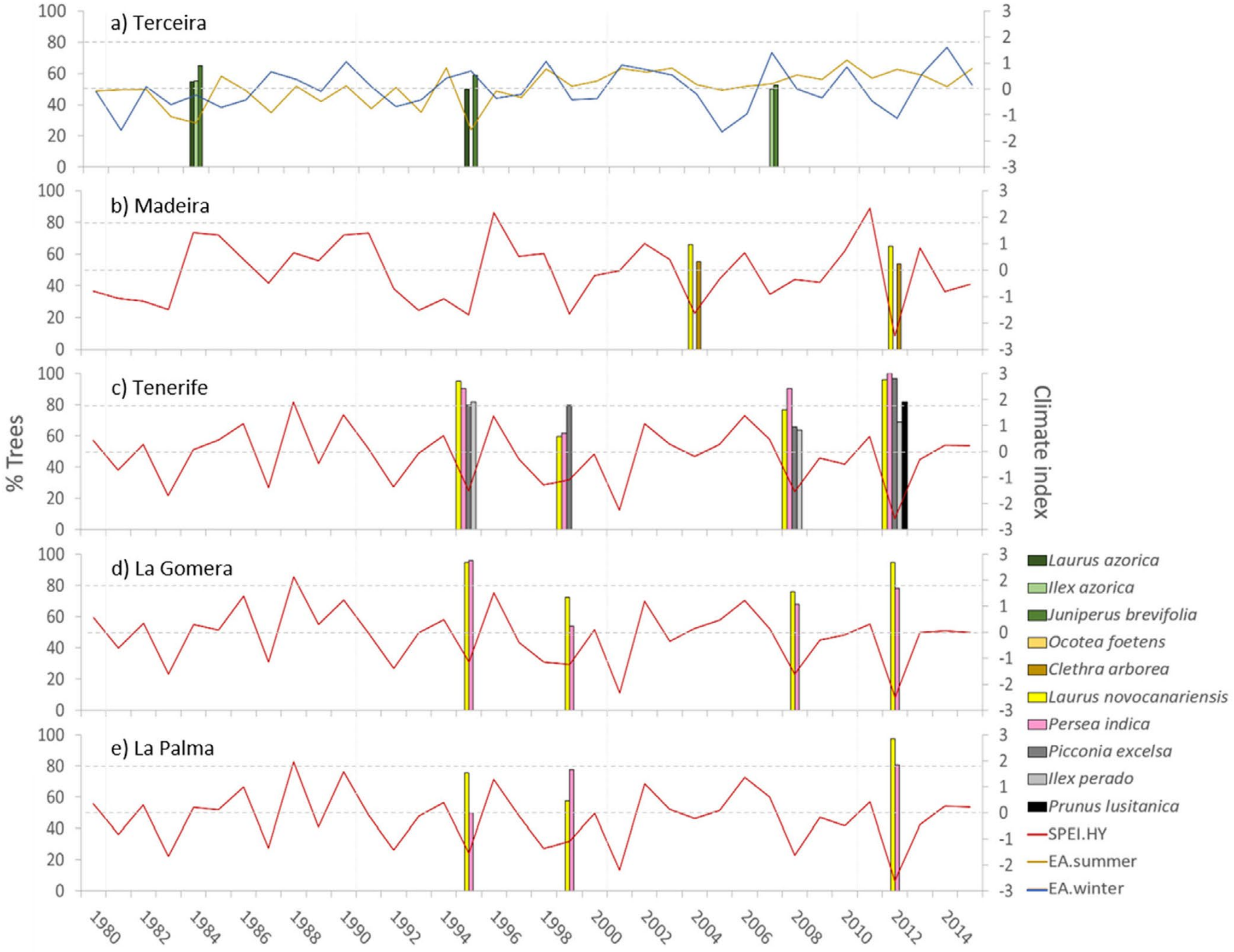

FIGURE 5 | Pointer years identified as percentage of trees of each chronology with annual growth reduction of at least 50% of standard deviation from the local mean within 13-yr moving window (bars, left y axis) in Terceira (a), Madeira (b), Tenerife (c), La Gomera (d) and La Palma (e) and annual variation of SPEI values (red lines, right axis) for the hydrological year (from October of the previous year to September of the current year), EA values for summer and winter (brown and orange lines, right y axis in a). We identified negative pointer years as those in which more than 50% of the tree-ring series of each species and site showed an annual growth reduction of at least 50% of standard deviation from the local mean. Dashed horizontal lines indicate the 50% and the 80% of the tree-ring series of each chronology. Dashed vertical lines mark the decades.

In Terceira, the pointer year 1984 was found to be shared by the three species studied, while 1995 was found only in *L. azorica* and *J. brevifolia*, and 2007 was found only in *J. brevifolia* and *I. azorica* (Figure 5a). The negative pointer years 2004 and 2012 were found in Madeira and were common in *L. novocanariensis* and *C. arborea* (Figure 5b). The negative pointer years 1995, 1999 and 2012 occurred in all the study species in La Gomera (Figure 5d) and La Palma (Figure 5e), as well as in *L. novocanariensis*, *P. indica* and *P. excelsa* on Tenerife (Figure 5c). 2008 was also a negative pointer year for all species from La Gomera and Tenerife, with the exception of *P. lusitanica*, for which only 2012 was a negative pointer year. For *I. perado* on Tenerife, 1995, 2008 and 2012 were found as the negative pointer years. The negative pointer years that the islands had in common were 1995, shared by Terceira and the three Canary Islands (Tenerife, La Gomera and La Palma), and 2012, shared by the three Canary Islands and Madeira (Figure 5).

The variation in drought responsiveness (R_c, R_t, and R_s) of cloud forest trees depended significantly on both the species (Figure S1, Table S4) and the island (Table S3). *Laurus novocanariensis, P. indica*, and *P. excelsa* showed the highest average recovery indices (R_c) in response to drought events, while *C. arborea, J. brevifolia and O. foetens*, were the species with the lowest average recovery rates (Figure S1a). Regarding the resistance index (R_t), *P. lusitanica, L. azorica, and O. foetens*, were the most drought-resistant species. The less resistant species to drought events were *L. novocanariensis, P. indica* and *P. excelsa* (Figure S1b). *Laurus azorica* was found to be the species with the highest resilience to drought events, while *C. arborea* was the least resilient species (Figure S1c).

The power models showed the best fit for the relationship between resistance and recovery of each species, except for *C. arborea*, for which the linear model showed a better fit (Figure 6). In all species, the relationship between resistance and recovery was significant ($p<0.05$). *Laurus novocanariensis*, *P. indica*, *P. lusitanica*, *P. excelsa*, and *I. perado* were the species that showed the best fit, with an $R^2>0.5$, while *L. azorica*, *C. arborea*, and *J. brevifolia* were the ones that showed a poorer fit, with an $R^2<0.2$. On the other hand, *I. azorica* and *O. foetens* showed intermediate fit values with R^2 of 0.448 and 0.316, respectively (Figure 6).

The results obtained by comparing the indices of tree-ring growth response to drought among islands (Table S3) showed similar resistance rates from Terceira, Madeira, and La Palma (Figure 7a), significantly higher than on the other islands. Regarding recovery (Figure 7b), the rates were higher in Tenerife and La Gomera, in contrast to Madeira and La Palma, which had significantly lower values. The lowest resilience values were observed for Madeira (Figure 7c).

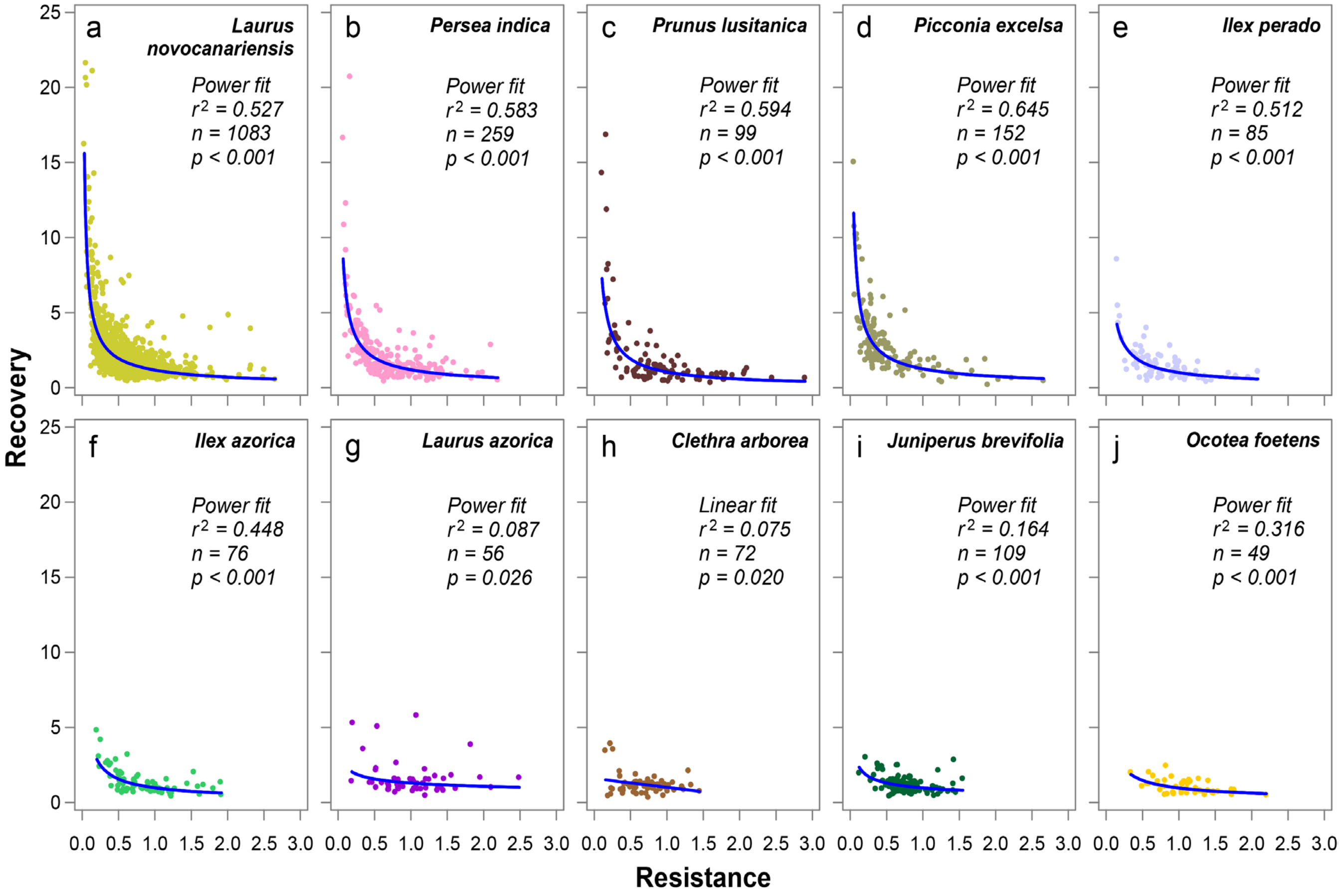

FIGURE 6 | Relationship between resistance and recovery values based on the negative pointer years identified in the tree-ring series of the 10 studied species, considering all studied islands together. Fitted model (blue line) and its statistics for each species are shown.

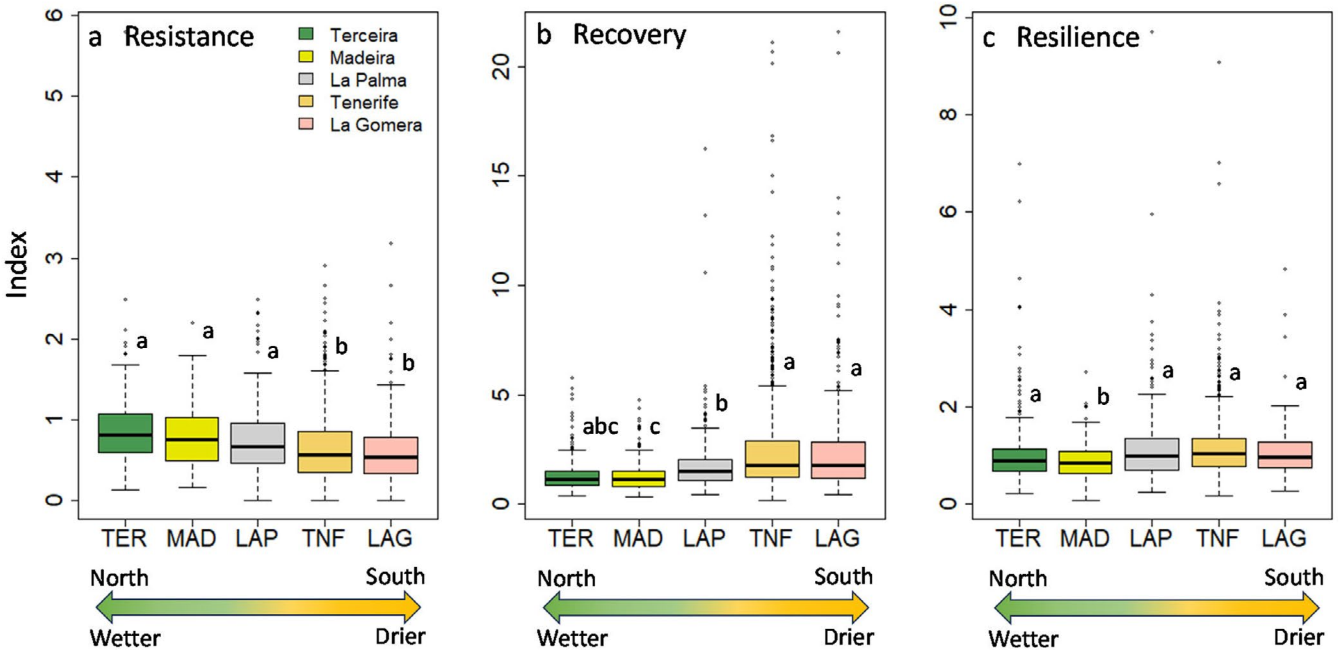

FIGURE 7 | Boxplots of the resistance (a), recovery (b) and resilience (c) indices calculated from the negative pointer years for all tree species sampled in each of the five islands studied (TER Terceira, MAD Madeira, LAP La Palma, TNF Tenerife, LAG La Gomera). The error bars represent mean ± standard error. Letters 'a', 'b' and 'c' indicate significant differences between islands ($p < 0.05$). The sampling sites in the horizontal axis are ordered from left to right according to their location along the north–south moisture gradient.

For the genus *Laurus*, resistance increased and recovery decreased with increasing latitude (Figure S2a,b). Resilience values for *L. novocanariensis* were similar in the Canary Islands and exceeded those of *L. novocanariensis* from Madeira and fell below those of *L. azorica* individuals from Terceira (Figure S2c). In the case of *P. indica*, the resistance and recovery indices increased (Figure S2d) and decreased (Figure S2e) respectively with longitude. The resilience values were similar between Tenerife and La Palma, and between La Gomera and La Palma (Figure S2f).

4 | Discussion

4.1 | Tree Growth Patterns Were Geographically Structured

The local environmental conditions associated with the latitudinal and longitudinal location of the studied islands had a strong influence on the growth patterns of cloud forest tree taxa. Analysis of tree-ring chronologies revealed clustering of species by archipelago, indicating greater similarity among species with the same geographical origin than among different populations of the same species. This suggests a common influence of local climate on growth, with macroclimatic differences between islands being responsible for this grouping (de Nicolás et al. 1989). Furthermore, these findings suggest that the radial growth of cloud forest trees is determined by local environmental constraints rather than the phenotypic characteristics of the species. Our results are consistent with previous studies indicating that geographical and climatic site characteristics have a greater influence on growth response than the biological characteristics of tree species (Babst et al. 2013; Tei et al. 2021).

On the other hand, principal component analyses between chronologies and local climatic variables highlighted stronger similarity among growth patterns with decreasing latitude. This analysis revealed greater homogeneity of growth patterns among species in environments with higher water stress (Madeira and the Canary Islands), suggesting that water deficit modulates species growth and leads to a convergence of tree growth patterns (Ferrero et al. 2013; López, Rodríguez-Catón, and Villalba 2019). The greater heterogeneity in growth patterns among species in Terceira may be related to endogenous forest dynamics and changes in interspecific relationships. On this island, water availability favours the development of dense forests with fast canopy closure. Therefore, although climate may be relevant for tree growth in wet sites, light availability and biotic interactions may lead to species-specific differences in growth rates and, consequently, greater heterogeneity in growth patterns (López, Rodríguez-Catón, and Villalba 2019). This result is supported by the data obtained in the correlation matrix, with the Canary Islands having higher correlation values and a greater number of significant correlations between climatic variables and species growth, indicating a stronger influence of local climate on growth. However, Terceira showed less influence of local climate on growth, with very low correlation values, being *I. azorica* the only species that showed significant correlations.

4.2 | Tree Growth in Macaronesian Cloud Forests Was Controlled by Local Climate Variations

The most influential climatic factor on tree growth in the cloud forests of Macaronesia was water availability, quantified as both SPEI and precipitation. We found specific differences in the timing of growth response to water availability. The findings suggest that the growth of *L. novocanariensis* and *P. excelsa* in Tenerife, and *L. novocanariensis* and *P. indica* in La Gomera, is closely associated with winter precipitation and with a positive water balance during the hydrological year (Oct- Sep). Similarly, in Madeira, the growth of *L. novocanariensis* appears to be mainly influenced by winter precipitation, which leads to high annual total precipitation and a positive water balance. However, in Terceira, the growth of *I. azorica* was favoured by positive water balance in summer, despite annual precipitation and relative humidity are high in the Azores archipelago. Greater water availability early in the growing season likely promotes radial tree growth (Sun et al. 2021). In addition, the low water retention capacity of the soils on which the sampled forests in Terceira develop, being composed of young and poorly developed soils on solidified lava flows, could lead to a greater physiological water deficit in summer, which might also justify the absence of a climatic signal on tree growth during the wettest period (López, Rodríguez-Catón, and Villalba 2019; Cruz and Silva 2001).

Several studies have observed the negative effect of high temperatures on tree growth in tropical and subtropical forests (Ferrero et al. 2013; Brienen, Schöngart, and Zuidema 2016; Jing et al. 2022; Argüelles-Marrón et al. 2023). This is consistent with our results for all studied species in the Canary Islands and for *C. arborea* in Madeira, which showed that high temperatures generally had a negative impact on radial growth, with the unique exception of *L. novocanariensis* in La Gomera. In contrast, a positive influence of temperature on tree growth was observed in Terceira as well as in *L. novocanariensis* and *O. foetens* in Madeira, although not statistically significant. This differential effect of temperature between archipelagos is mainly due to the fact that precipitation in Macaronesia follows a latitudinal gradient decreasing from north to south, making the Canary Islands drier than the Azores and Madeira. The positive effect of temperature on growth was also observed by Pavão, Jevšenak, Silva, et al. (2023) in their study on the relationship between climate and growth in *L. azorica*. They found that warmer temperatures in late spring and early summer enhanced photosynthetic performance during the rest of the growing season. *For I. azorica*, the positive influence of temperature on growth contrasts with the results of Pavão, Jevšenak, Engblom, et al. (2023), who predominantly observed a negative effect of the previous year's temperature on the growth of this species.

Trees on La Palma showed particular growth patterns and dependence on the climate, which differentiated them from the rest of the Canary Islands. At La Palma, the radial growth of *L. novocanariensis* and *P. indica* showed a negative influence of autumn precipitation and SPEI. Due to its more westerly location, La Palma is the wettest Canary island (Herrera et al. 2001), and experiences high amounts of precipitation and abundant associated cloud cover, which reduces incoming solar radiation, decreasing photosynthesis rates and therefore tree growth (Graham et al. 2003). This result was also reported by Rozas et al. (2013) in a *Pinus canariensis* population at the windward slope of Tenerife. Something similar was observed for *C. arborea* in Madeira, whose growth was significantly negatively affected by annual and spring precipitation and SPEI. *Clethra arborea* is an opportunistic species with strong vertical growth into canopy openings and edges of the canopy (Fernández-Palacios et al. 2004). The negative influence of SPEI and precipitation during the growing season and the hydrological year on the growth of *C. arborea* suggests that the decrease in solar radiation caused by precipitation-associated cloudiness could be a limiting factor for this species.

4.3 | NAO And EA Had Local Impacts on the Growth of Cloud Forest Trees

The negative correlations of winter NAO on growth were common to all studied species, but only showed significant correlations with the growth of *L. novocanariensis* in La Gomera and *L. novocanariensis* and *P. indica* in La Palma. The negative effect of winter NAO on growth of cloud forest trees is consistent with the results observed for *Pinus canariensis* in Tenerife (Rozas et al. 2013), where tree ring growth on the leeward slope depended on NAO-related water input. A negative correlation was also reported by Vieira, Campelo, and Nabais (2017) between the NAO in May and June and the ring width of *Pinus pinaster* on Pico Island (Azores archipelago). Previous research has shown that the positive phase of the NAO is associated with higher than average westerly winds and drier conditions in the Mediterranean region, while its negative phase is linked to increased precipitation in southern Europe (Visbeck et al. 2001; Báez, Gimeno, and Real 2021). In Spain, the positive phase of the NAO correlates positively with temperature, especially in the northern and western parts of the peninsula (Ríos-Cornejo et al. 2015a), and negatively with precipitation in the westernmost part (Ríos-Cornejo et al. 2015b). In the Azores, the NAO modulates the magnitude of precipitation, particularly in winter, when high NAO values are negatively correlated with precipitation (Marques et al. 2008). As the low-pressure system over the North Atlantic Ocean strengthens, wetter and colder conditions are likely to occur in the Canary Islands and Madeira. However, high winter pressure produces the opposite pattern, leading to warm and dry winters in these two archipelagos (Rozas et al. 2011, 2013; Cropper and Hanna 2014; Espinosa and Portela 2020).

Regarding the EA, its positive phase is associated with a warm anomaly in Western Europe (Moore and Renfrew 2012; Ríos-Cornejo et al. 2015a), which leads to increasing air temperatures all year around. The positive phase of the EA is also linked to above-average precipitation in Northern Europe and below-average precipitation in Southern Europe (Mikhailova and Yurovsky 2016). A detailed study for the Iberian Peninsula relates high winter EA values to higher precipitation in the western part of the peninsula, while in summer, high EA values are reflected in lower precipitation (Ríos-Cornejo et al. 2015b). In cloud forests, where water availability and relative humidity are generally high, the high temperatures favoured by the positive phases of the EA may stimulate photosynthesis and water uptake without water acting as a limiting factor. This situation probably promotes the growth of species that develop within the canopy, but negatively affects the growth of opportunistic trees that establish in clearings within or at the edges of the canopy. This would explain the positive association between EA and the growth of all species, with the exceptions of *J. brevifolia* in Terceira, *C. arborea* in Madeira, and *P. lusitanica* in the Canary Islands.

While *J. brevifolia* and *C. arborea* regenerate from seedlings recruited in open areas or after gap formation (Elias and Dias 2009; Elias, Dias, and Pereira 2011), *P. lusitanica* regenerates primarily through suckers and is considered a gap maker in mature forests, being one of the main gap generators in cloud forests (Arévalo and Fernández-Palacios 1998; Arévalo, Fernández-Palacios, and Palmer 1999). Due to the particular biological strategies of these three species, they are associated with gaps or open spaces where solar radiation is higher and results in an increase in air and soil temperature and a decrease in relative humidity compared to the forest understory (Clinton 2003). In this context, it would be expected that the increase in temperature during positive EA periods would lead to a decrease in the growth of these three species.

4.4 | Droughts Had a Greater Impact in Madeira and the Canary Islands Than in the Azores

The agreement between the SPEI minimum values from October to September and the occurrence of negative pointer years in the radial growth series of trees in the Canary Islands and Madeira, highlights the significant impact of drought events on tree growth in Macaronesian cloud forests. There is already evidence of impacts of drought events on tree growth in Tropical Montane Cloud Forest in South America (Argüelles-Marrón et al. 2023; Rodríguez-Ramírez et al. 2022, 2024). The negative effects of high temperatures and droughts on tree growth worldwide are well known (Harvey et al. 2020; Bosela et al. 2021). This would be expected since water availability and drought are the main drivers of tree growth and forest productivity in the tropics and subtropics (Bonal et al. 2016; Brienen, Schöngart, and Zuidema 2016; Wagner et al. 2012). The exception was the island of Terceira, where the minimum growth rates observed in 1984, 1995 and 2007 did not correspond to droughts, but rather to a combination of high winter EA values and low summer EA values. A study conducted in the Iberian Peninsula showed that in the westernmost part (climatically more similar to the Azores archipelago), high EA values in winter cause greater precipitation, as do low EA values in summer (Ríos-Cornejo et al. 2015b). The combination of EA values could lead to an increased annual precipitation, accompanied by an increase in cloud cover and a reduction in solar radiation and photosynthesis rates, leading to a sharp decline in tree radial growth on the wetter island of Terceira.

The observed results of tree growth resistance, recovery and resilience to drought across Macaronesia suggest that the impacts of drought occurrence on cloud forest tree growth are different across the five islands studied. According to the results obtained per island, tree growth in Terceira, Madeira, and La Palma showed greater resistance to drought, with the greatest reductions in growth during drought events occurring in the islands of Tenerife and La Gomera. However, the growth recovery after drought occurrence showed an opposite pattern, with higher rates on Tenerife and La Gomera, indicating that the ability of trees to recover growth rates after the drought event was faster on these two islands. These results are consistent with previous findings that the growth of tree populations in drier areas have lower drought resistance and higher recovery ability after drought compared to populations in wetter areas (Gazol et al. 2017; Sánchez-Salguero et al. 2018; Correa-Díaz et al. 2023). Furthermore, we found strong geographic variation in resilience indices associated with the two precipitation gradients distributed from south to north (increasing precipitation with latitude) and from East to West (increasing precipitation with longitude) in the Macaronesian region (see Figure 7). We found evidence of this pattern of geographical variation of precipitation both in the analysis of resilience indices with all species on each island, and in the analyses conducted individually with both species of the genus *Laurus* across Macaronesia and with *P. indica* in the Canary Islands. These analyses revealed an increase in drought resistance and a decrease in drought recovery capacities with increasing latitude and longitude. Gazol et al. (2017) found a similar result in their analysis of the impacts of drought on the growth resilience of forests in the Northern Hemisphere, where higher resistance values and lower recovery values were recorded at higher latitudes. These results revealed a trade-off in tree growth between drought resistance and recovery after drought events across Macaronesia, where lower resistance capacity is associated with higher recovery rates and vice versa (see Figure 6), as already observed in several previous studies (Hoffmann et al. 2018; Sánchez-Salguero et al. 2018; Urrutia-Jalabert et al. 2021).

We also observed particular responsiveness of each tree species in resistance and recovery indices to drought events across Macaronesia. We found that the species with the highest recovery capacities and the lowest resistance rates (*L. novocanariensis, P. indica* and *P. excelsa*), also had the highest correlations of growth with climate. On the other hand, *L. azorica* showed low correlations of growth with climate, was the most resilient species and showed higher growth resistance to drought. The results obtained at the island level also showed that tree species adapted to higher water availability had higher resistance rates, while species adapted to drier conditions had greater recovery capacity.

Overall, these results are consistent with previous findings in which trees were less resistant to drought but showed greater recovery ability after droughts when located in areas with more xeric conditions (Sánchez-Salguero et al. 2018; Urrutia-Jalabert et al. 2021; Correa-Díaz et al. 2023). However, this idea does not fully explain the different responses of all species studied. In addition to regional climatic conditions and other site-dependent environmental factors, such as stand health, slope, and soil conditions (Gazol and Camarero 2012; Sánchez-Salguero et al. 2018), the specific physiological and anatomical attributes of each species are closely related to their response and tolerance to drought (Meinzer et al. 2013). All tree species we studied exhibit a diffuse porous wood with generally small vessels, but also show contrasting anatomical traits that could confer different functional responses (pers. obs.). For example, tree species that are more resistant to cavitation have conduits with thicker walls (Bouche et al. 2014), while tree species with ring-porous wood and large vessel lumens in the earlywood are more susceptible to cavitation (Hacke et al. 2006). Furthermore, changes in the size and distribution of conducting vessels have been observed during periods of severe water stress (von Arx, Archer, and Hughes 2012).

This study represents the first evaluation of the impact of changing climatic conditions on tree growth of cloud forests across the latitudinal and longitudinal gradients of Macaronesia. Contrary to expectations, the results obtained did not show high sensitivity in the southernmost islands, although these areas experience more severe and frequent droughts. These findings suggests that it is not entirely clear which islands would be most affected by drought. On the other hand, these results highlight the importance of a thorough understanding of the functional implications of tree anatomy and physiology on the responses of Macaronesian cloud forests to climate warming and drought impacts. The future study of the anatomical features of Macaronesian species and the dynamics of these forests would provide an integrated view of the functioning of cloud forests, allowing for a more precise assessment of their response to environmental challenges and providing a solid basis for their future conservation and management.

5 | Conclusions

This is the first dendrochronological study focused on assessing growth patterns and responsiveness of cloud forest tree species to climatic variations across the Macaronesian region. Growth patterns were more similar among species from the same island than among conspecifics of different islands. Furthermore, we found greater homogeneity in the growth patterns of trees growing in environments with more pronounced hydric stress, suggesting that water deficit modulates the growth of trees in the cloud forests of Macaronesia and leads to a convergence of growth responses to climate in trees growing in the same island. In Madeira and Canary Islands, greater water availability in winter and early in the growing season favoured radial tree growth. We also observed a negative association between precipitation, especially in winter, and the NAO, resulting in a reduction in annual ring width in the positive NAO phases. We found a strong decline in radial growth of trees associated with the occurrence of drought events in almost all species and islands with the exception of Terceira, where abrupt growth reductions were associated with a combination of high EA values in winter and low EA values in summer. We also found species-specific responses to drought, with species adapted to higher water availability showing higher resistance rates overall, while species adapted to drier conditions showed greater ability to recover growth, which could be extrapolated to the island level. This study highlights the strong dependence of cloud forest trees on water availability and reveals the sensitivity of the Macaronesian cloud forest to local climate conditions, mainly precipitation, and large-scale climatic patterns. These results provide new insights into the behaviour of cloud forest tree species in response to climate variability and provide important information for the knowledge and conservation of this vulnerable island ecosystem.

Author Contributions

Ana I. García-Cervigón, José María Fernández-Palacios, José M. Olano, and Vicente Rozas conceived the ideas and designed the research. All authors conducted the fieldwork and collected the data with additional support from collaborators. María A. García-López and Victoria Calvo-Donate conducted the laboratory work. María A. García-López analysed the data with assistance from Ana I. García-Cervigón and Vicente Rozas. María A. García-López led the writing with assistance and edits from Ana I. García-Cervigón and Vicente Rozas. All authors contributed with comments and editing to the manuscript and gave final approval for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data will be made available on request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.